

190 Years of *Sargassum* Taxonomy, Facing the Advent of DNA Phylogenies

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Abstract *Sargassum* C. Agardh is one of the morphologically most complex phaeophyceae genera and represents the most species-rich genus of the brown algal order Fucales Bory de Saint-Vincent (Phaeophyceae). The genus' classification system dates back to the 19th century and is based on observed differences in macromorphological characters. Those morphological characters may display important variation within individual species, and several authors have linked the taxonomic complexity of the genus to its highly polymorphic nature and phenotypic plasticity. Among the large choice of existing species and subspecies epithets (about 1000), identifying taxa accurately is a difficult task, often relying on authors' interpretation of short Latin diagnoses or descriptions published in local Floras. Recently, the study of individual species' morphological range and DNA phylogenies underlined inconsistencies within low taxonomic levels (sections, subsections, series and species groups). Results highlighted the weak taxonomic value of traditional characters used to classify species, and pointed out significant taxonomic issues. The four *Sargassum* subgenera (*S.* subgen. *Arthrophyucus*, *Bactrophyucus*, *Sargassum* and *Phyllotrichia*) are now subdivided into a total of 12 sections and further subdivisions were abandoned. Two possible new sections need to be assessed. In the present paper, we raise the hypothesis that *S.* subgen. *Arthrophyucus* could be merged to *S.* subgen. *Bactrophyucus*, and that *S.* subgen. *Phyllotrichia* could be transferred to the recently reinstated genus *Sargassopsis* Trevisan. We also propose that two sections of the *S.* subgen. *Bactrophyucus*: *S.* sect. *Halochloa* and *Repentia* be merged. A summary of the actual classification is given along with an identification key for *Sargassum* subdivisions.

Résumé *Sargassum* C. Agardh représente le genre le plus complexe et le plus riche de l'ordre des Fucales Bory de Saint-Vincent (Phaeophyceae). La classification du genre remonte au 19^{ème} siècle et se base sur l'observation de plusieurs caractères macromorphologiques, lesquels peuvent montrer des variations importantes au niveau intra-spécifique. Plusieurs auteurs ont mis en évidence le lien existant entre la complexité taxonomique du genre et sa nature polymorphique ainsi que sa plasticité phénotypique. Ainsi parmi le large choix d'épithètes d'espèces et de sous-espèces disponible pour *Sargassum* (près de 1000), identifier un taxon de façon précise est

une tâche difficile reposant souvent sur l'interprétation de courtes diagnoses en Latin ou de descriptions disponibles dans des Flores locales. Récemment, l'analyse combinée de la variabilité morphologique et ADN pour des espèces étudiées individuellement, ont permis de mettre en évidence des incohérences au niveau infra-générique (sections, subsections, series et groupes d'espèces). Les résultats ont souligné la faible valeur taxonomique des caractères utilisés pour classer les espèces, et mis en évidence un certain nombre de conséquences taxonomiques. Les quatre sous-genres de *Sargassum* (*S.* subgen. *Arthrophyucus*, *Bactrophyucus*, *Sargassum* et *Phyllotrichia*) sont dorénavant sous-divisés en 12 sections, et les sous-divisions inférieures ont été abandonnées. Deux nouvelles sections potentielles nécessitent d'être évaluées. Dans ce papier, nous émettons deux hypothèses: (i) la fusion de *S.* subgen. *Arthrophyucus* avec *S.* subgen. *Bactrophyucus*, et (ii) le transfert de *S.* subgen. *Phyllotrichia* au genre *Sargassopsis* Trevisan récemment réintégré. Nous proposons la fusion de deux sections de *S.* subgen. *Bactrophyucus*: *S.* sect. *Halochloa* et *Repentia*. Un résumé de la classification actuelle est donné avec une clef d'identification pour les sous-divisions du genre *Sargassum*.

Keywords Classification · DNA markers · Fucales · Section · Systematic · Taxonomic review

Introduction

Taxonomy is the discipline describing, naming and classifying living organisms, it is essential to the inventory and understanding of biodiversity. Knowing and describing organisms in sufficient details allows (1) to identify and classify them accurately, (2) to study their biology and ecology, (3) to understand their geographical distribution, estimate biodiversity hotspots and define regions of interest for conservation, as well as (4) selecting species with economic potential. Incorrect identifications lead to errors on the quantification of biodiversity, on biological and ecological processes, on the definition of conservation zones, or on the wrong selection of the species containing the targeted molecule of interest. Taxonomy is in constant evolution and tributary of technology progress. The advents of electronic microscopy, as well as biochemical and molecular analyses have been factors responsible for the evolution of our view of taxonomy. Two hundred years ago, phycologists were describing species based on fragments collected as drifts during the first expeditions around the world (Turner, 1808, 1809, 1811; C. Agardh, 1820; Montagne, 1845). Nowadays, the world has been more extensively explored and phycologists study the morphological and molecular variability of populations based on tens of specimens collected at various geographical levels (Tatarenkov et al., 2007; Zhao et al., 2007; Cheang et al., 2008), sequence genomes (Oudot-Le Secq et al., 2002, 2006), and attempt to identify species with genetic barcodes (Saunders, 2005; Robba et al., 2006; Chase et al., 2007).

Sargassum C. Agardh, described 190 years ago (C. Agardh, 1820), represents today the most species rich genus of the marine macrophytes (estimated from Guiry & Guiry, 2010) and the morphologically most complex phaeophyceae genera. Species are distributed worldwide and the genus is especially well represented in

tropical and inter-tropical regions where it forms dense submarine forests. These forests structure an essential habitat for numerous marine species, and are equivalent to the temperate *Fucus* Linnaeus, *Cystoseira* C. Agardh or Kelp forests (Nizamuddin, 1962; Phillips, 1995; Steneck et al., 2002; Thibaut et al., 2005). Some species are economically important, especially in Asian countries where they are exploited by agro-food, textile, cosmetic and pharmaceutical industries. Chemical properties may vary from one species to another (Prud'homme van Reine, 2002; Smit, 2004). However, with roughly 1000 taxa, of which less than 40% are recognized as current, identifying a species is often a difficult task (Mattio et al., 2010). The placement of species within a section of the genus or its subdivisions is often difficult and illustrates the challenge between a high intra-specific morphological variability and a classification system based on ancient and fragmentary material not representative of species' polymorphy (pers. obs.). Although *Sargassum*'s taxonomy has been the focus of increased attention since 1985 (Abbott, 2004), it is still in need of systematic re-examination (Mattio et al., 2010).

Morphology

The morphology of *Sargassum* is characterised by a thallus composed of a fixation holdfast, one to several main axes ramified into 'branches' of several orders which differentiate into foliar appendices named 'leaves', vesicles (aerocysts) and receptacles (reproductive organs). The overall shape of the thallus may be more or less linear or bushy, it may measure a few centimetres in exposed habitats (ex. *S. spinuligerum* var. *crispata* (Sonder) J. Agardh in Kiuva reef, Fiji—pers. obs.) to several meters in sheltered areas [ex. *S. sp.* in Colombia, O. Camacho-Hadad pers. comm.; up to 10 m for the invasive *S. muticum* (Yendo) Fensholt in France (Belsher & Pommellec, 1988)]. The holdfast is discoid, conical or rhizoidal and do not penetrate the substratum. Main axes are perennial, short, cylindrical or flattened in section, and bear the scars of deciduous branches. Secondary or other order axes or branches are cylindrical or flattened in section, with a smooth or 'spiny'¹ surface, and are distichously or spirally arranged. In species belonging to *S.* section *Polycystae* Mattio et Payri some of the secondary branches are differentiated into stoloniferous axes bearing haptera (or secondary holdfasts). The shape of leaves is highly diversified (Fig. 1). They can be simple, bifid or divided several times, rond, spatulate, turbinate, lanceolate, ovoid, linear or of any intermediate forms. The basis of leaves is rounded or attenuate, symmetrical or not. The pedicel is inexistent or of variable length, cylindrical or flattened in section and smooth or 'spiny'. The leaves' margin may be simple or double at the apex, and be smooth, undulate, finely serrate, deeply dentate or any intermediate aspect. The midrib may be short and thick or thinner and reaching the apex, or any intermediate length. The apex may be acute, rounded or truncated, simple or showing a cup-like shaped depression. Cryptostomata, of variable number and size, are either randomly distributed over the leaves'

¹ Note that the term 'spiny' is commonly employed in *Sargassum* taxonomy, however, it may refer to various types of spine-like protuberances which depending on their aspect may be of taxonomic significance.

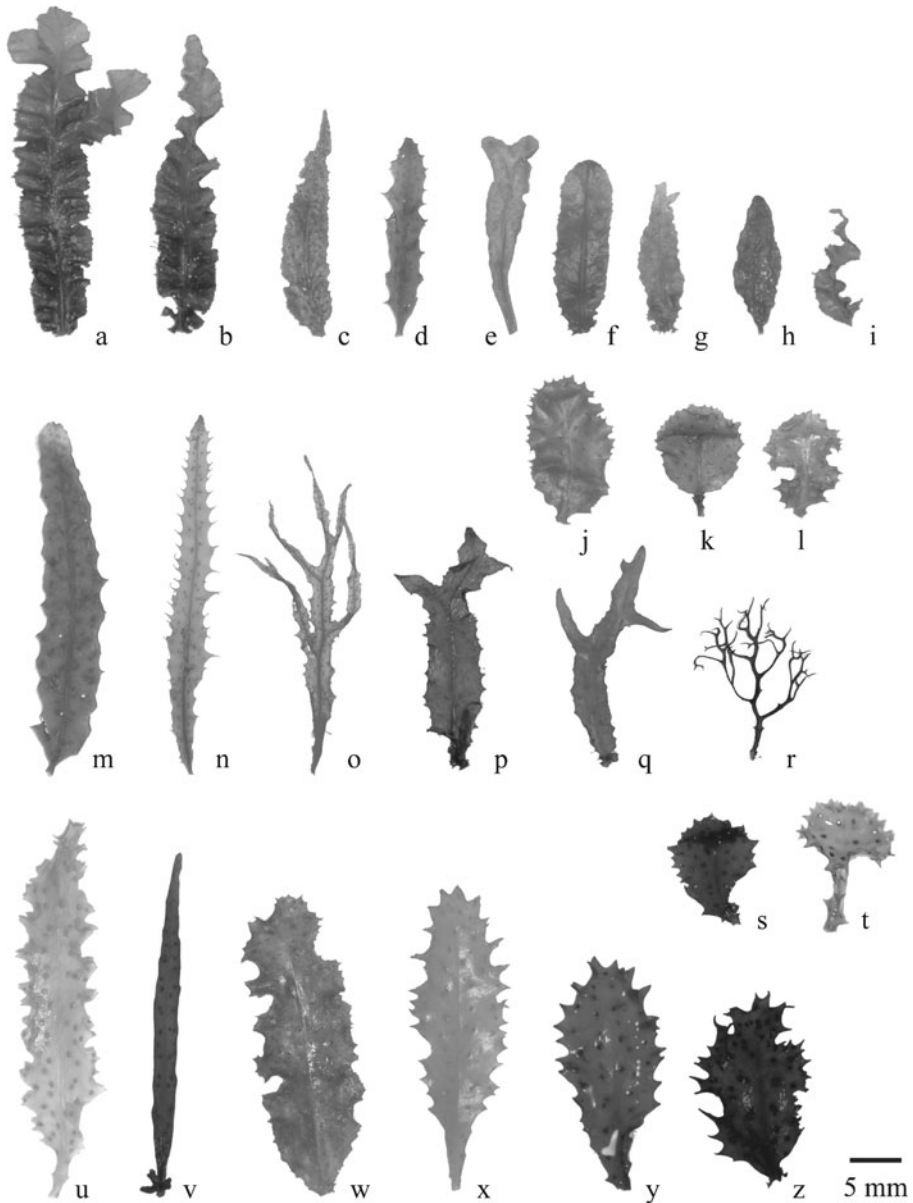


Fig. 1 Leaves morphology (*S.* subgen. *Sargassum*). Leaves may be simple (eg. c, m, u), bifid (eg. e), trifid (eg. a, p), divided several times (eg. o, q, r); the general shape may be round (eg. k), spatulate (eg. s, x, y), turbinate (eg. t), lanceolate (eg. b, c), ovoid (eg. h), or oblong (eg. f, j, w), linear (eg. n, v); undulate (eg. a, j, w) or strait in lateral view (eg. n, v, x). The basis may be rounded (eg. a, k) or attenuate (eg. e, n, x), symmetrical (eg. v, x) or asymmetrical (eg. p, s, z). The margin may be smooth (eg. e, v), finely serrulate (eg. d, p, w), profoundly dentate (eg. u, x, y); simple (eg. c, n, w), or double (eg. t, y). The apex may be acute (eg. c, v), or obtuse (eg. f, j, s); simple (eg. d, m) or with a depression (eg. j, k)

surface or aligned on each side of the midrib in one to several rows. Vesicles (or aerocysts) may be spherical, ovoid, pyriform or of any intermediate shape; they are smooth or bear a mucron which may be simple or multiple, thin and spine-like, foliar, or in crown. Vesicles are held by a pedicel variable in size, cylindrical, flattened or foliar. For some species, the vesicle may develop in the middle of leaf and is named phyllocyst (Fig. 2). Receptacles are either solitary or in tight to open clusters, simple, branched, bearing or not small vesicles and/or leaves (mixed receptacles), lanceolate or linear, smooth or 'spiny', of cylindrical or flattened section. Receptacles are said zygoecarpic (composed or mixed), malacocarpic (cylindrical and smooth) or acanthocarpic (spiny), qualified of carpophylles or pseudocarpophylles, arranged in cymes, racemes or glomerules. In case of a dioecious species, a male/female dimorphism may be observed with male receptacles often slender than female receptacle shorter and stockier (Fig. 3). Sexual dimorphism may concern the whole thallus.

Morphological characters may present a high intra-specific morphological plasticity, either between populations, within populations or even within one individual. Kilar and Hanisak (1989) have identified as many as 47 different morphotypes within the same *S. polyceratium* Montagne population in Florida. They have also pointed out that a number of morphological variations depend on seasons, habitat type, and water motion. In a review on the phenotypical variability of

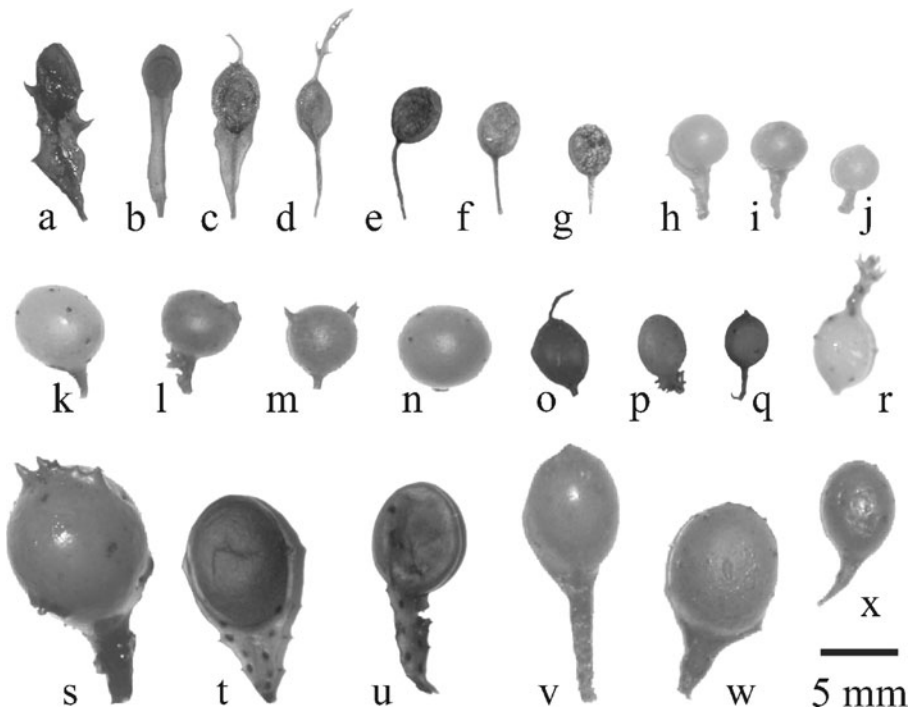


Fig. 2 Vesicles morphology (*S.* subgen. *Sargassum*). The general shape may be spherical (eg. h, n, s), or ovoid (eg. c, t, v); vesicles may be smooth (eg. e, k, p), with a mucron which may be thin (eg. c, o, q), foliar (eg., d, r), expanded into a crown (eg. t) or forming ear-like expansions (eg. m). The pedicel may be of variable size cylindrical (eg. g, m, q), flattened (eg. v, x) or foliar (eg. a, c, u)

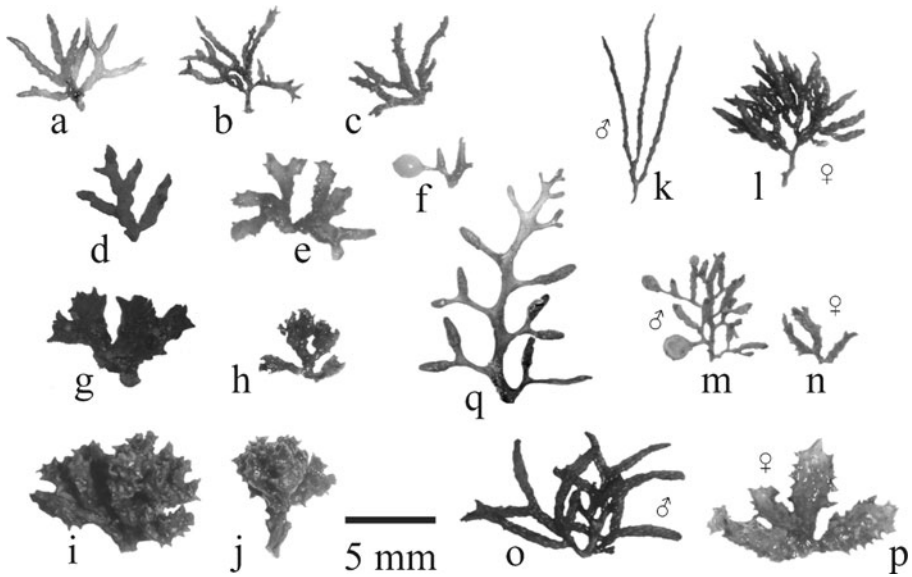


Fig. 3 Receptacles morphology (*S.* subgen. *Sargassum*). The general shape of receptacles may be lanceolate (eg. f, q) or linear (eg. a, k), margins may be smooth (eg. a, l) or with spine-like protuberances (eg. c, g, p), with a section cylindrical (eg. b, o) or more or less flattened (eg. e, p); arranged in cymes (eg. a, h, o), in racemes (eg. d, m) or in glomerules (eg. i, j). Receptacles may be zygocarpic (eg. m, f), acanthocarpic (eg. h, i, p) or malacocarpic (eg. a, k, o). Example of male/female dimorphism (k/l, m/n, o/p)

Sargassum, Kilar et al. (1992) underlined the influence of environmental conditions, age and period of reproduction on the size, shape and aspect of leaves. According to these authors, the morphological characters of a given species may vary in time, at intra- or inter-individual level, depending on environmental conditions and spatially (inter-population).

The systematic of *Sargassum* is based on various morphological characters. Subgenera are mainly recognizable by the organisation and aspect of their axes, but *S.* subgen. *Bactrophyucus* J. Agardh and *Arthrophyucus* J. Agardh are differentiated by their receptacle morphology (Yoshida, 1989a, b). However, the several morphological characters used for distinguishing further subdivisions do not show a consensus. Sections of *S.* subgen. *Bactrophyucus* are first recognizable by the shape and organisation of axes, and then by the receptacle morphology while sections of *S.* subgen. *Sargassum* are originally exclusively recognizable based on receptacle morphology. The sub-divisions of these sections are based on a more detailed description of receptacle morphology and reproduction strategies (dioecy, monoecy, male/female dimorphism or not), and to a less extent on the morphology of vesicles, holdfast or axes. Within each subdivision, species are identified on supplementary morphological characters including, most often, morphological variation in the aspect and shape of leaves, vesicles and receptacles. Infra-specific ranks such as varieties and formas are mainly identified according to minor morphological variations which are difficult to differentiate from a simple ecomorph. For instance, some taxa are distinguished by the absence or presence of vesicles (eg. *S. tahitense* Grunow and *S. boraborensis* (Grunow) Setchell), whereas the abundance of vesicles

is clearly influenced by environmental conditions such as hydrodynamism (Kilar et al., 1992; Mattio et al., 2008).

Taxonomical Ambiguities

Nomenclatural ambiguities have been documented since the establishment of *Sargassum* (Silva et al., 1996: 930), which is consensually recognized as a difficult genus in need for a significant taxonomic revision. Taxonomic ambiguities are found at two levels: (i) the level of terminal taxa, ie. ambiguities in species distinction, and (ii) the level of classification, ie. ambiguities in the attribution of a particular species to one of the genus' numerous subdivisions. The classification and description of most species date back to the 19th century mainly with the works of C. Agardh (1820, 1824) and J. Agardh (1848, 1889). Monographies and collections of these authors are representative of the genus taxonomy at this time. Diagnoses mainly consist in short paragraphs describing briefly the type material, which was most of the time not properly designated. The latter is often represented by an incomplete dry sample in bad shape, collected as drift in an imprecise locality during the first expeditions around the world (pers. obs. Museum of Lund, Agardh's collection). As a consequence and without knowledge of individuals in their natural habitat, C. and J. Agardh and their contemporaries may have described several taxa from fragments belonging to the same species. The situation is even increased by the substance of diagnoses, which without illustrations, may correspond to several very different species (pers. obs.). In addition, it is difficult to retrieve collections and type specimens as some of them might have disappeared or been destroyed (eg. the fire of the Berlin's Museum during the Second World War).

The origin of these taxonomic confusions is probably linked to the high polymorphy of the genus as it was likely underestimated at this time. Morphological characters used for *Sargassum* taxonomy may show important phenotypic variations related to habitat diversity, exposition or seasons (De Wreede, 1976; Magruder, 1988; Kilar et al., 1992; Trono, 1992; Gillespie & Critchley, 1997, 2001). This polymorphy has sometimes been wrongly interpreted as inter-specific variations, thus creating several epithets for the same species (Womersley & Bailey, 1970; Guiry & Guiry, 2010). Considering this morphological variability, Grunow (1915, 1916a, b) described numerous varieties and formas, thus increasing the complexity of the genus taxonomy. Many of these infra-specific taxa have been considered as superfluous by various authors (Womersley, 1987; Yoshida, 1987; Mattio & Payri, 2009) and there is often a lack of information about taxa's morphological variability. Consequently, identifying species often remains uncertain.

According to Kilar et al. (1992), taxonomic ambiguities are linked to a considerable variability in species description. Authors list 11 potential reasons for taxonomic confusions: (i) an important morphological plasticity, (ii) variable ontogenic forms, (iii) a high polymorphism, (iv) morphological characters which may be absent (eg. vesicles and receptacles), (v) too much importance given to highly variable characters such as leaves, (vi) hybridization which may produce specimens with intermediate forms, (vii) the possibility of polyploidy which may produce divergent morphologies, (viii) the number of varieties and formas described

in the literature, (ix) the absence of polymorphy representation by type specimens which are often fragments, (x) absence of a consensus underlying characters of taxonomic importance, (xi) absence of relevant information concerning ecology, development, and reproduction of most of the species. With the aim of circumscribing taxa's morphological variability, Kilar et al. (1992) made several recommendations notably including studies on a sufficient number of specimens, in various seasons and issued from populations submitted to various environmental conditions. These authors also recommend *in vitro* reproduction tests and genetic analyses.

Once species have been identified, classifying them into the various subdivisions of the genus is often confusing (Womersley, 1954; Yoshida, 1983; Mattio et al., 2009, 2010). This is mainly due to the combination of factors such as a high intra-specific polymorphy, and a classification system based on ancient and fragmentary material. For example, *S. mclurei* Setchell was first placed within *S.* subgen. *Arthrophyucus* (Setchell, 1933), then transferred to *S.* subgen. *Bactrophyucus* sect. *Phyllocystae* Tseng (Tseng et al., 1985), and finally to *S.* subgen. *Sargassum* when *S.* sect. *Phyllocystae* was transferred to this subgenus by Stiger et al. (2000). Womersley (1954) proposed to include *S.* subgen. *Schizophycus* J. Agardh into *S.* subgen. *Sargassum* and did not recognize the various subdivisions of *S.* subgen. *Phyllotrichia* (Areschoug) J. Agardh, which according to him are based on insignificant morphological variations. Later, in an attempt to resolve main ambiguities, Yoshida (1983) proposed to classify *Sargassum* subgenera in two groups: (i) those with leaves perpendicular to main axis (ie. horizontally oriented) (*S.* subgen. *Bactrophyucus* and *Arthrophyucus*), and (ii) those with leaves parallel to the main axis (ie. vertically oriented) (*S.* subgen. *Phyllotrichia*, *Schizophycus*, and *Sargassum*). In their revision of *S.* subgen. *Sargassum* from China, Tseng and Lu (1988, 1992a, b, 1995a, b, c, 1997a, b, 1999, 2002a, b, c, d) clarified and synthesized characters having taxonomic significance for the identification of sections, subsections, series and species groups. But according to Abbott (1992: 1–3), the entire *Sargassum* classification system is confusing and in some cases too vague to be useful. The author points out inconsistencies at all levels including for the distinction of subgenera. According to her, abandoning subgenera wouldn't be the solution, and a new taxonomic approach is necessary to better appreciate the composition and organisation of the genus.

***Sargassum* Taxonomy, First Period (1820–1988)**

In botany, even if several genera are divided into subgenera, there are only few taxa with sufficient species number to justify the use of inferior sub-divisions such as for example sections, subsections and series. In the case of *Sargassum*, the hundreds of taxa attributed to one subgenus are traditionally classified into sections, subsections, series and species groups, the latter having not taxonomic value according to the International Code of Botanical Nomenclature (ICBN, McNeill et al., 2006). The first sargasso species, originally attributed to the genus *Fucus*, were described by Linnaeus (1753) (*F. natans* Linnaeus, *F. acinarium* Linnaeus, *F. lendigerus* Linnaeus), then by Turner (1808, 1809, 1811) (36 species). The genus *Sargassum* was established by C. Agardh (1820), who was the first to lay the foundations of a

new classification system for seaweeds. *Sargassum* represents the first genus listed in C. Agardh's order Fucoidea, and contains 62 species partitioned into seven unnamed groups recognizable by the following morphological characters: (i) axillary receptacles and whole leaves; (ii) axillary receptacles and pinnatifid leaves; (iii) vesicles and leaves of small size (*Microphylla*); (iv) terminal receptacles; (v) leafy vesicles, and spatulate and inflated leaves; (vi) axes flattened, pinnatifid and foliar, and axillary vesicles and receptacles; (vii) leaves without midribs, receptacles marginal and fixed to leaves, and solitary capsules in each tubercle. Later on, two of these groups were recognised as genera: *Turbinaria* Lamouroux (group iv) and *Carpophyllum* Greville (group vii). This classification was used by Montagne (1842, 1845) and Greville (1848, 1849). Nevertheless, Kützing (1843, 1845) proposed a completely different classification system, maintaining only part of the species in the genus *Sargassum* (mainly those corresponding to J. Agardh (1889)'s *S.* series *Malacocarpicae* and *Zygocarpicae* according to Setchell 1931), and attributing the other part to the genera *Carpacanthus* Kützing, *Halochloa* Kützing, *Pterocaulon* Kützing, *Spongocarpus* Kützing and *Stichophora* Kützing. J. Agardh (1848) did not retain Kützing's work and proposed a new classification composed of sections divided into 'tribus' (no taxonomic value according to ICBN) themselves divided into species groups which were organised according to morphological characters or a common geographical distribution. At this stage, the genus *Sargassum* contained three sections organised as follows:

- (i) *S.* sect. *Pterophycus* J. Agardh with one tribus:
 - tribus *Pterocaulon* (Kützing) J. Agardh (type unknown);
- (ii) *S.* sect. *Arthrophyucus* J. Agardh with three tribus:
 - tribus *Schizophylla* J. Agardh (type unknown),
 - tribus *Holophylla* J. Agardh (type unknown),
 - tribus *Heterophylla* J. Agardh (type: *S. heterophyllum* C. Agardh);
- (iii) *S.* sect. *Eusargassum* with eighth tribus:
 - tribus *Carpophylla* J. Agardh (type: *S. carpophyllum* J. Agardh),
 - tribus *Glandularia* J. Agardh (type unknown),
 - tribus *Siliquosae* J. Agardh (type: *S. siliquosum* J. Agardh),
 - tribus *Biserrulae* J. Agardh (type: *S. biserrula* J. Agardh),
 - tribus *Acanthocarpa* J. Agardh (type unknown),
 - tribus *Acinaria* J. Agardh (type: *S. acinaria* C. Agardh),
 - tribus *Ligularia* J. Agardh (type: *S. ligulatum* C. Agardh),
 - tribus *Cymosae* J. Agardh (type: *S. cymosum* C. Agardh).

Later, J. Agardh (1889), following the basis of his 1848's classification, published the most complete classification and divided the genus *Sargassum* into five subgenera, themselves divided into several series, each sub-divided into 'tribus':

- (i) *S.* subgen. *Phyllotrichia* (Areschoug) J. Agardh with five tribus:
 - tribus *Heteromorphae* J. Agardh (type: *S. heteromorphum* J. Agardh),
 - tribus *Cladomorphae* J. Agardh (type unknown),

- tribus *Phyllomorphae* J. Agardh (type unknown),
- tribus *Pteromorphae* (Kützing ?) J. Agardh (type unknown),
- tribus *Dimorphae* J. Agardh (type unknown);
- (ii) *S.* subgen. *Schizophycus* J. Agardh (type: *S. patens* C. Agardh) monospecific;
- (iii) *S.* subgen. *Bactrophycus* J. Agardh (type unknown) with two unnamed species groups;
- (iv) *S.* subgen. *Arthrophycus* J. Agardh (type *S. heterophyllum* C. Agardh) with two unnamed species groups;
- (v) *S.* subgen. *Eusargassum* with three series:
 - *S.* ser. *Zygocarpicae* (J. Agardh) Setchell with one tribus:
 - * tribus *Carpophyllae* J. Agardh (type: *S. carpophyllum*) with two unnamed species groups;
 - *S.* ser. *Acanthocarpicae* J. Agardh with two tribus:
 - * tribus *Glomerulatae* J. Agardh (type unknown) with four unnamed species groups;
 - * tribus *Biserrulae* J. Agardh (type: *S. biserrula*) with four named species groups:
 - # *Ilicifolia* (founding species: *S. ilicifolium* (Turner) C. Agardh),
 - # *Coriifolia* (founding species: *S. coriifolium* J. Agardh),
 - # *Parvifolia* (founding species: *S. parvifolium* (Turner) C. Agardh),
 - # *Dentifolia* (founding species: *S. dentifolium* (Turner) C. Agardh);
 - *S.* ser. *Malacocarpicae* J. Agardh with three tribus:
 - * tribus *Fruticuliferae* J. Agardh (type unknown),
 - * tribus *Cymosae* J. Agardh (type: *S. cymosum*),
 - * tribus *Racemosae* J. Agardh divided into three ‘sub-tribus’:
 - *Acinariae* (type: *S. acinaria*),
 - *Glandulariae* (type unknown),
 - *Siliquosae* (type: *S. siliquosum*).

In 1849, Kützing described two supplementary genera: *Anthophycus* Kützing and *Platylobium* Kützing for *Sargassum longifolium* (Turner) C. Agardh (1820) and *S. platylobium* (Mertens) C. Agardh (1820), respectively. The J. Agardh (1848)’s classification was largely adopted by subsequent authors such as Grunow (1915, 1916a, b), Setchell (1931, 1933, 1935a, b, 1936, 1937) and Yoshida (1983), and was slightly modified till recently. The main modifications were those of Abbott et al. (1988), and Tseng and Lu (various works) who proposed a number of corrections to J. Agardh’s classification, mainly to follow the Art.4.1 of the ICBN, by transferring the majority of series to the rank of section and ‘tribus’ to the rank of subsections. Certain species groups proposed by J. Agardh (1889) and Grunow (1915, 1916a, b) were transferred to the rank of series, and authors, including Tseng and Lu (various works) and Ajisaka et al. (1995), have defined several new species groups. Species groups are meant to cluster taxa *a priori* related but the ICBN do not recognize a

taxonomic status for them. However according to Art.4.2, species groups may be used as supplementary ranks under subseries. According to Ajisaka et al. (1995), after thorough population study, a species group could be either elevated to a recognized rank or reduced to only one species, all members of the species groups being then considered as conspecific. A view of *Sargassum* classification at this stage is given in Appendix 1. More recently, studies using DNA markers have underlined the necessity to reassess the whole *Sargassum* classification.

***Sargassum* Taxonomy, Second Period (2000–2010): The Advent of DNA Phylogenies**

Molecular analyses of DNA offer an alternate method to test taxonomic, systematic and phylogenetic traditional concepts. In phycology, systematic studies using nucleic acids have apprehended phylogenies in a new way as soon as the 1980s (Olsen, 1990). Since then, numerous studies have demonstrated how useful DNA markers are to understand taxa's evolutionary history (Kooistra et al., 1992; Hoarau et al., 2007; Phillips et al., 2008a, b), and phylogenetic relationships (Kogame et al., 1999; Coyer et al., 2006; De Clerck et al., 2006), or resolve taxonomic ambiguities (Coyer et al., 2001; Hayden et al., 2003; Faye et al., 2004; Mattio et al., 2010). Regarding Phaeophyceae, the first complete phylogenies (Draisma et al., 2001; Rousseau et al., 2001) have confirmed the monophyly of the majority of orders whereas the Laminariales and Sphacelariales appeared as paraphyletic. The phylogeny of Fucales was explored by several authors using nuclear markers SSU and LSU (rDNA) (Rousseau et al., 1997; Rousseau & de Reviere, 1999) or chloroplastic *psaA* (Cho et al., 2007). These studies have pointed out the monophyly of Fucales as well the majority of families currently classified into this order, exception of Cystoseiraceae. Two new families have been proposed and the Cystoseiraceae were merged to the Sargassaceae. More recently, Draisma and Rousseau (2010) have proposed several significant revisions within the Sargassaceae using a combined analysis of *psbA* and *mt23S*. A considerable number of studies have been dedicated to Fucales and in particular to *Fucus* species which play a major role in European marine ecosystems (Wallace et al., 2004; Engel et al., 2005; Coyer et al., 2006; Oudot-Le Secq et al., 2006). However, only few authors take an active interest in *Sargassum* despite its ecological importance in inter-tropical regions and taxonomic significance.

The first authors to challenge the traditional classification and phylogenetic relationships in *Sargassum* using DNA markers were Phillips (1998), Phillips and Fredericq (2000), Phillips et al. (2005), Stiger et al. (2000, 2003), and Yoshida et al. (2000, 2002, 2004). These studies only led to few taxonomic revisions as markers for the *ITS-2* region and the partial *rbcLS*-operon, used independently, showed poor taxon representation and limited interspecies resolution. Stiger et al. (2000, 2003) transferred *S. sect. Phyllocystae* from *S. subgen. Bactrophycus* to *S. subgen. Sargassum* and the genus *Hizikia* Okamura to section level within *S. subgen. Bactrophycus*. Yoshida et al. (2004) merged *S. subgen. Schizophycus* into *S. subgen. Sargassum*. These rearrangements provided strong evidence of the necessity to reassess taxonomic concepts within *Sargassum*. In more recent studies, combining

detailed results provided by a three markers-DNA phylogeny, analyses of morphology, and old herbarium collections including types, Mattio and Payri (2009) and Mattio et al. (2008, 2009, 2010) provided taxonomic clarifications of *Sargassum* diversity for South Pacific islands. The authors confirmed the polyphyletic nature of *S.* sect. *Acanthocarpicae*, re-assessed the status of numerous species, resolved several taxonomic incongruities, and provided an advanced revision of *S.* subgen. *Sargassum*'s sections. A detailed review of each *Sargassum* subgenera is discussed hereafter.

Sargassum* subgen. *Phyllotrichia* & *Schizophycus

Phyllotrichia was described by Areschoug as a distinct genus [Areschoug, 1854: 332, type species: *Phyllotrichia sonderi* (J. Agardh) Areschoug, basionym: *Cystoseira sonderi* J. Agardh, 1848: 247] and was later considered as a subgenus of *Sargassum* by J. Agardh [1889: 35, type species: *S. sonderi* (J. Agardh) J. Agardh]. J. Agardh (1889) further subdivided this subgenus into five 'tribus' mainly established based on differences in vesicles' shape: (i) *Heteromorphae* (2 species), (ii) *Cladomorphae* (3 species), (iii) *Phyllomorphae* (4 species), (iv) *Pteromorphae* (4 species) et (v) *Dimorphae* (2 species). Beside, *Sargassum* subgen. *Schizophycus* was originally described by J. Agardh (1848) as a 'tribus' of his section *Arthrophycus* and later elevated to subgenus rank (J. Agardh, 1889) containing only one species: *S. patens* J. Agardh.

In his revision of Australian species of *S.* subgen. *Phyllotrichia*, Womersley (1954) proposed that *S.* subgen. *Schizophycus* be merged to *S.* subgen. *Phyllotrichia* based on morphological evidences. The author further enumerates eight Australian species of *S.* subgen. *Phyllotrichia* (*S. decurrens* (R. Brown ex Turner) C. Agardh, *S. peronii*, *S. heteromorphum*, *S. sonderi*, *S. decipiens* (R. Brown ex Turner) C. Agardh, *S. howeanum* Lucas, *S. varians* Sonder, et *S. verruculosum* C. Agardh), three East Asian species (*S. piluliferum* (Turner) C. Agardh, *S. pinnatifidum* Harvey, et *S. patens*), and one from Canary Islands (*S. desfontainesii* (Turner) C. Agardh). Womersley (1954) also pointed out that the 'tribus' of J. Agardh were a source of confusion and should be avoided. Later, Goldberg and Huisman (2004) described a new *S.* subgen. *Phyllotrichia* species: *S. kendrickii* N. A. Goldberg et Huisman, while five species were transferred to *S.* subgen. *Sargassum*: *S. desfontainesii* (Diaz-Villa et al., 2007), *S. howeanum* (Goldberg & Huisman, 2004), *S. piluliferum* and *S. patens* (Stiger et al., 2003), and *S. pinnatifidum* (along with three other ex-*S.* subgen. *Schizophycus* species, Yoshida et al., 2004). Finally, Draisma and Rousseau (2010), using molecular markers and a large Sargassaceae dataset, demonstrated that *S. decurrens* (= *S. scabripes* J. Agardh and *S. boryi* C. Agardh) should be placed back in *Sargassopsis* Trevisan (1843: 332) (not *Sargassopsis* Nizamuddin et al., 1993) of which it should be considered the type species. The authors recommend a thorough revision before other *S.* subgen. *Phyllotrichia* species may be transferred to *Sargassopsis*. All these taxonomic changes point out the necessity for a re-evaluation of the species traditionally ascribed to *S.* subgen. *Phyllotrichia* as well as the morphological characters used to characterize this subgenus. Currently, only seven species should be attributed to *S.* subgen. *Phyllotrichia*: *S. peronii*, *S.*

heteromorphum, *S. sonderi*, *S. decipiens*, *S. varians*, *S. verruculosum*, and *S. kendrickii*.

Sargassum* subgen. *Bactrophycus* & *Arthrophyucus

Sargassum subgen. *Bactrophycus* was described by J. Agardh (1889) based on 14 species distributed in four morphological groups mainly defined by the organisation of axis and the shape of vesicles. This subgenus was studied in detail by Yoshida (1983, 1989a) and Tseng et al. (1985), and *S. horneri* was designated as type of *S. subgen. Bactrophycus* (Yoshida, 1983). *Sargassum* subgen. *Bactrophycus* currently contains 35 taxa including 22 species and one variety endemic to Japan. These taxa were divided into four sections by Yoshida (1983): *S. sect. Halochloa* (Kützing) Yoshida, *S. sect. Repentia* Yoshida, *S. sect. Spongocarpus* (Kützing) Yoshida and *S. sect. Teretia* Yoshida. Tseng (1985) described a fifth section: *S. sect. Phyllocystae* Tseng to classify species with phyllocysts. Later, based on molecular studies, Stiger et al. (2000, 2003) proposed to transfer *S. sect. Phyllocystae* from *S. subgen. Bactrophycus* to *S. subgen. Sargassum*, as well as the reinstatement of *S. fusiforme* (Harvey) Setchell (= *Hizikia fusiformis* (Harvey) Okamura) to be placed in a new section: *S. sect. Hizikia* (Okamura) Yoshida.

Sargassum subgen. *Arthrophyucus* was described by J. Agardh (1889) based on 20 species distributed into four morphological groups mainly distinguished on the shape of receptacles. According to Yoshida (1989b), no type species has ever been designated for the subgenus. The basionym of *S. subgen. Arthrophyucus* is *S. sect. Arthrophyucus* which was divided into three ‘tribus’: *Schizophylla*, *Holophylla* and *Heterophylla* (J. Agardh, 1848). Only eight species of ‘tribus’ *Heterophylla* were transferred by J. Agardh (1889) to *S. subgen. Arthrophyucus*. The other two ‘tribus’ were respectively transferred to *S. subgen. Schizophycus* and *Bactrophycus* (J. Agardh, 1889). In this context, we propose to consider *S. heterophyllum* (nomen typificatum for ‘tribus *Heterophylla*’) as the type species of *S. subgen. Arthrophyucus*. In a general trend, *S. subgen. Arthrophyucus* is badly known and only sequences for two species are currently available on GenBank (*S. fallax* Sonder, partial Rubisco, Phillips & Fredericq, 2000—*S. sinclairii* J. D. Hooker et Harvey, ITS-2, Mattio & Payri, 2009). Lindauer et al. (1961) listed three taxa belonging to *S. subgen. Arthrophyucus* in New Zealand: *S. sinclairii*, *S. undulatum* J. Agardh and *S. undulatum* f. *serratifolium* Lindauer. However, according to Adams (1994) the two latter should be considered as synonyms of *S. sinclairii* which is the most common *Sargassum* species in New Zealand. According to Womersley (1987), five species of *S. subgen. Arthrophyucus* are common along the coast of Australia. These studies appear to be ones of the rare works undertaken about this subgenus.

Sargassum subgen. *Bactrophycus* and *Arthrophyucus* are morphologically close and distinguished only by the shape of receptacles and their distinct geographical distribution. Hence, *S. subgen. Arthrophyucus* is distinguished from *S. subgen. Bactrophycus* by the presence of compound receptacles (Yoshida, 1983), and according to Setchell (1931), species of *S. subgen. Arthrophyucus* are exclusively

found in the southern hemisphere along the coast of Australia, Tasmania, New Zealand and South Africa. Nevertheless, Setchell (1933) attributed two species from Hong-Kong (*S. mclurei* Setchell, *S. herklotsii* Setchell) to *S.* subgen. *Arthrophyucus*. Yoshida (1983, 1989b) prefers to consider that this subgenus is only distributed in the southern hemisphere while *S.* subgen. *Bactrophyucus* is restricted to the northern hemisphere, mainly in the East Asian region.

Analyses of the nuclear *ITS-2* marker were carried out for 26 species of *S.* subgen. *Bactrophyucus* (available on GenBank from Stiger et al., 2000, 2003) and one species of *S.* subgen. *Arthrophyucus* (*S. sinclairii*, available on GenBank from Mattio & Payri, 2009). Results (Appendix 2) demonstrate a low genetic polymorphism between members of the *S.* sect. *Halochloa* and *Repentia* suggesting that both taxa should be considered as only one section. Based on the same results, Stiger et al. (2003) interpreted the low genetic polymorphism to a recent radiation of both sections. However, because sequences for both section's type (respectively *S. siliquosum* and *S. okamurae*, see Appendix 2 table) are identical, we propose to merge *S.* sect. *Repentia* Yoshida into *S.* sect. *Halochloa* (Kützing) Yoshida. Results of the *ITS-2* analysis also show the clustering of sequences available for *S. sinclairii* from New Zealand with the *Halochloa/Repentia* clade. Consequently, we propose the transfer of *S. sinclairii* from *S.* subgen. *Arthrophyucus* to *S.* subgen. *Bactrophyucus*. The geographical distribution of *S.* subgen. *Bactrophyucus* should not anymore be considered as restricted to the Northern hemisphere. The study of further markers and samples of *S.* subgen. *Arthrophyucus*, especially for the type species *S. heterophyllum*, should provide us with a revised view of *S.* subgen. *Arthrophyucus* and *Bactrophyucus*.

Sargassum* subgen. *Sargassum

Sargassum sect. *Sargassum* (75 species subdivided in eight 'tribus') was elevated to subgenus rank by J. Agardh (1889) who subdivided it into three series: *Zygocarpicae*, *Malacocarpicae* and *Acanthocarpicae* (95 species in total). Series were later elevated to sectional rank (Setchell, 1935b; Abbott et al., 1988) and subdivided into subsections, series and species groups (cf. Appendix 1). The traditional identification of *S.* subgen. *Sargassum*'s sections is exclusively based on the morphology of receptacles. *Sargassum* sect. *Acanthocarpicae* is conventionally recognized on the basis of flattened and spiny receptacles arranged in dense glomerules (*S.* subsect. *Glomerulatae*) or racemes (*S.* subsect. *Biserrulae*), and possibly exhibiting malacocarpic male receptacles (*S.* subsect. *Biserrulae* ser. *Plagiophyllae*). *Sargassum* sect. *Zygocarpicae* is conventionally identified by 'mixed' receptacles (ie. receptacles associated to small leaves and/or vesicles) which pedicels may be absent and only associated with leaves or with leaves and vesicles (*S.* subsect. *Holozygocarpicae*) or which pedicels are often present and only associated with leaves or only with vesicles (*S.* subsect. *Pseudozygocarpicae*). *Sargassum* sect. *Malacocarpicae* is traditionally recognized by the presence of smooth and cylindrical receptacles which may be arranged in cymes brush-like and pedicelate (*S.* subsect. *Fruticuliferae*), in fascicules and branched (*S.* subsect. *Cymosae*), or arranged in racemes with branches supported by a sterile pedicel

(*S.* subsect. *Racemosae*) (Appendix 1). This system of classification was accepted by the majority of the authors but because in practice it is based on very slight variations of receptacles' morphology, it has been used by few of them.

Recently, Norris (2010) published four new sections of *S.* subgen. *Sargassum* according to four morphological groups described by Dawson (1944): *S.* sect. *Johnstonii* E. Y. Dawson ex J. N. Norris, *S.* sect. *Lapazeanum* E. Y. Dawson ex J. N. Norris, *S.* sect. *Sinicola* E. Y. Dawson ex J. N. Norris and *S.* *Herporhizum* E. Y. Dawson ex J. N. Norris. These four sections are mainly identified on the morphology of leaves, vesicles and/or attachment type.

With the advent of DNA markers in *Sargassum* taxonomy, several revisions have been proposed for *S.* subgen. *Sargassum*. Stiger et al. (2000) proposed the transfer of *S.* sect. *Phyllocystae* from *S.* subgen. *Bactrophyucus* to *S.* subgen. *Sargassum* based on *ITS*-2 sequences analysis of *S. meclurei* and *S. quinhonense* Nguyen Huu Dai. However, Mattio et al. (2010) underlined that the effective transfer of the section should await confirmation by an analysis of the sequences for the section's type (*S. phyllocystum* Tseng et Lu). Using combined analyses of nuclear *ITS*-2, chloroplastic partial *Rubisco* and mitochondrial *cox3* markers, Mattio et al. (2009, 2010) have: (i) described *S.* sect. *Polycystae* Mattio et Payri. to fit species with stolon-like branches; (ii) synonymised *S.* sect. *Malacocarpicae* and *Acanthocarpicae* to the autonomous *S.* sect. *Sargassum*; and (iii) elevated *S.* ser. *Binderiana* Tseng et Lu and *S.* ser. *Ilicifolia* (J. Agardh) Tseng et Lu to sectional rank and emended their descriptions according to new sets of morphological characters to accommodate species with respectively cylindrical to slightly compressed axes possibly twisted, alternately and spirally arranged, and strongly flattened axes distichously arranged in one plan.

For the purpose of the present work, analyses of the nuclear *ITS*-2 marker (Appendix 3) were carried out for 19 taxa of *S.* sect. *Sargassum* (available on GenBank from Stiger et al. 2000, 2003; Mattio & Payri, 2009; Mattio et al., 2008, 2009). Results show six well sustained clades, five of them representing *S.* sect. *Sargassum*, *Zygocarpicae*, *Polycystae*, *Binderiana* and *Ilicifolia*. One clade, clustering sequences for *S. piluliferum* and *S. yendoii* Okamura et Yamada, form a sister group to the clade representing *S.* sect. *Sargassum*. These results are similar to those of Stiger et al. (2003) but the low representation of *S.* sect. *Sargassum* (two species) in their work did not allow the authors to interpret this clade as a distinct group from *S.* sect. *Sargassum*. Similarly using partial *Rubisco* marker, Mattio et al. (2010) showed *S. platycarpum* Montagne as a sister group to *S.* sect. *Sargassum* and *Zygocarpicae* and raised the hypothesis of a new section to be elevated from *S.* ser. *Platycarpae*. The hypothesis of a sixth section to fit *S. piluliferum*- and *S. yendoii*-like species and a seventh section to fit *S. platycarpum*-like species need to be confirmed with the help of further markers and morphological analysis. Similarly, we recommend that the four sections published by Norris (2010) (*S.* sect. *Johnstonii*, sect. *Lapazeanum*, sect. *Sinicola*, and sect. *Herporhizum*) be assessed with DNA markers and diagnostic morphological characters be revised. Actually, the three species classified within *S.* sect. *Herporhizum* (*S. herporhizum* Setchell et N. L. Gardner, *S. brandegeei* Setchell et N. L. Gardner, and *S. liebmanni* J. Agardh) exhibit stolon-like branches arising from a discoid holdfast which is a diagnostic character of *S.* sect. *Polycystae*. The

examination of *S. herporhizum* syntypes (UC 484236, 484241, 484252, 484253) confirmed that *S. sect. Herporhizum* should be considered as a synonym of *S. sect. Polycystae*.

Sargassum subgen. *Sargassum* assembles the majority of the genus' species but it is difficult to estimate an accurate species number. If we consider the current genus species number (344) given by Guiry and Guiry (2010), and the species number estimated for other subgenera from the above discussions (*S. subgen. Phyllotrichia*=7; *S. subgen. Bactrophyucus*=27; *S. subgen. Arthrophyucus*=about 20), the number of *S. subgen. Sargassum* species could be around 300. This number may be largely overestimated considering the numerous possible synonym epithets which have not yet been proposed. Actually, recent studies have demonstrated that the current species diversity as listed by Guiry and Guiry (2010) is wider than the existing diversity in the field. As an example, latest works by Mattio and collaborators (2008, 2009, 2010) pointed out 47 new synonymies and underlined numerous misidentifications thus reducing the 67 epithets listed in the literature for South Pacific Islands to 14 taxa (20%). By the transfer of *S. decurrens* to the reinstated genus *Sargassopsis*, Draisma and Rousseau (2010) further reduced this number to 13 species (Table 1). These works are based on the analysis of types corresponding to 103 taxa, relevant original diagnoses, vouchers listed in the literature and new extensive collections from worldwide localities. It must be noted here that Guiry and Guiry (2010)'s list does not encompass all existing *Sargassum*'s taxon names (species, varieties and formas; pers. obs.) which renders the estimation of *Sargassum* taxa number even more uncertain.

Table 1 Number of *Sargassum* taxa listed in the literature and number of actual taxa after taxonomic revision for South Pacific Islands according to (a) Mattio et al. (2008), (b) Mattio et al. (2009), and (c) Mattio and Payri (2009)

| Locality | Nb of taxa before revision | Nb of taxa after revision | References |
|-------------------|----------------------------|---------------------------|------------|
| Cook Is. | 3 | 3 | (a) |
| Easter Is. | 1 | 2 | (a) |
| Fiji Is. | 10 | 4 | (b) |
| French Polynesia | 18 | 3 | (a) |
| Nauru | 2 | 2 | (b) |
| New Caledonia | 45 | 11 | (c) |
| Pitcairn | 1 | 2 | (a) |
| Samoa | 9 | 3 | (b) |
| The Solomon Is. | 7 | 3 | (b) |
| Tonga | 4 | 3 | (b) |
| Vanuatu | 0 | 2 | (b) |
| Wallis | 1 | 1 | (b) |
| Total Nb. of taxa | 67 | 13 | – |

Conclusion, Perspectives and Recommendations

Currently, *Sargassum* is divided into four subgenera (*S.* subgen. *Sargassum*, *Bactrophyucus*, *Arthrophyucus* and *Phyllotrichia*). However, new insights have led to the hypothesis that *S.* subgen. *Arthrophyucus* could be merged to *S.* subgen. *Bactrophyucus*, and that *S.* subgen. *Phyllotrichia* could be transferred to the reinstated genus *Sargassopsis*. These hypothesis need to be tested implementing studies based on a larger sampling, including the type species for these subdivisions. Beside, only *S.* subgen. *Bactrophyucus*, and *S.* subgen. *Sargassum* are subdivided into sections. In this paper, we propose that two sections of the *S.* subgen. *Bactrophyucus*: *S.* sect. *Halochloa* and *Repentia* be merged, thus reducing the number of *S.* subgen. *Bactrophyucus* sections from five to four (*S.* sect. *Halochloa*, *Hizikia*, *Spongocarpus*, and *Teretia*). The subdivisions of *S.* subgen. *Sargassum* were considerably simplified since its establishment by J. Agardh (1889), all below-section ranks have been abandoned and traditional sections have been significantly revised. The subgenus is now currently subdivided into eight sections: *S.* sect. *Sargassum*, *Zygocarpicae*, *Polycystae*, *Ilicifolia*, *Binderiana*, *Johnstonii*, *Lapazaenum*, and *Sinicola*. The last three sections as well as two possible new ones need to be assessed further. A summary of the actual classification is given in Fig. 4 and Appendix 4 along with an identification key for *Sargassum* subdivisions in Table 2.

Phylogenetic methods have become routinely used in systematic. According to Stuessy and König (2008), the main rules of these methods are: (i) only synapomorphies are important for the discrimination of a phylogenetic tree's branches, (ii) only monophyletic groups are acceptable, (iii) the classification must only be based on topologic patterns, and (iv) sister clades should be of same rank. DNA markers used recently in the study of *Sargassum* (*ITS-2*, partial *Rubisco*, *cox3*, 23S) have led to significant new insights on the genus' phylogeny and allowed reconsidering the taxonomic placement of several entities. Notably, they confirmed the monophyly of *S.* subgen. *Sargassum* and detected the polyphyly of several of its subdivisions (*S.* sect. *Zygocarpicae* and *Acanthocarpicae*) thus pointing out to the incongruity of morphological characters traditionally used to define them. Several new sections have been proposed and part of the genus has been revised according to a simplified scheme (Fig. 4, Table 2, Appendix 4).

The efficiency of traditional morphological characters used to differentiate taxa (subgenera, sections or infrageneric taxonomic ranks) has been questioned, and the consideration of these characters, one by one, showed few synapomorphies (Mattio et al., 2010). Molecular phylogenies are not based on morphological characters; it is thus not surprising that they cluster taxa, originally classified in groups considered as morphologically homogeneous into different clades. For example, *S.* sect. *Acanthocarpicae*, which was traditionally identified on 'spiny' receptacles, appeared as polyphyletic (Mattio et al., 2010). In this case, the appendices traditionally named 'spines' are probably from different ontogenic origin. Thus, the 'spines' of *S. hystrix* (*S.* sect. *Sargassum*) are different from that of *S. aquifolium* (*S.* sect. *Binderiana*) or *S. ilicifolium* (*S.* sect. *Ilicifolia*). In the first one, they appear as extensions on the surface of receptacles, thin and linear like a 'hair', whereas in the latter two the receptacle's margin is dented. These expansions of different types, and probably different origins, had been interpreted

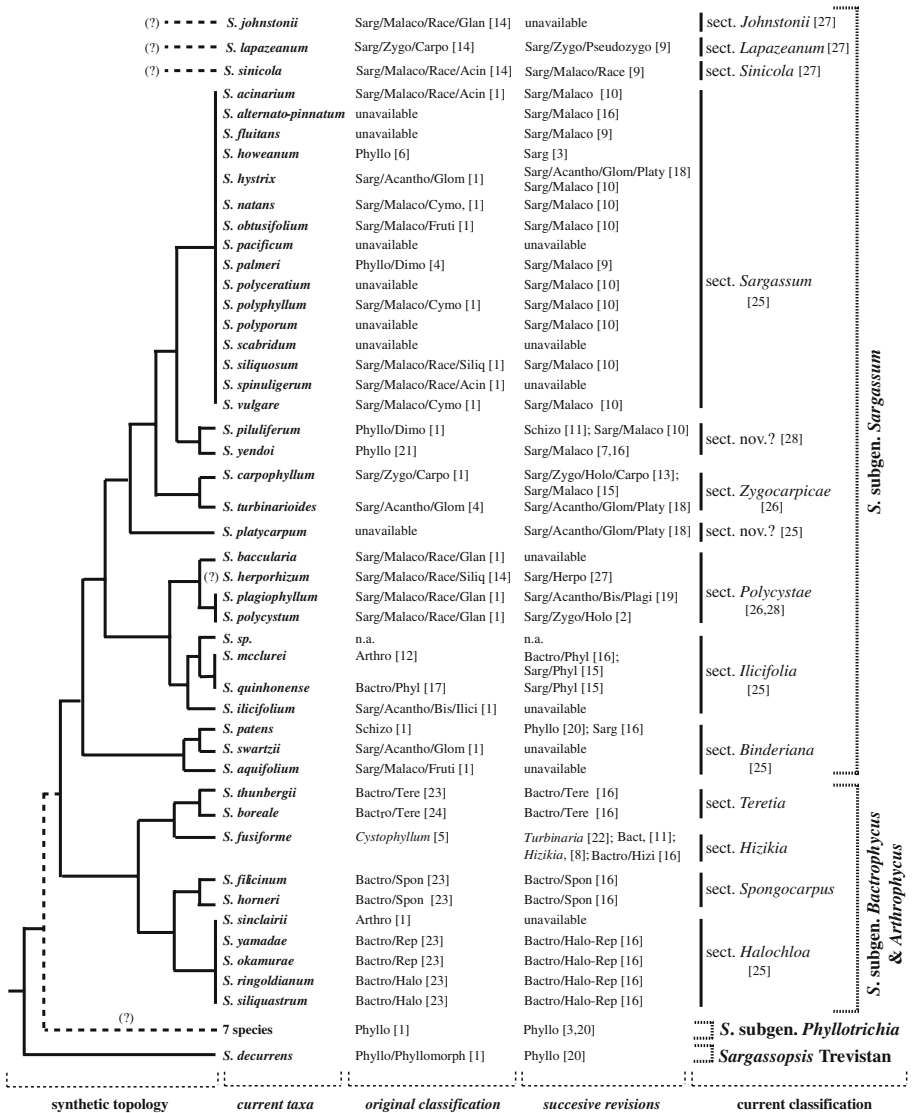


Fig. 4 Taxonomy history synthesis for taxa sequenced since year 2000. The synthetic topology presented was compiled visually from results obtained with *ITS-2*, partial *Rusbisco* and *cox3* by Stiger et al. (2000, 2003), Phillips and Fredericq (2000), Phillips et al. (2005), Mattio et al. (2008, 2009, 2010); Mattio and Payri (2009), and Draisma and Rousseau (2010). (?) indicate the likely position of taxa not yet confirmed by DNA analyses. The classification proposed by the authors of taxa (by default by J. Agardh, 1889), the revision of this classification by following authors, and the latest classification as proposed the most recently are indicated. Abbreviations follow Table 3 and bibliographic references are listed in Table 4

as the same character named ‘spine’ leading previous authors to classify *S. hystrix* and *S. ilicifolium* within the same section (*S. sect. Acanthocarpicae*). Similar situations may be encountered for other *Sargassum* infrageneric groups.

To overcome these difficulties and to progress toward a simplified taxonomy, more representative of the real diversity of the genus, we recommend that the genus be

Table 2 Identification key for *Sargassum* subdivisions. NB: Norris (2010)'s sections could not be considered for the construction of the key because the available diagnoses could fit several of the below sections (cf. main text for more details)

| | |
|--|--------------------------------|
| 1. Main axis cylindrical, flattened to foliar, leaf es pinnatifid, little or not differentiated..... | subgen. <i>Phyllotrichia</i> |
| 1. Main axis distinctly differentiated in secondary axis, leaves (mainly simple) and vesicles..... | →2 |
| 2. Axis bicuspid or angular, leaves retroflex..... | →3 |
| 2. Axis cylindrical, compressed, or flattened (not foliar), leaves rarely retroflex..... | subgen. <i>Sargassum</i> →4 |
| 3. Receptacles simple, axillary or terminal..... | subgen. <i>Bactrophycus</i> →8 |
| 3. Receptacles compound..... | subgen. <i>Arthrophyucus</i> |
| 4. Stolon-like axis present..... | sect. <i>Polycystae</i> |
| 4. Stolon-like axis absent..... | 5 |
| 5. Axis cylindrical and spindly..... | 6 |
| 5. Axis slightly compressed to flattened and thick..... | 7 |
| 6. Receptacles mixed with leaves and/or vesicles (zygocarpic)..... | sect. <i>Zygocarpicae</i> |
| 6. Receptacles forming cymes, cylindrical and warty (malacocarpic)..... | sect. <i>Sargassum</i> |
| 7. Axis flattened, leaves elongated and distichously arranged..... | sect. <i>Binderiana</i> |
| 7. Axis slightly compressed, leaves wide, spatulate, and spirally arranged..... | sect. <i>Ilicifolia</i> |
| 8. Main axis long, primary axis absent..... | sect. <i>Spongocarpus</i> |
| 8. Main axis shorter, primary axis well developed..... | →9 |
| 9. Receptacles compressed to triquetrous..... | sect. <i>Halochoa</i> |
| 9. Receptacles cylindrical..... | →10 |
| 10. Leaves flattened, with or without midrib, vesicles differentiated..... | sect. <i>Teretia</i> |
| 10. Leaves cylindrical or compressed, vesicles not differentiated similar to leaves..... | sect. <i>Hizikia</i> |

drastically revised following a two-pronged approach: first, the revision of the species diversity carried out by geographical region and second, the revision of the classification.

The species diversity may be re-evaluated through a four step taxonomic revision approach including:

- (i) An alpha-taxonomic study of the specimens based on morphological characters of traditional taxonomic value (see section *Morphology* of this paper) to distinguish morphotypes. Morphotypes are considered as groups of morphologically similar specimens, showing characters included within a morphological range which may represent a taxonomic entity corresponding to a species or an inferior taxonomic rank. The morphological range is defined according to the polymorphism of the specimens of interest as observed at intra-individual, and intra and inter-population levels taking into account as much as possible the ontogenic and phenotypic variability for various worldwide localities.

Table 3 Abbreviations used in Fig. 4

| | | | |
|---------|-------------------------------------|-------------|---------------------------------------|
| Acantho | S. sect. <i>Acanthocarpicae</i> | Malaco | S. sect. <i>Malacocarpicae</i> |
| Acin | S. ser. <i>Acinariae</i> | Phyl | S. sect. <i>Phyllocystae</i> |
| Arthro | S. subgen. <i>Arthrophyucus</i> | Phyllo | S. subgen. <i>Phyllotrichia</i> |
| Bactro | S. subgen. <i>Bactrophycus</i> | Phyllomorph | S. trib. <i>Phyllomorphae</i> |
| Bis | S. subsect. <i>Biserrulae</i> | Plagio | S. ser. <i>Plagiophyllae</i> |
| Carmo | S. ser. <i>Carpophyllae</i> | Platy | S. ser. <i>Platycarpae</i> |
| Cymo | S. subsect. <i>Cymosae</i> | Pseudozygo | S. subsect. <i>Pseudozygocarpicae</i> |
| Dimo | S. trib. <i>Dimorphae</i> | Racemo | S. subsect. <i>Racemosae</i> |
| Fruti | S. subsect. <i>Fruticuliferae</i> | Rep | S. sect. <i>Repentia</i> |
| Glan | S. ser. <i>Glandulariae</i> | Sarg | S. subgen. <i>Sargassum</i> |
| Glom | S. subsect. <i>Glomerulatae</i> | Schizo | S. subgen. <i>Schizophycus</i> |
| Halo | S. sect. <i>Halochoa</i> | Siliq | S. ser. <i>Siliquosae</i> |
| Holo | S. subsect. <i>Holozygocarpicae</i> | Spon | S. sect. <i>Spongocarpus</i> |
| Herpo | S. sect. <i>Herporhizum</i> | Tere | S. sect. <i>Teretia</i> |
| Ilici | S. ser. <i>Ilicifolia</i> | Zygo | S. sect. <i>Zygocarpicae</i> |

Table 4 Bibliographic references used in Fig. 4

| | | |
|------------------------------------|----------------------------------|----------------------------|
| [1] J. Agardh (1889) | [11] Setchell (1931) | [21] Yamada (1956) |
| [2] Ajisaka et al. (1995) | [12] Setchell (1933) | [22] Yendo (1907) |
| [3] Goldberg and Huisman (2004) | [13] Setchell (1935b) | [23] Yoshida (1983) |
| [4] Grunow (1915) | [14] Setchell and Gardner (1924) | [24] Yoshida et al. (2000) |
| [5] Harvey (1859) | [15] Stiger et al. (2000) | [25] Mattio et al. (2010) |
| [6] Lucas (1935) | [16] Stiger et al. (2003) | [26] Mattio et al. (2009) |
| [7] Noro et al. (1995) | [17] Tseng et al. (1985) | [27] Norris (2010) |
| [8] Okamura (1932) | [18] Tseng and Lu (1997b) | [28] This study |
| [9] Phillips et al. (2005) | [19] Tseng and Lu (2002b) | |
| [10] Phillips and Fredericq (2000) | [20] Womersley (1954) | |

- (ii) An analysis of at least three DNA markers for which comparative data are available in the literature and on GenBank, in the case of *Sargassum*: the nuclear *ITS-2*, the chloroplastic partial *Rubisco* and the mitochondrial *cox3*. Supplementary and more variable markers need to be assessed for discriminating the closely-related species of *S. sect. Sargassum*. Draisma and Rousseau (2010) underlined that the mitochondrial spacer proposed by Coyer et al. (2006) could be used as DNA barcode marker in *Sargassum*. However, its usefulness has yet to be tested.
- (iii) A comparison of morphological and DNA data. The aim is to test the monophyly of morphotypes defined above, the taxonomic value of morphological characters used to define them, and the subjectivity linked to the interpretation of these characters' variability. Two results may arise: either morphotypes are congruent with clades or not. In the latter case, the morphotype may be poly- or paraphyletic, or several morphotypes may be found within the same clade. If the morphotype is poly- or paraphyletic, going back to the morphological observations may help to identify new morphological characters which taxonomic informativeness was not suspected, or morphological variations were misinterpreted as intra-specific polymorphism. If several morphotypes are found within the same clade, either the morphological variations were wrongly interpreted as inter-specific differences or the DNA marker(s) used is (are) not variable enough to discriminate the morphologically well differentiated morphotypes. The main limit encountered when using above listed markers is the lack, even the absence, of variability in sequences obtained for *S. sect. Sargassum* taxa yet discriminated based on well established morphological differences. This lack of variability has been interpreted as the mark of recent radiation (Mattio et al., 2008; Mattio & Payri, 2009), but more variable markers have to be explored to test this hypothesis. It is important to note that if the DNA analysis cannot *a priori* replace a traditional taxonomic study, it may put forward inconsistencies in the interpretation of morphological characters and thus represents a supplementary taxonomic character to be considered for species delineation.

- (iv) Finally, a first identification of morphotypes may be done with data from local literature (identification keys, Floras, and phylogenies) which would have to be confirmed through the careful study of original diagnoses and types (loan or visit to herbaria) for the suspected species. A comparison of morphology and DNA sequences with specimens from the type locality is recommended. If several names can be applied to the same morphotype, and only after effective examination of types, the taxon earliest published would be considered as the current name while the other epithet(s) may be proposed as heterotypic synonym(s) (Art. 11.4, ICBN).

The classification may be re-evaluated by testing the following nul hypothesis: “the traditional classification is similar to the phylogenetic classification”. If the nul hypothesis is accepted it is then possible to be confident with the traditional classification. If the nul hypothesis is rejected, it is necessary to understand why the traditional classification is different from the phylogenetic classification and how to adapt it (or revise it) to find consistency between the two. One of the main source of inconsistency is of topologic order, ie. the arrangement of taxa in the traditional and phylogenetic classifications are different. The most frequent case is that of non-monophyly of traditional taxa: a taxon may be either polyphyletic or paraphyletic.

- (i) If a section (or another infrageneric entity) is paraphyletic (ie. it doesn't include all taxonomic entities found in the relevant clade), the relevant taxa may be transferred from the section, within which they are traditionally classified, to that indicated by phylogenetic analyses. A second option may be to merge the sections which taxonomic entities form a single clade.
- (ii) If a section is polyphyletic, ie. taxonomic entities traditionally attributed to this section are found in two (or more) distinct clades, only taxa grouped in the same clade as the type for the section should be considered as part of the section. Taxa found in a different clade may be either transferred to the section corresponding to the relevant clade or attributed to a new section.

In both instances, when amending or describing a section, it is necessary to know (i) the position of the section's type which will ascertain the clade corresponding to the section(s) of interest (Art. 7 & 10 ICBN), (ii) the anteriority of taxa which will determine the epithet to be conserved when merging two taxonomic groups (Art. 11.4 & 11.5 ICBN), and (iii) the diagnostic characters of the group.

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Appendix 1

Table 5 Bibliographic synthesis of the *Sargassum* classification before the advent of molecular analyses; key morphological characters and type species as compiled from J. Agardh (1848, 1889), Womersley (1954), Yoshida (1983, 1989a, b), Abbott et al. (1988), Tseng and Lu (1988, 1992a, b, 1995a, b, c, 1997a, b, 1999, 2002a, b, c, d); the list of species in each subdivision is non exhaustive

| Taxonomic rank | Epithet | Key morphological characters | Type species | Other species |
|----------------|--|--|--|--|
| Genus | <i>Sargassum</i> C. Agardh | Specialized branch system (axes, branches); only one egg per oogone; three-sided apical cell. | <i>S. bacciferum</i> (Turner) C. Agardh (Basionym <i>Fucus baccifer</i> ; Turner 1802: 56, Falmouth) (= <i>S. natans</i> (Linnaeus) Gaillon) | <i>S. boryi</i> C. Agardh, <i>S. decurrens</i> (R. Brown ex Turner) C. Agardh, <i>S. peronii</i> C. Agardh, <i>S. heteromorphyum</i> J. Agardh, <i>S. decipiens</i> (R. Brown ex Turner) J. Agardh, <i>S. varians</i> Sonder, <i>S. verruculosum</i> C. Agardh, <i>S. piluliferum</i> (Turner) C. Agardh |
| I. subgenus | <i>Phyllotrichia</i> (Aresch.) J. Agardh | Primary branches emerging from the stem or main axis as 'foliar expansions', which are pinnatifid and usually flattened below, but may become cylindrical above where they bear vesicles and receptacles; vesicles essentially without terminal outgrowth. | <i>S. sonderi</i> (J. Agardh) J. Agardh | |
| II. subgenus | <i>Bactrophyucus</i> J. Agardh | Branch bicuspid or angulate; leaves retroflex and perpendicular to branches; simple axillary or terminal receptacles; distributed only in the northern hemisphere. | <i>S. horneri</i> (Turner) C. Agardh (1820: 38, type BM?, Corea Strait) | |
| II.1. sectio | <i>Spongocarpus</i> (Kützting) Yoshida | Stem erect, elongated; branches always arising in axils of leaves and shorter in length than the stem; receptacles terete and siliqueiform | <i>S. horneri</i> (Turner) C. Agardh (1820: 38, type BM?, Corea Strait) | <i>S. filicinum</i> Harvey |
| II.2. sectio | <i>Teretia</i> Yoshida | Main axis shorter or longer; primary axis angular; secondary axis always shorter than primary axis; receptacles cylindrical | <i>S. confusum</i> C. Agardh (1824: 301, lectotype LD3230, Japan) | <i>S. boreale</i> Yoshida et Horig., <i>S. thunbergii</i> (Mert. ex Roth) Kuntze, <i>S. muticum</i> (Yendo) Fensholt, <i>S. hemiphyllyum</i> (Turner) C. Agardh, <i>S. fulvellum</i> (Turner) C. Agardh |

| | | | | |
|-----------------------------|---|--|--|---|
| II.3. sectio | <i>Halochloa</i> (Kützting) Yoshida | Main axis upright and short; primary axes bicuspid to tricuspid; secondary axis always shorter than primary axis; basal leaves retroflex; receptacles flattened or triquetrous with smooth or serrulate margins. | <i>S. siliquastrum</i> (Mert. ex Turner) C. Agardh (1820: 22, lectotype BM, port Nagasaki, Japan) | <i>S. ringgoldianum</i> Harvey, <i>S. giganteifolium</i> Yam., <i>S. trichophyllum</i> (Kützting) Kuntze, <i>S. autumnale</i> Yoshida, <i>S. serratifolium</i> (C. Agardh) C. Agardh |
| II.4. sectio | <i>Repentia</i> Yoshida | Main axis procumbent or decumbent forming secondary haptera on the ventral face; primary axes branched on the dorsal face of main axis; receptacles compressed to flattened. | <i>S. okamurae</i> Yoshida et Konno (1983: 153, holotype SAP-03691, Kominato, Japan) | <i>S. nigrifolium</i> Yendo, <i>S. yamadae</i> Yoshida et Konno, <i>S. yezoense</i> (Yamada) Yoshida et Konno |
| III. subgenus | <i>Arthropophycus</i> J. Agardh | Branch bicuspid or angulate; leaves retroflex and perpendicular to branches; compound receptacles; distributed only in the Southern hemisphere | Type: unknown | <i>S. fallax</i> Sonder, <i>S. lacrifolium</i> (Turner) C. Agardh, <i>S. paradoxum</i> (R. Brown ex Turner) Gaillon, <i>S. robustum</i> J. Agardh, <i>S. sinclairii</i> Hooker et Harvey, <i>S. trischium</i> Sonder, <i>S. vestitum</i> (R. Brown ex Turner) C. Agardh |
| IV. subgenus | <i>Sargassum</i> | Axis cylindrical compressed or flattened (not leaf-like); leaves parallel to axis and rarely retroflex; vesicles arising from the distal portion of leaves; receptacles compound, smooth or bearing spine-like protuberances | <i>S. bacciferum</i> (Turner) C. Agardh (Basionym <i>Fucus baccifer</i> ; Turner 1802: 56, Falmouth) (= <i>S. natans</i> (Linnaeus) Gaillon) | |
| IV.1. sectio | <i>Zygozarpicacae</i> (J. Agardh) Setchell | Receptacles associated to leaves and/or vesicles. | Type: unknown | |
| IV.1.1. subsectio | <i>Holozycopicacae</i> Setchell | Receptacles with pedicel that may be absent, associated only with leaves or both with leaves and vesicles. | Type: unknown | |
| IV.1.1.1. series | <i>Carpophyllae</i> (J. Agardh ex Setchell) Abbott et al. | Missing information | <i>S. carpophyllum</i> J. Agardh (1848: 304, holotype LD2306 herb. Agadh, Sri-Lanka) | |
| IV.1.1.1.1. groupe d'espèce | <i>Carpophyllae</i> J. Agardh | Receptacles bisexual, cylindrical to fusiform, smooth or with a few spines. | <i>S. carpophyllum</i> J. Agardh (1848: 304, holotype: LD2306, Sri-Lanka) | <i>S. angustifolium</i> C. Agardh |
| IV.1.1.1.1.2. species group | <i>Tenerrima</i> Setchell | Receptacles bisexual, compressed to triquetrous, bearing spines at the apex. | <i>S. tenerrimum</i> J. Agardh (1848: 305–306, holotype LD2345, Bombay, India) | <i>S. assimile</i> Harvey, <i>S. aemulum</i> Sonder, <i>S. subtilissimum</i> Tseng et Lu |

Table 5 (continued)

| Taxonomic rank | Epithet | Key morphological characters | Type species | Other species |
|---------------------------|--|---|--|---|
| IV.1.1.1.3. species group | <i>Longifructa</i> Tseng et Lu | Receptacles unisexual, male and female receptacles cylindrical, smooth or with few spines. | <i>S. longifructum</i> Tseng et Lu (1987: 516, holotype AST551767, China) | <i>S. nozhouense</i> Tseng et Lu |
| IV.1.1.1.4. species group | <i>Tenuia</i> Setchell | Receptacles unisexual, male receptacles cylindrical and smooth, female receptacles compressed to triquetrous with spines. | <i>S. tenue</i> J. Agardh <i>nom illeg.</i> (1848: 303–304, type?, India) (= <i>S. steinitzii</i> Lipkin et Silva 2002: 50–51) | <i>S. polycystum</i> C. Agardh, <i>S. laxifolium</i> Tseng et Lu, <i>S. myriocystum</i> J. Agardh |
| IV.1.1.1.5. species group | <i>Vietnamensa</i> Ajsaka | Receptacles unisexual, male and female receptacles compressed to triquetrous, bearing spines. | <i>S. vietnamense</i> Zinova et Dinh (according to Nguyen 1986) | |
| IV.1.2. subsectio | <i>Pseudozygocarpicac</i> Setchell | Receptacles often pedicelate, associated only with leaves or vesicles. | Type: unknown | |
| IV.1.2.1. series | <i>Cinerea</i> Tseng et Lu | Receptacles unisexual; thallus ash-grey. | <i>S. cinereum</i> J. Agardh (1848: 305, holotype: LD2349, Hong-Kong) | |
| IV.1.2.1.1. species group | <i>Vachelliana</i> Setchell | Receptacles unisexual, male and female receptacles cylindrical to fusiform smooth or with few spines. | <i>S. vachellianum</i> Greville (1848: 204, holotype E?, China) | <i>S. graminifolium</i> (Turner) J. Agardh, <i>S. crispifolium</i> Yamada |
| IV.1.2.1.2. species group | <i>Incana</i> Ajsaka | Receptacles bisexual, cylindrical to fusiform, smooth or with a few spines. | <i>S. incanum</i> Grunow (1915: 379, syntypes W?, Shangai-Canton, Hong-Kong) | <i>S. bulbiferum</i> Yoshida |
| IV.1.2.1.3. species group | <i>Cinerea</i> Setchell | Receptacles unisexual, male receptacles cylindrical smooth or with spines, female receptacles compressed with spines. | <i>S. cinereum</i> J. Agardh (1848: 305, holotype LD2349, Hong-Kong) | <i>S. glaucescens</i> J. Agardh |
| IV.1.2.1.4. species group | <i>Denticarpha</i> Ajsaka | Receptacles bisexual, compressed to triquetrous with spines. | <i>S. denticarpum</i> Ajsaka (1994: 394–396, type: photo in Ajsaka et al., 1995: 48, Vietnam) | |
| IV.2. sectio | <i>Acanthocarpicac</i> (J. Agardh) Abbott et al. | Receptacles flattened with spines. | Type : unknown | |

| | | | |
|------------------------------|---|--|---|
| IV.2.1. <i>subsectio</i> | <i>Glomerulatae</i> (J. Agardh) Tseng et Lu | Receptacles bisexual, flattened, arranged in dense glomerules. | Type: unknown |
| IV.2.1.1. series | <i>Binderiana</i> (Grunow) Tseng et Lu | Distichous axis, compressed to flattened. | <i>S. binderi</i> Sonder |
| IV.2.1.1.1. species group | <i>Swarzia</i> | Vesicles ellipsoidal and apiculate, with flattened pedicels longer than vesicles. | <i>S. acutifolium</i> Greville, <i>S. cervicorne</i> Greville, <i>S. dumosum</i> Greville, <i>S.</i> <i>echinocarpum</i> J. Agardh, <i>S. wightii</i> Greville |
| IV.2.1.1.2. species group | <i>Binderia</i> | Vesicles spherical, with pedicels generally longer than or as long as the vesicles. | <i>S. binderi</i> Sonder ex J. Agardh 1848: 328, syntypes TCD1110-113a, China Sea and Sunda Strait) |
| IV.2.1.2. series | <i>Platycarpae</i> (Grunow) Tseng et Lu | Apical part of axis multiple, filiform or subcylindrical. | <i>S. platycarpum</i> Montagne (1842: 248, holotype PC-MA9209, Martinique) |
| IV.2.2. <i>subsectio</i> | <i>Biserrulae</i> (J. Agardh) Tseng et Lu | Receptacles uni- or bisexual arranged in racemes. | <i>S. biserrula</i> J. Agardh (1848: 318, syntypes TCD1118, India) |
| IV.2.2.1. series | <i>Plagiophyllae</i> Tseng et Lu | Receptacles unisexual, female receptacles acanthocarpic, male receptacles malacocarpic. | <i>S. plagiophyllum</i> C. Agardh |
| IV.2.2.1.1 species group | <i>Plagiophylla</i> | Holdfast discoid. | <i>S. plagiophyllum</i> C. Agardh (1824: 304, neotype: PC ABI4948, Indian Ocean) |
| IV.2.2.1.2. species group | <i>Rhizophora</i> | Holdfast rhizoidal. | <i>S. rhizophorum</i> Tseng et Lu (2002b: 18, holotype: AST 55-1843, China) |
| IV.2.2.2. series | <i>Illicifoliae</i> (J. Agardh) | Receptacles unisexual, male and female receptacles | <i>S. illicifolium</i> (Turner) C. Agardh <i>S. cinctum</i> J. Agardh, |

Table 5 (continued)

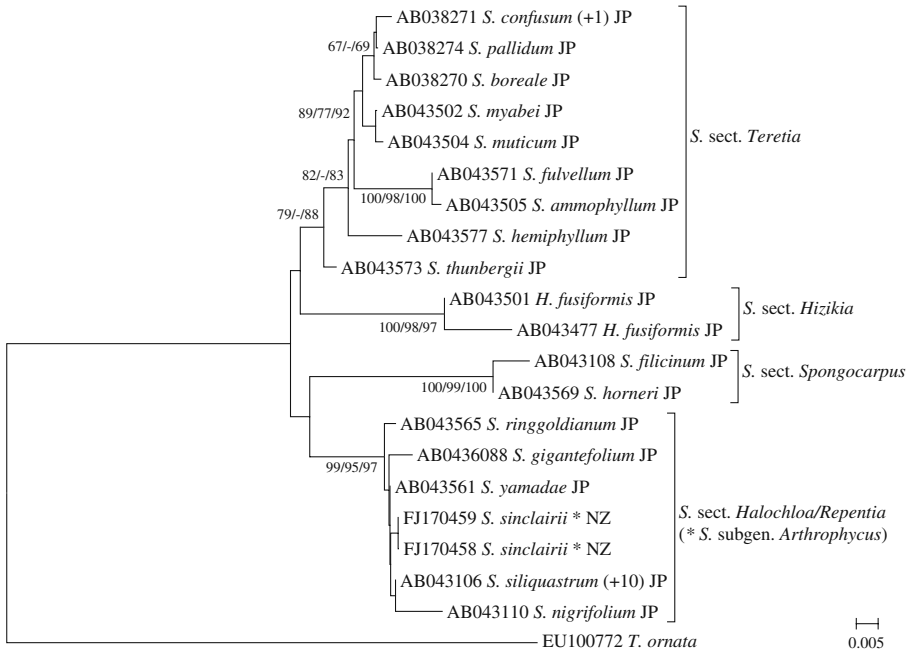
| Taxonomic rank | Epithet | Key morphological characters | Type species | Other species |
|-------------------|---|--|---|--|
| | Tseng et Lu | acanthocarpic; basis of leaves asymmetrical, internal margin smooth or slightly serrulate, external margin distinctly dentate. | (Turner, 1807:113, holotype BM 562953, Sunda Strait) | <i>S. parvifolium</i> (Turner) C. Agardh, <i>S. sandei</i> Reinbolt |
| IV.2.2.3. series | <i>Odontocarpicae</i> Tseng et Lu | Receptacles bisexual; leaves lanceolate to linear often with an asymmetrical basis. | <i>S. odontocarpum</i> Sonder (1871:43, India) | <i>S. spinifex</i> C. Agardh, <i>S. turbinatifolium</i> Tseng et Lu |
| IV.3. sectio | <i>Malacocarpicae</i> (J. Agardh) Abbott et al. | Receptacles cylindrical, smooth, arranged in cymes or racemes. | Type: unknown | |
| IV.3.1. subsectio | <i>Fruiculiferae</i> (J. Agardh) Tseng et Lu | Receptacles brush like, arranged in cymes, pedicelate and without sterile parts. | Type: unknown | <i>S. polyporum</i> Montagne, <i>S. longicaulis</i> Tseng et Lu, <i>S. aquifolium</i> (Turner) C. Agardh, <i>S. obtusifolium</i> J. Agardh |
| IV.3.2. subsectio | <i>Cymosae</i> (J. Agardh) Tseng et Lu | Receptacles branched, arranged in cymes, ramuli arranged in groups of fascicles, with acuminate apex. | <i>S. cymosum</i> C. Ag. (1820: 20, syntypes: LD2979, 2990, Brazil) | <i>S. bacciferum</i> (Turner) C. Agardh, <i>S. vulgare</i> C. Agardh, <i>S. desfontainesii</i> (Turner) C. Agardh, <i>S. torvum</i> J. Agardh, <i>S. polyphyllum</i> J. Agardh |
| IV.3.3. subsectio | <i>Racemosae</i> (J. Agardh) Tseng et Lu | Receptacles arranged in racemes, with sterile pedicels. | Type: unknown | |
| IV.3.3.1. series | <i>Acinariae</i> J. Agardh | Receptacles lanceolate to conical, with short fertile and axil ramuli. | <i>S. acinaria</i> C. Agardh nom. illeg. (1820: 22, cf. Silva et al., 1996: 701, 930) | <i>S. spinuligerum</i> Sonder, <i>S. podacanthum</i> Sonder, <i>S. leptodum</i> Sonder |
| IV.3.3.2. series | <i>Glandulariae</i> J. Agardh | Receptacles with short, axial and glandular ramuli. | Type : unknown | <i>S. bacularia</i> (Mertens) C. Agardh, <i>S. plagiophyllum</i> Montagne, <i>S. granuliferum</i> C. Agardh |
| IV.3.3.3. series | <i>Siliquosae</i> J. Agardh | Receptacles with long and pedicelate ramuli, cylindrical siliquaeform, pinched in some points, alternate position on axis. | <i>S. siliquosum</i> J. Agardh (1848: 316, syntype LD3260, Singapor) | <i>S. henslowianum</i> C. Agardh, <i>S. kuetzingii</i> Setchell, <i>S. paniculatum</i> J. Agardh |
| IV.4. sectio | <i>Phyllocystae</i> Tseng | Modified leaves characterised by a central inflated part | <i>S. phyllocystum</i> Tseng et Lu | <i>S. emarginatum</i> Tseng et Lu, <i>S.</i> |

| | | | |
|---|--|--|---|
| <i>Incertae sedis</i> <i>Schizophycus</i> J. Agardh | (1979: 1, China) <i>S. patens</i> C. Agardh ^a (1820: 27, lectotype: LD2838, Japan) | (Phyllocysts): receptacles bisexual, generally compound and arranged in short racemes, female receptacles flattened or triquetrous, generally dentate. Primary axis arising from foliar expansions; leaves and axis developed in the same plan; vesicles bearing a coronal leaf. | <i>mcclurei</i> Setchell, <i>S. herklotsii</i> Setchell, <i>S. quinhomense</i> Nguyen <i>S. kashiwajimanum</i> Yendo, <i>S. kashimotense</i> Yendo, <i>S. pinnatifidum</i> Harvey, <i>S. tosaense</i> Yendo, |
|---|--|--|---|

^a *S. patens* represents the type species of *S. subgen. Schizophycus* because it is the only species conserved by the J. Agardh (1889) when transferring tribus *Schizophylla* to subgenus rank. The four other species of tribus *Schizophylla* were transferred to subgenera *Phyllotrichia* and *Bactrophycus* (J. Agardh, 1889)

Appendix 2

ITS-2 analyses based on the alignment of 31 GenBank sequences available for species of *S.* subgen. *Bactrophycus* and *Arthrophyucus*



Neighbour-Joining (NJ) analysis based on 31 GenBank sequences, 475 pb-long (including gaps), representing 27 taxa of *S.* subgen. *Bactrophycus* and *Arthrophyucus*. Bootstrap values are indicated for NJ/MP(Maximum Parsimony)/ML(Maximum Likelihood) when above 60% and were based on 1000 (NJ/MP) or 100 (ML, GTR+G+I) replicates. Root: *Turbinaria ornata*. JP: Japan, NZ: New Zealand. The number of identical sequences is indicated between brackets when relevant and detailed the table below. **S. sinclairii* is traditionally classified in *S.* subgen. *Arthrophyucus*.

List of identical sequences not shown on the tree

References on the tree

AB043106 *S. siliquastrum*

AB038271 *S. confusum*

Identical sequences not on tree

AB043575 *S. autumnale*

AB043574 *S. macrocarpum*

AB043610 *S. micracanthum*

AB043609 *S. micracanthum*

AB043578 *S. okamurae*

AB043579 *S. okamurae*

AB043612 *S. serratifolium*

AB043568 *S. trichophyllum*

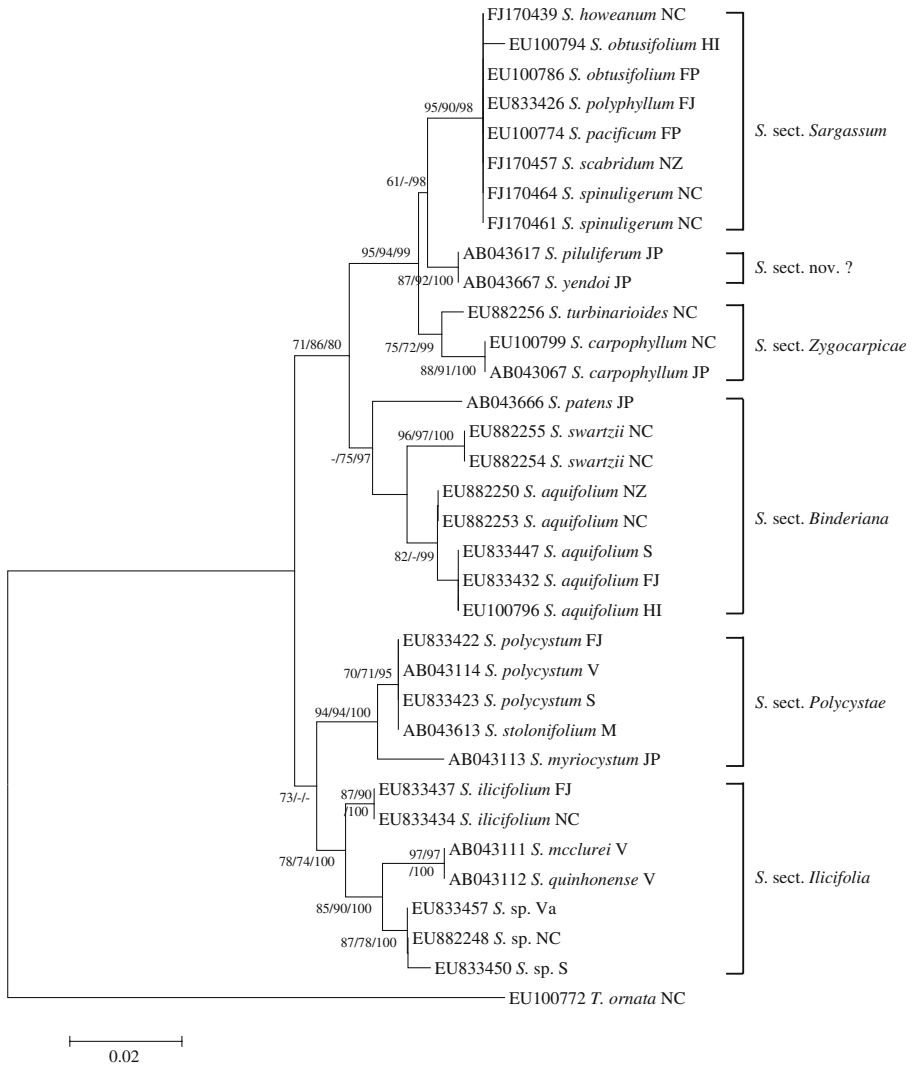
AB043107 *S. yamamotoi*

AB043611 *S. yesoense*

AB038273 *S. microceratium*

Appendix 3

ITS-2 analyses based on the alignment of 33 GenBank sequences available for species of *S.* subgen. *Sargassum*.



Neighbour-Joining (NJ) analysis based on 33 GeneBank sequences, 475 pb-long (including gaps), representing 19 taxa of *S.* subgen. *Sargassum*. Bootstrap values are indicated for NJ/MP (Maximum Parsimony)/ML (Maximum Likelihood) when above 60% and were based on 1000 (NJ/MP) or 100 (ML, GTR+G+I) replicates. Root: *Turbinaria ornata*. FJ: Fiji Islands, FP: French Polynesia, HI: Hawaii, JP: Japan, M: Malaysia, NC: New Caledonia, S: the Solomon Islands, Va: Vanuatu, V: Vietnam.

Appendix 4

Table 6 Synthesis of the current *Sargassum* classification; key morphological characters; details of type species; example of species for each subdivision (non exhaustive list); compiled from J. Agardh (1848, 1889), Womersley (1954), Yoshida (1983, 1989a, b), Abbott et al. (1988), Tseng and Lu (1988, 1992a, b, 1995a, b, c, 1997a, b, 1999, 2002a, b, c, d), Stiger et al. (2003), Mattio and Payri (2009), Mattio et al. (2009, 2010), Norris (2010)

| Taxonomic rank | Epithet | Key morphological characters | Type species | Other species ^a |
|----------------|---|---|---|--|
| Genus | <i>Sargassum</i> C. Agardh | Specialized branch system (axes, branches); only one egg per oogone; three-sided apical cell. | <i>S. bacciferum</i> (Turner) C. Agardh (Basionym : <i>Fucus baccifer</i> Turner 1802: 56, no data about type, Falmouth) (= <i>S. natans</i> (Linnaeus) Gaillon) | |
| I. subgenus | <i>Arthrophyucus</i> J. Agardh ³ | Branch bicuspoid or angulate; leaves retroflex and perpendicular to branches; compound receptacles; distributed only in the Southern hemisphere. | <i>S. heterophyllum</i> C. Agardh ^b (1820: 21, syntype LD herb, Agadh?; Cape of Good Hope, Japan, Australia) (= <i>S. incisifolium</i> (Turner) C. Agardh) | <u><i>S. fallax</i> Sonder, <i>S. lacertifolium</i> (Turner) C. Agardh, <i>S. paradoxum</i> (R. Brown ex Turner) Gaillon, <i>S. robustum</i> J. Agardh, <i>S. tristichum</i> Sonder, <i>S. vestitum</i> (R. Brown ex Turner) C. Agardh</u> |
| II. subgenus | <i>Bactrophyucus</i> J. Agardh | Branch bicuspoid or angulate; leaves retroflex and perpendicular to branches; simple axial or terminal receptacles; distributed only in the northern hemisphere. | <i>S. horneri</i> (Turner) C. Agardh (Basionym : <i>Fucus horneri</i> Turner, 1808: 34, type BM-K, Korea Strait) | |
| II.1. sectio | <i>Hatolchloa</i> (Kützing) Yoshida | Main axis either upright and short; primary axis bicuspoid to tricuspoid; secondary axis always shorter than primary axis; basal leaves retroflex; receptacles flattened or triquetrous with smooth or serrulate margins. <i>NB. this description needs revision with regard to the fusion of S. sect.</i> | <i>S. siliquastrum</i> (Mert. ex Turner) C. Agardh (Basionym : <i>Fucus siquastrum</i> , lectotype BM, port Nagasaki, Japan) | <u><i>S. autumnale</i> Yoshida, <i>S. giganteifolium</i> Yam., <i>S. nigrifolium</i> Yendo, <i>S. okamurae</i> Yoshida et Konno, <i>S. ringgoldianum</i> Harvey, <i>S. sinclairii</i> Hook. et Harvey, <i>S. serratifolium</i> (C. Agardh) C. Agardh, <i>S. trichophyllum</i> (Kützing) Kuntze, <i>S. yamadadae</i> Yoshida et Konno, <i>S. yezoense</i> (Yamada) Yoshida et Konno</u> |

| | | | | |
|--|--|--|---|---|
| <p>Repentia: main axis procumbent or decumbent, forming secondary haptera on the ventral face; primary axis arising from the dorsal face; receptacles compressed to flattened.</p> | <p>II.2. sectio <i>Hizikia</i> (Okam.) Yoshida</p> | <p>Holdfast with creeping rhizomatous outgrowth; stem short; leaves cylindrical to compressed linear, with marginal teeth; vesicle fusiform; receptacles short, cylindrical, aggregated in axil of leaf.</p> | <p><i>S. fusiforme</i> (Harvey) Setchell (Basionym : <i>Cystophyllum fusiforme</i> Harvey 1860: 328, no data on type location, Shimoda, Japan)</p> | <p>To date this section contains only one species.</p> |
| <p>Stem erect, elongated; branches always arising in axils of leaves and shorter in length than the stem; receptacles terete and siliquaeform.</p> | <p>II.3. sectio <i>Spongocarpus</i> (Kützinger) Yoshida</p> | <p>Main axis shorter or longer; primary axis angular; secondary axis always shorter than primary axis; receptacles cylindrical.</p> | <p><i>S. horneri</i> (Turner) C. Agardh (Basionym : <i>Fucus horneri</i> Turner 1808: 34, type BM-K, Korea Strait)</p> | <p><i>S. filicinum</i> Harvey</p> |
| <p>Axis cylindrical compressed or flattened (not leaf-like); leaves parallel to axis and rarely retroflex; vesicles arising from the distal portion of leaves; receptacles compound, smooth or bearing spine-like protuberances.</p> | <p>III. subgenus <i>Sargassum</i></p> | <p>Main axis shorter or longer; primary axis angular; secondary axis always shorter than primary axis; receptacles cylindrical.</p> | <p><i>S. confusum</i> C. Agardh (1824: 301, lectotype LD3230 herb. Agardh, Japan)</p> | <p><i>S. boreale</i> Yoshida et Horriguchi, <i>S. fibvellum</i> (Turner) C. Agardh, <i>S. hemiphyllum</i> (Turner) C. Agardh, <i>S. muticum</i> (Yendo) Fensholt, <i>S. thunbergii</i> (Mertens ex Roth) Kuntze</p> |
| <p>Strongly flattened axes distichously arranged in one plan; elongated spatulate leaves with attenuated</p> | <p>IV.1. sectio <i>Binderiana</i> (Grunow) Mattio et al.</p> | <p>Axis cylindrical compressed or flattened (not leaf-like); leaves parallel to axis and rarely retroflex; vesicles arising from the distal portion of leaves; receptacles compound, smooth or bearing spine-like protuberances.</p> | <p><i>S. bacciferum</i> (Turner) C. Agardh (Basionym : <i>Fucus baccifer</i> Turner 1802: 56, no data about type, Falmouth) (= <i>S. natans</i> (Linnaeus) Gaillon)</p> | <p><i>S. aquifolium</i> (Turner) C. Agardh, <i>S. patens</i> C. Agardh, <i>S. swartzii</i> C. Agardh</p> |

Table 6 (continued)

| Taxonomic rank | Epithet | Key morphological characters | Type species | Other species ^a |
|---------------------|--|---|--|--|
| IV.2. <i>sectio</i> | <i>Illicifolia</i> (J. Agardh) Mattio et al. | base, cryptostomata thin to large, mostly aligned on each side of the midrib, and dentate margins; vesicles supported by a long pedicel, spherical to obovoid, smooth or with a short mucro, a foliar appendage or crown, or differentiated into phyllocysts; receptacles mostly bisexual, with serrate margins and arranged in dense cymose glomerules. | Sea) (= <i>S. aquifolium</i> (Turner) C. Agardh) | <i>S. quinhonense</i> Nguyen, <u><i>S. meclurei</i> Setchell</u> |
| IV.3. <i>sectio</i> | <i>Polycystae</i> Mattio et al. | Cylindrical to slightly compressed axes possibly twisted, alternately and spirally arranged; broadly spatulate leaves with cuneate or rounded unequal base, cryptostomata thin, numerous, dispersed, rarely aligned, and serrate to dentate margins; vesicles supported by a short pedicel, spherical to obovoid, smooth, with an ear-like or simple spine-like mucro; receptacles bearing spine-like protuberances, mostly unisexual and showing a male/female dimorphism. | <i>S. illicifolium</i> (Turner) C. Agardh (Basionym <i>Fucus illicifolius</i> Turner 1807: 113, holotype BM 562953, Sunda Strait). | <i>S. bacularia</i> (Mertens) C. Agardh, <u><i>S. herporhizum</i> Setchell et N. L.</u> Gardner, <u><i>S. plagiophyllum</i> Montagne</u> , <u><i>S. brandegeei</i> Setchell et N. L.</u> Gardner, <u><i>S. liebmanni</i> J. Agardh</u> |
| | | Lower part of the 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 may arise; upper | <i>S. polycystum</i> C. Agardh (1824: 304, syntypes TCD 1108, 1109, Sunda Strait) | |

parts of the secondary axis densely clothed with leaves, vesicles and receptacles.

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|---------------------|---|--|---|--|
| IV.4. <i>sectio</i> | <i>Sargassum</i> | Leaves and vesicles well differentiated, leaves not retroflex at basis; receptacles usually compound, cylindrical, smooth, arranged in cymes or racemes. <i>NB. this description needs revision.</i> | <i>S. bacciferum</i> (Turner) C. Agardh (Basionym : <i>Fucus baccifer</i> ; Turner 1802 : 56, no data about type, Falmouth) (= <i>S. natans</i> (Linnaeus) Gaillon) | <u><i>S. cynosomum</i></u> C. Agardh, <u><i>S. howeanum</i></u> Lucas, <u><i>S. lysterix</i></u> J. Agardh, <u><i>S. obtusifolium</i></u> J. Agardh, <u><i>S. pacificum</i></u> Boyl, <u><i>S. polyphyllum</i></u> J. Agardh, <u><i>S. polyporum</i></u> Montagne, <u><i>S. siliquosum</i></u> J. Agardh, <u><i>S. spinuligerum</i></u> Sonder, <u><i>S. vulgare</i></u> C. Agardh |
| IV.5. <i>sectio</i> | <i>Zygocarpicae</i> (J. Agardh) Setchell | Receptacles associated to leaves and/or vesicles. <i>NB. this description needs revision.</i> | <i>S. carpophyllum</i> J. Agardh ^c (1848: 304, holotype LD2306 herb. Agardh, Sri-Lanka) | <i>S. aemulatum</i> Sonder, <i>S. angustifolium</i> C. Agardh, <i>S. cinereum</i> J. Agardh, <i>S. denticarpum</i> Ajsaka, <i>S. glaucescens</i> J. Agardh, <i>S. incanum</i> Grunow, <i>S. tenerimum</i> J. Agardh, <i>S. turbinarioides</i> Grunow, <i>S. vachellianum</i> Greville, <i>S. vietnamense</i> Zinova et Dinh |
| IV.6. <i>sectio</i> | <i>Johnstonii</i> E. Y. Dawson ex J. N. Norris—need assessment with DNA markers | Leaves very narrow, subcylindrical to compressed, midrib absent, cryptostomata usually present; vesicles elliptical with long apiculate extensions. | <i>S. Johnstonii</i> Setchell et N. L. Gardner (1924: 737, type UC?, Georges Is., Gulf of California) | To date this section contains only one species. |
| IV.7. <i>sectio</i> | <i>Lapazeanum</i> E. Y. Dawson ex J. N. Norris—need assessment with DNA markers | Holdfast rhizomatous, leaves flattened, expanded, and asymmetrical, midrib absent or occasionally, if present, inconspicuous. | <i>S. lapazeanum</i> Setchell et N. L. Gardner (1924: 734, type UC?, La Paz California) | <i>S. acinacifolium</i> Setchell et N. L. Gardner, <i>S. macdougallii</i> E. Y. Dawson, <i>S. sonorense</i> E. Y. Dawson |
| IV.8. <i>sectio</i> | <i>Sinicola</i> E. Y. Dawson ex J. N. Norris—need | Holdfast woody, conical, or knotty, with short protuberances; leaves longer than wide, symmetrical, | <i>S. sinicola</i> Setchell et N. L. Gardner (1924: 736, type UC?, La Paz, | <i>S. sinicola</i> subsp. <i>Camoutii</i> (E. Y. Dawson) J. N. Norris et Yensen, <i>S. horridum</i> Setchell |

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|---|--|--|--|
| assessment with DNA markers | midrib present, dentate to serrate margins, cryptostomata present, often abundant; vesicles subspherical to spherical. | California) | et N. L. Gardner |
| IV. subgenus <i>Phyllotrichia</i> (Areschoug) J. Agardh | Primary branches emerging from the stem or main axis as 'foliar expansions', which are pinnatifid and usually flattened below, but may become cylindrical above where they bear vesicles and receptacles; vesicles essentially without terminal outgrowth. | <i>S. sonderi</i> (J. Agardh) J. Agardh (Basionym : <i>Cystophora sonderi</i> J. Agardh 1848: 247, type LD 2043 herb. Agardh, Western Australia) | <i>S. decipiens</i> (R. Brown ex Turner) J. Agardh, <i>S. heteromorphum</i> J. Agardh, <i>S. peronii</i> C. Agardh, <i>S. varians</i> Sonder, <i>S. verruculosum</i> C. Agardh |

^a underlined epithets correspond to taxa which taxonomic position was confirmed by DNA markers analysis

^b *S. sect. Arthrophyllus* J. Agardh (1848) was subdivided into three tribes: *Schizophylla*, *Holophylla* and *Heterophylla*. Only species of tribes *Heterophylla* were maintained by J. Agardh (1889) to form *S. subgen. Arthrophyllus*. The two first tribes were transferred to subgenus rank as respectively *S. subgen Schizophyllus* and *Bactrophyllus*. In this context, it is the founding species of tribus *Heterophylla* (*S. heterophyllum*) which we propose as type of *S. subgen. Arthrophyllus*

^c *S. carpophyllum* is proposed as the type species of *S. sect. Zygozarpicaceae* because it represents the nomen typificatum of its first subdivision (tribe *Carpophyllae* J. Agardh) as listed by J. Agardh (1889)

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