REVIEW

A concise review of the genus *Asperococcus* (Phaeophyceae: Chordariaceae)

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Abstract

Asperococcus J.V. Lamouroux is a genus of brown algae in the Chordariaceae family (Order Ectocarpales). This concise review compiles the published literature on *Asperococcus* taxonomy, morphology, geographical distribution, ecology, life cycles, cultivation, biochemical composition and bioactive properties, emphasizing its commercial potential. This genus, which is mainly distributed in temperate-cold latitudes, is represented by six species of which *A. fistulosus*, *A. ensiformis* and *A. bullosus* have been the most studied. Species of this genus have membranous saccate or filiform thalli with prominent sori protruding from the surface. The life cycle is heteromorphic, alternating between a macroscopic sporophyte and a microscopic branched gametophyte. They inhabit tidal pools or different depths in the subtidal zone. Some species have been reported as epiphytic and epizoic organisms. Although there is no record of the commercialization of *Asperococcus* species, the cultivation of *A. ensiformis* from the Argentine Patagonian coasts was recently assessed and the biochemical composition of some species was studied, revealing a commercial potential.

Keywords Taxonomy · Geographical distribution · Ecology · Life cycle · Cultivation · Bioactive properties

The genus *Asperococcus* includes a group of brown algae with a heteromorphic life cycle, belonging to the family Chordariaceae, Order Ectocarpales (Peters and Ramírez 2001). Six species of *Asperococcus* are flagged as taxonomically accepted in Algaebase (Guiry and Guiry 2023), however, the genus has a complex nomenclatural history that has led to uncertainty about the identity of the species that it encompasses. *Asperococcus* species are widespread around the world, however they have received less attention than other species of Chordariaceae and the literature on the genus is somewhat fragmented and scarce. The only available information for some species is the original description which is several decades old.

In recent years *Asperococcus* has been valued as a source of biologically active compounds (Zubia et al. 2009; Poza et al. 2022) which are of great interest to the pharmaceutical industry. Considering the global trend towards the production of macroalgae through aquaculture, the culture of some species of *Asperococcus* was studied, allowing the development of techniques that guarantee sustainable management of the natural populations (FAO 2020; Poza et al. 2022).

Historical background of the genus

The name *Asperococcus* means "rough seed" (*asper*=rough; *kok-koç*=seed or grain) and was established by J.V. F. Lamouroux to distinguish a seaweed that resembled the thallus of *Ulva*, but with prominent reproductive structures. Lamouroux (1813) described the fronds of *Asperococcus* as fistulous, generally cylindrical and rarely compressed, with a less bright color than *Ulva*. He clearly pointed out that *Asperococcus* could not be confused with *Ulva* because in the former, isolated and scattered "seeds"

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protruded from the surface of the frond when mature, giving the thallus a rough texture. Hence, he transferred the species *Ulva rugosa* of Linnaeus to the genus *Asperococcus* (as *Asperococcus rugosus*). In the same publication of 1813, Lamouroux designated the species *Asperococcus bullosus* from the Mediterranean, without including a formal description.

Botanists and phycologists through time have adopted different classifications for *Asperococcus*, placing the genus in different orders and families. Agardh (1820) was the first to classify this genus among the brown algae, in the order Fucoideae, however, he established the genus *Encoelium* to include the plants studied by Lamouroux with three species, *Encoelium echinatus* (=*A. rugosus*), *Encoelium bullosum* (=*A. bullosus*) and *Encoelium sinuosum*. In a later publication, Greville (1830) rescued the name *Asperococcus* indicating that the generic name given by Lamouroux should be preferred over *Encoelium* because it describes the most striking characteristic of these algae, the surface roughness given by the prominent sori. Other authors placed the genus in the Dictyoteae (Greville 1830; Hooker 1833; Harvey 1857), Punctariaceae (Kylin 1907), Encoeliaceae (MacCaughey 1918), Ectocarpales (Fritsch 1945) and Dictyosiphonales (Wynne 1982). The most recent classification adopted for this genus is based on the multilocus phylogeny of the Phaeophyceae proposed by Silberfeld et al. (2010), in which *Asperococcus*

is classified in the subclass Fucophycidae, order Ectocarpales, and family Chordariaceae (Guiry and Guiry 2023).

More than 40 species names of *Asperococcus* appear in the phycological literature, but the majority are considered synonyms of the three most common species *A. fistulosus*, *A. ensiformis* and *A. bullosus*. Many different generic or specific names have been given to the same species by different authors, resulting in a plethora of synonyms for some species. An example is that of *A. bullosus*, which was given that name in continental Europe (Cabioc´h et al. 2006), but the same alga was named *Asperococcus turneri* in Britain (Fletcher 1987; Morton 1994). Currently, only six species of *Asperococcus* are taxonomically accepted in Algaebase (Guiry and Guiry 2023): *Asperococcus bullosus* J.V. Lamouroux, *Asperococcus ensiformis* (Delle Chiaje) M.J. Wynne, *Asperococcus fistulosus* (Hudson) W.J. Hooker, *Asperococcus scaber* Kuckuck, *Asperococcus norvegicus* Kylin and *Asperococcus tortilis* Suhr (Table 1), and many still have uncertain taxonomic status. According to Greville (1830), *A. fistulosus* (=*A. rugosus,* in Lamouroux 1813) was once considered the type of the genus; however, it has never been formally designated, and currently *A. bullosus* is regarded as the type *non designatus* (Guiry and Guiry 2023).

Table 1 Species of *Asperococcus* that are currently taxonomically accepted according to Algaebase (Guiry and Guiry 2023), with their corresponding authorities, type localities and synonyms

	Type locality	Basionym	Synonyms
Asperococcus bullosus J.V.Lamouroux	France: Mediterranean coast		*Physidrum bullosum, Encoelium bullosum, Ulva turneri, Gastridium opuntium, Asperococcus bulbosus, Asperococcus turneri, Encoelium macgregori, Asperococcus turneri* var. *profundus*
Asperococcus ensiformis (Delle Chiaje) M.J.Wynne	Italy: Posilipo near Napoli	*Laminaria ensiformis*	*Laminaria ensiformis, Asperococcus compressus, Haloglossum griffithsianum, Haloglossum compressum*
Asperococcus fistulosus (Hudson) W.J.Hooker	England	*Ulva fistulosa*	*Ulva fistulosa, Scytosiphon fistulosus, Chordaria filum* var. *fistulosa, Scytosiphon filum* var. *fistulosus, Conferva echinata, Asperococcus rugosus, Asperococcus echinatus, Encoelium echinatum, Scytosiphon lomentaria* f. *fistulosus, Ectocarpus reptans, Ectocarpus repens, Ascocyclus reptans, Phycocelis reptans, Myrionema reptans, Chilionema reptans, Hecatonema reptans, Asperococcus echinatus* f. *villosa, Asperococcus fistulosus* f. *villosus, Hecatonema kjellmani, Phycocelis crouaniorum*
Asperococcus norvegicus Kylin	Norway: Bergen	-	-
Asperococcus scaber Kuckuck	Rovinj and Naples, Mediterranean Sea	-	-
Asperococcus tortilis Suhr	Ostindien	-	*Encoelium tortile, Scytosiphon tortilis*

Morphology

The macroscopic thallus of *Asperococcus* is the sporophyte, which has a simple morphology. The sporophytes may arise solitarily, but more frequently they appear in clumps or groups attached to the substratum by a small disc (Fig. 1a). The fronds may be tubular, filiform or elongate-saccate, solid, completely hollow or highly compressed in some parts with a ribbon-like shape. In some species, the hollow part of the fronds is irregularly inflated. The fronds are characterized by a slightly tapering or rounded apex, and a basal part that tapers gradually to the attachment disc, forming a sort of short stipe (Fig. 1b,c). The most remarkable feature of this genus is the prominent sori, scattered on the surface of the fertile thalli (Fig. 1b,c). Although the size of the thallus is variable, some species reach large sizes up to 1 m long and 5 cm wide.

The structure of the thallus is parenchymatous, polystichous, with diffuse growth. It is formed internally of a cortex of assimilatory pigmented cells with numerous chloroplasts, each with one or two pyrenoids, and a medulla of larger colorless cells (Fig. 1d,e). Phaeophycean hairs are scattered on the surface of the thallus, solitary or in groups, usually related to the sorus.

The macroscopic sporophytes have unilocular sporangia grouped in sori that are prominent and may be visible to the naked eye (Fig. 1c,f). Both types of sporangia (unilocular and plurilocular) can be found in the same sorus on one plant or on different plants. The paraphyses are multicellular. They are straight, club-shaped or pyriform, and are mixed with the sporangia (Fig. 1g). The microscopic thallus (gametophyte) is filamentous and forms a disc from which erect filaments arise, bearing plurilocular gametangia.

Several authors have provided descriptions of *A. fistulosus*, *A. ensiformis, A. bullosus* and *A. scaber* (Greville 1830; Sauvageau 1895; Fritsch 1945; Asensi 1972; Womersley 1987; Schneider and Searles 1991; Nelson and Knight 1995; D'Archino and Nelson 2006; Cormaci et al. 2012; Bárbara et al. 2015), whereas little is known about *A. tortilis* and *A. norvegicus*, of which only the original description is available.

The following descriptions summarize the main morphological characters found on the macroscopic thallus of the six species taxonomically accepted in Algaebase.

Asperococcus bullosus J.V. Lamouroux

(Greville 1830; Fritsch 1945; Womersley 1987; Nelson and Knight 1995; D'Archino and Nelson 2006; Cormaci et al. 2012).

Thalli are medium to dark brown, flabby, gelatinous, irregularly inflated to bullose, up to 100 cm long and 12 cm

wide. The base of the thallus tapers abruptly to a short stipe 2 mm to 10 mm long. The holdfast is 0.5–2 mm wide. The membrane is formed of 3 to 5 layers of cells. The cortex is formed of one layer of angular and isodiametric cortical cells, 20–35 µm in diameter in surface view, with numerous chloroplasts, each with 1 or 2 pyrenoids. The medulla is formed of 1 to 3 layers of large colorless cells. In the center of the membrane there is a large hollow cavity. Phaeophycean hairs are 16–20 µm in diameter, they grow singly or in groups from a basal meristem and each has a basal sheath. Unilocular sporangia are sessile, pyriform or clavate in transversal section, 30–40 µm long and 20–30 µm in diameter, and are located in rounded or elongated sori that measure 100 to 350 µm across. Plurilocular sporangia are lanceolate, ovoid or conical, 40–60 µm long and 30–40 µm in diameter, sessile or pedunculated. They are usually in the same sorus as the unilocular sporangia. Paraphyses are clavate, 2–4 cells long, with the apical cell rich in physodes.

Asperococcus ensiformis (Delle Chiaje) M.J. Wynne

(Womersley 1987; Sauvageau 1895; Asensi 1972; D'Archino and Nelson 2006; Cormaci et al. 2012; pers. obs.)

The thalli are yellowish, medium brown or olive-greenish, membranous, elongate-clavate or attenuated at the apex and flattened like a ribbon. Several fronds arise from a small discoid holdfast, 1–3 mm in diameter. They are up to 80 cm long and 4 cm broad, attenuating at the base to a short stipe 3–10 mm long. The fronds have the same width throughout the thallus. The membrane is formed of 1 or 2 layers of subquare cortical cells, or rectangular in surface view, measuring 13–20 µm × 8–12 µm, with numerous chloroplasts, each with one pyrenoid, and a medulla of 1 to 3 large rectangular colorless cells, measuring 60–90 µm × 25–45 µm. In cross-section, the thallus is strongly compressed in the center, forming a narrow cavity because the medullary cells are close together and are linked by irregular strands of long, cylindrical, colorless cells; while the margins are hollow, giving the thallus a flattened appearance. Plurilocular sporangia are rare, cylindrical or conical, 9–15 µm × 35 µm, sessile or pedunculated, and grouped in sori. Unilocular sporangia are rounded in surface view, 26–43 µm × 40–60 µm, globose or pyriform in cross-section, sessile or occasionally pedunculate, located in circular or irregularly shaped sori. Paraphyses are 2–4 cells long, cylindrical or clavate, 13–23 µm × 58–87 µm. Phaeophycean hairs in groups, 8–12 µm in diameter with a basal meristem and a basal sheath.
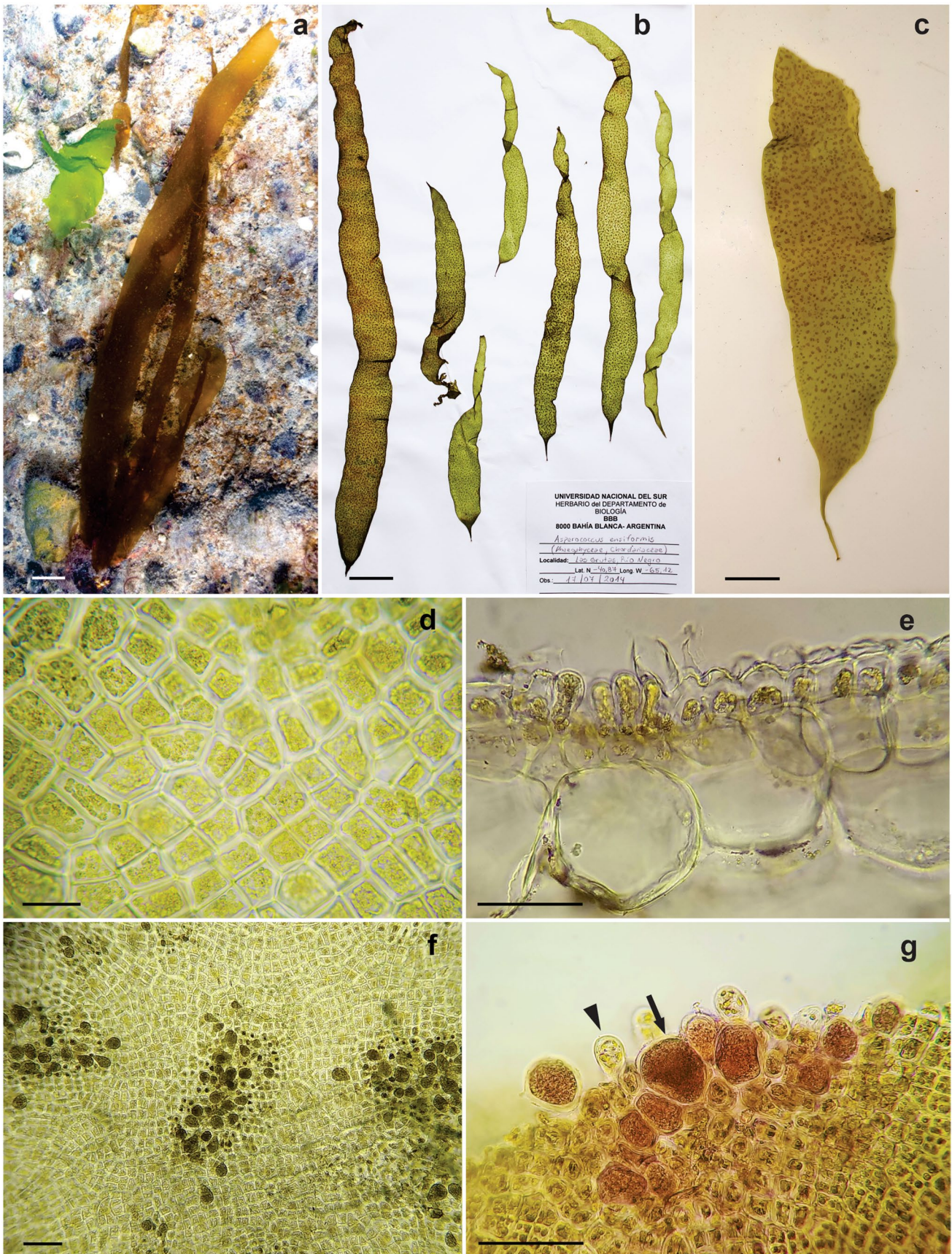
◄**Fig. 1** Morphological characteristics of *Asperococcus* (on the example of *A. ensiformis*). **a**) Macroscopic sporophytes in nature. Scale bar: 1 cm (Photo by Gonzalo Bravo www.proyectosub.org.ar). **b**) Pressed specimen of *A. ensiformis* from the BBB Herbarium of the Universidad Nacional del Sur. Scale bar: 2 cm. **c**) Fresh specimen showing sori as dark dots. Scale bar: 1 cm. **d**) Surface view of the cortical cells. Scale bar: 25 μm. **e**) Cross-section of the thallus. Scale bar: 50 μm. **f**) Surface view of a frond showing scattered sori. Scale bar: 100 μm. 5) Detail of a sorus protruding from the surface, with unilocular sporangia (arrow) and paraphyses (arrowhead)

Asperococcus fistulosus (Hudson) W.J. Hooker

(Greville 1830; Fritsch 1945; Womersley 1987; Schneider and Searles 1991; Cormaci et al. 2012).

Thalli are light to middle brown, flabby, cylindrical or with sparse bulges, up to 60 cm long and 30 mm broad, attenuating at the base. The attachment disc is 100–300 μm across. The membrane is formed of 2–4 layers of cells, with 1 layer of angular cortical cells, isodiametric or rectangular, 1 to 3 layers of large medullary cells and a large cavity in the center. Cortical cells are 15–40 μm across and 10–44 μm long in surface view, with numerous chloroplasts, each with 1 or 2 pyrenoids. Phaeophycean hairs are solitary or in groups, 14–20 μm in diameter, with a basal sheath. Unilocular sporangia are located in rounded to elongated sori and they are pyriform to globular, sessile, rounded in surface view and pyriform in cross-section, 45–100 μm long and 40–70 μm in diameter. Paraphyses are relatively straight or cylindrical, 3–8 cells long, 18–36 μm × 18–47 μm and rarely branched.

Asperococcus scaber Kuckuck

(Kuckuck 1899; Fritsch 1945; Cormaci et al. 2012; Bárbara et al. 2015).

The thallus is minute, cylindrical, and slightly attenuated at both ends, or elongate and clavate, up to 1 cm long and 0.5 mm broad, with a pseudo discoid basal portion. Cortical cells are angular in surface view and measure 10–21 μm × 10–27 μm, with numerous chloroplasts, each with 1 or 2 pyrenoids. In cross-section the thallus is compact, without a central hollow cavity; instead, the axes are occupied by 4 to 6 large colorless cells, surrounded by 1–2 layers of small pigmented cortical cells. Phaeophycean hairs are frequent, with a basal sheath. Plurilocular sporangia are frequent, measuring 24–36 μm × 12–20 μm and are grouped in irregular sori. They are cylindrical or conical, and rarely associated with multicellular paraphyses of 2–3 cells long. Unilocular sporangia are rare, spheric or pyriform, pedunculated, measuring 45–45 μm × 30–35 μm.

Asperococcus norvegicus Kylin

(Kylin 1910)

Thalli are simple, solid, cylindrical, filiform, thin, up to 3 cm long and 0.75 mm. In cross-section, the fronds are composed of 4 long and large central cells surrounded by an external layer composed of 1–2 small isodiametric cells. The basal portion has a Myrionema-like growth. The plurilocular sporangia, which are linear or linear-lanceolate, 30–55 μm long and 11–15 μm wide, are arranged in minute, scattered sori along with hairs and some 2–5 articulated paraphyses.

Asperococcus tortilis Suhr

(Suhr 1836).

The thalli are bright orange-yellow, coriaceous, cylindrical, tubular, and spirally twisted, simple, up to 10 cm long. The thalli emerge from a very small disc and are filiform at the base, spreading toward the apex. The apices are closed in young specimens and open and slashed in older ones. Sporangia are located in rounded sori.

Table 2 summarizes the main morphological differences between the six recognized species of *Asperococcus*. The species are mainly distinguished according to the shape of the thallus and the degree of compression of the membrane (e.g., flattened, compressed, terete, bullose, cylindrical, etc.). *Asperococcus ensiformis* and *A. bullosus* are the largest representatives within the genus. *Asperococcus ensiformis* is morphologically distinguished from *A. bullosus* by the ribbon-like shape of the thallus that is highly compressed in the center, and hollow at the margins. In addition, it usually lacks plurilocular sporangia. On the contrary, *A. bullosus* is saccate, bullose, with an intestine-like shape. *Asperococcus scaber* and *A. norvegicus* are the smallest representatives. Both species can be differentiated from the others because they have a compact cylindrical thallus, without a hollow central cavity; however, they share several morphological aspects. In both species, the substrate attachment structure consists of a disc with marginal growth similar to *Myrionema*, they present a solid thallus formed by 4 large and elongated inner cells and an outer layer of isodiametric cells. *Asperococcus scaber* sometimes has a third middle layer of isodiametric cells, and *A. norvegicus* is usually larger than *A. scaber*. *A. norvegicus* has not been described by any other author than Kylin (1910) and to date there is no molecular evidence to determine whether *A. norvegicus* could be conspecific with *A. scaber*. *Asperococcus fistulosus* shares some characteristics with *A. tortilis*, for example, the cylindrical thallus, attenuated at the base with a large cavity in

Table 2 Summary of the main morphological characters of the macroscopic thallus of *Asperococcus* species

	A. bullosus	A. ensiformis	A. fistulosus	A. scaber	A. norvegicus	A. tortilis
Form	Irregularly inflated to bullose Elongate- rounded at apex	Flattened like a ribbon Elongate- clavate or attenuated at the apex	Cylindrical and attenuated at the base, with sparse bulges	Cylindrical, and slightly attenuated at both ends, or elongate-clavate	Cylindrical	Cylindrical and spirally twisted
Texture	Flabby, gelatinous	Membranous	Flabby	-	-	Coriaceous
Height	Up to 100 cm	Up to 80 cm	Up to 60 cm	Up to 1 cm	Up to 3 cm	Up to 10 cm
Width	Up to 12 cm	Up to 4 cm	Up to 30 mm	Up to 0.5 mm	Up to 0.75 mm	—
Anatomy	Hollow *Cortex*:1 layer, angular and isodiametric cells *Medulla*:1–3 layers of large colorless cells	Hollow in the margins *Cortex*: 1–2 layer, subsquare cells, or rectangular *Medulla*:1- 3 layers of colorless cells with the cavity crossed by filaments of long, cylindrical and colorless cells	Hollow *Cortex*: 1 layer, angular cells, isodiametric or rectangular *Medulla*: 1–3 layers of large cells	Solid *Cortex*: 1–2 layer, angular cells, isodiametric or rectangular *Medulla*: 4–6 large cells	Solid *Cortex*:1–2 layer, angular cells, isodiametric or rectangular *Medulla*: 4 large cells	Hollow
Sporangia	Unilocular and plurilocular sporangia in the same sori	Unilocular sporangia in sori, plurilocular sporangia are rare	Unilocular sporangia in sori, plurilocular sporangia are rare	Unilocular sporangia are rare, plurilocular sporangia in sori	Plurilocular sporangia in sori	In sori (type of sporangia not described)
Sori	Irregular	Rounded or irregular	Elongated or rounded	-	Minute	Rounded
Reference	Greville 1830; Fritsch 1945; Womersley 1987; Nelson and Knight 1995; D'Archino and Nelson 2006, Cormaci et al. 2012	Womersley 1987; Sauvageau 1895; D'Archino and Nelson 2006; Asensi 1972; Cormaci et al. 2012; pers. obs	Greville 1830, Fritsch 1945, Womersley 1987; Schneider and Searles 1991; Cormaci et al. 2012	Kuckuck 1899; Fritsch 1945; Cormaci et al. 2012; Bárbara et al. 2015	Kylin 1910	Suhr 1836

not described in the literature

the center, however *A. tortilis* is distinguished by the thallus twisted into a spiral.

Molecular phylogeny

The family Chordariaceae is the largest and most diverse lineage within the order Ectocarpales (van den Hoek et al. 1995). However, to date only a few genera included in this family have been studied with molecular tools (Silberfeld et al. 2014; Kawai and Hanyuda 2021). The characteristics that allow the inclusion of *Asperococcus* species within the family Chordariaceae are the presence of discoid plastids and life cycles with heteromorphic alternation between haploid microscopic filamentous gametophytes and diploid macroscopic sporophytes, or direct asexual cycles, which regenerate diploid macrothalli (e.g., van den Hoek et al. 1995; Peters and Ramírez 2001). However, according to the current classification, the family Chordariaceae includes a large number of genera with a great variety of morphologies of which many are suspected to be polyphyletic (Silberfeld et al. 2014; Kawai and Hanyuda 2021). The phylogeny of the family should be revised with multimarker approaches.

Table 3 DNA sequences published in Genbank database under the name *Asperococcus*

Species	Molecular marker	Accession number	Locality or culture ID	Reference
Asperococcus fistulosus	*rbc*L	AF207796	unknown	Siemer and Pedersen (direct submission)
		MN184536	Norway: Askoy	Bringloe et al. (2019)
		MN184557	Norway: Bergen	Bringloe et al. (2019)
		MN184559	Norway: Ormhilleren	Bringloe et al. (2019)
	*rbc*L-*rbc*S	AY095321	UK: Isle of Mann	Cho et al. (2003)
	*psa*A	AY372940	UK: Isle of Man	Cho et al. (2003)
	*psb*A	AY528825	UK: Isle of Man	Cho et al. (2003)
Asperococcus bullosus	18S	L17013	Culture: Oregon State University	Tan and Druehl (1993)
	*cox*1	EU681392	France: Brittany	Silberfeld et al. (2010)
		LM995422	Culture: GR11-s#8–4	Peters et al. (2015)
		MN184423	Norway: Askoy	Bringloe et al. (2019)
		MN184437	Norway: Stora Lauvoyna	Bringloe et al. (2019)
		MN184505	Norway: Stora Lauvoyna	Bringloe et al. (2019)
		LC205693	Culture: KU-MACC:KU-570	Kawai et al. (2019)
		MW580393	Malta	Bartolo et al. (2021)
	*cox*3	EU681434	France: Brittany	Silberfeld et al. (2010)
		LC016522	Culture: KU-MACC:KU-570	Kawai et al. (2016)
	*nad*1	EU681475	France: Brittany	Silberfeld et al. (2010)
	*psa*A	EU681605	France: Brittany	Silberfeld et al. (2010)
		LC205706	Culture: KU-MACC:KU-570	Kawai et al. (2019)
	*atp*B	EU681668	France: Brittany	Silberfeld et al. (2010)
		LC205701	Culture: KU-MACC:KU-570	Kawai et al. (2019)
	*nad*4	EU681518	France: Brittany	Silberfeld et al. (2010)
	*atp*9	EU681548	France: Brittany	Silberfeld et al. (2010)
	*rbc*L	EU681590	France: Brittany	Silberfeld et al. (2010)
		LC016509	Culture KU-	Kawai et al. (2019)
		MN510448	MACC:KU-570 Australia	Bringloe et al. (2019)
		MN184531	Norway: Hellesoy	Bringloe et al. (2019)
		MN184561	Norway: Stora Lauvoyna	Bringloe et al. (2019)
	*psb*A	EU681628	France: Brittany	Silberfeld et al. (2010)
		LC205711	Culture: KU-MACC:KU-570	Kawai et al. (2019)
	*nad*2	LC636594	Japan: Ehime	Kawai and Hanyuda (2021)
	*nad*5	LC636607	Japan: Ehime	Kawai and Hanyuda (2021)
	*nad*6	LC636623	Japan: Ehime	Kawai and Hanyuda (2021)
	*rbc*L-*rbc*S	MW659858	Malta	Bartolo et al. (2021)

Regarding the genus *Asperococcus*, there are 35 DNA sequences with the names *A. bullosus* and *A. fistulosus* available in Genbank (Table 3), however no species delimitations or phylogenetic studies based on DNA markers have been published specifically for this genus. Most of the public sequences are partial sequences of mitochondrial *cox*1 and chloroplast *rbc*L markers obtained from specimens collected in Norway, Britain, France, Malta, Australia, Chile and Japan, or from cultured specimens. Many of these sequences appear in phylogenetic studies of Phaeophyceae taxa, which have shown that *Asperococcus* is close to Chordariaceae genera, such as *Punctaria, Leathesia, Striaria, Delamarea* and *Hecatonema* (Siemer et al. 1998; Cho et al. 2003; Silberfeld et al. 2010; Kawai and Hanyuda 2021).

In Fig. 2 we present a Maximum Likelihood tree constructed with 11 *rbc*L sequences with the name *Asperococcus* and 95 *rbc*L sequences of species representative of families of Ectocarpales, all of which were retrieved from GenBank. The tree shows high or full support (100% or 98% bootstrap percentage, BP) for five of the six families of Ectocarpales delimited by Peters and Ramírez (2001) and Racault et al. (2009), Adenocysaceae, Acinetosporaceae, Ectocarpaceae, Petrospongiaceae and Scytosiphonaceae, but the family Chordariaceae was not well resolved in this phylogeny.

Asperococcus sequences formed a monophyletic group with two sequences of *Striaria attenuata,* that were highly supported (93% BP). This close relationship between *Asperococcus* and *Striaria* has been demonstrated by several authors (Cho et al. 2003; Kawai et al. 2019; Kawai and Hanyuda 2021). It is worth noting that the sequences representing *Asperococcus* are separated from genera of the Scytosiphonaceae, which sometimes used to be confused with *Asperococcus* due to some morphological similarities.

Within the *Asperococcus* group, two clades were highly supported with 97 and 100% BP, which may represent two of the known species of *Asperococcus*. Clade 1 included sequences from Norway and Britain named *A. fistulosus* and clade 2 included sequences from Norway, Japan, France, and Malta named *A. bullosus*. A sequence from Australia named *A. bullosus* (MN510448) segregated from both clades. Intraclade distances were between 0 and 0.09% in clade 1 and between 0.08% and 0.84% in clade 2. These values show that the genetic variability between specimens from clade 1 is lower than the variability within clade 2, which is expected given that the sequences from *A. bullosus* represent a wider distribution range, whereas those of *A. fistulosus* are from Norway and Britain. Distances between members of clades 1 and 2 were between 1.8% and 2.1%, whereas distances between the sequence MN510448 and clades 1 and 2 were between 2.1 and 2.5%.

The Australian sequence MN510448, named *A. bullosus*, clearly represents a third species. Considering the geographical distribution of the genus and the morphology of the six species of *Asperococcus,* this third species that appears in the ML tree could correspond to a specimen of *A. ensiformis*, a species that has been recorded in at least two coasts of Australia (Womersley 1987).

The Norwegian *Asperococcus* specimens, previously analyzed by Bringloe et al. (2019), segregate into two groups, which correspond to *A. fistulosus* and *A. bullosus*. Surprisingly, no molecular evidence of the species *A. norvegicus* can be derived from the tree, since all the sequences from Norwegian specimens, including the one from Bergen (MN184557) that is the type locality of *A. norvegicus,* are segregated in either the *A. bullosus* or *A. fistulosus* clades. The only morphological characterization available of *A. norvegicus* is the original description of Kylin (1910), which describes it as short and narrow (up to 3 cm long and up to 0.75 mm wide), solid and filiform, with plurilocular sporangia, with no mention of the presence of unilocular sporangia. It is unlikely that authors of the published sequences may have confused the morphology of *A. norvegicus* with that of *A. fistulosus* or *A. bullosus*, given the evident differences with the other two species that are larger, hollow, and somewhat inflated. An alternative explanation would be that the specimen studied by Kylin in 1910 was a young immature individual of *A. fistulosus,* given that *A. fistulosus* is a common seaweed in the northeast Atlantic and Baltic Sea (references in the section Geographic distribution). However, we cannot question the taxonomic validity of *A. norvegicus* unless a more comprehensive study of this species is conducted. Bringloe et al. (2019) already denoted that *Asperococcus* species need further scrutiny because there are cryptic groups around the world. In order to elucidate the identity of the *Asperococcus* species, the genus needs an urgent revision based on molecular markers and morphology of the representative specimens of the distribution range reported for the species.

Life cycle

Asperococcus is characterized by a heteromorphic life cycle, alternating between a macroscopic sporophytic thallus (diploid phase) and a microscopic branched gametophytic thallus (haploid phase) (Asensi 1972; D'Archino and Nelson 2006; Poza et al. 2022); and depending on the species, plurilocular sporangia may or may not be present on the sporophytic thallus.

To date, a few studies have described the life cycle of some species of the genus, e.g., *A. bullosus* was studied by Clayton (1982) as *A. turneri*; *A. ensiformis* was studied by Asensi (1972) as *Haloglossum compressum* and recently by Poza et al. (2022); and *A. fistulosus* was studied by Knight et al. (1935) and Pedersen (1984).
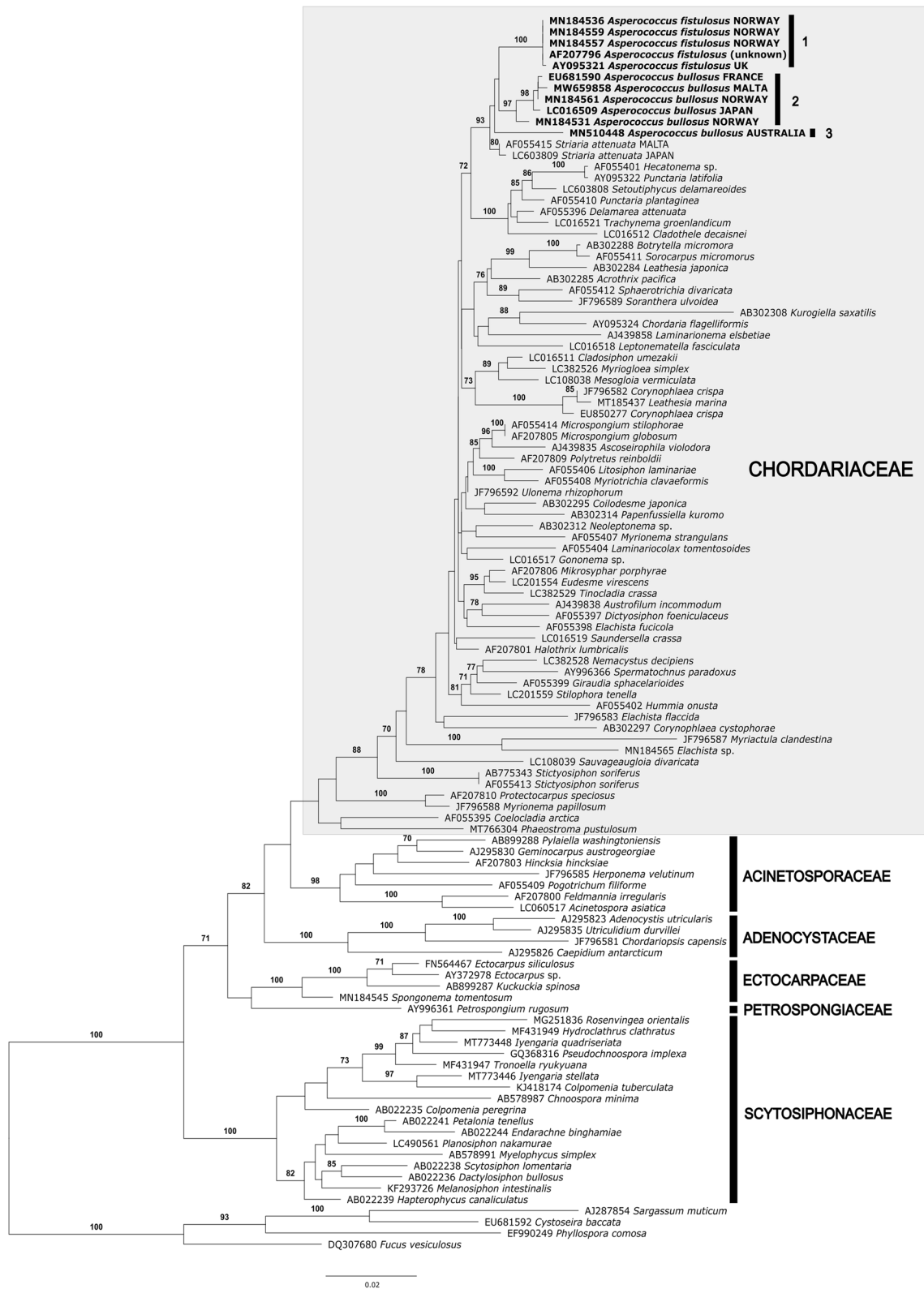
Fig. 2 Maximum likelihood tree phylogenetic based on 106 *rbc*L sequences of Ectocarpales obtained from Genbank. Four sequences of species representative of Fucales were used as outgroups. Values above branches are Bootstrap Percentages (> 70%). Analysis was conducted with RAxML-NG with the CIPRES web service (Miller et al. 2010)

In the life cycle of *A. bullosus*, both a direct and an indirect (or sexual) cycle can be distinguished. In the direct cycle, diploid spores from the plurilocular sporangia germinate, first forming a prostrate microscopic phase, known as plethysmothalli and constituting the basal part of the sporophyte (Fig. 3). Studies of *A. bullosus* populations from the Australian coasts revealed that plethysmothalli have the ability to reproduce and regenerate by means of plurilocular sporangia during the cold season. Then, during the warm season these thalli develop the young *Asperococcus* sporophyte (Chapman 1962; Clayton 1982). In the indirect cycle, unilocular sporangia release haploid spores (generated by meiosis) that give rise to the microscopic gametophytes, which produce plurilocular gametangia when mature. If the gametes produced by these gametangia fuse, the zygote develops into a plantule from which a new macroscopic plant arises, but if there is no fusion then they merely develop parthenogenetically into a new gametophytic generation (Chapman 1962; Pedersen 1984).

In *A. ensiformis* the haploid spores from the unilocular sporangia exhibit unipolar germination and develop a germ tube with transverse divisions, forming uniseriate branched filaments that develop into a prostrate microscopic gametophyte with occasional hyaline hairs (Fig. 3). Gametophytes give rise to plurilocular, terminal or intercalary gametangia. The female gametes (3.7–4.5 μm in diameter) settle first, becoming spherical, and are subsequently fertilized by male gametes (1–2.5 μm in diameter). The zygotes exhibit bipolar germination, forming two germ tubes. Some germlings form a little branched protonema with globose cells, from which, one or two erect laminae emerge, corresponding to the erect part of young sporophyte. The erect laminae can also emerge from a single basal cell, instead of a protonema. The erect lamina forms a uniseriate filament of cylindrical cells by transverse divisions and, subsequently, longitudinal divisions occur, forming a pseudoparenchymatous tissue with intercalary growth. On the other hand, although Sauvageau (1895) mentioned that the sporophyte of *A. ensiformis* rarely presents plurilocular sporangia, these structures have not been reported since by any other authors. In populations of *A. ensiformis* on the Patagonian coast, the presence of plurilocular sporangia has never been reported.

Knight et al. (1935) and Pedersen (1984) found that the life cycle of *A. fistulosus* depends on the behavior of the haploid spores from the unilocular sporangia. On one hand, once the haploid spores settle, they may form a prostrate thallus from which a macroscopic sporophyte emerges. This phenomenon, known as heteroblasty, is common in some *Ectocarpus* species where meiospores develop directly into haploid partheno-sporophytes (Coelho et al. 2020). On the other hand, the haploid spores may give rise to a filamentous microscopic phase (possibly gametophytic) that forms plurilocular reproductive structures and regenerates

parthenogenetically (Knight et al. 1935; Pedersen 1984). However, these authors did not record the syngamy and assumed that the sexual cycle could be repressed.

Geographic distribution

Asperococcus is a genus mostly distributed in temperate-cold latitudes, with higher occurrences in the northeast Atlantic and Mediterranean zone. The species *A. bullosus*, *A. ensiformis*, and *A. fistulosus* have a wider world distribution compared to the other *Asperococcus* species. *Asperococcus norvegicus* was reported by Athanasiadis (1996) at Bergen on the Norwegian coast and *A. tortilis* is restricted to Indian Ocean Island (Silva et al. 1996) (Fig. 4).

Asperococcus scaber has a wider distribution, but is restricted to the northeast Atlantic marine zone (Newton 1931; Fletcher 1987; Hardy and Guiry 2003; Guiry 2012; Brodie et al. 2015; Anon 2017; Burel et al. 2019), the Mediterranean area (Giaccone 1978; Ribera et al. 1992), and the West African marine zone (Gallardo et al. 2016) (Fig. 4).

According to the phycological literature the most common species, *A. bullosus*, *A. ensiformis* and *A. fistulosus,* have a much wider distribution range than the other three species. *Asperococcus bullosus* has been reported in the Arctic zone (Nielsen and Gunnarsson 2001; Bringloe et al. 2019), in the northeast Atlantic (Wollny 1881; Hauck 1889; Adams 1908; Cotton 1912; Kuckuck 1912; Lyle 1920; Newton 1931; Rees 1931; Miranda 1934; Feldmann 1954; De Mesquita Rodrigues 1963; Ardré 1970; Flores-Moya et al. 1995; Bartsch and Kuhlenkamp 2000; Báez et al. 2001; Hardy and Guiry 2003; Bárbara et al. 2005; Valenzuela Miranda 2005; Peña and Bárbara 2008, 2010; Araújo et al. 2009; Bunker et al. 2010, 2017; Cires Rodriguez and Cuesta Moliner 2010; Silberfeld et al. 2010; Guiry 2012; Brodie et al. 2015; Anon 2017), in the Mediterranean (Feldmann 1937; Diannelidis 1953; Giaccone 1969, 1978; Cinelli 1971; Güven and Öztig 1971; Coppejans 1972; Feoli and Bressan 1972; Cinelli et al. 1976; Boudouresque and Perret 1977; Ercegovic 1980; Güner et al. 1985; Rodríguez Prieto et al. 1993; Borg et al. 1998; Furnari et al. 1999; Aysel et al. 2005; Taşkin et al. 2008; Antolic et al. 2010; Bunker et al. 2010; Joher et al. 2012; Ould-Ahmed et al. 2013; Tsiamis et al. 2013; Burel et al. 2019; Taşkın et al. 2019; Bartolo et al. 2021; Boudouresque et al. 2022), in the Baltic Sea (Nielsen et al. 1995; Kontula and Fürhapter 2012; Nielsen and Lundsteen 2019), in West Africa (Kylin 1907, 1947; Price et al. 1978; Seagrief 1984; Silva et al. 1996; Gil-Rodríguez et al. 2003; John et al. 2004; Moro et al. 2011; Afonso-Carrillo 2014; Gallardo et al. 2016; Sabri et al. 2021), in the northeast Pacific (Pedroche et al. 2008; Pedroche and Sentíes 2020), in the northwest Pacific (Holmes 1896; Okamura 1936; Segawa 1981; Yoshida et al. 1990, 2015), in the South

Fig. 3 Heteromorphic life cycle of *A. ensiformis* and *A. bullosus*. Parth: parthenogenesis
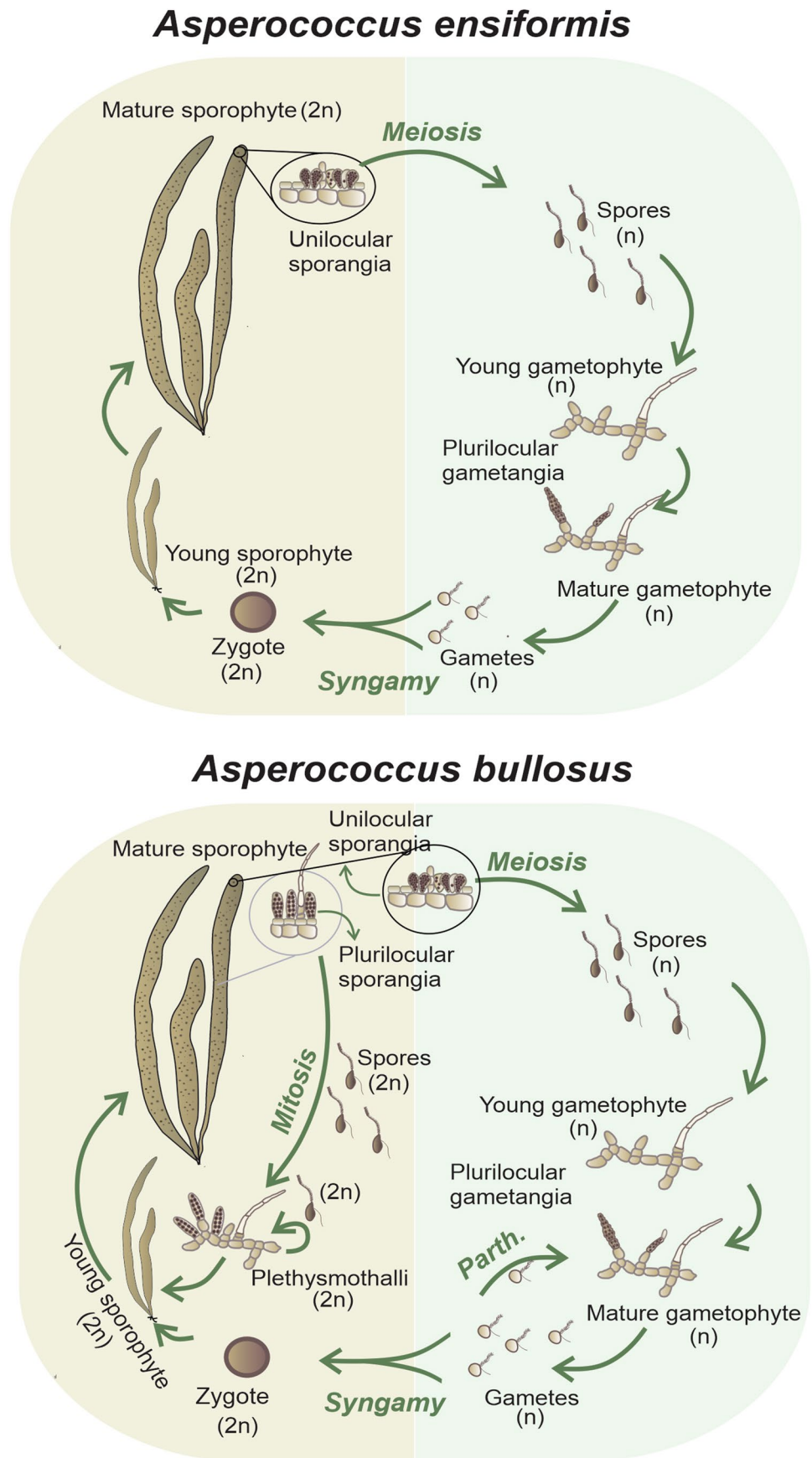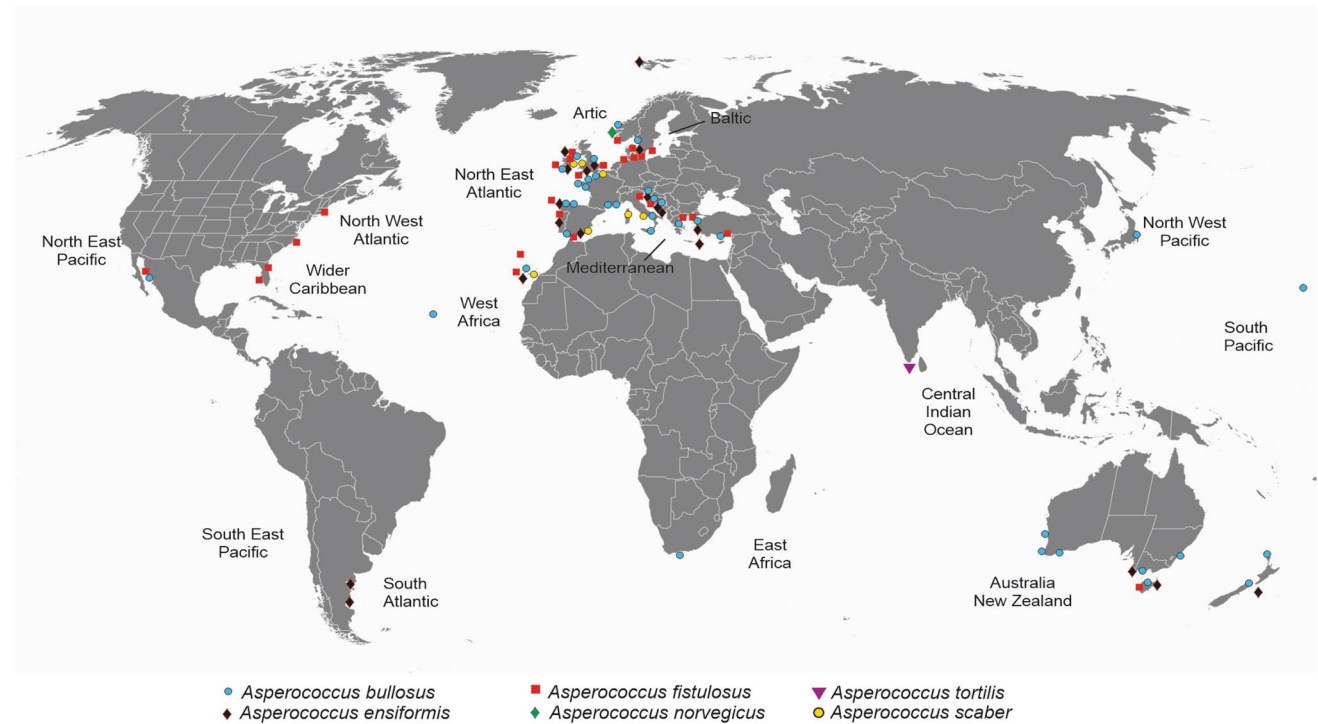
Fig. 4 World distribution of species of *Asperococcus* (colored symbols represent the records of each species)

Pacific (MacCaughey 1918) and in the Australia and New Zealand area (Womersley 1987; Huisman and Walker 1990; Adams 1994; Nelson and Knight 1995; Huisman 1997, 2000; 2019; Nelson 1999; D'Archino and Nelson 2006; Harper et al. 2012; Bringloe et al. 2019; Nelson et al. 2021). *Asperococcus bullosus* was also reported as *A. turneri* and as *A. turneri* var. *profundus* in the Arctic (Irvine 1982), in the northeast Atlantic (Fletcher 1987) in the Mediterranean (Rodríguez and Femenías 1889; Gerloff and Geissler 1974; Munda 1979; Ribera Siguán 1983; Verlaque 1984; Ribera Siguán and Gómez Garreta 1985; Athanasiadis 1987; Ballesteros 1989), and West Africa (Price et al. 1978; Haroun et al. 2002; Gil-Rodríguez et al. 2003; John et al. 2004; Moro et al. 2011).

Asperococcus ensiformis shares a distribution range with *A. bullosus* in the northeast Atlantic (Bárbara et al. 2005; Peña and Bárbara 2008; Araújo et al. 2009; Cires Rodriguez and Cuesta Moliner 2010; Bermejo et al. 2012; Guiry 2012; Brodie et al. 2015; Burel et al. 2019), the Mediterranean (Taşkin et al. 2008; Temniskova et al. 2008; Boudouresque et al. 2022), Baltic Sea (Kontula and Fürhapter 2012; Nielsen and Lundsteen 2019), West Africa (Afonso-Carrillo 2014; Gallardo et al. 2016) and Australia and New Zealand (Harper et al. 2012; Nelson et al. 2021). *Asperococcus ensiformis* is the only *Asperococcus* species reported in the South Atlantic on the Patagonian coast by Asensi (1972, as *Haloglossum compressum*) and Boraso de Zaixso (2013).

Nevertheless, *A. ensiformis* was cited as *A. compressus* in the Arctic (Rueness 1997; Brattegard and Holthe 1997; Fredriksen et al. 2019), in the northeast Atlantic (Heape 1888; Adams 1908; Newton 1931; Blackler 1951; Cullinane 1971; Guiry 1978; De Valéra et al 1979; Whelan and Cullinane 1985; Fletcher 1987; Morton 1994; Coppejans and Kling 1995; Bárbara et al. 2005; Brodie et al. 2015), in the Mediterranean (Feldmann 1937; Giaccone 1969; Edwards et al. 1975; Ercegovic 1980; Ribera et al. 1992; Flores-Moya et al. 1995; Furnari et al. 1999; Rindi et al. 2002), in the Baltic Sea (Nielsen et al. 1995) in the West Africa area (Price et al. 1978; Stegenga et al. 1997; Gil-Rodríguez et al. 2003; John et al. 2004; Moro et al. 2011; Gallardo et al. 2016), in the South Atlantic zone (Asensi and Küpper 2012) and Australia and New Zealand (Womersley 1987).

Asperococcus fistulosus is widely distributed. This species was reported in the Arctic (Caram and Jónsson 1972), northeast Atlantic (Adams 1907; Cotton 1912, 1913; Newton 1931; De Valéra et al. 1979; Maggs 1983; Whelan and Cullinane 1985; Fletcher 1987; Morton 1994; Bartsch and Kuhlenkamp 2000; Hardy and Guiry 2003; Brodie et al. 2015; Bunker et al. 2017), West Atlantic (Neto et al. 2001; Haroun et al. 2002; Gil-Rodríguez et al. 2003; John et al. 2004; Moro et al. 2011; Afonso-Carrillo 2014; Ferreira et al. 2018), Mediterranean (Gerloff and Geissler 1974; Ribera et al. 1992; Furnari et al. 1999; Rindi et al. 2002; Taşkin et al. 2008), Baltic Sea (Nielsen et al. 1995; Kontula and

Fürhapter 2012; Nielsen and Lundsteen 2019), in the wider Caribbean and North Carolina (USA) (Schneider and Searles 1991), in the northwest Atlantic from Virginia to New Hampshire (Humm 1979; Schneider et al. 1979), in the northeast Pacific (Pedroche et al. 2008), and on the Australia and New Zealand coasts (Womersley 1987).

Asperococcus bullosus and *A. ensiformis*, were also reported by D'Archino and Nelson (2006) as introduced species in New Zealand, and *A. ensiformis* (cited as *A. compressus*) was reported in Australia by Womersley (1987). *Asperococcus bullosus*, a native species from Europe, was first recorded in New Zealand waters at Stewart Island by Lindauer (1957) and later, in the late 1980s and early 1990s, it was recorded in South Island (D'Archino and Nelson 2006). In Australia, *A. bullosus* was found from Rottnest Island (West Australia) to Pittwater, Sydney (NSW) and also on the north and east coasts of Tasmania. *Asperococcus ensiformis* (cited as *A. compressus*) was observed solely at Flinders and Port Phillip (Victoria), and *A. fistulosus* was found from Kangaroo Island (South Australia) to Apollo Bay (Victoria), and in southeastern Tasmania (Womersley 1987).

Given that Asperococcus species are predominantly distributed in the northern hemisphere, and its presence in the southern hemisphere (Australia and New Zealand) is related to possible introduction, the records of *A. ensiformis* in the Atlantic Patagonian coast could represent another potential introduction.

Ecological aspects

Asperococcus species have been found in the intertidal zone, in intertidal pools (Fritsch 1945; Blackler 1951) and at different depths in the subtidal zone, reaching depths of up to 46 m (Cinelli 1971; Borg et al. 1998; Bárbara et al. 2005; D'Archino and Nelson 2006; Taşkin et al. 2008; Bartolo et al. 2021).

Several checklists reported the presence of other genera of Chordariaceae coexisting with *Asperococcus,* of which the most represented are *Acrospongium, Acrothrix, Adriogloia, Botrytella, Chilionema, Chordaria, Cladosiphon, Climacosorus, Corynophlaea, Cylindrocarpus, Delamarea, Dermatocelis, Dictyosiphon, Elachista, Endodictyon, Eudesme, Giraudia, Halothrix, Hecatonema, Isthmoplea, Kuetzingiella, Laminariocolax, Leathesia, Leblondiella, Leptonematella, Litosiphon, Mesogloia, Microcoryne, Microspongium, Mikrosyphar, Myriactula, Myriocladia, Myrionema, Myriotrichia, Nemacystus, Phaeostroma, Protectocarpus, Punctaria, Saundersella, Sauvageaugloia, Spermatochnus, Sphaerotrichia, Spongonema, Stictyosiphon, Stilophora, Streblonema, Striaria* and *Ulonema* (Haroun et al. 2002; Bárbara et al. 2005; Antolic et al. 2010; Kontula and Fürhapter 2012; Sabri et al. 2021).

Some species of *Asperococcus* have been reported as epiphytic and epizoic organisms. *Asperococcus ensiformis* (cited as *A. compressus*) was found growing on shells together with *Chorda filum* (Blackler 1951) and on fronds of *Cystoseira barbata* (Taşkin et al. 2008). Also, the basal holdfast of *A. ensiformis* was associated with *Urospora, Enteromorpha* (*Ulva*), *Bangia* and *Ectocarpus* spp. (Rees 1931). This author even highlighted the association with *Bangia-Urospora*, outside of the usual tidal level where *Asperococcus* occurs. On the Atlantic Patagonian coasts *A. ensiformis* (cited as *Haloglossum compressum*, Asensi 1972) was observed in lower intertidal pools, associated with calcareous algae such as *Jania*.

Asperococcus fistulosus was reported as an epiphyte on *Fucus, Himanthalia lorea, Laminaria saccharina, Punctaria latifolia* and *Cystoseira* and *Cladophora* thalli. Furthermore, it was observed bearing other seaweeds, such as *Myriotrichia filiformis, Myriotrichia clavaeformis, Sphacelaria cirrosa, Ceramium rubrum, Ceramium strictum*, filamentous diatoms and *Ectocarpus* sp. (Rees 1931). This species was also cited as an epiphyte on seagrasses. In South Australia it was collected from tidal flats on *Heterozostera* and on the brown seaweed *Scaberia* (Womersley 1987).

Asperococcus bullosus was also reported by Taşkin et al. (2008), growing as an epiphyte on the seagrass *Posidonia oceanica* on Turkish coasts. Furthermore, it was observed growing on *Posidonia sinuosa, Posidonia australis* and *Amphibolis antarctica* on the Australian coast, and as an epiphyte on *Heterozostera* in low intertidal pools in Tasmanian coastal areas (Womersley 1987). In New Zealand, many of the *A. bullosus* thalli found at Rangaunu harbor were attached to fragments of *Zostera* (Nelson and Knight 1995).

Seaweed phenology, like in terrestrial plants, is susceptible to temperature mediated changes, such as shifts in the timing of their reproduction. Also, temperature can affect individual performance regarding photosynthesis, growth, and reproduction rates, and it determines the tolerance or survival limits (Breeman 1990; Eggert 2012). Possible northern boundaries of seaweeds have been determined, whose ranges are established by lethally low winter temperatures, or by summer temperatures too low for growth and/or reproduction, while southern boundaries are established by lethally high summer temperatures, or by winter temperatures too high for induction of the crucial step in the life cycle (Breeman 1990). These thermal thresholds are commonly related to the tolerance of the hardiest life history stage, the microthallus stage, and temperature requirements for reproduction and growth. In particular, seaweeds are extremely sensitive to the effect of temperature on their distributional range. However, changes in temperature, such as warming, may favor opportunistic and tolerant seaweeds by increasing their competitive ability (Dukes 2007).

Some studies indicated the occurrence of *A. bullosus*, *A. ensiformis* and *A. fistulosus* macrothalli during summer and autumn in the northeast Atlantic zone, bearing mature unilocular sporangia (Harvey 1857; Heape 1888; Blackler 1951; Peña and Bárbara 2008). In southern latitudes, such as the Patagonian coast in the southwest Atlantic, *A. ensiformis* macrothalli were reported in summer, mostly in February and March (Asensi 1972).

Cultivation

Current state and perspectives

Traditionally seaweed production came mainly from the harvest of wild populations (FAO 2018, 2020). However, in recent decades, the worldwide demand of seaweed has increased notably due to its use in the food, cosmetic, nutraceutical and pharmaceutical industries, as well as for the production of organic fertilizers and biofuel (Cai et al. 2021; Grand View Research 2021). This has generated the need to develop algae cultures on a large scale to ensure sustainable management of the natural populations.

This situation encouraged the study of a large number of species with industrial potential or nutraceutical benefits, such as bioactive foods or superfoods (Chopin and Tacon 2021).

To date, there are no published records of commercialization of *Asperococcus*, but *A. fistulosus* was included in a list of seaweed species that could be used for human consumption (Drennan 2016; Mendes et al. 2022) and recently, a study evaluated the optimal conditions for the cultivation of *A. ensiformis* from the Patagonian coasts of Argentina (Poza et al. 2022).

Spore-based culture

Seeding spores or zygotes on collectors has been a traditional method for the production of seaweed seedlings for mass cultivation (Critchley and Ohno 1998). Due to the heteromorphic life cycle of *Asperococcus,* the cultures can be started from spores released from pluri or unilocular sporangia, depending on the species. The ones that present both types of spores (haploid and diploid), such as *A. bullosus*, present two ways to generate sporophytes; asexually through a direct cycle or sexually following an indirect cycle (Chapman 1962; Pedersen 1984). Other species, such as *A. ensiformis*, follow an indirect cycle, interspersed with a sexual phase (gametophytes), that ensures genetic recombination and a greater variability in the population (Asensi 1972; Poza et al. 2022). The culture from spores is advantageous because it can be started from a small amount of fertile biomass, it provides wide genetic variability and could be highly productive due to the vigor of the germlings produced

from spores (Hales and Fletcher 1990; Peteiro et al. 2016; Gupta et al. 2018; Hu et al. 2021). Culture studies of *A. ensiformis* were carried out under different temperatures and nutrient conditions where the viability of spores, zygotes and germlings was evaluated (Poza et al. 2022). It was observed that the number of settled spores was higher than the number of settled zygotes, generating a high number of gametophytic microscopic stages, and also that the subsequent survival of sporophytes and gametophytes germlings was around 40%.

However, when the cultivation starts from fertile fronds (spores), it depends on the seasonality and the availability of fertile specimens in the natural beds (Macchiavello et al. 2010; Camus and Buschmann 2017; Gupta et al. 2018; Hu et al. 2021). Therefore, the management and conservation of banks of microscopic forms (gametophyte germlings in *Asperococcus*) could represent an alternative for aquaculture development of rare species, since it allows the long-term preservation of more productive or diverse strains, which will then be used to generate new macroscopic sporophytes, avoiding the dependence on a continuous supply of fertile fronds from natural beds (Wade et al. 2020; Schoenrock et al. 2021).

Culture methods

Asperococcus ensiformis has been successfully cultivated on seeding ropes under controlled environmental conditions in the laboratory (Poza et al. 2022). Cultivation on ropes is a traditional method of cultivation that consists in producing macroalgae on ropes. This can be started from spores released from mature sporophytes extracted from natural populations or from gametes obtained from banks of microscopic forms (gametophytes in *Asperococcus*), which can then be transferred to the sea once they reach a certain size (Peteiro 2018). This technique is very effective and low cost, because it only requires a reduced biomass of fertile fronds to start the cultivation, and also because the thalli grown on ropes have lower production costs, due to the shorter time required in the hatchery and smaller hatcheries (Macchiavello et al. 2010; Camus and Buschmann 2017). Another hatchery technique is the free-floating system (Westermeier et al. 2006), which allows larger individuals to be stocked. However, it has higher production costs, due to a greater need for water and nutrients.

The culture procedure used for *A. ensiformis* in Poza et al. (2022) was an adaptation from the methodologies established for other species of brown algae with heteromorphic life cycles, where the production of seedlings on rope under laboratory conditions is divided into two steps: a first step where a culture of microscopic gametophytes is settled, and another stage where macroscopic thalli are produced under controlled environmental conditions.

Briefly the method used involves (i) collection of fertile thalli from nature, which are easily identified by the prominent sori visible as dark dots; (ii) thallus conditioning, to remove epiphytes and possible pathogens, and also to stimulate the maturation of the sporangia; (iii) laboratory incubation, which consists of fixing the fertile fragments to a mesh with an interlaced polypropylene rope, allowing the release of the spores and their settlement on the rope. Then the meshes are placed in transparent containers that allow the passage of light and they are kept in the laboratory under controlled abiotic conditions for 5 months, until the seedlings can be moved to the sea. This technique makes it possible to inoculate several meters of rope in a small area.

The collections, transportation and conditioning of fertile thalli used for cultivation are critical stages since the subsequent health of the culture will largely depend on them.

Some authors recommend transporting the fertile fronds at low temperatures, on moist paper towels and in black bags to avoid light. They also recommend never submerging the thalli in seawater since it could cause premature sporulation (Oliveira et al. 1995; Redmond et al. 2014; Forbord et al. 2018).

Regarding thallus conditioning to remove epiphytes and pathogens, different methodologies are mentioned in the literature; in Poza et al. (2022) the fertile sporophytes of *A. ensiformis* were first brushed and then immersed in freshwater with 0.5% chlorine for 10 s and rinsed with freshwater. Treatment with surface disinfectants allows the removal of epiphytes, animals, and microorganisms. Other surface disinfectants normally used are copper sulfate, which can remove epiphytic algae including phytoplankton and even fungi, and Betadine (an iodine-based antiseptic) which can also eliminate a wide range of microorganisms (Sulu et al. 2004; Redmond et al. 2014; Forbord et al. 2018).

To stimulate the maturation of the sporangia and the subsequent release of spores, the cleaned thalli have to be subjected to stress conditions generated by desiccation and darkness (Forbord et al. 2018; Suebsanguan et al. 2021). In Poza et al. (2022) the disinfected thalli of *A. ensiformis* were dried with paper towels and preserved in the dark at 8 °C for 12 h, without leaving the surface withered.

The early post-settlement phases of spores and zygotes of macroalgae is critical for the successful establishment of populations, so several studies have focused on evaluating the optimum temperature and radiation conditions, and nutrient concentration that affect the settlement and recruitment in macroalgae cultures (Vadas et al. 1992; Bogaert et al. 2016; Camus and Buschmann 2017; Lind and Konar 2017; Poza et al. 2018, 2022; Suebsanguan et al. 2021).

Temperature conditions

In the cultivation of *A. ensifomis*, the effect of temperature on the early stages of gametophytes and sporophytes was evaluated by Poza et al. (2022). A temperature range of 8–12 °C was favorable for the growth of *A. ensiformis* gametophytes on seed-rope with densities that reached 74 ± 2 individuals/2 mm. On the other hand, they observed that the sporophytes were able to develop in a wider temperature range of 8–16 °C, with densities that reached 13 ± 1 individuals/2 mm of rope. Seaweeds with a wide geographical range, such as *A. ensiformis*, exhibit a wide tolerance range to different temperatures, as they experience great seasonal temperature changes under natural conditions, which represents an advantage when it comes to cultivation (Eggert 2012).

Nutrient enrichment

Another determining factor is the flow of nutrients received at the hatchery stage, since proper handling reduces production costs and minimizes the amount of time and energy used for the production of the young sporophytes (Camus and Buschmann 2017; Charrier et al. 2017; Boderskov et al. 2022). There is evidence that certain nutrients, such as nitrate and phosphate, not only affect the growth in the brown algae, but also gametogenesis (Harries 1932; Amsler and Neushul 1990; Liu et al. 2016; Boderskov et al. 2022). Also, nutrient variations can affect the chemotaxis of spores and zygotes, which actively detect nutritionally favorable microhabitats for settlement and subsequent algal growth and survival (Amsler and Neushul 1990). Therefore, selection of the seawater to be used at the hatchery stage is essential because some nutrients may be limited under natural conditions (Peteiro et al. 2016) and external nutrient sources are needed to complete a successful hatchery operation in those situations.

Provasoli culture medium (PES) is an artificial medium that has traditionally been used for growing macroalgae, containing nitrogen and phosphorus in relatively high concentrations, macro and micronutrients, vitamins, and a chelating solution for poorly soluble ions. The use of artificial media continues to play an important role in overcoming nutrient supply problems because it allows the amounts of macro and micronutrients or other compounds to be manipulated according to the need (Berges et al. 2001; Camus and Buschmann 2017). Seaweed extracts are currently being tested as biostimulants for the hatchery stage, as an alternative to reduce the quantities of Provasoli used or, in some cases, to replace it (Robertson-Andersson et al. 2006; Hurtado et al. 2012; Vatsos and Rebours 2015; Umanzor et al. 2019, 2020).

The effect of biostimulant was tested in the *Asperococcus* culture combined with the traditional PES culture medium (Poza et al. 2022). These authors cultivated gametophytes and sporophytes of *A. ensiformis* by the seeding rope method using the traditional PES medium and also a biostimulant based on seaweed extracts called Kelpak® (Kelp Products Pty Ltd., Simon's Town, South Africa). They observed that the growth of *A. ensiformis* gametophytes was favored by the Povasoli culture medium at concentrations of 20 mL PES L^{-1} of seawater with densities that reached 104 ± 5 individuals/2 mm. However, the highest sporophyte density and greater growth of the thallus was achieved with the combination of 5 mL PES L^{-1} plus 1 mL L^{-1} of Kelpak, with 21 ± 1 individuals/2 mm and 6 ± 2 mm in length after 45 days of incubation. Kelpak is a liquid concentrate derived from the stipes and laminae of the subtidal kelp *Ecklonia maxima*, that contains phytohormones (auxins and cytokinins) (Stirk and van Staden 1997), alginate, amino acids, and small amounts of macro and microelements (Lötze and Hoffman 2016).

Initially the seaweed extracts gained popularity as agricultural supplies because of the presence of fucoidans and other sulfate esters or alginates, which provide a plant response similar to that produced by the application of composted seaweed (Milton 1964). Currently there are few studies that evaluate the effect of biostimulants on the growth of brown algae (Umanzor et al. 2019). The promotion of the use of algae-based biostimulants is not only focused on reducing the production costs, but also because previous studies highlighted their function as growth enhancers and improvers of the health status of the cultures (Robertson-Andersson et al. 2006; Hurtado et al. 2012; Vatsos and Rebours 2015; Umanzor et al. 2019).

Although the commercial cultivation of macroalgae does not use seaweed extracts as biostimulants nowadays, more and more studies are focusing on analyzing their effects on macroalgae cultivation with very promising results. For example, studies carried out on commercial red seaweeds, such as *Kappaphycus alvarezii,* revealed that the use of commercial biostimulants derived from brown seaweeds (Acadian®) increased the growth rate, shoot formation and yield of carrageenans (Hurtado et al. 2012; Loureiro et al. 2014a, b; Hurtado and Critchley 2020). Similarly, in *Eucheumatopsis isiformis* cultures supplemented with Kelpak®, Acadian®, and Ocean Organics biostimulant products, a larger number of shoots per propagule was observed (Umanzor et al. 2020). Also, brown algae cultures, such as the sporophytes of *Saccharina* spp. supplemented with biostimulants (Acadian), showed blades more than three times thicker than those without any supplementation, and their growth capacity was enhanced (Umanzor et al. 2019).

Chemical composition and bioactive properties

Seaweeds have been used for food since ancient times, especially in the Asia–Pacific region (Wells et al. 2017). Human consumption of algae varies from country to country, for example in Japan it ranges from 9.6 to 11 g of macroalga per day (MHLW 2014). The use of algae for human consumption and food additives is increasing due to the growing awareness about its health benefits (Wells et al. 2017). Seaweeds contain 10 to 20 times more minerals than terrestrial plants and they are a good source of proteins, minerals, vitamins, amino acids, lipids, fatty acids, polysaccharides, and carotenoids (Arasaki and Arasaki 1983). In addition, a large number of compounds isolated from different algae species have biological activity, as antiviral, antioxidant, antifungal, antidiabetic, neuroprotector, among others (Kumar et al. 2008).

Regarding the direct consumption of *Asperococcus* species as human food, there is only one record that mentions *A. fistulosus*, called *thin sausage weed*, as a possible edible seaweed, but this species has not been traditionally consumed (Drennan 2016).

Information about the chemical composition of *Asperococcus* species is really scarce and data on proximal composition, pigments and polysaccharides have only been recorded for *A. ensiformis* from the Atlantic Patagonian coasts in Argentina (Poza et al. 2022).

The protein content determined in samples from that population of *A. ensiformis* was around 2.8% dry weight, a value higher than the protein content reported for other brown algae from the same coastal area, such as *Macrocystis pyrifera*, *Undaria pinnatifida* and *Leathesia marina* (Viera et al. 2013; Poza et al. 2018). Although it is a low value, it is important to note that brown algae usually have a low protein content (3–15%) when they are compared with green and red seaweeds (Fleurence 1999).

Asperococcus ensiformis from the Patagonian coasts also has lower values of total carbohydrate content $(6.45 \pm 0.50$ mg $(100$ mg$)^{-1}$ organic matter) in comparison to other brown algae from the same area, e.g., *M. pyrifera*, *U. pinnatifida* (Viera et al. 2013) and *L. marina* (Poza et al. 2018), and it is the only record of total carbohydrate content for species of *Asperococcus*.

The ash content refers to the inorganic residue remaining after ignition in biological material and represents the amount of total minerals and trace elements (Liu 2019). It is an important parameter of seaweed nutritional quality since high ash content in most algae prevents their use as human food and hampers the inclusion of intact seaweed in animal diets (Austic et al. 2013; Bikker et al. 2020). However, since edible brown seaweeds usually contain high amounts of K, Na, Ca, Mg, Fe, Zn, Mn, P, a controlled intake of small portions (between 8 and 10 g dw) can supply most of the

recommended daily intake of some essential minerals (Rupérez [2002](#); Mišurcová et al. [2011](#)). The ash content recorded for *A. ensiformis* from the Atlantic Patagonian coast was higher than 40% dry weight (Poza et al. [2022](#)), a high value compared to most land plants (Rupérez [2002](#); Liu [2019](#)) and also to other seaweeds, which present values ranging from 20 to 35% (Verma et al. [2017](#)). Moreover, brown seaweeds usually show values of ash content between 20 and 40% (Pereira [2011](#); Kumar et al. [2015](#)).

Another compound studied in a species of *Asperococcus* was the iodine content. Iodine content is an important quality parameter to evaluate in edible seaweeds, since a regular consumption of iodine-rich seaweeds, such as kelps, could severally affect thyroid function; however, the occasional intake (once or twice a week) or their use as a dietary supplement is unlikely to be harmful (Smyth [2021](#)). Iodine was measured in *A. echinatus* from Woods Hole (USA), showing very low values of I_2 (0.056 mg g^{-1} alga) (Grimm [1952](#)). The iodine content of seaweed and its chemical form varies with different species and also varies depending on factors, such as season, geographical location, parts of the alga and growth stages, but the iodine content is generally greater in kelps than in other algae groups (Teas et al. [2005](#); Mussig [2009](#); Roleda et al. [2018](#)).

The cell walls of brown algae are mainly composed of alginic acid, cellulose, and sulfated polysaccharides in an average weight ratio 3:1:1 (Kloareg and Mabeau [1987](#)). These polysaccharides are arranged in two layers, the innermost is a skeleton of cellulose microfibrils that provides rigidity to the cell, and the outermost is mainly made of alginic acid and fucoidans conforming an amorphous matrix in which the set of microfibrils is embedded (Davis et al. [2003](#); Ponce and Stortz [2020](#)).

Alginic acid (or alginate) constitutes between 18.9 to 66.7% of the dry weight in brown algae (Li et al. [2021](#)). This polysaccharide is responsible for the springiness and flexibility required by the algae to withstand the forces of the ocean and waves. It also helps to prevent desiccation and facilitates the bonding of salts present in the seawater, particularly Ca^{2+}, Na^+, Mg^{2+}, Sr^{2+}, and Ba^{2+} ions (Haug [1964](#)).

Alginate is a linear polymer of residues of mannuronic (M) and glucuronic acid (G) connected through 1,4-glycosidic linkages (Brownlee et al. [2005](#)). The blocks are composed of consecutive G residues, consecutive M residues, and alternating M and G residues (Lee and Mooney [2012](#)). The M/G ratio varies among different algal species, as well as with season, age, tissue type, and geographic location (Kraemer and Chapman [1991](#); Donati et al. [2003](#)). In general, alginates that are rich in G residues exhibit stronger stiffness and gelling properties, so they are widely used in the food and cosmetic industry (Kim et al. [2018](#)).

Alginate yield of *A. ensiformis* from the Atlantic Patagonian coast is around 30% (Poza et al. [2022](#)), a yield similar to kelp species, such as *Macrocystis pyrifera*, *Laminaria hyperborea*, *Laminaria digitata* and *Saccharina japonica*, which are industrially important species for alginate production (Peteiro [2018](#)).

Fucoidans are a group of fucose-rich sulfated polysaccharides, usually built of a backbone of α-linked L-fucose residues accompanied by variable amounts of other monosaccharides, like galactose, xylose, mannose, rhamnose, and glucuronic acid (Ale and Meyer [2013](#); Ponce and Stortz [2020](#)). Fucoidans are believed to play a key role in cell wall architecture, by cross-linking alginates and cellulose microfibrils (Kloareg et al. [1986](#)). They would also help to retain water in the fronds by preventing desiccation during the emersion period, since when the fronds are in contact with seawater, the ester sulfate groups are associated with magnesium ions that are highly hydrated (Percival [1979](#)). Proof of this is that brown seaweeds growing in the upper parts of the shores have a high fucoidan content, whereas subtidal species contain very little or no fucoidans (Carlberg et al. [1978](#)).

A yield of 18.5% of fucoidans was found in *A. ensiformis* from the Atlantic Patagonian coast, being the first record of fucoidans yield in Asperococcus species (Poza et al. [2022](#)). This yield of fucoidans is high compared to other brown algae inhabiting the same shores, such as *Leathesia marina* and *Scytosiphon lomentaria* (Feldman et al. [1999](#); Ponce et al. [2019](#)), but similar to those yields found in *Undaria pinnatifida* from the same coastal area (Viera et al. [2013](#)).

Fucoidans have demonstrated a number of promising biological activities, including immunomodulatory, antitumor (Ale et al. [2011](#)), anti-inflammatory (Cumashi et al. [2007](#)), antithrombotic, and anticoagulant (Wang et al. [2010](#)) activity. Such bioactivities have been related to their chemical structure, i.e., monosaccharide composition, sulfate content, position of sulfate ester groups, and molecular weight (Li et al. [2008](#)).

The pigment profile of brown algae is mainly composed of chlorophylls *a* and *c*; carotenes, principally α and β carotene; and xanthophylls, mainly neoxanthins A and B, fucoxanthin and violaxanthin (Garcia-Perez et al. [2022](#)). Fucoxanthin is the pigment responsible for the characteristic golden-brown color of this group of algae (Kumar et al. [2013](#)) and its biological function is to enhance light harvesting due to its ability to absorb blue-green light (450–570 nm) which is poorly absorbed by the chlorophylls (Kim et al. [2011](#)). It also may function as a photoprotective pigment under overexposure to solar radiation (Frank et al. [1997](#); Griffiths et al. [2016](#)).

Pigment composition varies significantly between populations and also between individuals as a result of the influence of local environmental conditions. Therefore, adjustments in the chlorophyll *a* + *c* concentration reflect the acclimatation to the *in-situ* radiation and are applied in order to balance light harvesting and photoprotection (Marambio et al. [2017](#)).

Concentrations of photosynthetic pigments in *Asperococcus* species have only been recorded for *A. ensiformis* from Atlantic Patagonian coasts, being chlorophyll *a* the most abundant pigment (Poza et al. 2022). *Asperococcus ensiformis* also shows high levels of fucoxanthin (Poza et al. 2022), similar to those found in other phaeophycae, such as *Sargassum linearifolium* and *Spatoglossum asperum* (Verma et al. 2017).

Pigments from brown seaweed have been used as coloring agents in food products and in animal feed, and also to improve the appearance of pet foods and dairy products (Aryee et al. 2018). In addition, numerous studies show the beneficial impact of pigments on human health, for example fucoxanthin has been demonstrated to have antidiabetic and anti-obesity properties, blood-pressure lowering properties and anticancer, antioxidant, immune modulatory, antiangiogenic, antimalarial and anti-inflammatory activities (Brown et al. 2014; Namvar et al. 2014; Déléris et al. 2016; Pangestuti and Siahaan 2018).

Regarding biological activity, data on the antioxidant activity have only been obtained for *A. ensiformis* from the Atlantic Patagonian coast and for *A. bullosus* from the Britany coasts. *A. ensiformis* shows high radical scavenging activity, with an IC_{50} of 9.54 mg mL^{-1} and vitamin C equivalent of 41.84 mg VCE per 100 g of dry algae, whereas *A. bullosus* presented lower IC_{50} values for radical scavenging activity and low antioxidant activity evaluated using another methodology (β-carotene–linoleic acid system and reducing activity) (Zubia et al. 2009; Poza et al. 2022).

Numerous studies indicated a direct relationship between the antioxidant activity and the total content of phenolic compounds (Velioglu et al. 1998; Kim et al. 2005; Connan et al. 2006; Zhang et al. 2007; Le Lann et al. 2008). Phenolic compounds are secondary metabolites made up of an aromatic benzene ring with one or more hydroxyl substituents, they have a protective role against abiotic stressors such as UV radiation (de la Coba et al. 2009). The postulated protective mechanism involves the ability to donate a phenolic hydrogen as well as the stabilization of the resulting antioxidant radical through electron delocalization and/or intramolecular hydrogen bonding or further oxidation (Frankel and Meyer 2000). In this regard, total phenolic content data of *A. ensiformis* and *A bullosus* has been recorded in the literature (Zubia et al. 2009; Poza et al. 2022). However, no profile of the main phenolic compounds has yet been published for the genus.

Regarding antitumoral activity, there is only one paper evaluating the cytotoxic activity of *A. bullosus* from the Britany coasts against different tumoral cells lines, Daudi (human Burkitt's lymphoma), Jurkat (human leukaemic T cell lymphoblast) and K562 (human chronic myelogenous leukaemia); however, this study did not detect any antitumoral activity (Zubia et al. 2009).

Conclusions

Asperococcus is a genus of Chordariaceae little studied in terms of its biology, ecological dynamics, and phenology, despite its wide distribution in most oceans around the world. Species of this genus have simple thalli and can be easily distinguished in the field from other brown intertidal seaweeds by the notorious sori. Although a plethora of species names and synonyms for *Asperococcus* can be found in the literature, only a few species have been thoroughly described and the phylogenetic relationships between them are still uncertain. Given the simple morphology of the different species, the taxonomy of this group needs a critical revision on the basis of molecular data. The life cycle of *Asperococcus* has only been studied in *A. ensiformis, A. bullosus* and *A. fistulosus*, however there are some aspects of the cycle that need further study, for example the coexistence of unilocular and plurilocular sporangia in the macroscopic sporophyte.

Although there is no tradition of cultivating species of this genus, the results of cultivation trials carried out with *A. ensiformis* under laboratory conditions have shown that it is feasible to cultivate this seaweed by the rope seeding method, which is traditionally used for large brown algae with heteromorphic life cycles. To determine the actual potential of the species for mariculture, the performance of the sporophytes transplanted in the sea should be evaluated.

A few studies have evaluated the chemical compositions and bioactive properties of *Asperococcus* species, which have shown similar performance and characteristics to other commercially important brown algae; however, the scarce literature on this topic shows that further studies are needed on the uses and implementation of the species. Given that the species of *Asperococcus* are widely distributed and present promising features for the successful development of nursery stages, these seaweeds should be regarded as a promising alternative source of seaweed bioproducts, such as alginates and fucoidans.

Declarations

Competing interests The authors declare no competing interests.

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