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The Mediterranean *Cystoseira* Complex (Fucales, Ochrophyta): An Updated Illustrated Guide and Identification Key

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Abstract

Macroalgal forests dominated by *Cystoseira sensu lato* (*s.l.*) (genera *Cystoseira sensu stricto*, *Ericaria*, and *Gongolaria*) are among the most ecologically significant habitats in the Mediterranean Sea, providing structural complexity, biodiversity support, and key ecosystem services. Despite their ecological importance and protected status under multiple international directives, they are experiencing a severe decline and local extinction driven by anthropogenic pressures and climate change, making accurate monitoring and species identification a conservation priority. However, identification at the species level remains challenging, even for expert researchers, due to the high variability of diacritical characters and the lack of comprehensive photographic documentation in existing identification tools. To address this gap, we developed a photographic atlas key covering all *Cystoseira s.l.* taxa with confirmed presence in the Mediterranean Sea. The atlas consists of an identification key, a glossary, and species-specific descriptive cards. The cards, arranged alphabetically within each genus, include photos of complete thalli alongside macro-scale diacritical characters, captured in the field and in the laboratory, taxonomic synonymies, ecological and distributional information, and notes on potentially confounding species. This resource provides a user-friendly, stepwise identification tool accessible to both expert and non-expert users, with the aim of improving knowledge of the species-level distribution and ecological status of *Cystoseira s.l.* across Mediterranean coastal waters.

Keywords: *Cystoseira*; *Ericaria*; *Gongolaria*; Fucales; Mediterranean Sea; photographic atlas key

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1. Introduction

1.1. Mediterranean Forests

Macroalgal forests, one of the most productive and valuable habitats in the Mediterranean Sea, play a significant ecological role in the structuring and functioning of marine ecosystems, providing habitats, food sources, and nurseries for a diverse range of species, as well as important ecosystem services [1]. In the Mediterranean Sea, these forests are mainly composed of Sargassaceae Kützing (Fucales, Phaeophyceae) belonging to the genera *Cystoseira* C.Agardh *sensu lato* (*s.l.*) (comprising *Cystoseira sensu stricto* (*s.s.*), *Ericaria* Stackhouse, and *Gongolaria* Boehmer [2,3]) and *Sargassum* C.Agardh, which are pivotal

habitat-forming species in several assemblages along rocky shores [4]. The diversity and phylogenetic relationships within the genus *Cystoseira s.l.* were examined using both multigene molecular phylogenetic analyses and anatomical and morphological features, thus allowing researchers to recognise these three genera [2,3]. The genus *Cystoseira s.l.* has its centre of diversity in the Mediterranean Sea, where most of the occurring species are endemic (23 of the 48 species to date taxonomically accepted according to Guiry & Guiry [5]), while the remaining species extend their distribution mainly into the warm-temperate northeast Atlantic [6].

1.2. Genus Cystoseira s.l.

1.2.1. General Characters

These canopy-forming species are characterised by a vegetative body (thallus), usually attached to the substrate, with a single axis or several axes arising from a discoid holdfast or from haptera (except for the free-floating forms, i.e., pleustophytic forms), and by variable structural complexity (from a few centimeters to over 1 m high). Some species have a prostrate primary axis (stolon) that functions as an anchorage structure. They have an apical growth, a smooth or spinous apex, and abundant radial or distichous branching, sometimes with small spine-like or filiform appendages. Primary branches are repeatedly branched, and spinose branchlets may be present. Ovoid or elliptic-elongated aerocysts, isolated or arranged in chains and formed by the enlargement of branches, can also be found. Some species bear tophules (swollen storage structures) arranged along the axis or grouped in the apical zone. Cryptostomata (flask-shaped cavities opening to the surface) are present in most species, normally sunk into the branchlets and, only occasionally, pedicellate.

In cross-section, thalli of *Cystoseira s.l.* show a compact parenchymatous structure, consisting of an external meristoderm layer, several cortex layers, and an internal medulla, organised differently in the three genera [2]. *Cystoseira s.s.* shows cortical cells with thickened and shiny walls, arranged in a palisade and progressively decreasing in size toward both the medulla and the square meristoderm cells; *Gongolaria* presents cortical cells with thickened walls and square meristoderm cells; in *Ericaria*, cortical cells with thin walls and ellipsoidal to rounded rectangular meristoderm cells twice as long as wide are present.

Fertilisation is oogamous, with antheridia and oogonia located in cavities called conceptacles that are grouped in receptacles, variable in shape, and placed in terminal (sometimes intercalary) position at the end of higher-order branchlets. The life cycle is characterised by one diploid free-living generation in which gametes (haploid), produced by meiosis, are released into the water column, and fertilisation is external (Figure 1).

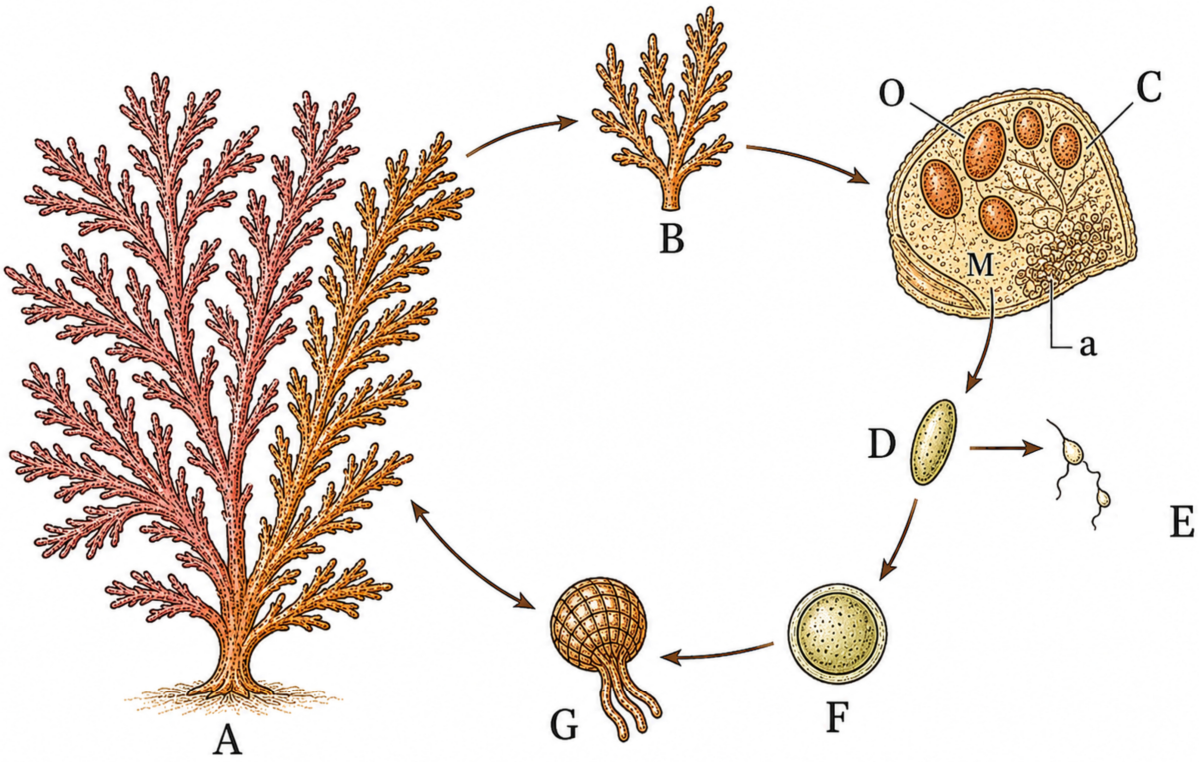


Figure 1. Schematic life cycle of *Cystoseira s.l.*: (**A**) adult thallus; (**B**) fertile branch with receptacles; (**C**) cross-section of a conceptacle showing gametangia (O = oosphere, a = antheridia, M = meiosis); (**D**,**E**) released gametes (oosphere and antheridia); (**F**) zygote; (**G**) embryo (modified from Gómez-Garreta et al. [7]).

1.2.2. Ecology

Species belonging to the genus *Cystoseira s.l.* inhabit the photophilous rocky substrates from the infralittoral fringe to the upper circalittoral zone, although they are more abundant in the infralittoral and their distribution is mainly influenced by light and hydrodynamic conditions [8]. In more superficial zones, characterised by multi- or bidirectional currents, species typically display a caespitose habit, such as *Ericaria amentacea* (C.Agardh) Molinari & Guiry and *Ericaria brachycarpa* (J.Agardh) Molinari & Guiry, whereas in the lower zones with weak, unidirectional currents, species tend to exhibit a non-caespitose habit, such as *Gongolaria montagnei* (J.Agardh) Kuntze and *Gongolaria sauvageauana* (Hamel) Molinari & Guiry. In addition, in sediment-rich environments, species develop prostrate cauloids with short primary branches, as seen in *Ericaria corniculata* (Turner) Neiva & Serrão ([8,9], as *Cystoseira corniculata* (Turner) Zanardini) and *Ericaria dubia* (Valiante) Neiva & Serrão.

1.2.3. Conservation Status and Monitoring

Since they are very sensitive to anthropogenic pressures (including climate change), *Cystoseira s.l.* forests are currently suffering a severe decline and/or local extinction in many areas of the Mediterranean [10–13]. As *Cystoseira s.l.* forests play an important ecological role, different regulations have been adopted at the international level to protect and conserve these habitats. Currently, except for *Cystoseira compressa* (Esper) Gerloff & Nizamuddin, they are included in the "List of endangered or threatened species" [14] and classified as endangered by several international organisations (e.g., RAC/SPA, Med-Pan, IUCN). Five species, [*Cystoseira amentacea* (C.Agardh) Bory (currently regarded as a synonym of *E. amentacea*), *Cystoseira mediterranea* Sauvageau (currently regarded as a synonym of *Ericaria mediterranea* (Sauvageau) Molinari & Guiry, *Cystoseira sedoides* C.Agardh (currently regarded as a synonym of *Ericaria sedoides* Neiva & Serrão), *Cystoseira spinosa*

Sauvageau (currently regarded as a synonym of *G. montagnei*), and *Cystoseira zosteroides* C.Agardh (currently regarded as a synonym of *Ericaria zosteroides* (C.Agardh) Molinari & Guiry)], are currently strictly protected under the Berne Convention [15] and the Barcelona Convention [16]. However, Mediterranean canopy-forming macroalgae were not considered priority habitats under the Habitats Directive [17] but rather as habitats of critical importance [18]. Therefore, they are included together with other marine habitats (e.g., erect macroalgae, turfs, or barren habitats) under the habitat type Reefs (Habitat Type 1170). Moreover, the photophilic communities with canopy-forming algae in Mediterranean sublittoral rock (Part 1, Annex A; [19]) are classified as Endangered in the European Red List of Habitats.

Furthermore, since their decline may have significant negative impacts on ecosystem biodiversity and functioning, they are also considered bioindicators of the environmental quality of Mediterranean coastal waters under the Water Framework Directive (2000/60/EC) [20] (i.e., the ecological indexes EEI and CARLIT) [21,22].

Therefore, it is essential to prioritise the monitoring of *Cystoseira s.l.* forests, particularly in Marine Protected Areas [23], to assess their distribution and ecological status in order to implement conservation and restoration strategies for these highly valuable habitats [23–26].

Monitoring *Cystoseira s.l.* forests and evaluating their health status, which underpin biodiversity conservation, depend strictly upon accurate identification skills [27]. We know that identification of this macroalgal group at the species level, based on diacritical characters that are often highly variable and difficult to interpret, is quite complex [28,29] and remains challenging even for expert researchers. A further limitation lies in the lack of comprehensive photographic documentation of the diacritical characters, typically illustrated by drawings, in most existing identification tools. To address this gap, we developed a photographic atlas key covering all *Cystoseira s.l.* taxa with confirmed presence in the Mediterranean Sea.

2. Materials and Methods

The main goal of this photographic atlas key is to make it easier to correctly identify Mediterranean species belonging to the *Cystoseira* complex. Therefore, it is addressed not only to expert phycologists but also to marine biologists and professionals in environmental monitoring and restoration. This tool is based on a critical review of the specific taxonomic literature (dated and recent), an analysis of personal herbaria specimens of the authors, and also on the long personal experience in the field of the authors. Moreover, the key has been carefully validated by the same authors and used with trainees and master's students. It consists of a dichotomous identification key, accompanied by photographs illustrating the diacritical characters used and specific illustrated descriptive cards, integrating photos of complete thalli alongside macro-scalemorphological diacritical characters, and a glossary.

In the illustrated descriptive cards, one for each taxon and arranged in alphabetical order within each genus (*Cystoseira*, *Ericaria*, and *Gongolaria*), the users will find the taxonomic accepted name (following Guiry & Guiry [5]), the synonyms, a short description, the habitat, the distribution, and descriptive photos, captured in the field and/or in the laboratory (from the same authors and other colleagues), and in a few cases taken from literature. The distribution mainly comes from Guiry & Guiry [5], except for some cases supported by recent taxonomic studies and discussed in the Results or in the relevant remarks. Furthermore, endemic taxa are marked with an asterisk (*) before the binomial name. Moreover, if a species may be easily confused with others, the users will find the distinguishing characters of the species in the section "Identity confusion," thus avoiding any possible confusion with similar species. The taxonomy of the Mediterranean *Cystoseira*

complex is still an evolving issue owing to morphological plasticity, historical nomenclatural issues, incomplete geographic sampling, and limited availability of molecular data. For this reason, the atlas adopts a conservative taxonomic framework based primarily on the most recent taxonomic literature and the nomenclature currently accepted by AlgaeBase. Taxa with a confirmed occurrence in the Mediterranean and with sufficiently documented morphological diagnostic characters were included in the identification key. Conversely, taxa regarded as synonyms, taxa with doubtful Mediterranean occurrence, or taxa with unresolved identities pending molecular investigation, were excluded.

Consequently, when the taxonomic position of a taxon remains debated and therefore requires further investigation (e.g., molecular analyses), or if misidentifications have been reported in the literature, some remarks are included, both general and specific in the illustrated descriptive cards. Taxa with uncertain generic placement (due to the lack of molecular data) are enclosed in quotation marks.

3. Results

3.1. General Remarks

Although 68 taxa (at the specific and intraspecific level) are recognised in Guiry & Guiry [5], the users will find here only the 40 taxa whose presence in the Mediterranean Sea has been confirmed. At the beginning of the key, the first considered character refers to the habit of the plant with respect to the substrate, i.e., unattached (pleustophytic forms) or attached plants. Since pleustophytic forms lack distinctive diagnostic characters, they are included in the identification key only to distinguish them from species fixed to the substrate and are not further differentiated at the species level. Some remarks concerning debated taxa are given below. Following Molinari-Novoa & Guiry [3], *Ericaria caespitosa* Sauvageau was excluded from the key as it is considered a synonym of *E. brachycarpa*. Similarly, *Cystoseira spicata* Ercegović was omitted due to its synonymy with *E. amentacea*, (although according to Blanfuné et al. [30], new unpublished genetic data question such a synonymy), while *Cystoseira pycnoclada* Schiffner *ex* Gerloff & Nizamuddin was omitted pending further examination of the original material. Following Neiva et al. [31], *Gongolaria mauritanica* (Sauvageau) Molinari & Guiry [=the Atlantic *Gongolaria nodicaulis* (Withering) Molinari & Guiry] was also omitted, while *Gongolaria gibraltarica* (Sauvageau) Neiva, Bermejo & Serrão was included. Similarly, *Cystoseira humilis* Schousboe *ex* Kützing was omitted, as Mediterranean records may represent misidentifications referring to *Cystoseira pustulata* (Ercegović) Neiva & Serrão [31]. However, further molecular analyses are required to clarify its taxonomic position. Following Nizamuddin's [32] description, we included *Gongolaria susanensis* (Nizamuddin) Molinari & Guiry among the caespitose species. We assume that the Sicilian specimens, considered as pseudocaespitose by Cormaci et al. [33], should instead be attributed to *Cystoseira barbata* (Stackhouse) C.Agardh [31,34], currently regarded as a synonym of *Gongolaria barbata* (Stackhouse) Kuntze. Certainly, further samples must be morphologically but also genetically analysed to definitively resolve this issue. Below are the photographs illustrating the key diacritical characters and the dichotomous identification key.

3.2. Diacritical Characters

In *Cystoseira* complex, we can recognise both stable (anchorage structure, main axis, apical region, and tophules) and seasonal (branches, branchlets, receptacles, aerocysts, and cryptostomata) diacritical characters, essential for taxonomic identification. Photographs illustrating the key diacritical characters are presented below (Figures 2–8). They provide a comprehensive photographic documentation of the thallus morphology, focusing on the origin and anchorage structure of the main axis and the apical region, and on specialised

structures, including tophules, vegetative branches, ultimate branchlets, fertile receptacles, and aerocysts.



Figure 2. Axis origins and anchorage structure details: (**a**) creeping axis (stoloniferous habit); (**b**) several axes arising simultaneously from an encrusting holdfast (caespitose habit); (**c**) a single extremely short axis that branches immediately, giving the appearance of a thallus with multiple axes (pseudocaespitose habit); (**d**) a single axis arising from a compact discoid holdfast (non-caespitose habit); (**e**) discoid holdfast with haptera. Scale bars = 1 cm.

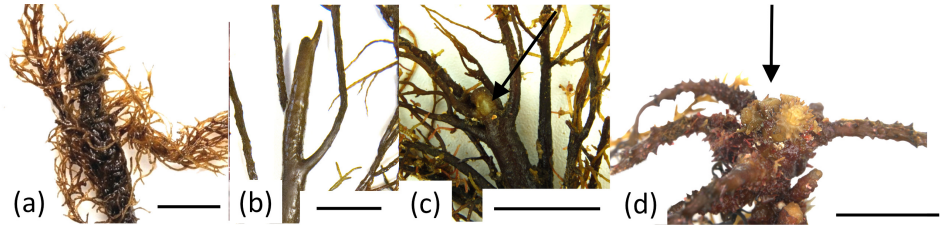


Figure 3. Apex details: (**a**) prominent and spiny; (**b**) highly prominent (≥1 cm) and smooth; (**c**) slightly prominent (≤0.5 cm) and smooth (black arrow); (**d**) not prominent, flattened, and smooth (black arrow). Scale bars = 1 cm.



Figure 4. Tophule details: (**a**) warty; (**b**) smooth; (**c**) spiny. Scale bars = 1 cm.

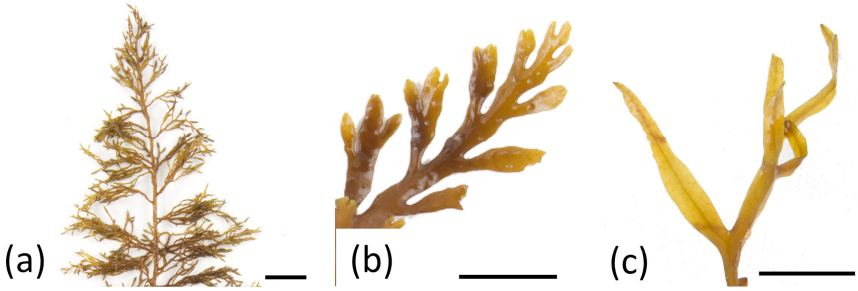


Figure 5. Branch details: (**a**) cylindrical; (**b**) compressed; (**c**) flattened with a midrib. Scale bars = 1 cm.

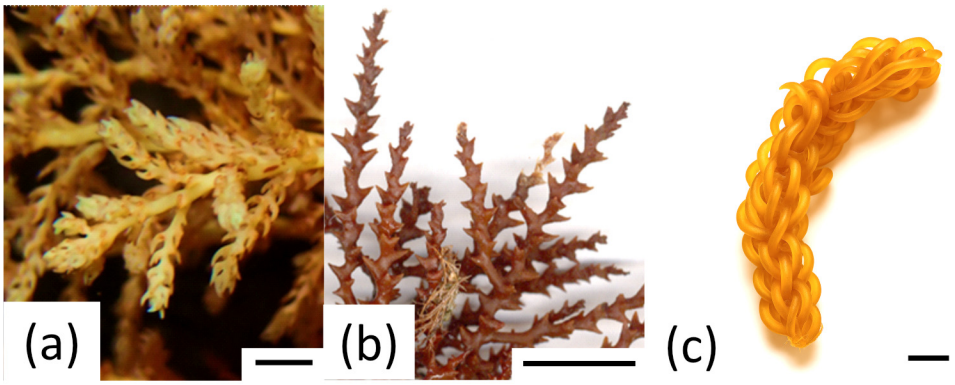


Figure 6. Ultimate branchlet details: (**a**) short, spiniform, and crowded on the branches; (**b**) short, spiniform, and triangular with a broad base and a bifid to multifid apex; (**c**) short, spiniform, deeply subulate, and uniformly imbricate along the branches. Scale bars = 1 cm.

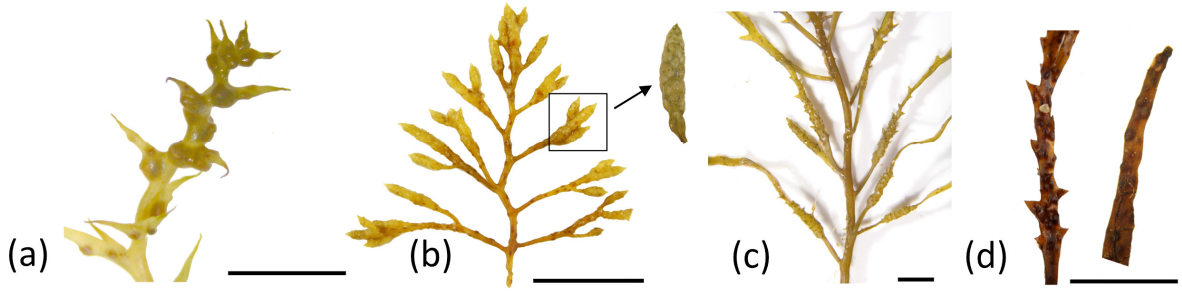


Figure 7. Receptacle details: (**a**) loosely compact, protruding from the base of the spiny branches; (**b**) terminal, compact, and lanceolate; (**c**) intercalary on the branches; (**d**) conceptacles scattered on the side of the subapical section of the flattened branches. Scale bars = 0.5 cm.

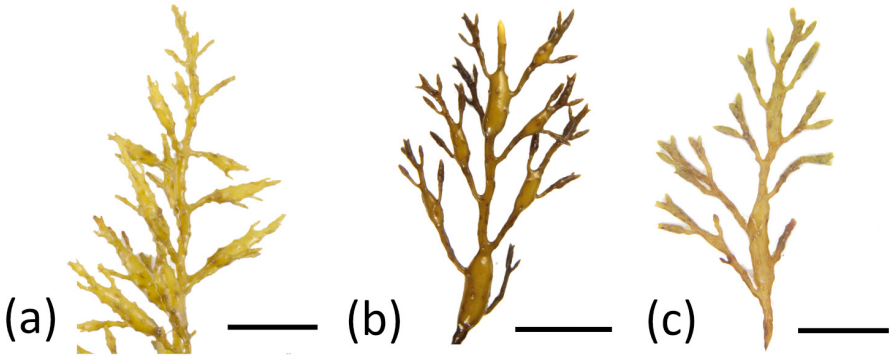


Figure 8. Aerocyst details: (**a**) fusiform with an obtuse or briefly mucronate tip; (**b**) ovoid; (**c**) cylindrical and arranged in chains. Scale bars = 1 cm.

3.3. Dichotomous Key to Identify Mediterranean Species Belonging to the Cystoseira Complex

1a. Plants unattached, free-floating (pleustophytes). Thalli without anchorage structures (no holdfast) and axes (cauloids) not evident ..... ***Cystoseira foeniculacea*** f. ***dubia***
Cystoseira schiffneri
Gongolaria barbata f. ***aurantia***
Gongolaria barbata f. ***repens***

1b. Plants attached to the substrate. Thalli with anchorage structures always recognisable [encrusting or discoid (with or without haptera)]; axes evident, erect or prostrate **2**

2a. Creeping axis on the substrate (stoloniferous habit) **3**
2b. Erect axes [one (non-caespitose or pseudocaespitose habit) or many (caespitose habit)] **5**

3a. Spinose branchlets absent; secondary axes erect, flattened with a midrib; distichous branching ..... ***Ericaria dubia***
3b. Spinose branchlets present **4**

4a. Secondary erect axes cylindrical, inserted at right angles, sparingly branched; all orders of branches densely covered with spine-like branchlets .....***Ericaria corniculata***
4b. Secondary erect axes cylindrical, highly branched, bare at base; branches of all orders covered with regularly spaced spine-like branchlets ..... G***ongolaria abies-marina***

5a. Thallus with numerous axes arising from an encrusting holdfast, with or without haptera (caespitose habit) **6**
5b. Thallus with a single axis, long or very short, raising from a single discoid holdfast (non-caespitose or pseudocaespitose habit), compact or with digitate haptera **17**

6a. Higher-order branches densely covered by short spinose branchlets; apex spinose, slightly prominent (≤0.5 cm); receptacles terminal, compact, cylindrical-tuberculate, spinose, attenuate at base ..... ***Ericaria amentacea***
6b. Higher-order branches without spinose branchlets, or spinose branchlets loosely arranged; receptacles with different combinations of traits (never as above) **7**

7a. Axes cylindrical or clavate, densely covered along almost their entire length, by small simple spines..... **8**
7b. Axes cylindrical or compressed, smooth, at most warty/nodular due to scars or basal stumps of old fallen branches **9**

8a. Axes clavate, covered with spines; apex spinose highly prominent, branches above the first order from compressed to strongly flattened (sometimes with a midrib) and with loosely arranged spinose branchlets; receptacles terminal, spindle-shaped, loosely compact (single conceptacles may remain isolated) ..... ***"Cystoseira" pelagosae***
8b. Axes cylindrical, primary branches densely covered, along almost their entire length, by small simple spines; apex spinose, not highly prominent; spinose branchlets absent; receptacles terminal, compact, fusiform:

→ with both cylindrical and flattened branches .. ***Cystoseira foeniculacea* f. *foeniculacea***
→ with cylindrical branches only ..... ***C. foeniculacea* f. *tenuiramosa***
→ with flattened branches only ..... ***C. foeniculacea* f. *latiramosa***

9a. Axes cylindrical or compressed, primary branches cylindrical or slightly compressed; secondary branches cylindrical, cryptostomata not prominent, often arranged in regular rows; aerocysts numerous, sub-terminal, isolated or in series of 2 (–3) ..... ***Cystoseira compressa* f. *compressa***

→ with very short cylindrical axis (1–3 cm), compressed branches only, aerocysts absent ..... ***Cystoseira compressa* f. *plana***
→ with a prostrate growth, compressed branches only, aerocysts absent .....***Cystoseira compressa* f. *rosetta***

9b. Axes cylindrical **10**

10a. Primary branches from cylindrical to slightly compressed, alternate or distichous; cryptostomata prominent (pustulate appearance); higher-order branches thin, cylindrical; receptacles thin, fusiform, simple or bifurcate, supported by flattened aerocysts ..... ***Cystoseira pustulata***

10b. Branches of all orders cylindrical (including in the proximal part) **11**

11a. Apex of the axis prominent and spinose **12**

11b. Apex of the axis smooth, either prominent and bare or not prominent/flattened and bare, sometimes surrounded by cylindrical appendages **13**

12a. Axes cylindrical, generally bare on the lower third and blackish brown; primary branches cylindrical, without spinose branchlets; higher-order branches very thin, cylindrical, spineless ..... ***Ericaria crinita***

12b. Axes often swollen at base, greenish; primary branches cylindrical with spinose branchlets mainly at the basal part; higher-order branches cylindrical or slightly flattened with loosely arranged spinose branchlets; frequent adventitious branches from scars of deciduous branches ..... ***"Cystoseira" crinitophylla***

13a. Apex of the axis not prominent, flattened and smooth, surrounded by cylindrical or spinose appendages **14**

13b. Apex of the axis prominent and smooth **15**

14a. Base not compact, without lateral haptera; primary branches with numerous spinose branchlets at the basal part; ultimate spinose branchlets, if present, few and loosely arranged ..... ***Ericaria balearica***

14b. Base compact, with lateral haptera; primary branches with numerous spinose branchlets at the basal part; ultimate spinose branchlets more numerous and thickened ..... ***Ericaria brachycarpa*** v. ***brachycarpa***

→ with spinose swelling at the base of primary branches (hemitophules) ..... ***Ericaria brachycarpa*** v. ***claudiae***

15a. Apex highly prominent (≥1 cm) relative to the insertion of primary branches; base not compact; primary axes thin (diameter 2–3 mm); branches of all orders cylindrical (including proximal part) with few, scattered, prominent cryptostomata; receptacles are terminal, small, cylindrical, compact, verrucose to tuberculate ..... ***Ericaria barbatula***

15b. Apex slightly prominent (≤0.5 cm) relative to the insertion of primary branches; base compact **16**

16a. Axes robust (4–5 mm diameter), long (2–10 cm); primary branches with a cupressoid habit (due to the subequal development of higher-order branches); spinose appendages absent except on fertile branches; cryptostomata abundant and prominent. Receptacles are terminal, cylindrical, compact; verrucose to tuberculate ..... ***Ericaria giacconei***

16b. Axes thin (1–5 mm diameter), short (5–40 mm) branching immediately above the base; spinose appendages absent; cryptostomata few, scattered, and not prominent. Receptacles terminal, small, and compact, fusiform and apiculate, surface varying from smooth to tuberculate ..... ***Gongolaria susanensis***

17a. Holdfast digitate or with branched haptera **18**

17b. Holdfast discoid, more or less regular and compact (sometimes digitate) **21**

18a. Tophules large (to 20 × 8 mm), cylindrical-ovoid, completely smooth **19**
18b. Tophules small, rugged to spinose **20**

19a. Primary branches cylindrical or slightly flattened; higher-order branches flattened with soft midrib; flattened, triangular spinose branchlets; aerocysts absent .....***Ericaria zosteroides***
19b. Primary branches cylindrical; higher-order branches cylindrical, except those at the base of primary branches which are leaf-like with a soft midrib; aerocysts abundant.....***Gongolaria usneoides***

20a. Thallus with wide frond; axis radially branched; spinose tophules spaced and splayed along the axis which has a coralloid aspect. Receptacles moniliform, branched, with spine-like appendages ..... ***Ericaria funkii***
20b. Thallus with thin frond; axis thin, simple or loosely branched; tophules verrucose or smooth, densely crowded on the axis which has not coralloid aspect; receptacles moniliform, spineless, and loosely branched .....***"Cystoseira" jabukae***

21a. Axis generally long ≥ 10–15 cm. During the maximum vegetative development, ratio cauloid length, thallus height (Lc/At), frond included, >0.5 ..... **22**
21b. Axis generally long 1–8 cm. During the maximum vegetative development, Lc/At, frond included, <0.5 ..... **27**

22a. Thalli cylindrical; primary branches short and subequal, giving a cylindrical brush habit ..... ***Ericaria sedoides***
22b. Thalli with a different habit **23**

23a. Tophules present **24**
23b. Tophules absent **25**

24a. Tophules spinose when young, smooth-tuberculate when older; receptacles both basal/intercalary, just above the tophule, and terminal on the branches ..... ***"Cystoseira" micheleae***
24b. Tophules spinose; receptacles only terminal:
→ branches mainly cyilindrical ..... ***Gongolaria montagnei*** v. ***montagnei***
→ branches compressed ..... ***Gongolaria montagnei*** v. ***compressa***
→ branches cylindrical, sometimes slightly flattened in the terminal part ..... ***Gongolaria montagnei*** v. ***tenuior***

25a. Apex smooth and highly prominent (≥1 cm) ..... ***Gongolaria barbata***
25b. Apex spinose (prominent or slightly prominent) **26**

26a. Apex prominent (up to 1 cm) relative to the insertion of the primary branches, covered with spines; basal disc compact, regular, without haptera; aerocysts absent .....***Gongolaria sauvageauana***
26b. Apex slightly prominent (≤0.5 cm) relative to the insertion of the primary branches; basal disc with irregular outline, often digitate with lateral haptera; ovoid aerocysts (to 5 mm long) often present along ultimate branches .....***Ericaria selaginoides***

27a. Tophules absent; apex slightly prominent (≤0.5 cm), surrounded by big, short spines; secondary/tertiary branchlets densely covered with spinose, pointed branchlets; aerocysts absent .....***Ericaria mediterranea***
27b. Tophules present; apex spinose or smooth **28**

28a. Apex spinose but obscured by a characteristic "cauliflower-like" axis tip; tophules spinose, closely appressed to the axis; branches of all orders slender, cylindrical; ultimate branchlets spiniform absent.....***Gongolaria elegans***
28b. Apex smooth; ultimate branchlets spiniform present **29**

29a. Lower young primary branches leaf-like (2–3 mm wide), flattened on one plane with a distinct midrib; upper branches cylindrical with spinose branchlets; tophules ovoid, smooth or rugged, occasionally slightly spinose.....***Gongolaria algeriensis***
29b. Lower primary branches not leaf-like, mostly cylindrical or slightly compressed, lacking a distinct midrib **30**

30a. Ultimate branchlets spiniform, simple and short, regularly spaced; primary branches with tophules often alternating with branches without tophules; aerocysts rare or absent.....***Gongolaria gibraltarica***
30b. Ultimate branchlets spiniform, triangular, broad-based, with bifid to multifid apex, imbricated toward branch tips; primary branches with tophules more consistently distributed; aerocysts absent **31**

31a. Spinose branchlets closely spaced, often imbricate (overlapping), frequently bifid to multifid; secondary axes suprabasal and subhorizontal; young primary branches slightly flattened; tophules rugged ..... ***Gongolaria squarrosa***
31b. Spinose branchlets widely spaced or concentrated at branch tips; primary branches typically smooth at the base; tophules variable (obovoid to oblong), concentrated at tips of axes; higher-order branches stouter with lateral spines …...***Gongolaria rayssiae***

3.4. Descriptive Cards

3.4.1. ***Cystoseira compressa*** (Esper) Gerloff & Nizamuddin **f. *compressa* (Figure 9)**

Synonyms: *Fucus compressus* Esper; *Cystoseira filicina* Bory; *Fucus fimbriatus* Desfontaines *nom. illeg*.; *Cystoseira fimbriata* Bory.

Morphology: Thallus caespitose, up to 30 cm high, attached to the substrate by a compact basal disc; axes, cylindrical or slightly compressed, short, with smooth and not very prominent apices; tophules absent; spiny branches absent; cryptostomata not protruding and arranged in regular rows. Aerocysts numerous, sub-terminal, isolated or in series of 2–3.

Reproductive morphology: Receptacles terminal, compact, lanceolate-fusiform, sometimes briefly pedicellate on the aerocysts, simple or branched, with an obtuse or briefly mucronate tip.

Habitat: Epilithic, in the upper infralittoral zone. Frequent in infralittoral pools.

Distribution: Mediterranean Sea: Spain, Balearic Islands, France, Corsica, Greece, Italy, Croatia, Adriatic Sea, Veneto, Apulia, Sicily, Malta, Israel, Cyprus, Turkey, Levant Basin, Syria, Morocco, Tunisia, Algeria, Libya, and Egypt. **Atlantic Ocean:** Canary Islands, Madeira, Azores, Bermuda, Cape Verde, Salvage Islands, Portugal, Spain, France, Morocco, and Tropical and Subtropical Western Atlantic.

Identity confusion: It cannot be confused with other species.

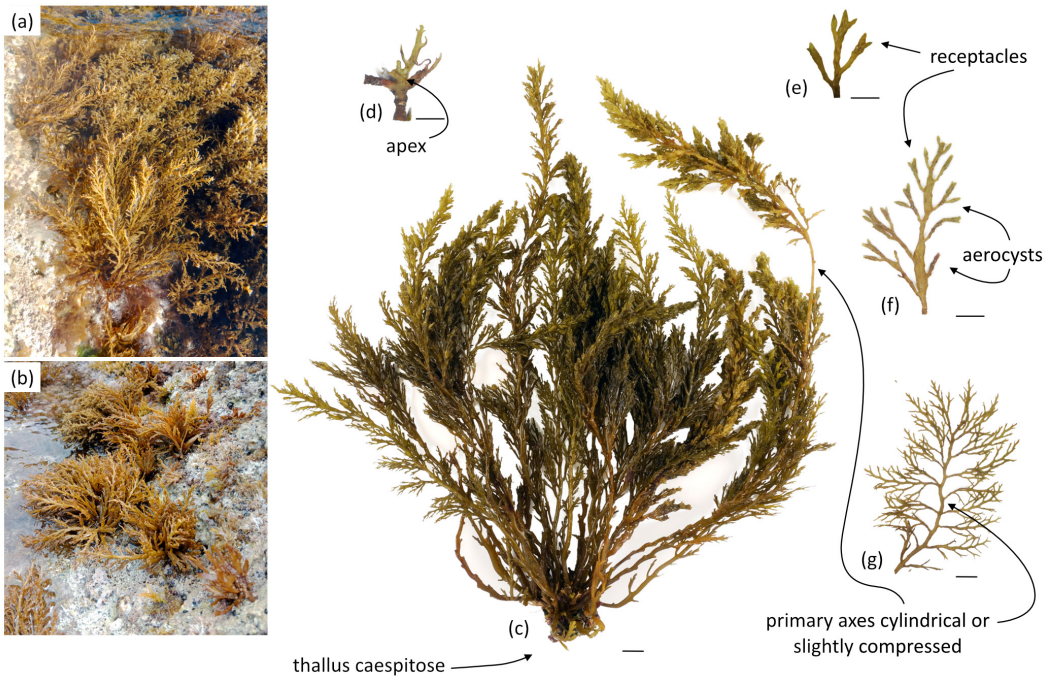


Figure 9. *Cystoseira compressa* f. *compressa*: (**a**,**b**) thalli in their habitat; (**c**) habit of the thallus (Scale bar = 1 cm); (**d**) details of the apex (Scale bar = 0.5 cm); (**e**) details of the receptacles (Scale bar = 0.5 cm); (**f**) details of the aerocysts (Scale bar = 0.5 cm), (**g**) details of a primary axis (Scale bar = 1 cm).

3.4.2. ***Cystoseira compressa* f. *plana*** (Ercegović) Cormaci, G. Furnari, Giaccone, Scammacca et Serio **(Figure 10)**

Morphology: characterised by a very short cylindrical axis (1–3 cm). Higher-order branches are entirely compressed; aerocysts absent.

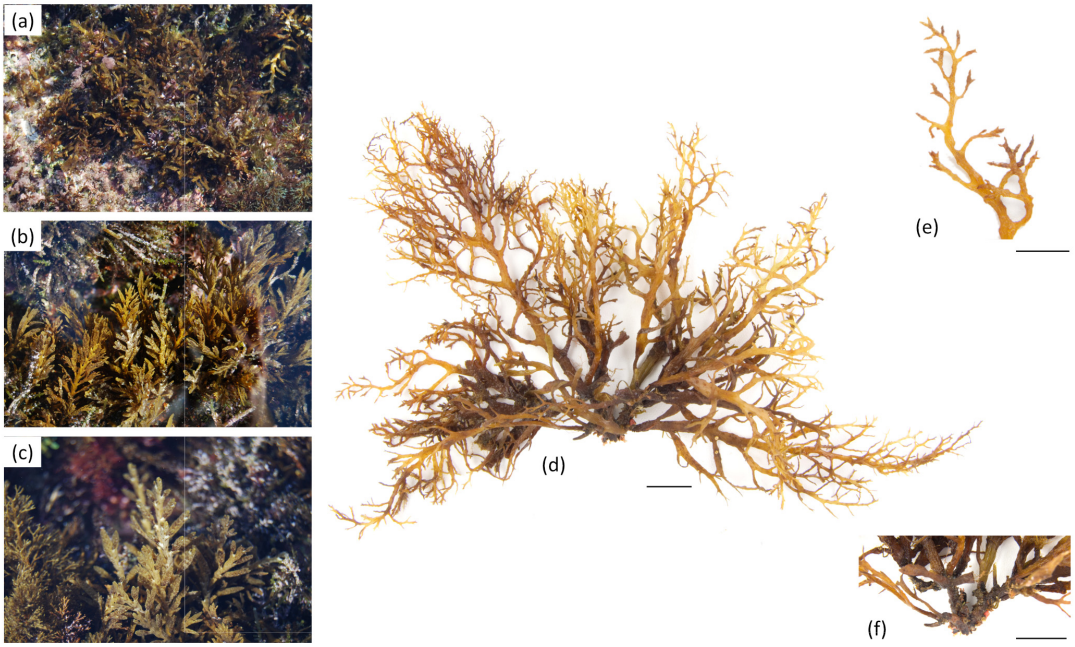


Figure 10. *Cystoseira compressa* f. *plana*: (**a**–**c**) thalli in their habitat; (**d**) habit of the thallus (Scale bar = 1 cm); (**e**) details of the receptacles (Scale bar = 0.5 cm); (**f**) details of the holdfast (Scale bar = 1 cm).

3.4.3. ***Cystoseira compressa* f. *rosetta*** (Ercegović) Cormaci, G. Furnari, Giaccone, Scammacca et Serio **(Figure 11)**

Morphology: characterised by a prostrate growth with morphological characteristics like those of the f. *plana* mentioned above.

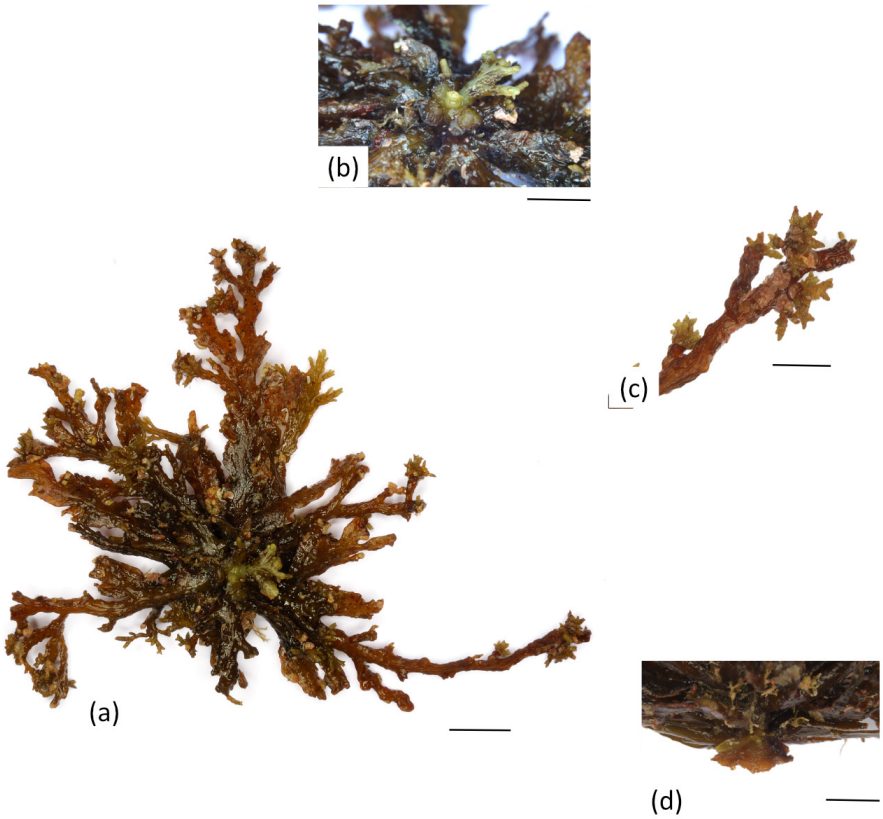


Figure 11. *Cystoseira compressa* f. *rosetta*: (**a**) habit of the thallus (Scale bar = 1 cm); (**b**) details of the apex (Scale bar = 0.5 cm); (**c**) details of the receptacles (Scale bar = 0.5 cm); (**d**) details of the holdfast (Scale bar = 1 cm).

3.4.4. (*) ***Cystoseira crinitophylla*** Ercegović **(Figure 12)**

Morphology: Thallus caespitose, olive-green to yellow-green, slight iridescence in situ in young individuals, 20–30 cm high; irregular basal holdfast; cylindrical axes, simple or branched, smooth to spiny; apex protruding and spiny; primary branches cylindrical with spinose appendages mainly at the basal part; higher-order branches cylindrical or slightly flattened with loosely arranged ultimate spinose branchlets, simple or divided, bifid to multifid, cylindrical-subulate or laterally compressed; frequent adventitious branches from scars of deciduous branches; cryptostomata more or less frequent; tophules absent; aerocysts absent.

Reproductive morphology: Receptacles compact, terminal, cylindrical, swollen, tuberculate, spiny, with an obtuse, non-mucronate apex.

Distribution: Mediterranean Sea: Adriatic Sea, Italy, Sardinia, Sicily, Corsica, France, Greece, Tunisia, Levant Basin, and Turkey.

Habitat: Epilithic, in the upper infralittoral zone up to 10 m depth.

Identity confusion: Often confused with *Ericaria crinita*, from which it differs by the greenish-yellow pigmentation (vs. blackish-brown axes) and the presence of abundant spinose branchlets on both higher-order branches and receptacles.

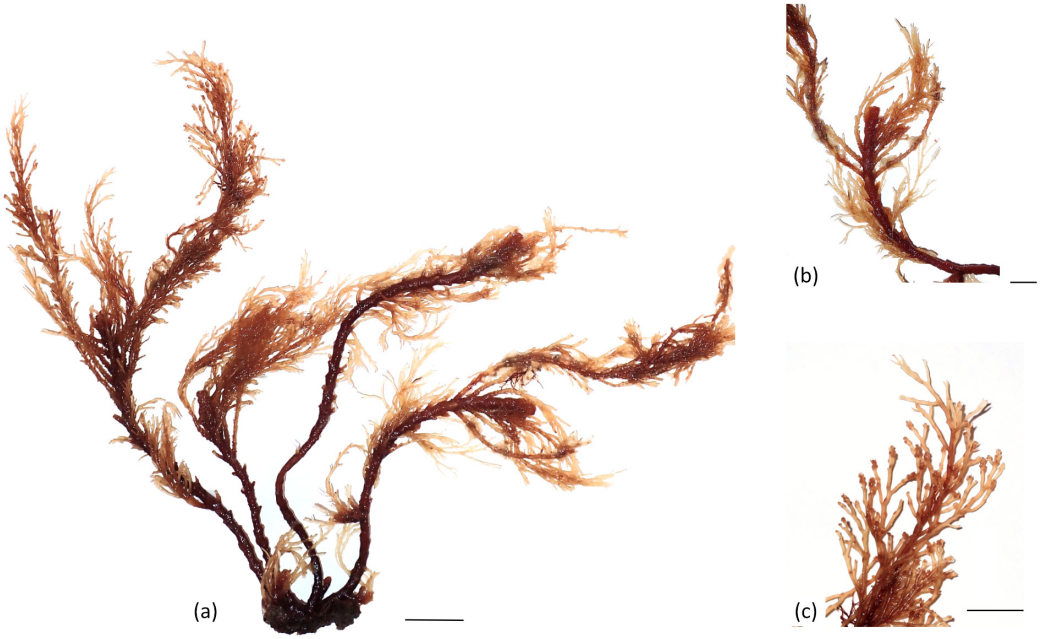


Figure 12. *Cystoseira crinitophylla*: (**a**) habit of the thallus; (**b**) details of the apex; (**c**) details of the receptacles. Scale bars = 1 cm.

3.4.5. ***Cystoseira foeniculacea*** (Linnaeus) Greville **f. *foeniculacea* (Figure 13)**

Synonyms: *Fucus foeniculaceus* Linnaeus; *Abrotanifolia foeniculacea* (Linnaeus) Stackhouse; *Fucus concatenatus* Linnaeus; *Fucus abrotanifolius* Linnaeus; *Fucus barbatus* Linnaeus; *Fucus discors* Linnaeus; *Abrotanifolia discors* (Linnaeus) Stackhouse; *Abrotanifolia loeflingii* Stackhouse; *Phryganella abrotanifolia* (Linnaeus) Stackhouse; *Phryganella concatenata* (Linnaeus) Stackhouse; *Phryganella discors* (Linnaeus) Stackhouse; *Cystoseira concatenata* (Linnaeus) C.Agardh; *Cystoseira abrotanifolia* (Linnaeus) C.Agardh; *Cystoseira discors* (Linnaeus) C.Agardh; *Phyllacantha concatenata* (Linnaeus) Kützing; *Cystoseira macrocarpa* Kützing; *Cystoseira abrotanifolia var. macrocarpa* (Kützing) De Toni.

Morphology: Thallus caespitose, 20–30 cm high, light to dark brown, not iridescent, attached to the substrate by an irregular discoid holdfast. Axes and primary branches are typically covered with small spines. Apex spinose slightly protruding from the insertion of the primary branches. Primary branches are flattened with distichous secondary ramifications or cylindrical with alternating secondary ramifications on different planes. Aerocysts present or absent, depending on the season.

Reproductive morphology: Receptacles, simple or bifurcated, fusiform and provided with a sterile peduncle at maturity.

Habitat: Grows on rocky substrates in the upper infralittoral zone, extending to a depth of 10 m. It is frequently found in infralittoral rock pools.

Distribution: Mediterranean Sea: Spain, Greece, Italy, Adriatic Sea, France, Israel, Turkey, Balearic Islands, Corsica, Morocco, Tunisia, Algeria, Cyprus, Levant Basin, and Syria.

Atlantic Ocean: France, Spain, Portugal, Madeira, Azores, Canary Islands, Cape Verde, Salvage Islands, Senegal, Western Sahara, Mauritania, Morocco, Britain, Channel Islands, Ireland, and the Netherlands.

Identity confusion: It cannot be confused with other species.

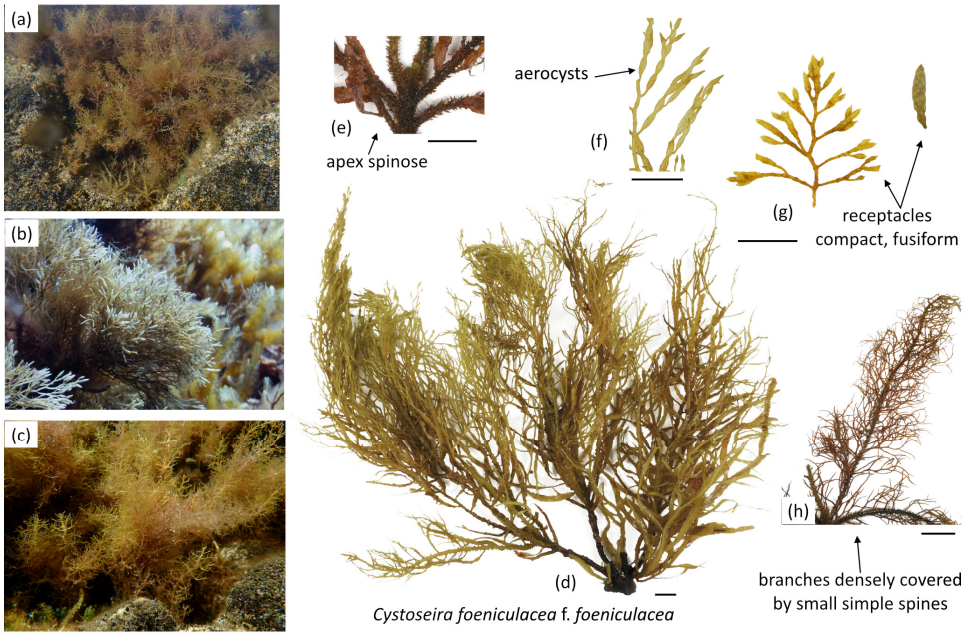


Figure 13. *Cystoseira foeniculacea* f. *foeniculacea*: (**a**–**c**) thalli in their habitat; (**d**) habit of the thallus; (**e**) details of the apex (Scale bar = 1 cm); (**f**) details of the aerocysts (Scale bar = 1 cm); (**g**) details of the receptacles (Scale bar = 0.5 cm); (**h**) details of the branches covered by small spines (Scale bar = 1 cm).

3.4.6. ***Cystoseira foeniculacea* f. *latiramosa*** (Ercegović) A. Gómez Garreta, Barceló, Ribera et Rull Lluch **(Figure 14a–c)**

Synonyms: *Cystoseira discors* (Linnaeus) C. Agardh subsp. *latiramosa* Ercegović; *Cystoseira ercegovicii* Giaccone f. *latiramosa* (Ercegović) Giaccone; *Cystoseira schiffneri* Hamel f. *latiramosa* (Ercegović) Giaccone.

Morphology: All branches are flattened, with a central midrib and toothed margins. Branching is sparse and distichous-alternate. Aerocysts absent.

Habitat: Epilithic, in the lower infralittoral zone.

Distribution: Mediterranean Sea: Greece, Italy, Adriatic Sea, Sardinia, Sicily, Malta, France, Corsica, Cyprus, Turkey, and Tunisia.

Identity confusion: It cannot be confused with other species.

3.4.7. ***Cystoseira foeniculacea* f. *tenuiramosa*** (Ercegović) A. Gómez Garreta, M.C.Barceló, M.A.Ribera & J.Rull Lluch **(Figure 14d,e)**

Synonyms: *Cystoseira discors* f. *tenuiramosa* Ercegović; *Cystoseira ercegovicii* f. *tenuiramosa* (Ercegović) Giaccone; *Cystoseira schiffneri* f. *tenuiramosa* (Ercegović) Giaccone.

Morphology: All branches are cylindrical; branching is sparse and alternate, ultimate branches filiform. Aerocysts absent.

Habitat: Epilithic, in the upper infralittoral zone up to 10 m depth.

Distribution: Mediterranean Sea: Balearic Islands, Italy, Adriatic Sea, Sardinia, Sicily, Cyprus, Turkey, Greece, France, Corsica, Slovenia, Spain, and Tunisia.

Identity confusion: It cannot be confused with other species.

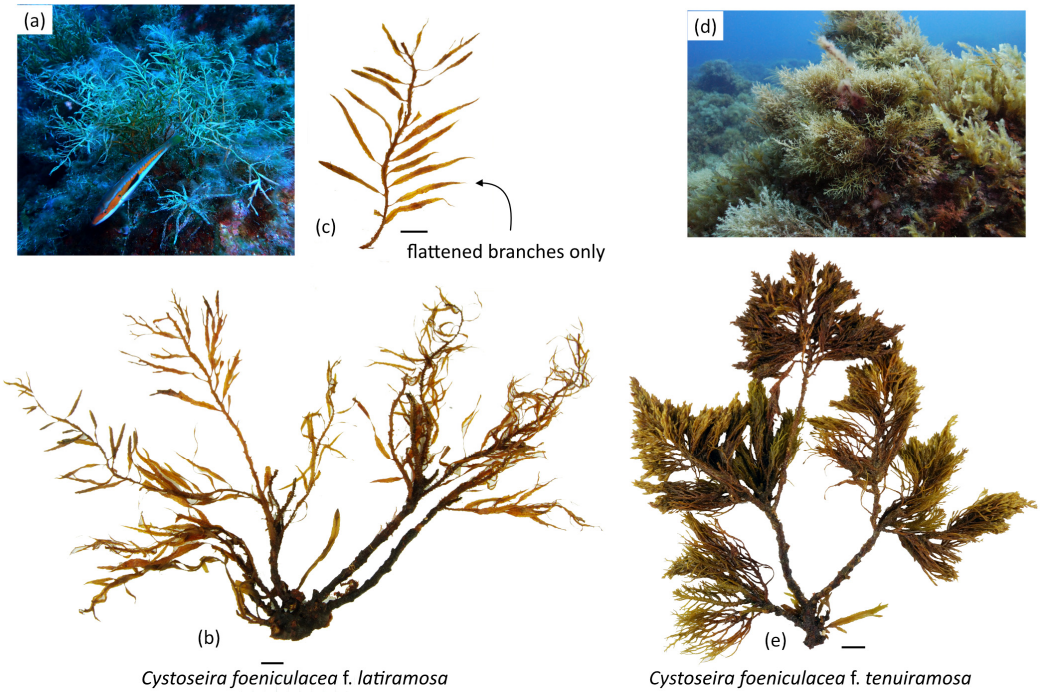


Figure 14. *Cystoseira foeniculacea* f. *latiramosa* (**a**–**c**): (**a**) thallus in its habitat; (**b**) habit of the thallus; (**c**) details of the apex; *Cystoseira foeniculacea* f. *tenuiramosa* (**d**,**e**): (**d**) thallus in its habitat; (**e**) habit of the thallus. Scale bars = 1 cm.

3.4.8. (*) ***"Cystoseira" jabukae*** Ercegović **(Figure 15)**

Morphology: Thallus non-caespitose, light olive-brown with a slight iridescence in situ; discoid basal holdfast, up to 2.5 cm in diameter; trunk-like axis, long and slender, up to 16 (–40) cm high and 0.2–0.5 (–1) cm in diameter, generally simple or with a lateral secondary axis. Spiny apex provided with a crown of young tophules. Primary branches thin, long, cylindrical; ultimate branches very slender, 0.2 mm in diameter; all branches smooth or sometimes with few simple and small spiniform ultimate branchlets. Tophules warty to smooth-tuberculated, arranged radially all along the axis and pressed against it. Aerocysts absent; cryptostomata spaced.

Reproductive morphology: Receptacles are diffuse, terminal, cylindrical, and markedly elongate, reaching up to 75 mm × 0.3–0.5 mm. They are loosely branched and may appear smooth or may bear conspicuous spiny appendages.

Habitat: Epilithic, in the lower infralittoral zone up to 35–50 m depth.

Distribution: Mediterranean Sea: Adriatic Sea, Italy, Sardinia, Corsica, and France.

Identity confusion: Frequently confused with *Ericaria funkii*, from which it is distinguished by the long, slender, trunk-like axis (up to 40 cm) with tophules pressed (appressed) against it.

Remarks: Verlaque et al. [35] regard *Cystoseira jabukae* as a separate species from *Ericaria funkii* (as *C. funkii).* Instead, Cormaci et al. [33] treat *C. jabukae* as a synonym of *Cystoseira spinosa* Sauvageau v. *tenuior* (Ercegović) Cormaci et al. [= *Gongolaria montagnei* var. *tenuior* to which also Guiry & Guiry [5], refer *C. jabukae*]. Following Verlaque et al. [35], we prefer to keep this taxon distinct pending specific molecular studies.

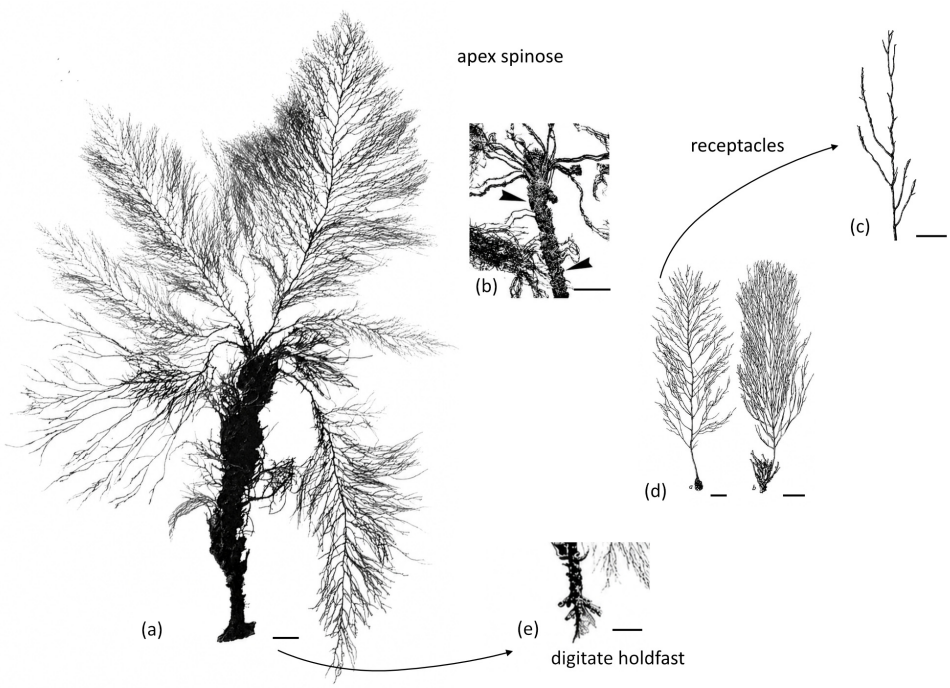


Figure 15. *"Cystoseira" jabukae*: (**a**) habit of the thallus (Scale bar = 1 cm); (**b**) details of the apex (Scale bar = 1 cm); (**c**) details of the receptacles (Scale bar = 0.5 cm); (**d**) details of the branches (Scale bar = 1 cm); (**e**) details of the holdfast (Scale bar = 1 cm) (modified from Verlaque et al. [35]).

3.4.9. (*) ***"Cystoseira" micheleae*** Verlaque, Blanfuné, Boudouresque, Thibaut & Sellam **(Figure 16)**

Replaced synonym: *Cystoseira granulata* (Linnaeus) C. Agardh var. *turneri* Montagne.

Morphology: Thallus non-caespitose, arising from a robust discoid holdfast; axis single or occasionally branched. Apex not prominent and generally surrounded by ovoid tophules from spiny to smooth-tuberculate with age. Primary branches of two different types: either slightly complanate with an inconspicuous midrib and irregularly alternately branched in one plane, or cylindrical and branched in all directions, with spaced simple to bifid spine-like branchlets. The habit varies with depth: shallow specimens have cylindrical branches while the deeper ones have complanate branches. Cryptostomata scattered along branches.

Reproductive morphology: Receptacles basal and intercalary near the tophules, as well as terminal on branchlets.

Habitat: Epilithic, in the infralittoral zone between 10 and 25 m depth.

Distribution: Mediterranean Sea: Algeria and Sicily. Some reports previously attributed to *Gongolaria montagnei* may represent misidentifications, indicating that the distribution of *C. micheleae* could be wider.

Identity confusion: It closely resembles *Gongolaria montagnei*, from which differs either in the tophules becoming tuberculate with age or the position of receptacles, which are basal and intercalary (near the tophules) as well as terminal.

Remarks: Originally described by Montagne [36] from Algeria as *C. granulata* var. *turneri* Montagne, this taxon was elevated to species rank by Sellam et al. [37] as *Cystoseira michaeleae* "*michelae*" Verlaque et al. new name, due to the existence of *C. turneri* (Yendo) Roberts. Earlier records of *G. montagnei* may represent misidentifications.

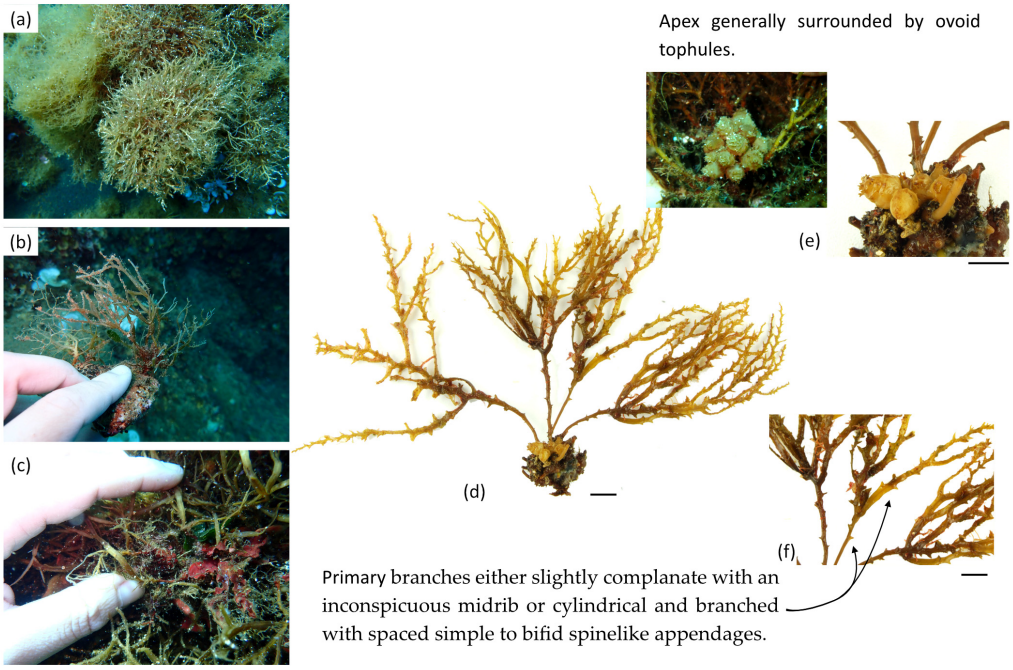


Figure 16. *"Cystoseira" micheleae*: (**a**–**c**) thallus in its habitat; (**d**) habit of the thallus (Scale bar = 1 cm); (**e**) details of the apex (Scale bar = 5 mm); (**f**) details of the primary branches and spine-like branchlets (Scale bar = 1 cm).

3.4.10. (*) ***"Cystoseira" pelagosae*** Ercegović **(Figure 17)**

Morphology: Thallus caespitose, erect, pale-yellow up to 30 cm high, non-iridescent in situ; axes simple, trunk-like, club-shaped, covered with small spines, 16 cm × 2–5 mm, arising from a small and breakable basal holdfast; protruding apex, truncated, rounded and densely spiny, primary branches spaced, 16–20 cm long, cylindrical, covered with small spines in their lower third and with a persistent base 1.0–1.5 cm long; secondary branches arranged radially, 3–4 cm long, quickly compressed to flattened, with a faint midrib, and with irregular branching in one plane; sparse short spiniform ultimate branchlets, triangular with a wide base, simple, rarely bifid; protruding sparse cryptostomata; tophules absent; aerocysts absent. Young thalli often consist of single axes giving a non-caespitose habit.

Reproductive morphology: Terminal receptacles, small, compact, tuberculated and spiny, a few mm to 1 cm long; axial conceptacles in the base of the spiniform ultimate branchlets.

Habitat: Epilithic, in the infralittoral zone up to 15 m depth.

Distribution: Mediterranean Sea: Adriatic Sea, Italy, Sardinia, and Sicily.

Identity confusion: It cannot be confused with other species.



Figure 17. *"Cystoseira" pelagosae*: (**a**) habit of the thallus; (**b**) details of the apex. Scale bars = 1 cm.

3.4.11. ***Cystoseira pustulata*** (Ercegović) Neiva & Serrão **(Figure 18)**

Synonyms: *Cystoseira abrotanifolia* subsp. *pustulata* Ercegović, *Cystoseira compressa* subsp. *pustulata* (Ercegović) Verlaque, *Cystoseira compressa* var. *pustulata* Ercegović *ex* Verlaque *nom. inval.*

Morphology: Thallus caespitose, delicate and slender, attached to the substrate by a small discoid holdfast. Apex smooth and not prominent. Primary branches cylindrical to slightly flattened with an alternate-distichous arrangement. Higher-order branches cylindrical and slender. The thallus surface is densely covered by prominent cryptostomata, conferring a characteristic pustulate appearance. Aerocysts present or absent.

Reproductive morphology: Tiny, fusiform, to lanceolate receptacles.

Habitat: Epilithic, in the subtidal zone, up to 20 m depth.

Distribution: Mediterranean Sea: Adriatic Sea, Sicily, Balearic Islands, France, Corsica, and Tunisia. **Atlantic**: Macaronesia [31].

Identity confusion: Possible confusion with *Cystoseira humilis* Schousboe *ex* Kützing, from which it is distinguished by the pustulate appearance caused by densely arranged and prominent cryptostomata.

Remarks: According to Neiva et al. [31] *C. humilis* is distributed in the Atlantic Ocean, and Mediterranean records may represent misidentifications referring to *C. pustulata*. Further molecular analyses are required to clarify its taxonomic position. The presence of *Cystoseira humilis* var. *myriophylloides* (Sauvageau) J. H. Price & D. M. John in the Mediterranean also needs to be confirmed pending further molecular investigations.

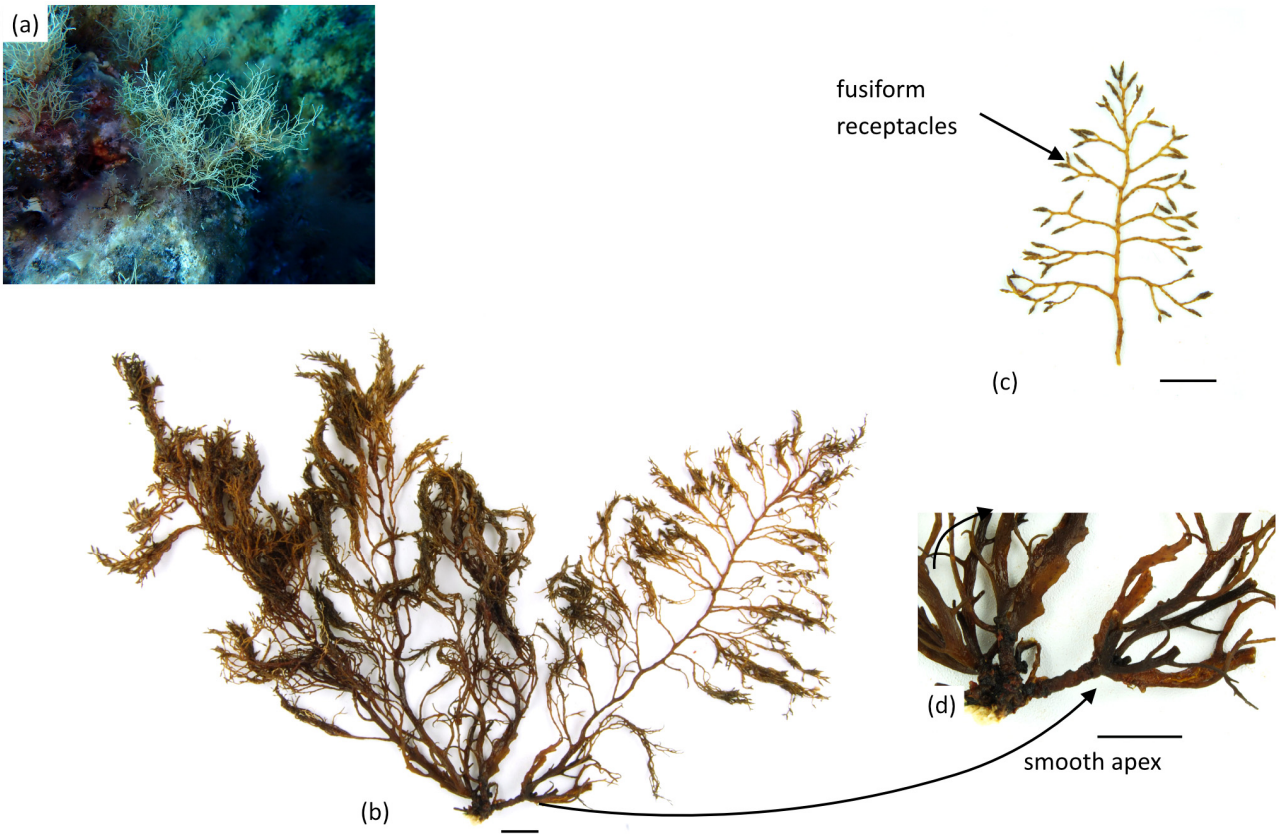


Figure 18. *Cystoseira pustulata*: (**a**) thallus in its habitat; (**b**) habit of the thallus (Scale bar = 1 cm); (**c**) details of the receptacles (Scale bar = 0.5 cm); (**d**) details of the apex (Scale bar = 1 cm).

3.4.12. (*) ***Ericaria amentacea*** (C.Agardh) Molinari & Guiry **(Figure 19)**

Synonyms: *Cystoseira ericoides* (Linnaeus) C. Agardh *var. amentacea* C. Agardh; *Cystoseira amentacea* (C. Agardh) Bory; *Halerica amentacea* (C. Agardh) Kützing; *Gongolaria amentacea* (C. Agardh) Kuntze; *Carpodesmia amentacea* (C. Agardh) Orellana & Sansón; *Cystoseira amentacea* var. *spicata* (Ercegović) Giaccone; *Cystoseira amentacea var. stricta* Montagne; *Cystoseira spicata* Ercegović; *Cystoseira spicata* ssp. *crassa* Ercegović; *Cystoseira spicata* ssp. *elegans* Ercegović; *Cystoseira stricta* (Montagne) Sauvageau; *Cystoseira stricta var. amentacea* (Bory) Giaccone.

Morphology: Thallus caespitose, numerous axes originating from a single anchoring structure formed by the confluence of the prostrate parts tenaciously adhering to the substrate. Primary branches cylindrical. Higher-order branches densely covered by short spiniform ultimate branchlets. Cryptostomata numerous. Apex spinose and not very prominent.

Reproductive morphology: Receptacles terminal, compact, cylindrical-tuberculate, spinose and attenuated at the base.

Habitat: Epilithic, in the upper infralittoral zone.

Distribution: **Mediterranean Sea:** Spain, Balearic Islands, France, Corsica, Greece, Italy, Apulia, Sicily, Adriatic Sea, Malta, Cyprus, Turkey, Levant Basin, Lebanon, Syria, Morocco, Tunisia, Algeria, Libya, and Egypt.

Identity confusion: Possible confusion with *E. mediterranea*, from which it is distinguished by the caespitose habit (multiple axes arising from a confluent, prostrate base) and the shorter, denser spinose branchlets.

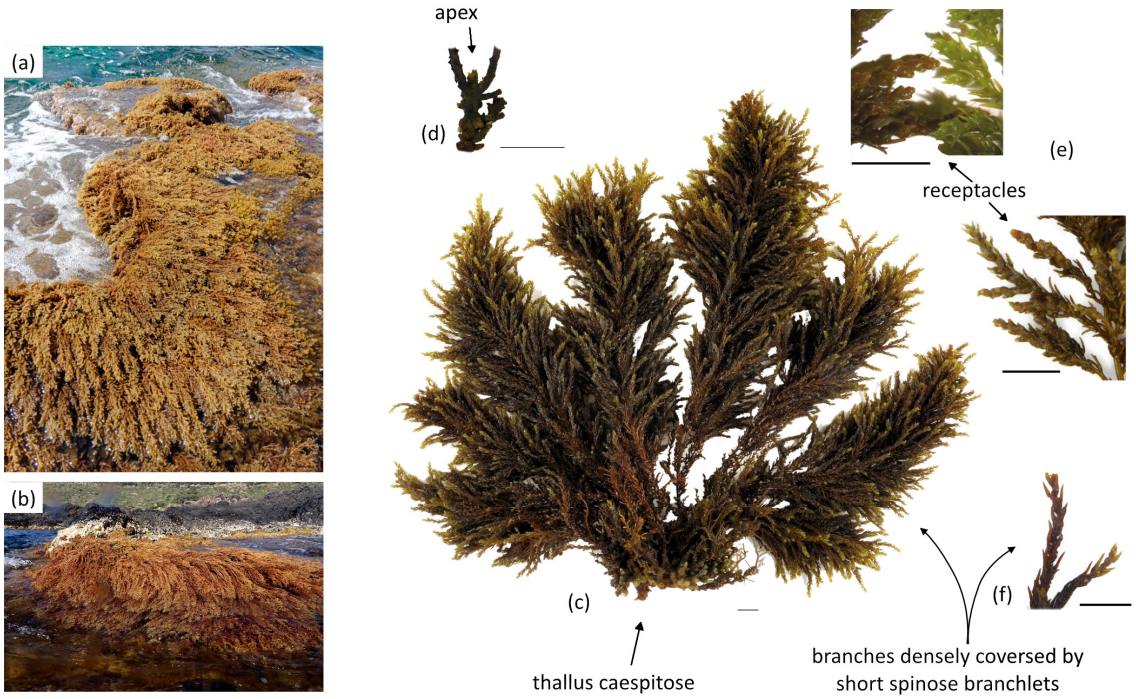


Figure 19. *Ericaria amentacea*: (**a**,**b**) thalli in their habitat; (**c**) habit of the thallus; (**d**) details of the apex; (**e**) details of the receptacles; (**f**) details of spinose branchlets. Scale bars = 1 cm.

3.4.13. (*) ***Ericaria balearica*** (Sauvageau) Neiva, Ballesteros & Serrão **(Figure 20)**

Synonyms: *Cystoseira balearica* Sauvageau; *Cystoseira brachycarpa* var. *balearica* (Sauvageau) Giaccone.

Morphology: Thallus caespitose with an irregular, spreading holdfast giving rise to multiple cylindrical and knotty axes, due to the basal stumps of deciduous branches. In situ, the thallus exhibits a marked dark blue-green iridescence, particularly on the apical branchlets. Apices non-prominent, bearing spinose appendages. Primary branches cylindrical, with spiniform appendages only in the basal portions; higher-order branches cylindrical and entirely non-spinose.

Reproductive morphology: Receptacles are diffuse, 3–10 mm long, and occasionally terminal in position.

Distribution: Mediterranean Sea: Balearic Islands, Spain, Isla de Alborán, France, Corsica, Italy, Sicily, Malta, Tunisia, Algeria, Libya, and Greece.

Habitat: Epilithic, in the infralittoral zone from 0.5 to 25 m of depth.

Identity confusion: It is morphologically similar to *E. brachycarpa*, from which it is recognised in situ by the marked dark blue-green iridescence. It is further distinguished by the presence of spinose appendages only in the basal part of primary branches, while higher-order branches remain entirely smooth.

Remarks: According to Neiva et al. [31] *E. balearica* and *E. brachycarpa* are two cryptic species with different biogeographical distribution.

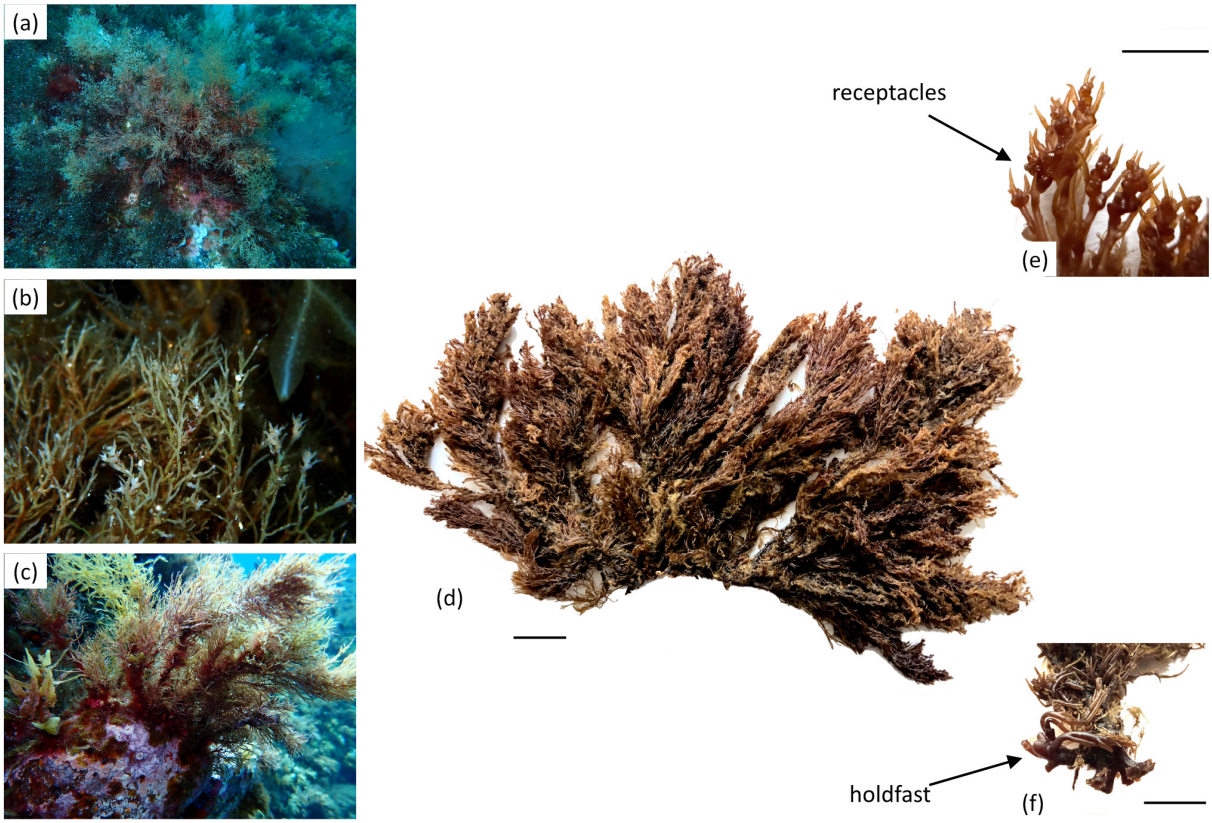


Figure 20. *Ericaria balearica*: (**a**–**c**) thalli in their habitat; (**d**) habit of the thallus; (**e**) details of the receptacles; (**f**) details of the holdfast. Scale bars = 1 cm.

3.4.14. (*) ***Ericaria barbatula*** (Kützing) Molinari & Guiry **(Figure 21)**

Synonyms: *Cystoseira barbatula* Kützing; *Carpodesmia barbatula* (Kützing) Orellana & Sansón; *Cystoseira graeca* Schiffner *ex* Gerloff & Nizamuddin.

Morphology: Thallus caespitose, attached to the substrate by an irregular basal disc, from which several thin, cylindrical and blackish axes take origin. The axes are tuberculate due to the presence of basal stumps of the fallen primary branches. The apices are strongly prominent and smooth. Primary and higher-order branches are cylindrical.

Reproductive morphology: The receptacles are borne on the apical parts of branchlets and are compact and tuberculate; they can bear 1–2 spinose appendages.

Habitat: Epilithic, in the upper infralittoral zone from 0.5 to 3 m of depth.

Distribution: Mediterranean Sea: Greece, Crete, Cyprus, Turkey, Levant Basin, Italy, Sicily, Malta, and Tunisia.

Identity confusion: Distinguished from *E. giacconei* by its strongly prominent and smooth apices (≥1 cm). It differs from *E. crinita* by the smooth (non-spinose) apex and from *C. crinitophylla* by the total absence of spiny branchlets.

Remarks: According to Neiva et al. [31], this entity falls within the *Ericaria crinita* complex, which includes specimens identified as *E. crinita*, *E. barbatula*, and *E. giacconei*. Further molecular analyses are required to clarify its taxonomic position.

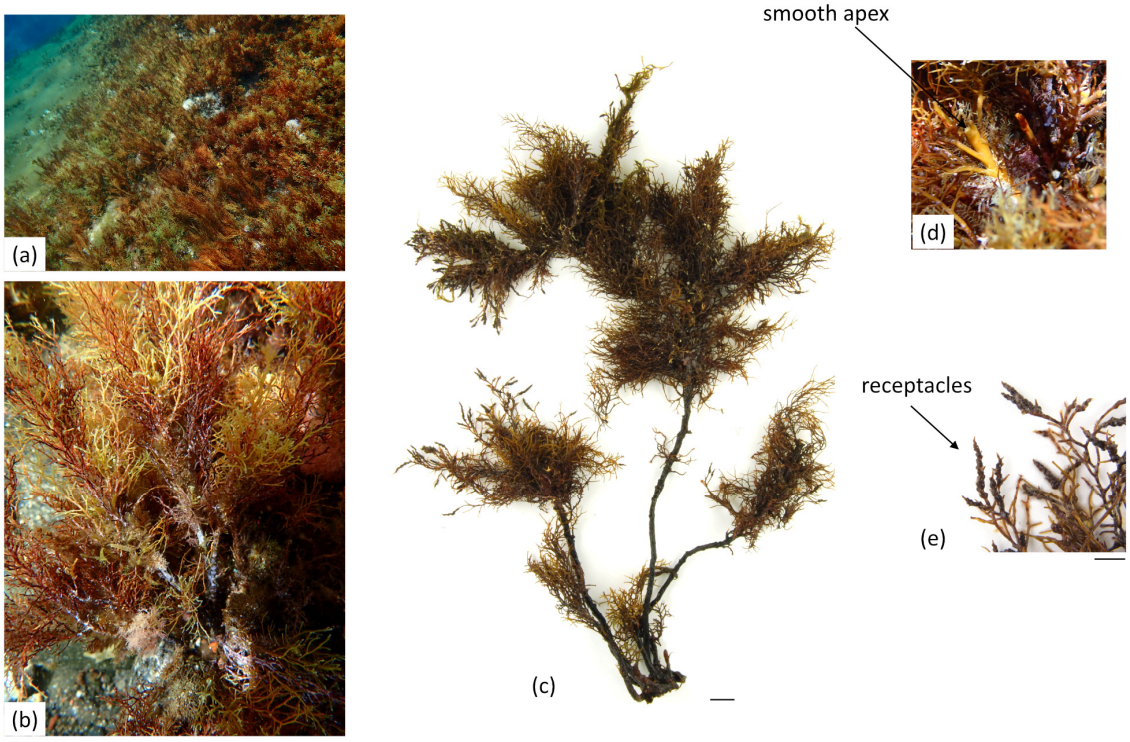


Figure 21. *Ericaria barbatula*: (**a**,**b**) thalli in their habitat; (**c**) habit of the thallus (Scale bar = 1 cm); (**d**) details of the apex; (**e**) details of the receptacles (Scale bar = 0.5 cm).

3.4.15. (*) ***Ericaria brachycarpa*** (J. Agardh) Molinari & Guiry **var. *brachycarpa* (Figure 22)**

Synonyms: *Cystoseira brachycarpa* J. Agardh, *Carpodesmia brachycarpa* (J. Agardh) Orellana & Sansón; *Cystoseira caespitosa* Sauvageau; *Carpodesmia caespitosa* (Sauvageau) Ballesteros & Mariani.

Morphology: Thallus caespitose, up to 20 cm high, attached to the substrate by an irregular basal disc and haptera. Apex of axes smooth, not prominent, surrounded by cylindrical appendages. The branches are both cylindrical and spiniform. Tophules and aerocysts absent.

Reproductive morphology: Receptacles loosely compact, protruding from the base of the spiny branches.

Habitat: Epilithic, in the upper infralittoral zone.

Distribution: Mediterranean Sea: Spain, Balearic Islands, France, Corsica, Greece, Italy, Sardinia, Sicily, Algeria, Tunisia, Morocco, Cyprus, Turkey, and Syria.

Identity confusion: Morphologically similar to *E. balearica*, it is further distinguished by having branches that are both cylindrical and spiniform.

Remarks: According to Neiva et al. [31], *E. brachycarpa* and *E. balearica* are two cryptic species with different biogeographical distribution. Further molecular analyses are required to clarify their taxonomic position.

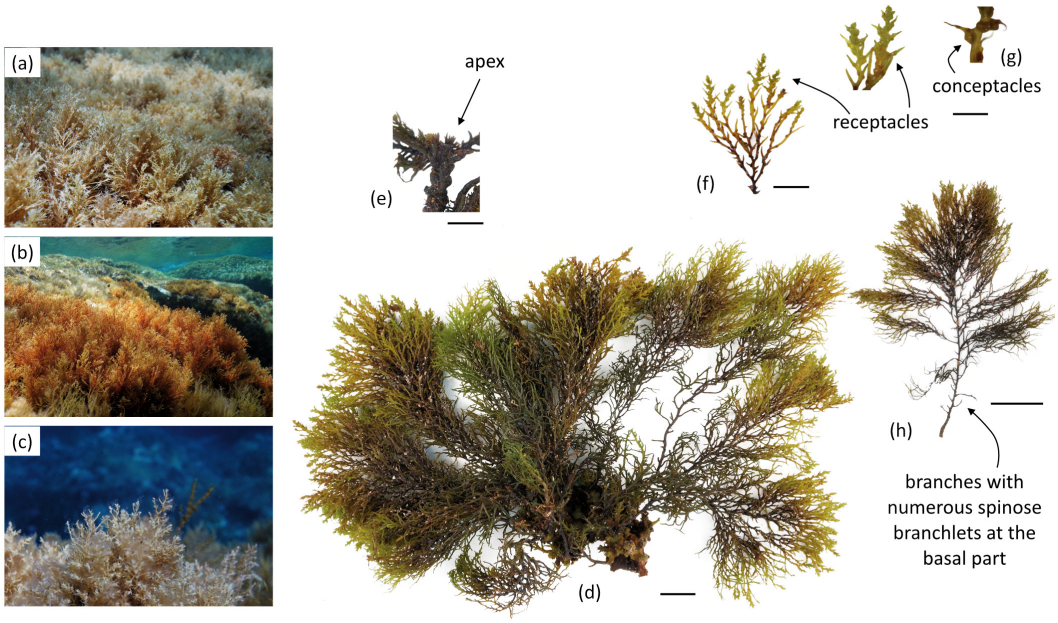


Figure 22. *Ericaria brachycarpa* var. *brachycarpa*: (**a**–**c**) thalli in their habitat; (**d**) habit of the thallus (Scale bar = 1 cm); (**e**) details of the apex (Scale bar = 0.5 cm); (**f**) details of the receptacles (Scale bar = 0.5 cm); (**g**) details of the conceptacles (Scale bar = 0.2 cm); (**h**) details of the primary branches (Scale bar = 1 cm).

3.4.16. ***Ericaria brachycarpa* var. *claudiae*** Boudouresque, Perret-Boudouresque & Blanfuné **(Figure 23)**

with hemitophules (swellings at the base of primary branches) spinose.

Synonyms: *Cystoseira balearica* var. *claudiae* Giaccone [*nom. inval.*];
Cystoseira brachycarpa var. *claudiae* Giaccone [*comb. inval.*]

Distribution: Mediterranean Sea: Spain, Balearic Islands, Italy, Sicily, France, and Tunisia.

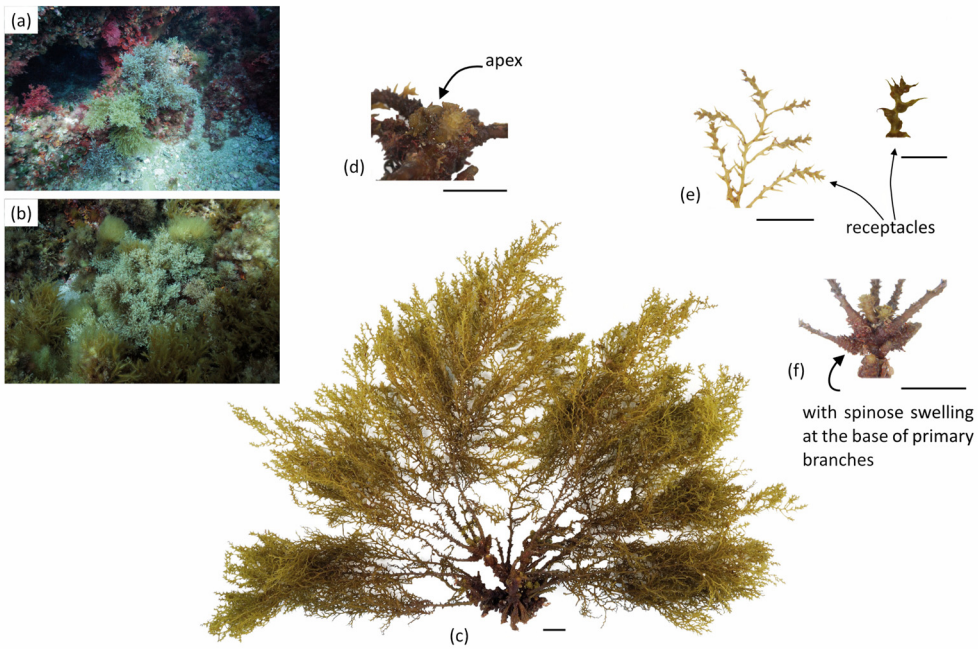


Figure 23. *Ericaria brachycarpa* var. *claudiae*: (**a**,**b**) thalli in their habitat; (**c**) habit of the thallus (Scale bar = 1 cm); (**d**) details of the apex (Scale bar = 0.5 cm); (**e**) details of the receptacles (Scale bar = 1 cm) and conceptacles (Scale bar = 0.5 cm); (**f**) details of the tophules (Scale bar = 1 cm).

3.4.17. ***Ericaria corniculata*** (Turner) Neiva & Serrão **(Figure 24)**

Synonyms: *Fucus ericoides* Linnaeus var. *corniculatus* Turner, *Cystoseira corniculata* (Turner) Zanardini, *Cystoseira corniculata* f. *clydonophila* Cormaci, G. Furnari, Giaccone, Scammacca & Serio *nom. inval.*, *Cystoseira corniculata* subsp. *divergens* Ercegović, *Cystoseira corniculata* var. *divergens* (Ercegović) Antolić & Span, *Cystoseira corniculata* f. *imperfecta* Ercegović, *Cystoseira corniculata* subsp. *laxior* Ercegović, *Cystoseira corniculata* var. *laxior* (Ercegović) Antolić & Span, *Halerica ericoides* var. *corniculata* (Turner) Kützing.

Morphology: Creeping, olive-brown to olive-green species, non-iridescent in situ, with stoloniferous axes 1–4 mm wide, branched at right angles, intertwined and anchored by haptera; vertical cylindrical primary branches 5–14 cm long near the surface and 14–21 cm below 30 m; secondary branches cylindrical or flattened, progressively shorter. All branch orders bear spines and imbricated bifid–multifid short spiniform ultimate branchlets, often palmate or "staghorn"-like; tophules absent; cryptostomata present; aerocysts absent.

Reproductive morphology: Terminal diffuse receptacles (0.2–2 cm); conceptacles at base of spiniform ultimate branchlets.

Habitat: Epilithic, in the infralittoral zone, hard bottoms, from wave-exposed to calm conditions, 0–50 (–70) m depth; in coastal lagoons too.

Distribution: Mediterranean Sea: Balearic Islands, Corsica, Adriatic Sea, Italy, Sardinia, Greece, Libya, Tunisia, Cyprus, Levant Basin, and Turkey. Tethyan relict with disjunct Mediterranean–Northern Indian Ocean distribution; western Mediterranean reports remain doubtful [30].

Identity confusion: It cannot be confused with other species.

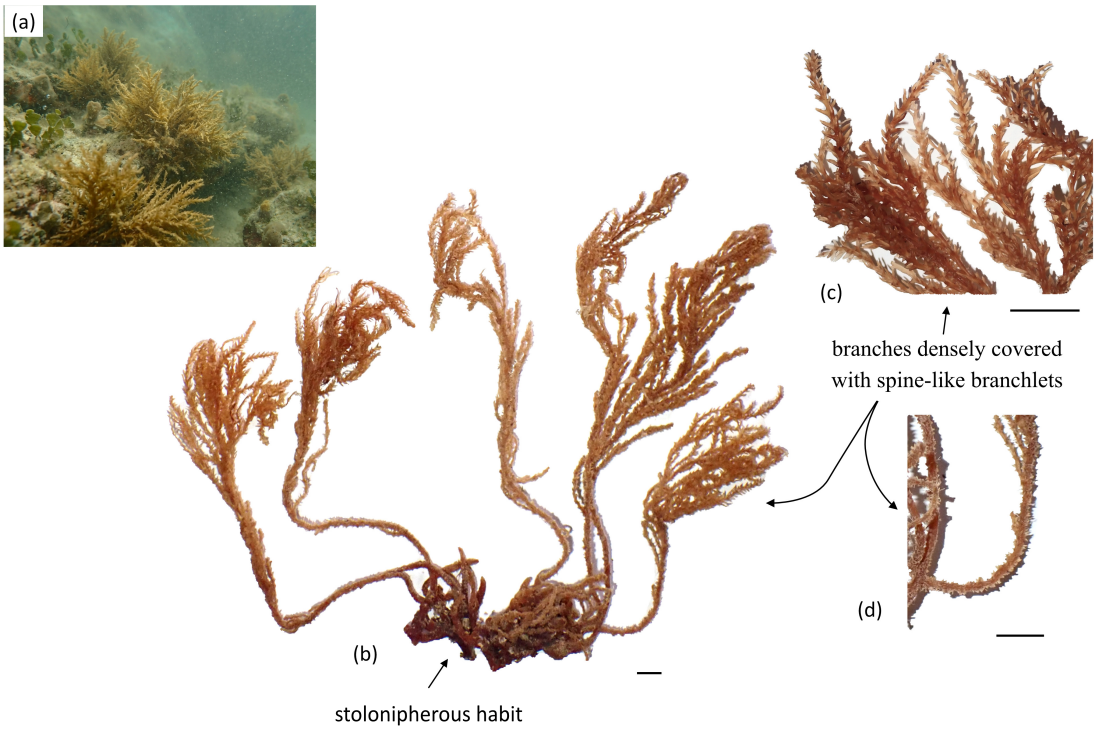


Figure 24. *Ericaria corniculata*: (**a**) thalli in their habitat; (**b**) habit of the thallus; (**c**,**d**) details of the branches. Scale bars = 1 cm.

3.4.18. (*) ***Ericaria crinita*** (Duby) Molinari & Guiry **(Figure 25)**

Synonyms: *Cystoseira crinita* Duby, *Carpodesmia crinita* (Duby) Orellana & Sansón, *Cystoseira granulata* Schousboe, *Gongolaria crinita* Kuntze.

Morphology: Thallus caespitose, arising from a thin basal crust from which several cylindrical, slender, and dark coloured axes originate. The axes are cylindrical, generally

devoid of branches in their lower third and exhibiting a blackish-brown pigmentation. Primary branches are cylindrical, with spinose appendages at their base, whereas higher-order branches are likewise cylindrical, very slender, and without spinose branchlets. The apex of the primary axis is conspicuously prominent and bears well-developed spines.

Reproductive morphology: Receptacles terminal, compact, and clearly differentiated, cylindrical to cylindrical-oval or cylindrical-lanceolate in shape.

Habitat: Epilithic, in the upper infralittoral zone.

Distribution: Mediterranean Sea: Spain, Balearic Islands, Adriatic Sea, Croatia, Corsica, France, Greece, Italy, Sicily, Algeria, Libya, Syria, Morocco, Tunisia, Cyprus, Egypt, Levantine Basin, Turkey, and Crete. **Atlantic Ocean:** Canary Islands and Morocco.

Identity confusion: It is distinguished from *E. barbatula* and *E. giacconei* by the conspicuously prominent and spinose apex. It is further separated from *C. crinitophylla* by its blackish-brown lower axes and the complete absence of spinose branchlets on primary and higher-order branches.

Remarks: According to Neiva et al. [31], this entity falls within the *Ericaria crinita* complex, which includes specimens identified as *E. crinita*, *E. barbatula*, and *E. giacconei*. Further molecular analyses are required to clarify its taxonomic position.

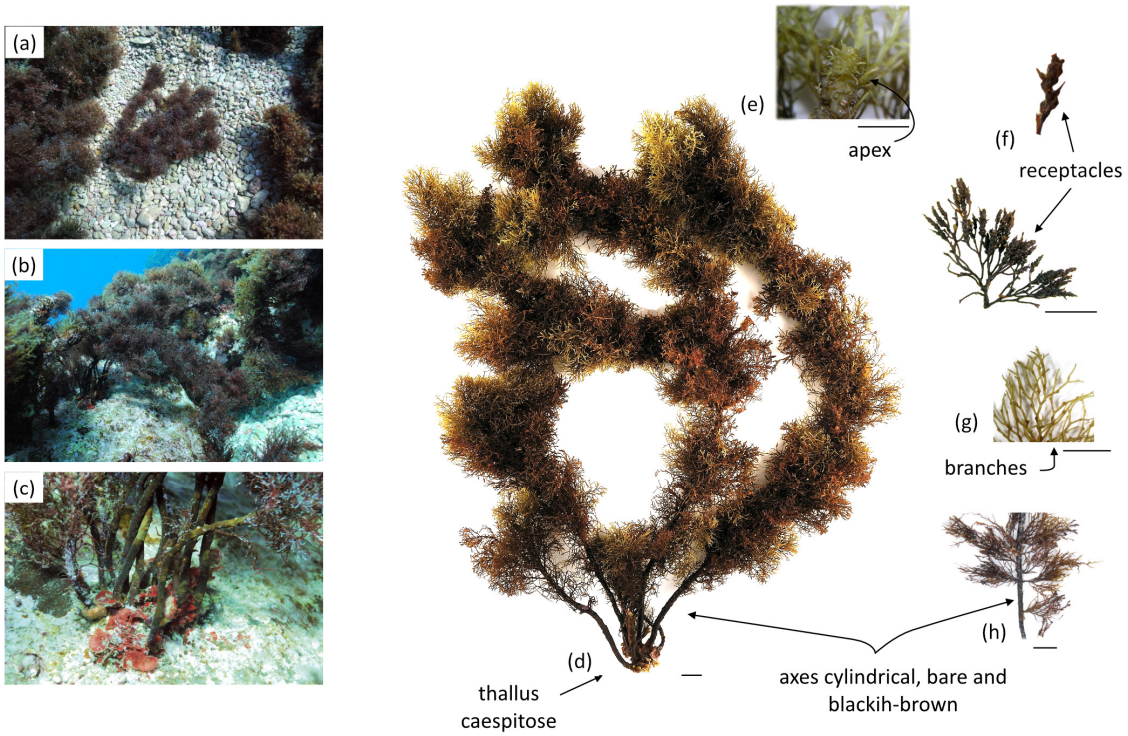


Figure 25. *Ericaria crinita*: (**a**,**b**) thalli in their habitat; (**c**) details of the holdfast in the field; (**d**) habit of the thallus (Scale bar = 1 cm); (**e**) details of the apex (Scale bar = 0.5 cm); (**f**) details of the receptacles (Scale bar = 0.5 cm); (**g**) details of the branchlets (Scale bar = 1 cm); (**h**) details of the axis (Scale bar = 1 cm).

3.4.19. (*) ***Ericaria dubia*** (Valiante) Neiva & Serrão **(Figure 26)**

Synonyms: *Cystoseira dubia* Valiante; *Cystoseira fucoides* Ercegović.

Morphology: Thallus non-iridescent, yellowish-brown, with a stoloniferous primary axis, branched into secondary axes. The apex is smooth, protruding, and occasionally slightly swollen. Primary branches are distichous, erect, and divided into two distinct portions: a proximal cylindrical or slightly fusiform part, and a distal strongly flattened, ribbon-like part (4–6 mm wide, 0.5 mm thick). The distal portion is subdichotomously

branched with entire margins, characterised by a prominent median midrib and covered with non-protruding cryptostomata.

Reproductive morphology: The conceptacles are scattered on both sides of the sub-apical section of the lamina, either isolated or, more rarely, in small contiguous groups of 3–4 (rarely more).

Habitat: Epilithic, on bottoms characterised by high sedimentation in the upper circalittoral zone.

Distribution: Mediterranean Sea: Adriatic Sea, Greece, Italy, Sicily, Tunisia, Israel, Levant Basin, Syria, and Turkey.

Identity confusion: It cannot be confused with other species.

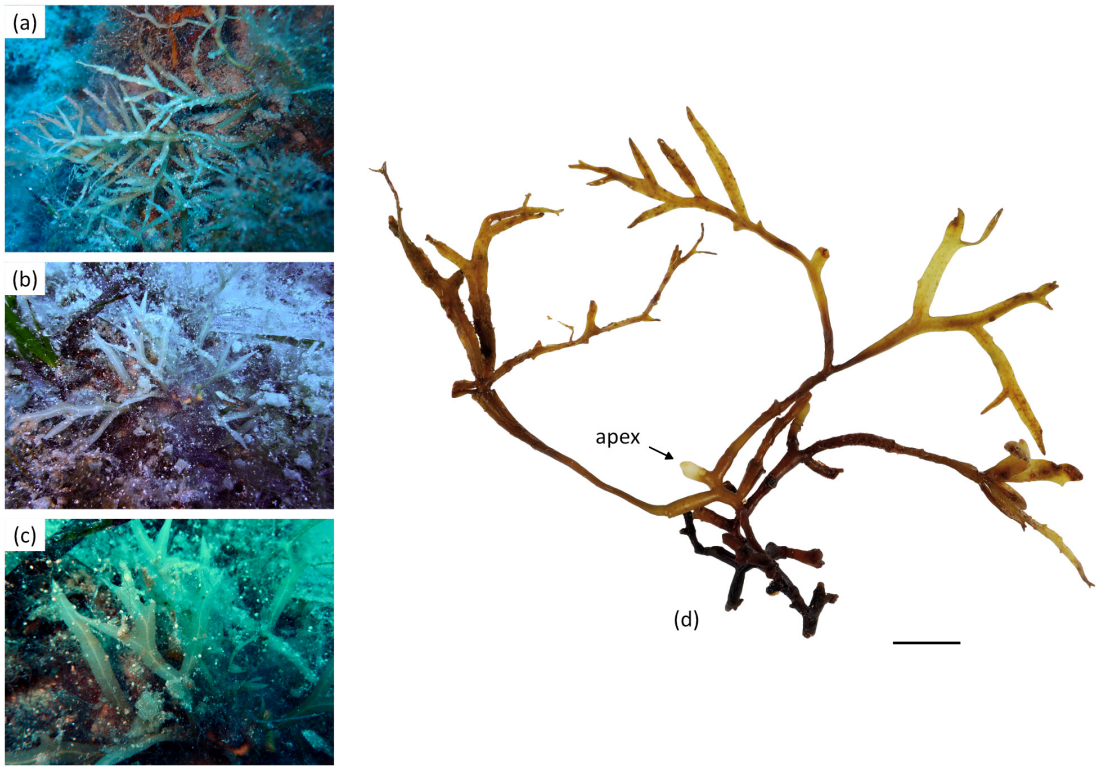


Figure 26. *Ericaria dubia*: (**a**–**c**) thalli in their habitat; (**d**) habit of the thallus (Scale bar = 1 cm).

3.4.20. (*) ***Ericaria funkii*** (Gerloff & Nizamuddin) Molinari & Guiry **(Figure 27)**

Synonyms: *Cystoseira funkii* Schiffner *ex* Gerloff & Nizamuddin, *Carpodesmia funkii* (Schiffner *ex* Gerloff & Nizamuddin) Orellana & Sansón.

Morphology: Thallus non-caespitose, 30–40 cm high, with greenish iridescence, fixed to the substrate by deeply digitate holdfast with branched haptera. Axis up to 8–10 cm high, abundantly and radially branched near the base with large, warty-spiny tophules, spaced and divaricate along the axis, giving the axis a coralloid appearance. Smooth apex. Higher-order branches provided with ultimate spiniform branchlets, rather long, some with the apex dichotomously divided, others grouped (fasciculate). Aerocysts absent.

Reproductive morphology: Receptacles are terminal, moniliform, slender, not very compact, provided with spines with bisexual conceptacles, which are formed at the base of the spiniform branchlets and/or spaced along the terminal parts of the branches of higher-order.

Habitat: Epilithic, in the lower infralittoral zone.

Distribution: Mediterranean Sea: Adriatic Sea, Corsica, France, Greece, Italy, Sicily, Levant Basin, and Turkey. According to Verlaque et al. [35], all previous reports of *Cystoseira jabukae* from the western Mediterranean and the Ionian Sea probably refer to this species.

Identity confusion: It is distinguished from "*C.*" *jabukae* by the deeply digitate holdfast and a shorter, coralloid axis with large, spaced, and divergent warty-spiny tophules.

Remarks: Verlaque et al. [35] regard *Ericaria funkii* (as *Cystoseira funkii*) as a separate species from *Cystoseira jabukae.* Instead, Cormaci et al. [33] treat *C. jabukae* as a synonym of *Cystoseira spinosa* Sauvageau var. *tenuior* (Ercegović) Cormaci et al. [=*Gongolaria montagnei* var. *tenuior* to which also Guiry & Guiry [5], refer *C. jabukae*]. Following Verlaque et al. [35], we prefer to keep this taxon distinct pending specific molecular studies.

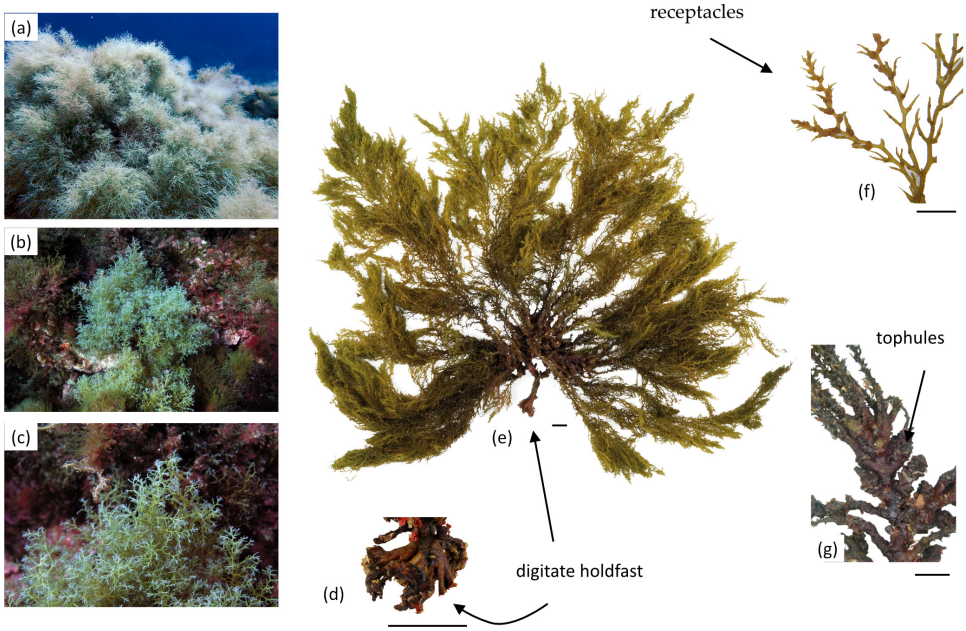


Figure 27. *Ericaria funkii*: (**a**–**c**) thalli in their habitat; (**d**) details of the holdfast (Scale bar = 1 cm); (**e**) habit of the thallus (Scale bar = 1 cm); (**f**) details of the receptacles (Scale bar = 0.5 cm); (**g**) details of the tophules (Scale bar = 1 cm).

3.4.21. (*) ***Ericaria giacconei*** Serio & G. Furnari **(Figure 28)**

Synonyms: *Cystoseira hyblaea* Giaccone.

Morphology: Thallus caespitose, axes robust (4–5 mm in diameter), long (2–10 cm); primary branches with a cupressoid habit (due to the subequal development of higher-order branches); spinose appendages absent except on fertile branches. Apices smooth, slightly prominent (≤0.5 cm); cryptostomata abundant; tophules and aerocysts absent.

Reproductive morphology: Terminal receptacles, compact; verrucose to tuberculate.

Habitat: Epilithic, in the upper infralittoral zone, up to 1 m depth.

Distribution: Mediterranean Sea: Italy, Sicily, Spain, and Tunisia.

Identity confusion: It differs from *E. crinita* and *E. barbatula* by having a robust, compact basal crust (vs. thin in both) and a smooth, slightly prominent axis apex (≤0.5 cm).

Remarks: According to Neiva et al. [31], this entity falls within the *Ericaria crinita* complex, which includes specimens identified as *E. crinita*, *E. barbatula*, and *E. giacconei*. Further molecular analyses are required to clarify its taxonomic position.

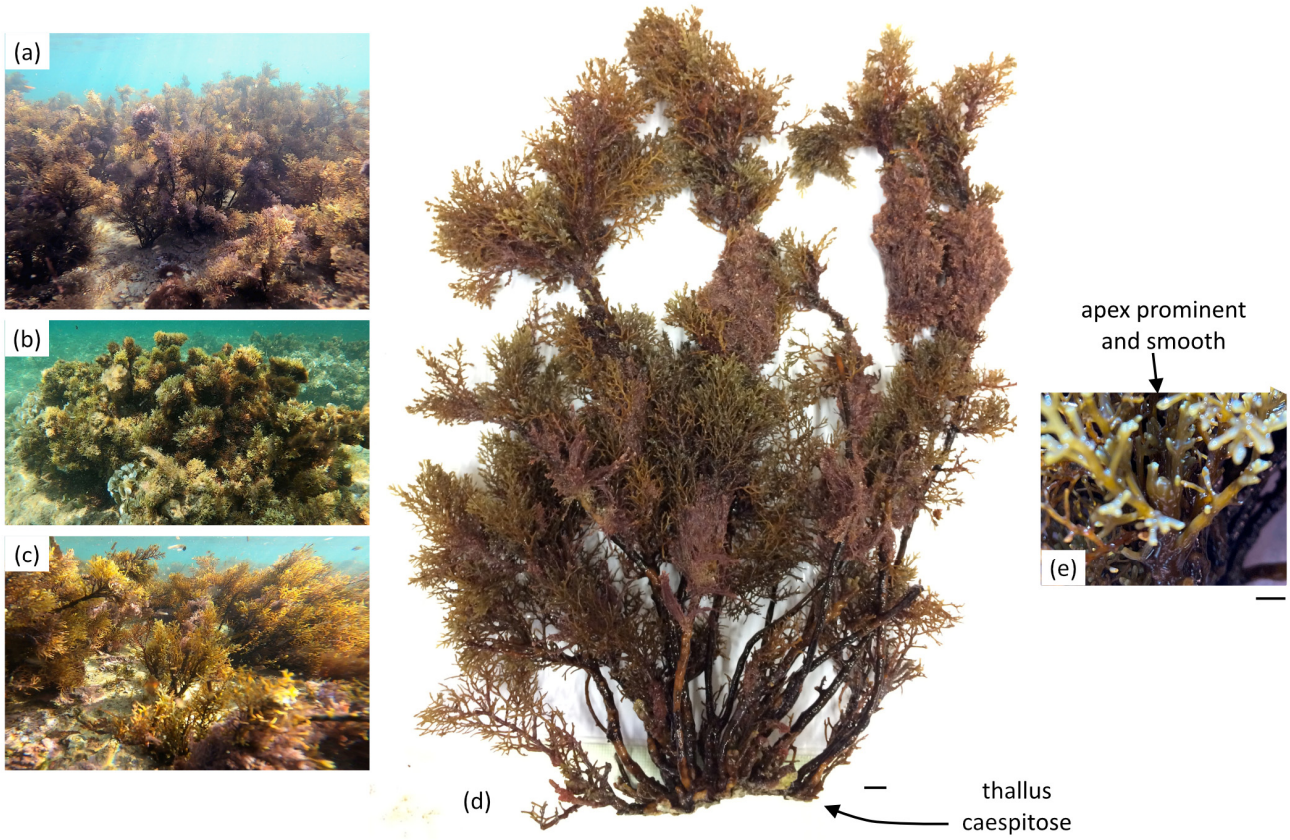


Figure 28. *Ericaria giacconei*: (**a**–**c**) thalli in their habitat; (**d**) habit of the thallus (Scale bar = 1 cm); (**e**) details of the apex (Scale bar = 0.5 cm).

3.4.22. (*) ***Ericaria mediterranea*** (Sauvageau) Molinari & Guiry **(Figure 29)**

Synonyms: *Cystoseira mediterranea* Sauvageau, *Carpodesmia mediterranea* (Sauvageau) Orellana & Sansón, *Cystoseira mediterranea* var. *valiantei* Sauvageau.

Morphology: Thallus non-caespitose, 15–40 (–50) cm high, with greenish iridescence. Short, truncate axis (generally 1–2 cm long, sometimes up to 8 cm long), fixed to the substrate by a robust basal disc, with an irregular outline, or more often digitate to form branched radiating haptera. Apices slightly prominent from the insertion of the primary branches. Deciduous cylindrical primary branches, with a pyramidal outline and close insertion, that leave a scar or a short stump to form adventitious branches. Secondary and tertiary branches covered by pointed and long attenuated spiny branchlets. Tophules absent; aerocysts present according to the season; cryptostomata present.

Reproductive morphology: Compact receptacles, formed by the fusion of the branch with very swollen bases of numerous simple or bifid spiny branchlets, with a reduced or developed pointed sterile portion.

Habitat: Epilithic, in the upper infralittoral zone.

Distribution: Mediterranean Sea: Spain, Balearic Islands, France, Greece, Italy, Sardinia, Sicily, Algeria, Morocco, Tunisia, Cyprus, Egypt, Lebanon, Turkey, and Levant Basin.

Identity confusion: Possible confusion with *E. amentacea*, from which it is distinguished by the non-caespitose habit, a truncated cauloid fixed by radiating haptera, and longer, attenuated spiny branchlets.

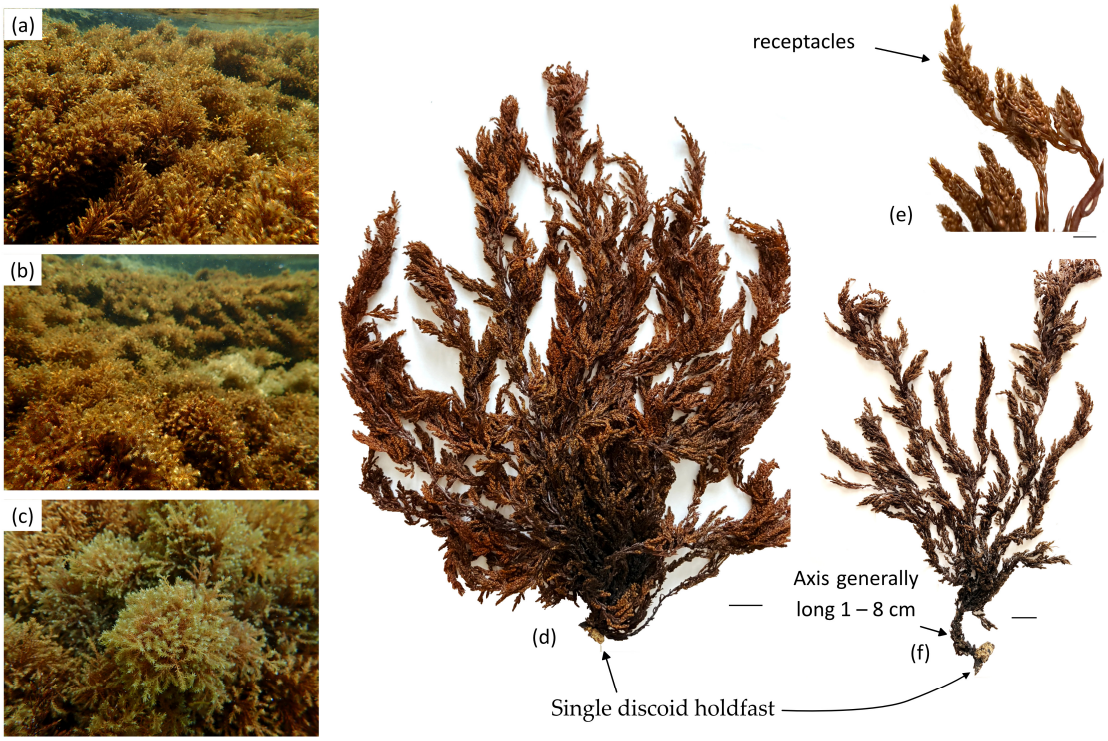


Figure 29. *Ericaria mediterranea*: (**a**–**c**) thalli in their habitat; (**d**) habit of the thallus with short axis (Scale bar = 2 cm); (**e**) details of the receptacles (Scale bar = 0.5 cm); (**f**) habit of the thallus with longer axis (Scale bar = 2 cm).

3.4.23. (*) ***Ericaria sedoides*** Neiva & Serrão **(Figure 30)**

Synonyms: *Fucus sedoides* Desfontaines *nom. illeg.*; *Fucus ericoides* Linnaeus var. *sedoides* Turner; *Cystoseira sedoides* C.Agardh.

Morphology: Thallus non-caespitose, with a characteristic brush-like habit; yellowish-brown, non-iridescent in situ. Holdfast discoid. Axis trunk-like, cylindrical (3–10 mm in diameter), simple or rarely branched once or twice, and entirely obscured by the dense branching pattern. Apex not visible. Primary branches of uniform length: 2–3 cm in early spring, 6–10 cm in early summer, and 1–5 cm before abscission in autumn; inserted densely and perpendicularly along the axis. Secondary branches usually simple and not extending to the apex of the primary branches. Short spiniform ultimate branchlets 2–3 mm long, deeply subulate, bifid, and uniformly imbricated along the branches. Aerocysts and tophules absent; cryptostomata present at the base of the short spiniform ultimate branchlets.

Reproductive morphology: Terminal receptacles diffuse, 3–20 mm long; conceptacles located in the basal portion of the short spiniform ultimate branchlets.

Habitat: Epilithic, in the upper infralittoral zone.

Distribution: Mediterranean Sea: Pantelleria (Sicily), Algeria, and Tunisia.

Identity confusion: This species is readily distinguished from others by its characteristic brush-like habit.



Figure 30. *Ericaria sedoides:* (**a**–**c**) thalli in their habitat; (**d**) habit of the thallus (Scale bar = 2 cm); (**e**) details of the conceptacles (Scale bar = 0.20 cm).

3.4.24. ***Ericaria selaginoides*** (Linnaeus) Molinari & Guiry **(Figure 31)**

Synonyms: *Fucus selaginoides* Linnaeus; *Cystoseira selaginoides* (Linnaeus) Bory *nom. illeg.*; *Fucus tamariscifolius* Hudson; *Fucus ericoides* Linnaeus; *Fucus erica-marina* S.G. Gmelin *nom. illeg.*; *Ericaria tamarisca* Stackhouse *nom. illeg*; *Ericaria selago* Stackhouse *nom. illeg*; *Phryganella ericoides* (Linnaeus) Stackhouse; *Cystoseira ericoides* (Linnaeus) C. Agardh; *Mackaia ericoides* (Hudson) S.F. Gray; *Cystoseira erica-marina* Naccari; *Gongolaria ericoides* (Linnaeus) Kuntze; *Cystoseira ericoides* var. *laevis* P.J.L. Dangeard; *Cystoseira ericoides* var. *divaricata* P.J.L. Dangeard; *Cystoseira tamariscifolia* (Hudson) Papenfuss; *Carpodesmia tamariscifolia* (Hudson) Orellana & Sansón.

Morphology: Thallus non-caespitose; light to dark brown with green-blue iridescence. Holdfast conical or with radiating haptera. Axis cylindrical, branched and rigid at the base; apex slightly spiny. Primary branches cylindrical, up to 60 cm, radially inserted. Tophules absent. Short spiniform ultimate branchlets abundant, 1–5 mm, simple or bifid; cryptostomata abundant. Aerocysts ovoid, isolated or in short series.

Reproductive morphology: Terminal receptacles small, simple or branched, cylindrical, tuberculate, with simple/bifid short spiniform ultimate branchlets. Axial and basal conceptacles protruding.

Habitat: Epilithic, in the upper infralittoral zone.

Distribution: Mediterranean Sea: Spain, Isla de Alborán, Italy, Sicily, Greece, Algeria, Morocco, Tunisia, Spanish North Africa, Libya, and Levant Basin. **Atlantic Ocean:** Canary Islands, Azores, Madeira, Cape Verde, Western Sahara, Britain, Channel Islands, France, Spain, Ireland, Mauritania, Morocco, the Netherlands, and Portugal.

Identity confusion: It is similar to *E. amentacea* and *E. mediterranea*, from which it can be distinguished by the intense green-blue iridescence in situ and the presence of

ovoid aerocysts. It differs from *E. amentacea* by having a non-caespitose, rigid axis (vs. the caespitose habit of *E. amentacea*).

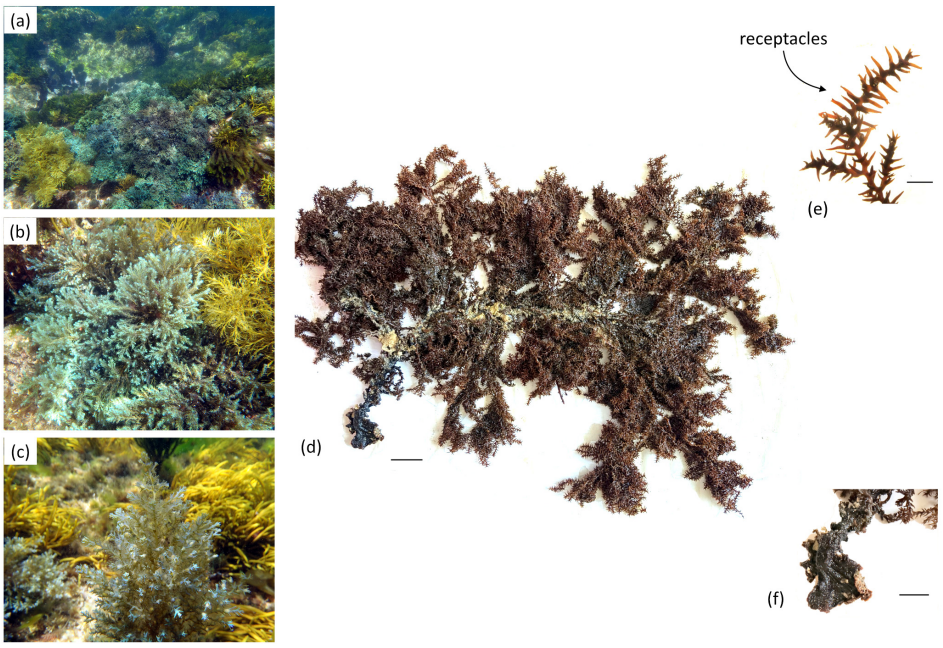


Figure 31. *Ericaria selaginoides*: (**a**–**c**) thalli in their habitat; (**d**) habit of the thallus (Scale bar = 2 cm); (**e**) details of spiniform ultimate branchlets and receptacles (Scale bar = 1 cm); (**f**) details of the holdfast (Scale bar = 1 cm).

3.4.25. (*) ***Ericaria zosteroides*** (C.Agardh) Molinari & Guiry **(Figure 32)**

Synonyms: *Cystoseira zosteroides* C.Agardh, *Carpodesmia zosteroides* (C.Agardh) Greville, *Cystoseira opuntioides* Bory *ex* Montagne, *Phyllacantha opuntioides* (Bory *ex* Montagne) Kützing, *Carpodesmia opuntioides* (Bory *ex* Montagne) Kützing, *Gongolaria opuntioides* (Montagne) Kuntze.

Morphology: Thallus non-caespitose, about 30 cm high, with a slightly iridescent frond, provided with gracile and flexible branches. Axis short (up to 10 cm high), simple or slightly branched, fixed to the substrate by robust haptera arranged radially and not welded together. Apex smooth slightly protruding. Tophules smooth, sessile or briefly pedunculated, from oblong to cylindrical (5–20 × 4–8 mm). Primary branches, up to 30 cm long, cylindrical or slightly flattened. Branches of the upper order, covered with cryptostomata, flattened with a thin median rib and provided with flattened spines. Aerocysts absent.

Reproductive morphology: Receptacles intercalary (rarely terminal) on the primary and/or secondary branches, compact, fusiform-lanceolate.

Habitat: Epilithic, in the circalittoral zone.

Distribution: Mediterranean Sea: Adriatic Sea, Spain, Balearic Islands, Corsica, France, Greece, Italy, Sicily, Algeria, Libya, Tunisia, Morocco, Cyprus, Lebanon, Syria, Turkey, and Levant Basin.

Identity confusion: It cannot be confused with other species.

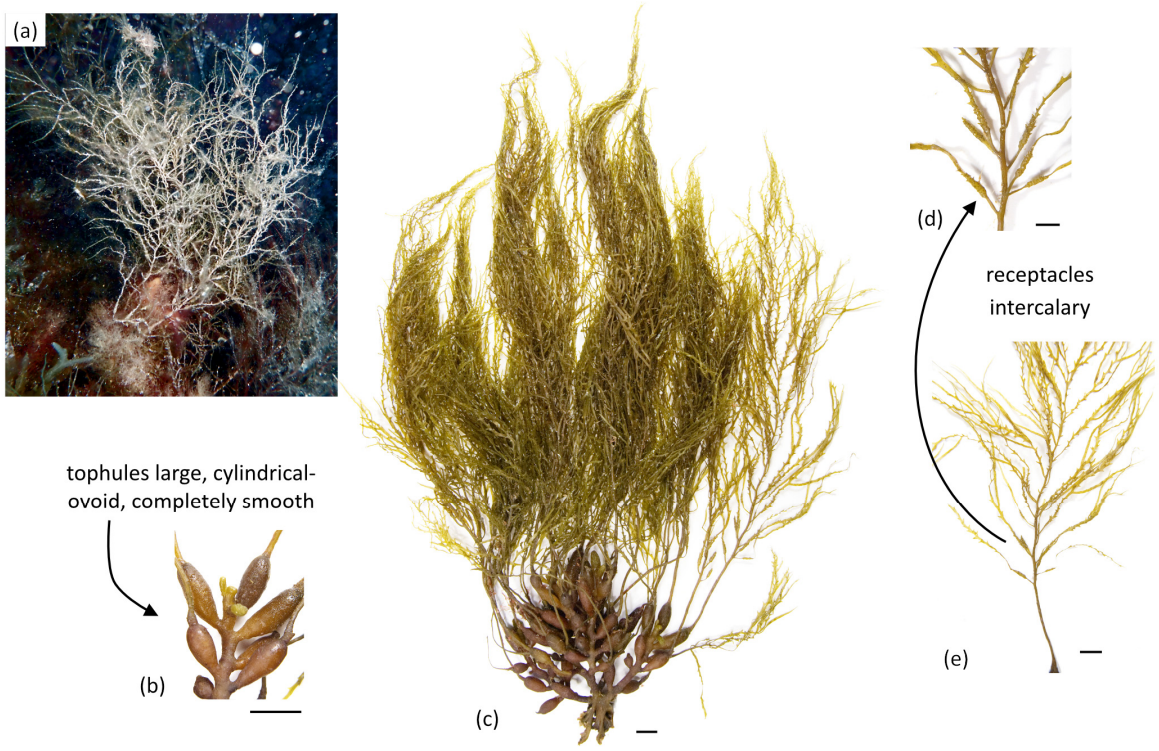


Figure 32. *Ericaria zosteroides:* (**a**) thallus in its habitat; (**b**) details of the tophules (Scale bar = 5 mm); (**c**) habit of the thallus (Scale bar = 1 cm); (**d**,**e**) details of the receptacles (Scale bars: (**a**) = 5 mm; (**b**) = 1 cm).

3.4.26. ***Gongolaria abies-marina*** (S.G. Gmelin) Kuntze **(Figure 33)**

Synonyms: *Fucus abies-marinus* S.G.Gmelin, *Cystoseira abies-marina* (S.G.Gmelin) C.Agardh, *Treptacantha abies-marina* (S.G.Gmelin) Kützing, *Fucus corniculatus* Wulfen, *Fucus abies* Bertoloni *nom. illeg.*, *Phyllacantha moniliformis* Kützing, *Treptacantha gracillima* Kützing, *Treptacantha montagnei* Kützing.

Morphology: Thallus spreading over the substrate at low tide (Atlantic) or upright (submerged in the Mediterranean), yellowish green-brown, lacking a distinct discoid base. Attached by an intricate, cylindrical prostrate axis emitting numerous small haptera (isolated or confluent). Creeping axis, cylindrical (1–2 mm in diameter), smooth, highly branched and intricate. Apex obtuse and rounded. Primary and adventitious branches reach 20 cm, ramified to 3rd or 4th order; branches thin (1.0–1.5 mm diameter) with short spiniform branchlets loosely arranged distally. Aerocysts and tophules absent; cryptostomata present seasonally.

Reproductive morphology: Receptacles terminal, poorly differentiated, 1–4 mm long; conceptacles situated in the slightly swollen base of the short spiniform ultimate branchlets.

Habitat: Atlantic: Lower intertidal zone. Mediterranean: rare, perennial, epilithic or epiphytic; associated with maërl (free-living coralline algae) and coarse sands/pebbles at 20–35 m depth.

Distribution: Mediterranean Sea: Spain, Italy, Sardinia, and Libya, but its presence in Spain has been confirmed only in Murcia, Andalusia, and the Balearic Islands. **Atlantic Ocean:** Canary Islands, Azores, Cape Verde, Madeira, Salvage Islands, Morocco, Senegal, and Western Sahara.

Identity confusion: It cannot be confused with other species.

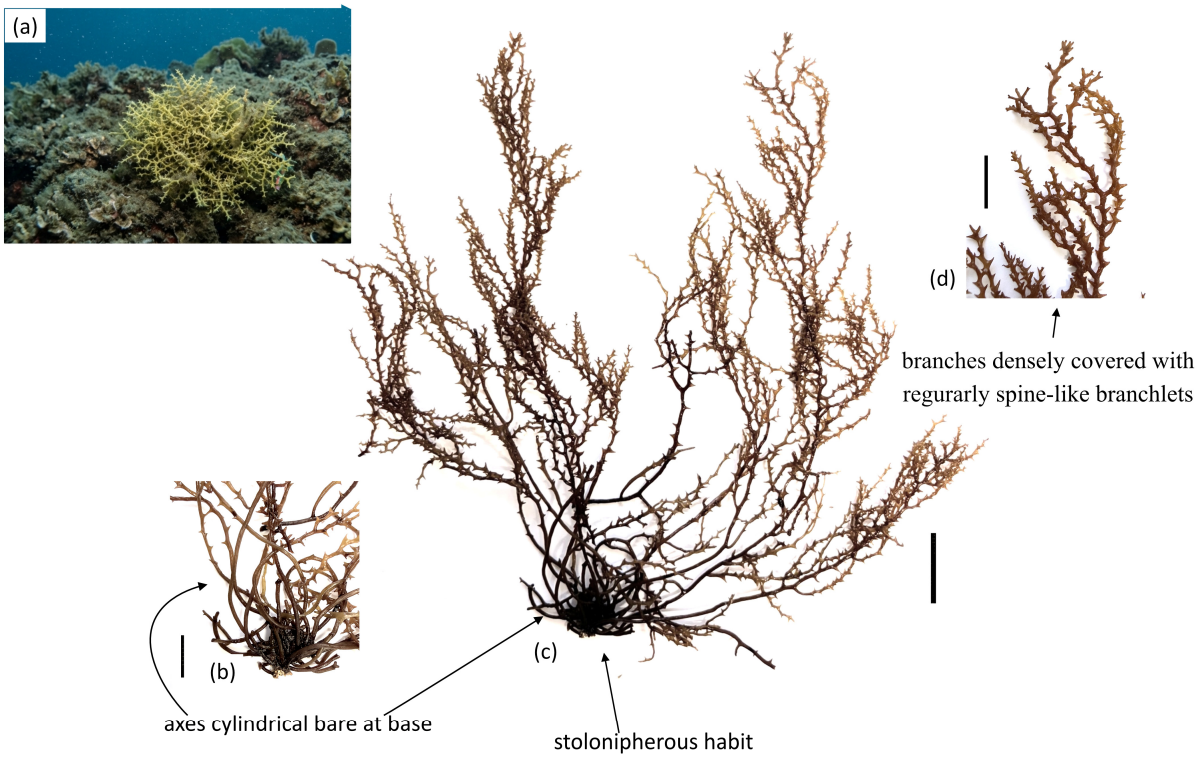


Figure 33. *Gongolaria abies-marina:* (**a**) thallus in its habitat; (**b**) details of the holdfast and axes (Scale bar = 1 cm); (**c**) habit of the thallus (Scale bar = 2 cm); (**d**) details of the branches (Scale bar = 1 cm).

3.4.27. (*) ***Gongolaria algeriensis*** (Feldmann) Molinari & Guiry **(Figure 34)**

Synonyms: *Cystoseira algeriensis* Feldmann, *Treptacantha algeriensis* (Feldmann) Orellana & Sansón.

Morphology: Thallus non-caespitose, up to 25 cm; yellowish-brown attached to the substrate by a robust discoid holdfast. Axis (to 10 cm), simple or 2–3 times divided. Smooth, non-protruding apex. Lower primary branches foliaceous, 2 mm wide, with a midrib and pinnate-distichous branching; upper primary branches and branches of higher orders cylindrical; simple or geminate short spiniform ultimate branchlets, up to 3–4 mm long, more or less spaced on the branches. Scattered triangular spines on primary branches; secondary/tertiary branches spinose. Tophules ovoid, smooth to rugose. Aerocysts absent; scattered cryptostomata.

Reproductive morphology: Diffuse terminal receptacles and conceptacles differentiated in the swollen base of the short spiniform ultimate branchlets.

Habitat: Epilithic, in the upper infralittoral zone up to 1 m depth.

Distribution: Mediterranean Sea: Spain, Balearic Islands, Italy, Algeria, and Tunisia.

Identity confusion: This species differs from *G. squarrosa* by the thinner habit and longer and more branched axis (vs. a very short, robust axis). It is further separated by its scattered, non-crowned tophules and flattened basal branches.

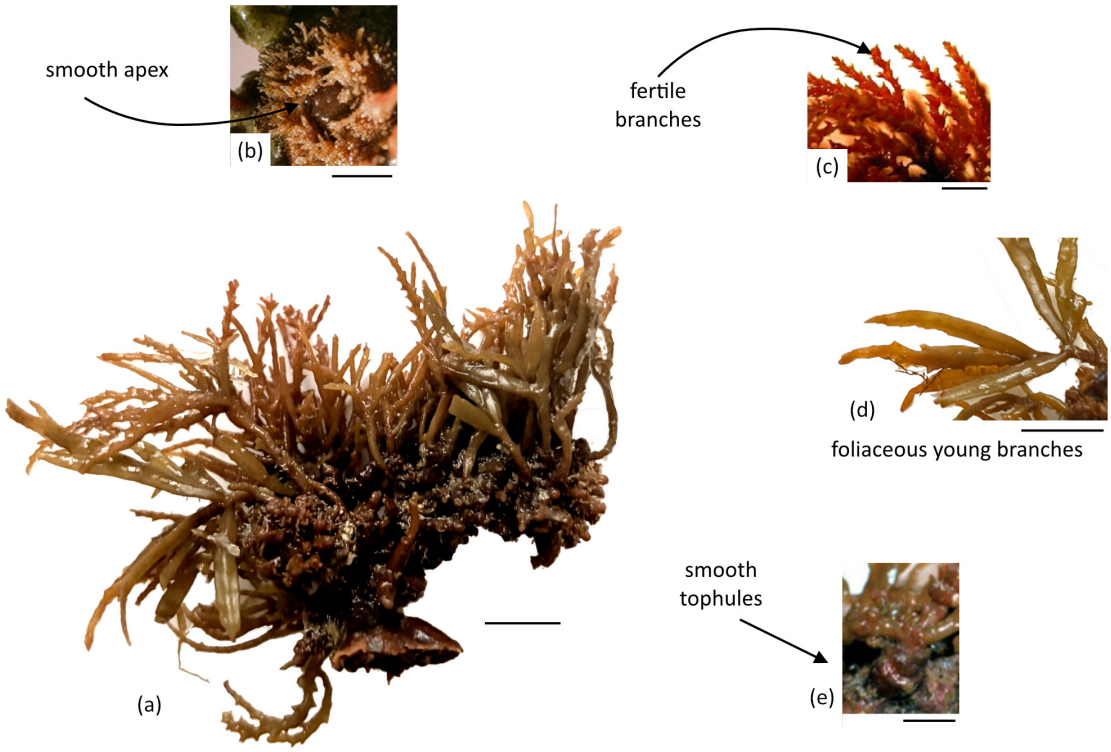


Figure 34. *Gongolaria algeriensis*: (**a**) habit of the thallus (Scale bar = 1 cm); (**b**) details of the apex (Scale bar = 2 mm); (**c**) details of the receptacles (Scale bar = 1 cm); (**d**) details of foliaceous branches (Scale bar = 1 cm); (**e**) details of the tophules (Scale bar = 5 mm).

3.4.28. ***Gongolaria barbata*** (Stackhouse) Kuntze **(Figure 35)**

Synonyms: *Abrotanifolia barbata* Stackhouse, *Phryganella barbata* (Stackhouse) Stackhouse, *Cystoseira barbata* (Stackhouse) C. Agardh, *Treptacantha barbata* (Stackhouse) Orellana & Sansón, *Fucus barbatus* Goodenough & Woodward *nom. illeg.*

Morphology: Thallus non-caespitose, iridescent, devoid of spiniform branchlets, attached to the substrate by a small basal disc. Single truncate axis, up to 60 cm high, cylindrical, with strongly protruding apex in relation to the insertion of the primary branches; primary branches well developed, especially in spring (40–70 cm long), with secondary and higher-order branches cylindrical-filiform. Tophules absent. Aerocysts abundant, isolated or in chains. Cryptostomata evident.

Reproductive morphology: Terminal receptacles, compact, silique-shaped (cylindrical-lanceolate), slightly wrinkled or smooth, simple, mucronate, pedicellate when surmounting an aerocyst.

Habitat: Growing on rocks in the upper infralittoral zone, well-lit coastal rock pools, bay bottoms, and coastal lagoons.

Distribution: Mediterranean Sea: Spain, Balearic Islands, Adriatic Sea, Croatia, France, Corsica, Greece, Italy, Veneto, Sicily, Malta, Algeria, Libya, Tunisia, Cyprus, Egypt, Syria, Turkey, Levant Basin, and Crete. **Atlantic Ocean:** Canary Islands, Salvage Islands, Portugal, and Morocco.

Identity confusion: It differs from *Ericaria barbatula* in the distinctive non-caespitose thallus.

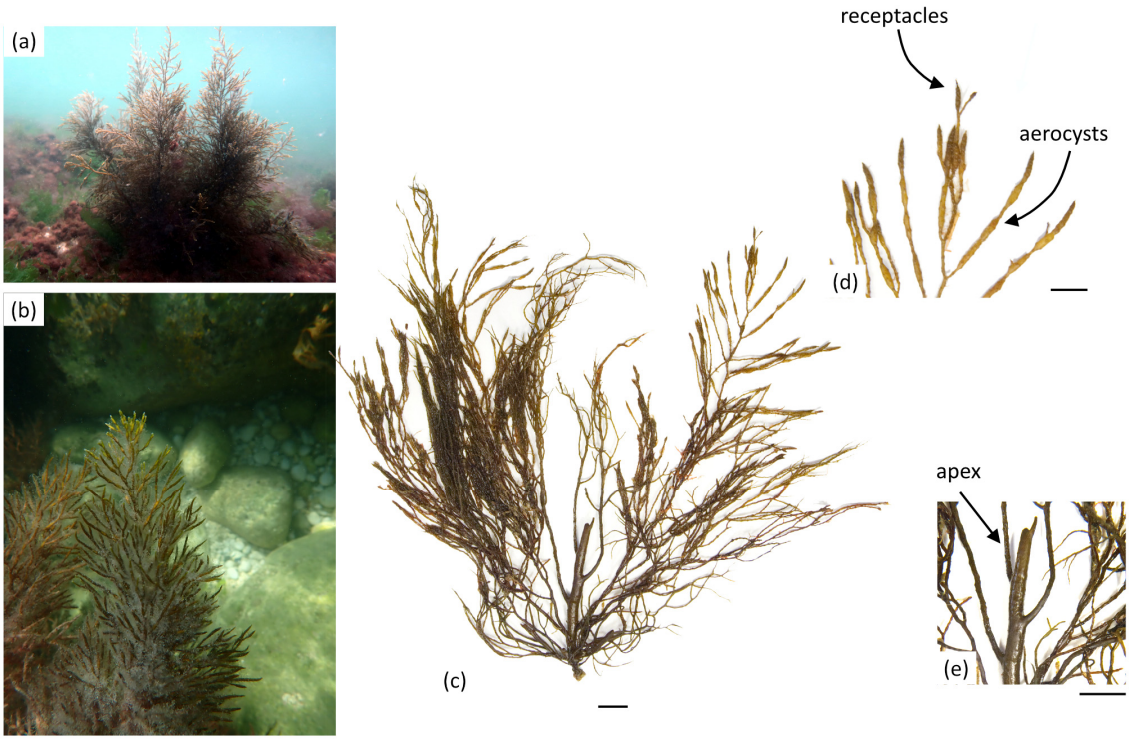


Figure 35. *Gongolaria barbata*: (**a**,**b**) thalli in their habitat; (**c**) habit of the thallus (Scale bar = 1 cm); (**d**) details of the receptacles and aerocysts (Scale bar = 5 mm); (**e**) details of the apex (Scale bar = 1 cm).

3.4.29. (*) ***Gongolaria elegans*** (Sauvageau) Molinari & Guiry **(Figure 36)**

Synonyms: *Cystoseira elegans* Sauvageau, *Treptacantha elegans* (Sauvageau) Orellana & Sansón.

Morphology: Thallus non-caespitose, tophulose. The axis, truncated, cylindrical, short (1–3 cm high, rarely up to 7–8 cm), branched 1–3 times (rarely more) and fixed to the substrate by a robust circular basal disc (1–2 cm in diameter); apex spinose but obscured by a characteristic "cauliflower-like" cauloid tip; tophules spiny and/or warty, ovoid (1–3 mm long), closely appressed to the axis. Aerocysts absent.

Reproductive morphology: Receptacles terminal, cylindrical ovoid to clavate, 0.5–1 cm long and 1–2 mm wide, with deciduous spinous appendages. Maximum vegetative and reproductive development in winter.

Habitat: Epilithic, in the upper infralittoral zone.

Distribution: Mediterranean Sea: Spain, Balearic Islands, Adriatic Sea, France, Corsica, Greece, Italy, Sicily, Sardinia, Algeria, Morocco, Tunisia, Cyprus, Turkey, and Levant Basin, **Atlantic Ocean:** Morocco.

Identity confusion: This species may be confused with *Gongolaria montagnei* var. *tenuior*. However, it is distinguished by a shorter axis (typically 1–8 cm) (10–15 cm in *G. montagnei* var. *tenuior*), the ratio between cauloid length and total thallus high (Lc/At), including the frond, is <0.5. Its apex is spinose but often obscured by a characteristic "cauliflower-like" appearance. During maximum vegetative growth, the Lc/At ratio, frond included, is >0.5, and a smooth apex surrounded by spinose tophules.

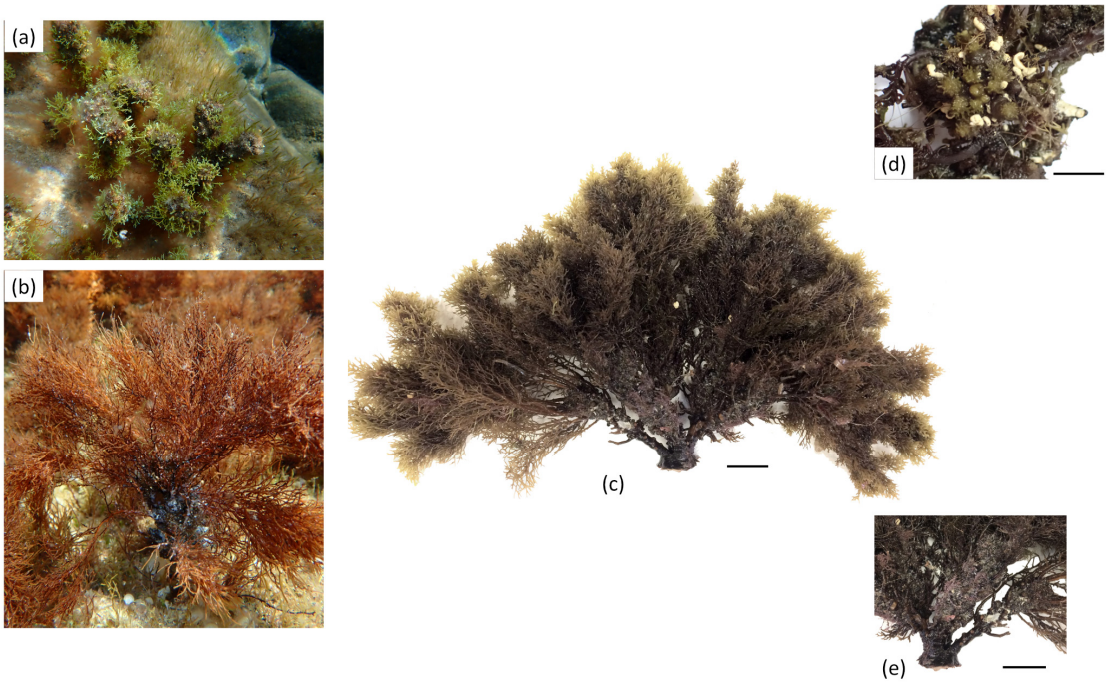


Figure 36. *Gongolaria elegans*: (**a**,**b**) thalli in their habitat; (**c**) habit of the thallus (Scale bar = 2 cm); (**d**) details of "cauliflower-like" cauloid tip (Scale bar = 1 cm); (**e**) details of the holdfast (Scale bar = 2 cm).

3.4.30. ***Gongolaria gibraltarica*** (Sauvageau) Neiva, Bermejo & Serrão **(Figure 37)**

Synonyms: *Cystoseira selaginoides sensu* Valiante var. *gibraltarica* Sauvageau; *Cystoseira gibraltarica* (Sauvageau) P. J. L. Dangeard; *Cystoseira sauvageauana* Hamel var. *gibraltarica* (Sauvageau) Hamel.

Morphology: Thallus non-caespitose, 15 to 20 cm high, dark brown; slight iridescence in situ; attached to substrate by a discoid basal holdfast; short axis, 1–3 cm high; smooth and slightly protruding apex; spaced tophules alternating with primary branches without tophules; oblong tophules, smooth to warty, rarely spiny; primary branches more or less cylindrical bearing spaced short spiniform branchlets; similar secondary branches, little branched and ending at the same level; simple short spiniform ultimate branchlets, regularly spaced; aerocysts rare or absent.

Reproductive morphology: Terminal cylindrical receptacles, not very spiny; reproduction in spring and summer.

Habitat: Epilithic, in the tide pools.

Distribution: Mediterranean Sea: Spain and Morocco.

Identity confusion: It represents a cryptic species, distinct from the Atlantic *Gongolaria mauritanica* (= *G. nodicaulis*) only through molecular phylogenetic analysis [31].

Remarks: Based on molecular data, in Neiva et al. [31] *Cystoseira selaginoides* var. *gibraltarica* was raised to the species rank as *Gongolaria gibraltarica*. As a result, specimens from the Strait of Gibraltar and the Moroccan coasts of the Alboran Sea, traditionally referred in the literature to as *C. mauritanica*, were reassigned to this species.

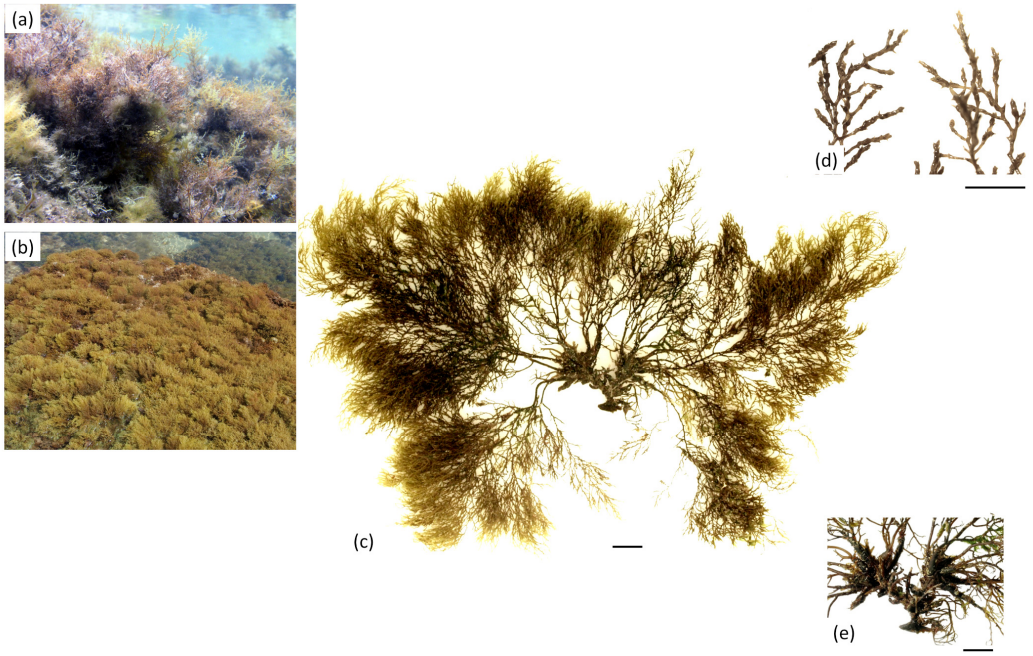


Figure 37. *Gongolaria gibraltarica*: (**a**,**b**) thalli in their habitat; (**c**) habit of the thallus (Scale bar = 1 cm); (**d**) details of the receptacles (Scale bar = 0.5 cm); (**e**) details of the axes and tophules (Scale bar = 1 cm).

3.4.31. (*) ***Gongolaria montagnei*** (J. Agardh) Kuntze **var. *montagnei* (Figure 38)**

Synonyms: *Cystoseira montagnei* J.Agardh, *Phyllacantha montagnei* (J.Agardh) Kützing, *Treptacantha montagnei* (J.Agardh) Orellana & Sansón *nom. illeg.*, *Cystoseira spinosa* Sauvageau, *Cystoseira adriatica* Sauvageau, *Treptacantha ballesterosii* Orellana & Sansón.

Morphology: Thallus non-caespitose, 30–40 cm high, tophulose, slightly iridescent in young portions, fixed to the substrate by a robust basal disc. Axis, cylindrical, with apex flat, smooth, not protruding relative to the insertion of the primary branches, and surrounded by cylindrical appendages and spinose tophules. Primary branches 10–20 cm long, initially cylindrical, then flattened, provided with spiny branchlets, spaced and irregularly distributed, of variable shape, bi-multifid, toothed. Secondary branches are shorter and less branched, with divaricated, triangular, spiny branchlets with bifid tips. Tophules, spherical or oblong, spiny, sometimes wrinkled or smooth with age.

Reproductive morphology: The conceptacles, initially scattered on the branches of the higher order, become increasingly dense to form true terminal receptacles that are rather long and not very compact.

Habitat: Epilithic, in the lower infralittoral zone.

Distribution: Mediterranean Sea: Spain, Balearic Islands, Adriatic Sea, France, Corsica, Greece, Italy, Sicily, Sardinia, Malta, Libya, Algeria, Morocco, Spanish North Africa, Tunisia, Egypt, Syria, Spanish North Africa, Turkey, Levant Basin, Cyprus, Israel, and Lebanon. **Atlantic Ocean:** Canary Islands.

Identity confusion: Possible confusion with *G. sauvageauana*, from which it is distinguished by possessing a smooth apex and distinctly spiny tophules.

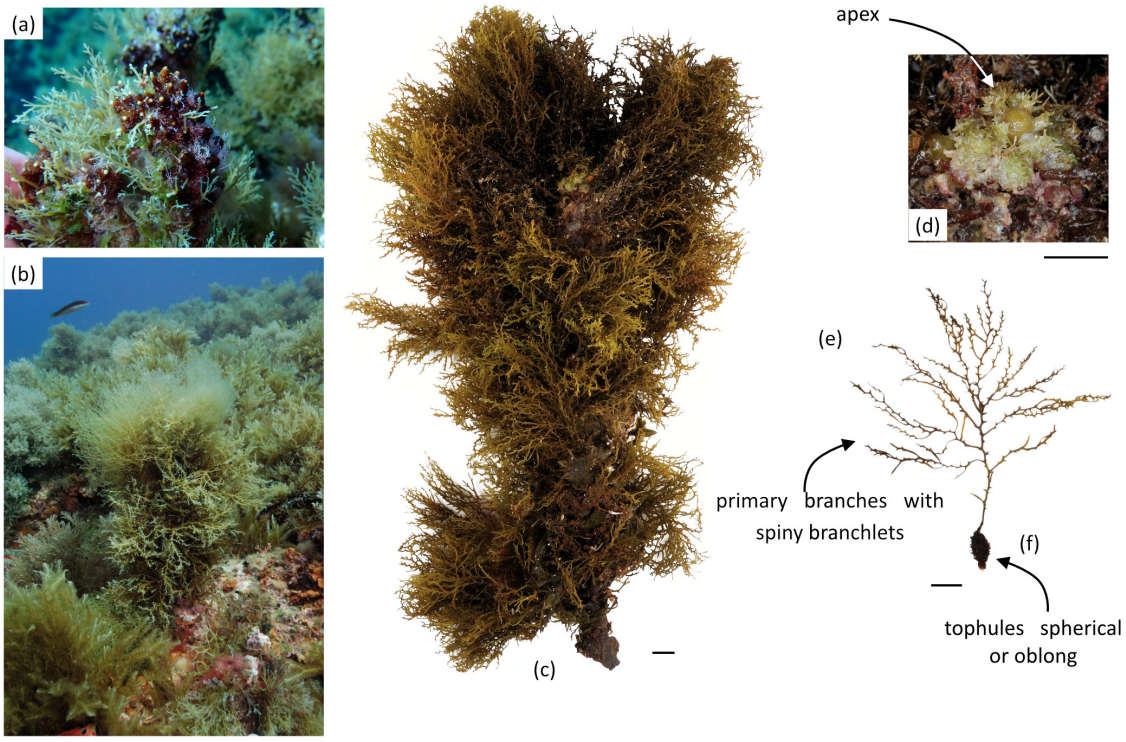


Figure 38. *Gongolaria montagnei* var. *montagnei*: (**a**,**b**) thalli in their habitat; (**c**) habit of the thallus (Scale bar = 1 cm); (**d**) details of the apex (Scale bar = 0.5 cm); (**e**,**f**) details of the primary branch with tophules (Scale bar = 1 cm).

3.4.32. ***Gongolaria montagnei* var. *compressa*** (Ercegovič) Verlaque, Blanfuné, Boudouresque & Thibaut **(Figure 39)**

Synonyms: *Cystoseira adriatica* subsp. *compressa* Ercegovič, *Cystoseira adriatica* var. *compressa* Ercegovič (Giaccone), *Cystoseira platyramosa* Ercegovič, *Cystoseira adriatica* subsp. *intermedia* Ercegovič, *Cystoseira adriatica* var. *intermedia* (Ercegovič) Giaccone, *Cystoseira spinosa* var. *compressa* (Ercegovič) Cormaci, G. Furnari, Giaccone, Scammacca & D. Serio, *Cystoseira montagnei* var. *compressa* (Ercegovič) M. Verlaque, Blanfuné, Boudouresque, Thibaut & Sellam.

Morphology: with primary branches initially cylindrical near the base, tending to become flattened. Higher-order branches are flattened with a central midrib.

Habitat: Epilithic, in the lower infralittoral zone.

Distribution: Mediterranean Sea: Spain, Balearic Islands, Adriatic Sea, Greece, Italy, Sicily, France, Corsica, Libya, Syria, Cyprus, Turkey, and Levant Basin.

Identity confusion: Similar to *C. micheleae*, but differing in the presence of spinose tophules and the arrangement of its terminal receptacles.

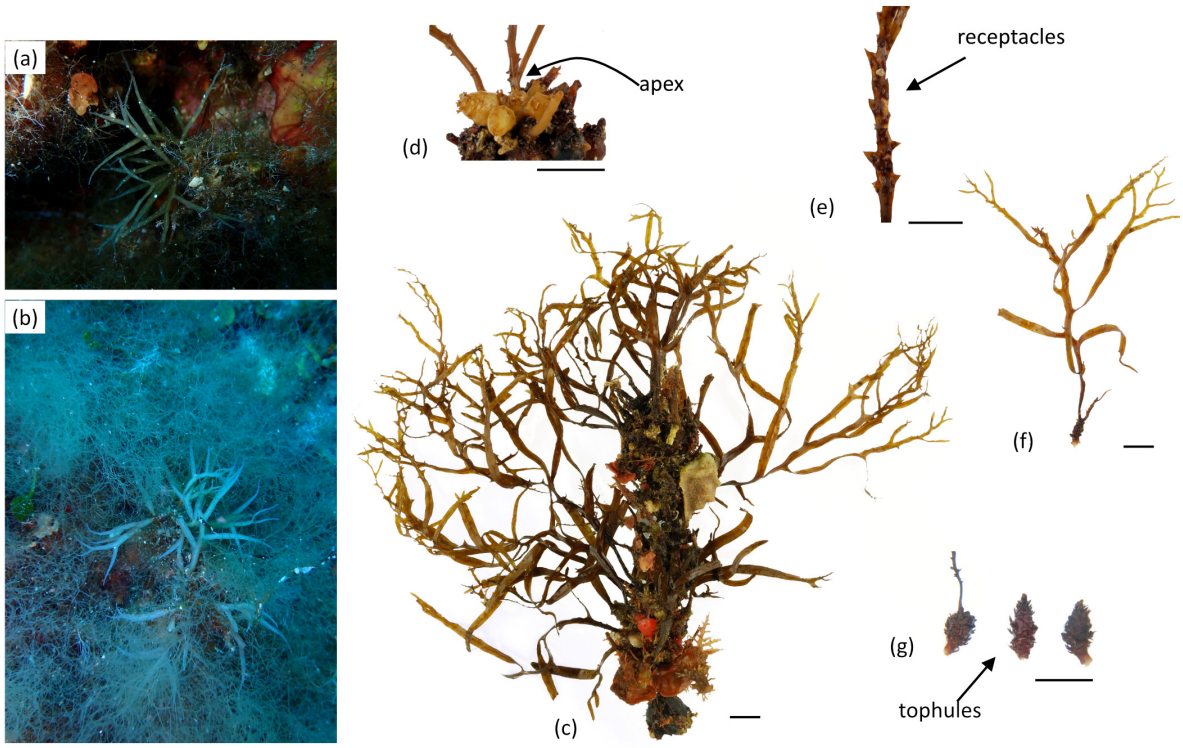


Figure 39. *Gongolaria montagnei* var. *compressa*: (**a**,**b**) thallus in its habitat; (**c**) habit of the thallus (Scale bar = 1 cm); (**d**) details of the apex (Scale bar = 1 cm); (**e**) details of the receptacles (Scale bar = 0.5 cm); (**f**) details of a branch (Scale bar = 1 cm); (**g**) details of the tophules (Scale bar = 1 cm).

3.4.33. ***Gongolaria montagnei* var. *tenuior*** (Ercegović) Molinari et Guiry **(Figure 40)**

Synonyms: *Cystoseira adriatica* subsp. *tenuior* Ercegović, *Cystoseira spinosa* var. *tenuior* (Ercegović) M.Cormaci, G.Furnari, G.Giaccone, B.Scammacca, & D.Serio, *Cystoseira montagnei* var. *tenuior* (Ercegović) Verlaque & al., *Cystoseira adriatica* subsp. *reducta* Ercegović, *Cystoseira adriatica* f. *reducta* (Ercegović) Giaccone, *Cystoseira adriatica* f. *tenuior* (Ercegović) Giaccone, *Cystoseira adriatica* f. *reducta* (Ercegović) Giaccone.

Morphology: with primary branches cylindrical or slightly flattened towards their tips, while higher-order branches are slightly flattened and slender.

Habitat: Epilithic, in the upper infralittoral zone.

Distribution: Mediterranean Sea: Adriatic Sea, France, Corsica, Greece, Italy, Sicily, Sardinia, Malta, Libya, and Tunisia.

Identity confusion: This taxon may be confused with *Gongolaria elegans*. However, it is distinguished by a longer axis (generally >10–15 cm). During maximum vegetative growth, the Lc/At ratio, frond included, is >0.5, and a smooth apex surrounded by spinose tophules. In contrast, *G. elegans* shows a shorter axis (typically 1–8 cm), and a ratio between cauloid length and total thallus high (Lc/At), including the frond, <0.5. Its apex is spinose but often obscured by a characteristic "cauliflower-like" appearance.

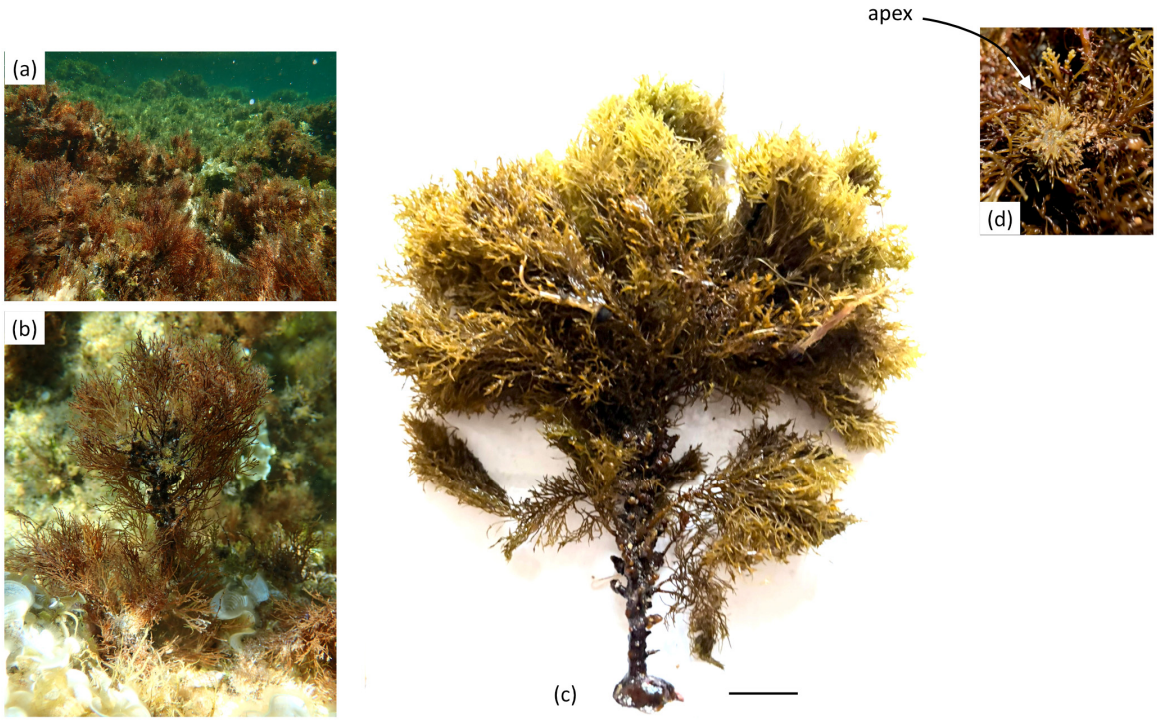


Figure 40. *Gongolaria montagnei* var. *tenuior*: (**a**,**b**) thalli in their habitat; (**c**) habit of the thallus (Scale bar = 1 cm); (**d**) details of the apex.

3.4.34. (*) ***Gongolaria rayssiae*** (Ramon) Molinari & Guiry **(Figure 41)**

Synonyms: *Cystoseira rayssiae* Ramon, *Treptacantha rayssiae* (Ramon) M. Mulas, J.Neiva & Á.Israel.

Morphology: Thallus non-caespitose, reaching up to 30 cm in height, olive-brown to dark brown, and non-iridescent in situ. Holdfast discoid to conical, 0.5–1.5 cm in diameter. Axis very short, cylindrical, simple or occasionally branched, with a smooth, non-protruding apex. Tophules oblong and smooth, rarely tuberculate or warty, never spiny; they are spread apart and grouped near the apices of the axes. Young primary branches are slender and translucent, bearing a very fine midrib; older branches are thicker and lack a midrib. Secondary branches are few, spaced, and alternate. Short spiniform ultimate branchlets are absent or extremely rare. Aerocysts absent. Cryptostomata are small and sparse.

Reproductive morphology: Receptacles terminal, long, and robust in relation to the supporting branch; compact, cylindrical, and branched, reaching up to 6 cm in length and 2–3 mm in diameter.

Habitat: Epilithic, in the upper infralittoral, 0–2 m depth.

Distribution: Mediterranean Sea: Egypt, Israel, and Levant Basin.

Identity confusion: It cannot be confused with other species.

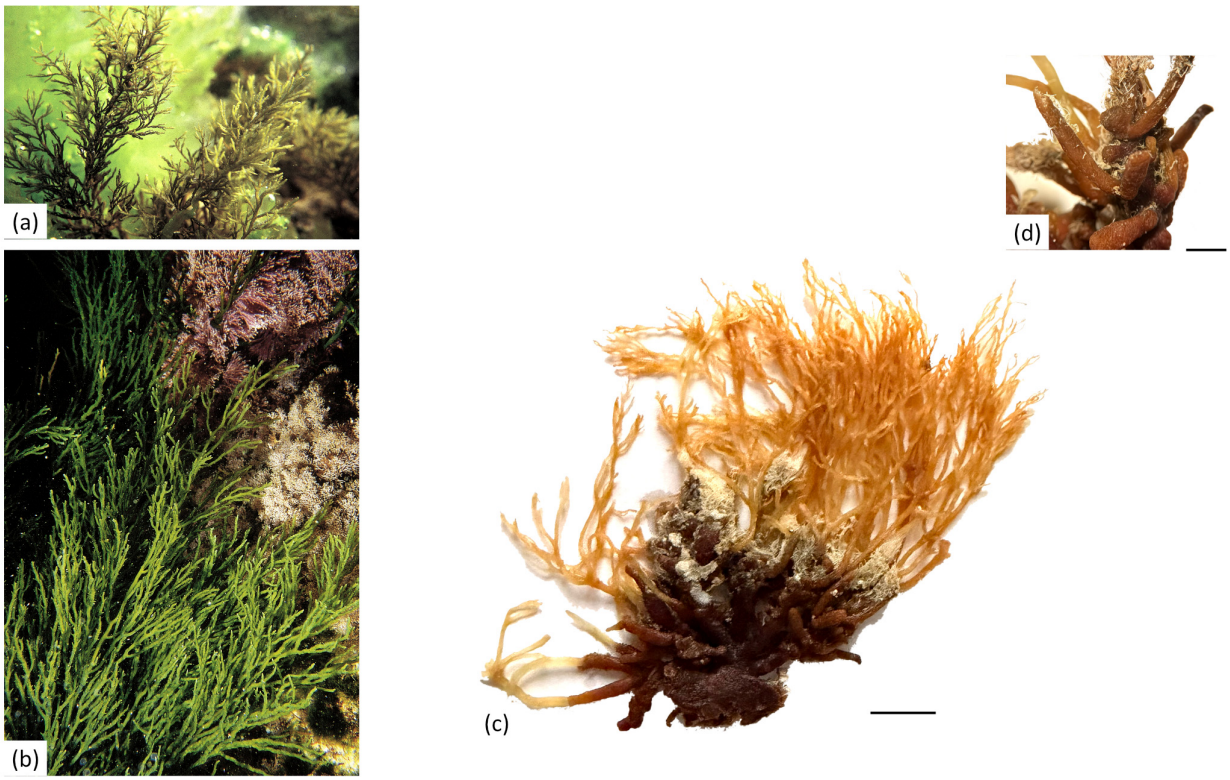


Figure 41. *Gongolaria rayssiae*: (**a**,**b**) thalli in their habitat; (**c**) habit of the thallus; (**d**) details of the tophules. Scale bars = 1 cm.

3.4.35. (*) ***Gongolaria sauvageauana*** (Hamel) Molinari & Guiry **(Figure 42)**

Synonyms: *Cystoseira sauvageauana* Hamel, *Treptacantha sauvageauana* (Hamel) Orellana & Sansón, *Cystoseira selaginoides* var. *polyoedematis* Sauvageau, *Cystoseira sauvageauana* var. *polyoedematis* (Sauvageau) Hamel, *Cystoseira sicula* Schiffner *ex* Gerloff & Nizamuddin.

Morphology: Thallus non-caespitose, 20–50 cm high, attached to the substrate by a regular basal disc. Single axis, 25–30 cm high, cylindrical (diameter 3–8 mm), repeatedly and irregularly branched into secondary axes. Spinose apex protruding from the insertion of the primary branches. Primary branches spaced, long (up to 20 cm), cylindrical, slender in relation to the diameter of the cauloid. Secondary branches cylindrical, variously and densely branched into branches that progressively decrease in length toward the top. Tophules and aerocysts absent.

Reproductive morphology: Receptacles terminal, compact, cylindrical (diameter 1–2 mm), long (from a few mm to 3 cm), simple or branched.

Habitat: Epilithic, in the middle infralittoral zone.

Distribution: Mediterranean Sea: Spain, Balearic Islands, France, Corsica, Italy, Abruzzo, Sicily, Adriatic Sea, Greece, Algeria, Morocco, Tunisia, and Turkey.

Identity confusion: This species is distinguished from *G. montagnei* var. *montagnei* by possessing a spinose, protruding apex and lacking tophules, whereas the latter is characterised by a smooth apex and distinctly spiny tophules.

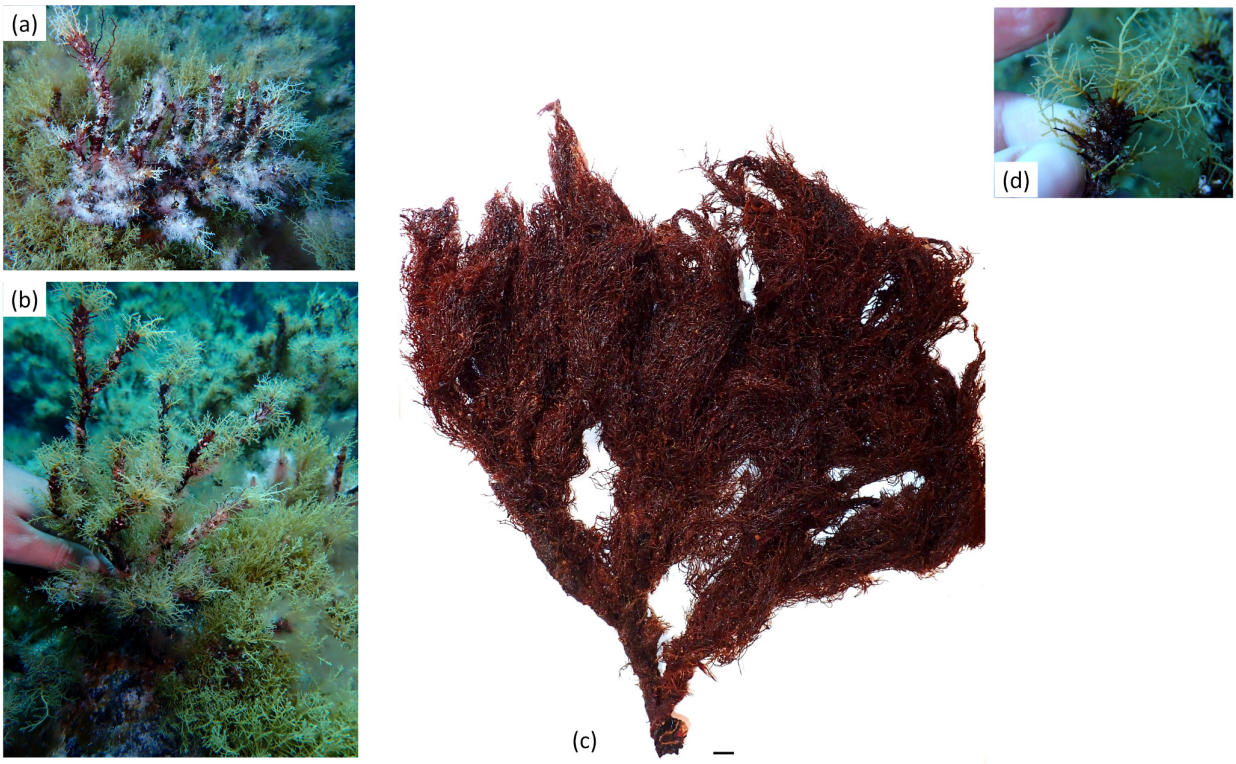


Figure 42. *Gongolaria sauvageauana*: (**a**,**b**) thalli in their habitat; (**c**) habit of the thallus (Scale bar = 1 cm); (**d**) details of the apex.

3.4.36. (*) ***Gongolaria squarrosa*** (De Notaris) Kuntze **(Figure 43)**

Synonyms: *Cystoseira squarrosa* De Notaris, *Cystoseira erica-marina* Naccari var. *squarrosa* (De Notaris) De Toni & Levi, *Cystoseira spinosa* Sauvageau var. *squarrosa* (De Notaris) Giaccone, *Treptacantha squarrosa* (De Notaris) S. Orellana et M. Sansón.

Morphology: Thallus non-caespitose, 6–20 cm high, bushy and rigid, with a thorny, cactus-like appearance; yellow-olive and non-iridescent in situ. Holdfast robust, discoid (≈2 cm). Axis short, trunk-like, and branched (4–5 cm), bearing 1–2(–4) perpendicular secondary axes. Apex smooth and slightly protruding. Tophules warty, 5–8 mm, forming a terminal crown. Each tophule bears 1–2 (–3) primary branches: the young ones flattened (2 mm wide, with midrib), the older ones cylindrical, 7–12 (–15) cm long. Ultimate branches cylindrical (8–10 cm). Short spiniform ultimate branchlets triangular, broad-based, with bifid to multifid apex, imbricated toward branch tips. Aerocysts absent; cryptostomata sparse.

Reproductive morphology: Diffuse terminal receptacles, 2–3 (–4) cm long; conceptacles grouped in the wide base of loosely imbricated short spiniform ultimate branchlets, with bifid, trifid to multifid apex.

Habitat: Epilithic, in the upper infralittoral zone, from the surface to about 15 m depth.

Distribution: Mediterranean Sea: Spain, Adriatic Sea, Croatia, France, Italy, Sicily, Malta, Greece, and Turkey.

Identity confusion: *G. squarrosa* differs from *G. algeriensis* in the "cactus-like" appearance, having a very short/robust axis and apically crowned tophules (vs. a longer axis and non-crowned tophules). Additionally, *G. squarrosa* possesses triangular multifid ultimate branchlets (simple in *G. algeriensis*).

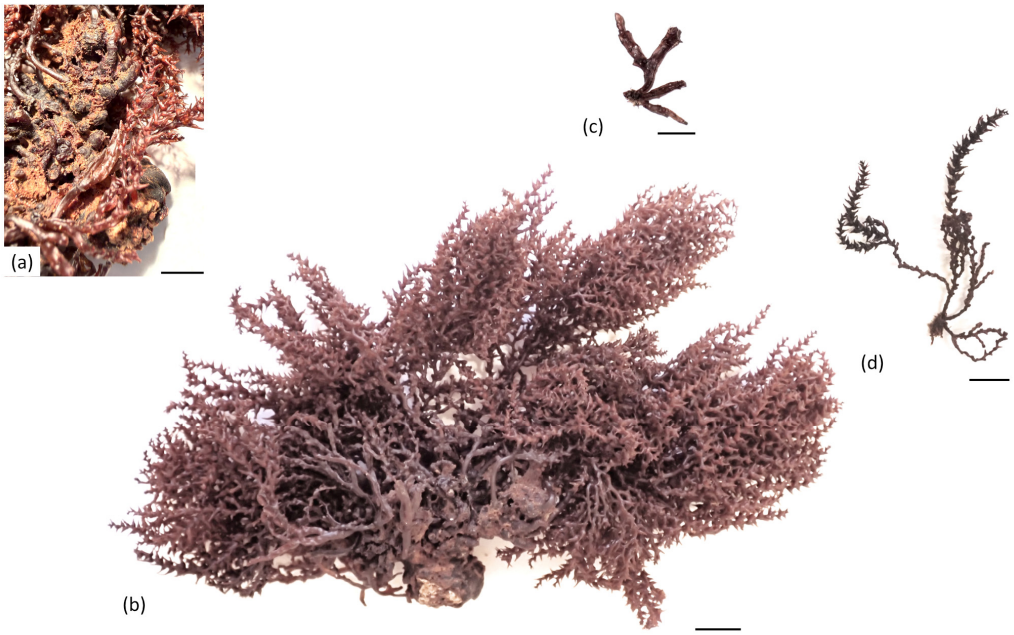


Figure 43. *Gongolaria squarrosa*: (**a**) Details of the tophules (Scale bar = 0.5 cm); (**b**) habit of the thallus (Scale bar = 1 cm); (**c**) details of young, flattened branchlets (Scale bar = 0.5 cm); (**d**) details of a branch with short spiniform ultimate branchlets imbricated (Scale bar = 1 cm).

3.4.37. (*) ***Gongolaria susanensis*** (Nizamuddin) Molinari & Guiry **(Figure 44)**

Synonyms: *Cystoseira susanensis* Nizamuddin, *Treptacantha susanensis* (Nizamuddin) Orellana & Sansón.

Morphology: Thallus caespitose, erect, brown-blackish, non-iridescent. Several short trunk-like axes, branched very near the holdfast; protruding and smooth apex; primary branches, very fine, rigid, 10–15 cm long and 0.6–1.0 mm in diameter, inserted radially on the axes and with a persistent enlarged base; loose alternate sub-dichotomous branching; secondary branches, up to 3 cm long and 0.5 mm in diameter; very fine ultimate branches, up to 1 cm long and 0.3–0.4 mm in diameter; short spiniform ultimate branchlets absent; sparse cryptostomata; aerocysts and tophules absent.

Reproductive morphology: Small compact terminal receptacles, 1.5–3 (–4) mm long and 0.7 mm in diameter, fusiform apiculate, smooth and tuberculated; axial conceptacles; reproduction in spring.

Habitat: Epilithic, in the upper infralittoral, superficial rocks and well-lit sandstone pebbles, medium hydrodynamics, 0–1 m depth; lagoonal environments, sandy bottoms; coastal rock pools.

Distribution: Mediterranean Sea: Greece, Italy, Sicily (its presence in Sicily needs confirmation), Spain, Libya, Tunisia.

Identity confusion: This species differs from *G. barbata* in the caespitose habit and trunk-like axes (vs. a solitary, tall thallus) and the absence of iridescence and aerocysts (vs. abundant aerocyst chains).

Remarks: Following the original description by Nizamuddin [32] and Tsiamis et al. [38] we consider G. *susanensis* as caespitose, rather than pseudocaespitose as made by Alongi et al. [39] and Cormaci et al. [33] for Sicilian specimens. The latter records have been questioned by Bouafif et al. [34] as potential misidentifications of *G. barbata*.

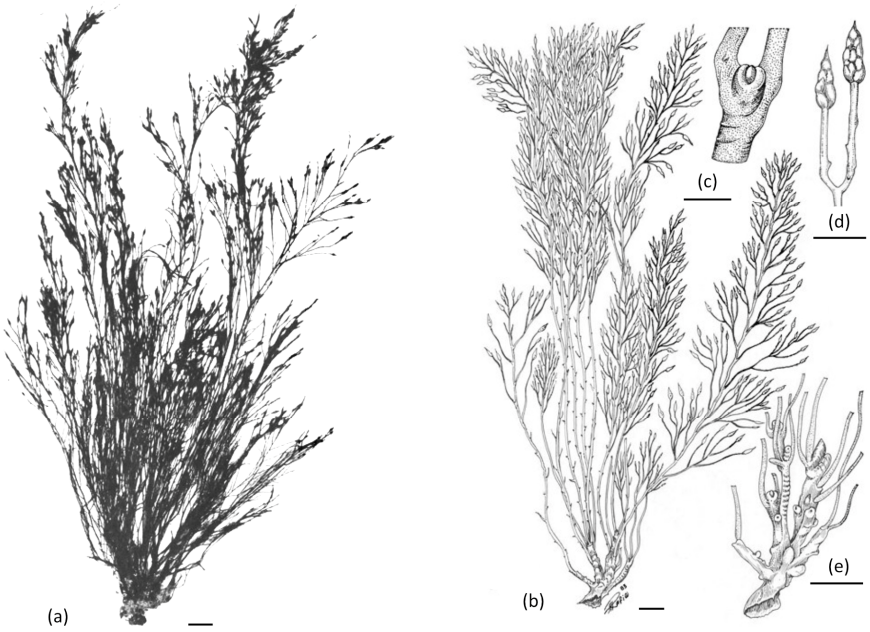


Figure 44. *Gongolaria susanensis*: (**a**,**b**) habit of the holotype (Scale bars = 1 cm); (**c**) details of the apex (Scale bar = 0.3 cm); (**d**) details of the receptacles (Scale bar = 0.3 cm); (**e**) details of the basal part (Scale bar = 1 cm) (modified from Nizamuddin [32]).

3.4.38. ***Gongolaria usneoides*** (Linnaeus) Molinari & Guiry **(Figure 45)**

Synonyms: *Fucus usneoides* Linnaeus, *Cystoseira usneoides* (Linnaeus) M.Roberts, *Treptacantha usneoides* (Linnaeus) Orellana & Sansón, *Fucus granulatus* Linnaeus *nom. illeg.*, *Fucus aculeatus* Esper *nom. illeg.*, *Cystoseira granulata* C.Agardh.

Morphology: Thallus non-caespitose, reaching up to 2 m in high, light brown to yellow-brown with pale green iridescence in situ. Attached to the substrate by a radiating holdfast. Axis trunk-like, cylindrical, up to 15 cm long, simple or branched; apex smooth and slightly protruding. Tophules are pedunculated, smooth, oblong-elongated (10–20 mm × 5–8 mm), spaced, and divaricate. Primary branches are long (often up to 100 cm) and cylindrical. Lower secondary branches are foliaceous (flattened), spaced, distichous, and often opposite; these branches are 3–4 cm long and 2–4 mm wide, with smooth margins and a midrib. Subsequent branches are cylindrical, either lacking or bearing a few rare short spiniform ultimate branchlets (simple or bifid). Ultimate branches are slender, spaced, often inserted in pairs, and carry 4 to 8 small aerocysts (2–3 mm × 1 mm) arranged in series. Cryptostomata are sparse and inconspicuous.

Reproductive morphology: Compact terminal receptacles, branched, slender, 3–20 mm × 1 mm, smooth-tuberculated, cylindrical, with or without short spiniform ultimate branchlets; axial conceptacles; reproduction all year round.

Habitat: Epilithic, in the middle and deep infralittoral, circalittoral, 15–40 m depth, subject to strong currents.

Distribution: Mediterranean Sea: Spain, Italy, Sicily, Malta, Algeria, Morocco, and Corsica. **Atlantic Ocean:** Scandinavia, Canary Islands, Cape Verde, Britain, Channel Islands, France, Ireland, Mauritania, Morocco, Senegal, Madeira, Spain, and Portugal.

Identity confusion: This species may be confused with the Atlantic species *G. nodicaulis*. However, it can be distinguished by its axes, which are never nodose (lacking swellings), but rather distinctly filiform and thread-like with very long internodes.

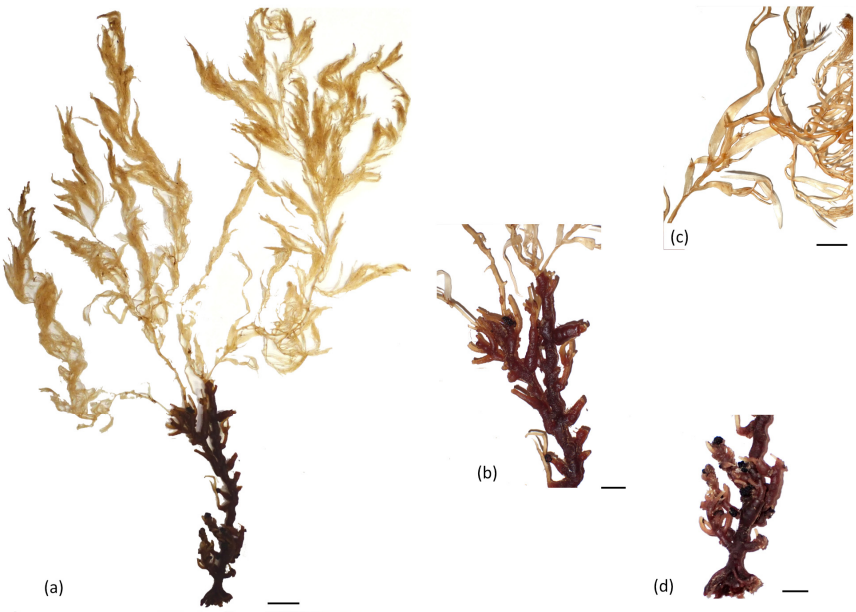


Figure 45. *Gongolaria usneoides*: (**a**) habit of the thallus (Scale bar = 2 cm); (**b**) details of the axis and tophules (Scale bar = 1 cm); (**c**) details of foliaceous (flattened) secondary branches (Scale bar = 1 cm); (**d**) details of the holdfast (Scale bar = 1 cm).

4. Conclusions

Species belonging to *Cystoseira s.l.* play a significant ecological role in the structuring of sublittoral marine ecosystems. However, they are currently experiencing declines and/or local extinction in many areas of the Mediterranean. This loss has significant negative impacts on biodiversity and ecosystem functioning, meaning these species deserve particular protection and conservation.

As natural recovery is hardly possible [40] due to their slow growth and low dispersal capacity [41], conservation regulations alone have not proven truly effective. In this regard, restoration programs are largely considered effective tools for the conservation of degraded or destroyed *Cystoseira s.l.* forests. Therefore, prompt restoration measures are currently considered necessary to preserve these habitats, aligning with initiatives such as the UN Decade on Ecosystem Restoration (2021–2030) [42], the EU Biodiversity Strategy for 2030 [43], and the proposed EU Nature Restoration Law [44].

Monitoring *Cystoseira s.l.* forests to assess their real distribution and ecological status is crucial for planning effective restoration programs. To this end, correctly identifying all species observed during monitoring campaigns is essential, and we are fully aware that this is quite complex and may represent a real challenge, even for expert researchers. This difficulty arises not only from the high variability and challenging interpretation of diacritical characters, but also from the fact that the existing literature (e.g., Floras and identification keys) generally illustrates both thalli and diacritical characters with drawings rather than with photos.

This key, thanks to the photos captured both in the field and in the laboratory, provides a complete photographic documentation of both thalli and diacritical characters, which is fundamental for the correct identification of species. This user-friendly tool will also allow non-expert researchers to arrive step by step at a correct identification of species. By filling this gap, we hope that this Atlas key will help to improve our understanding of the distribution and ecological status of *Cystoseira s.l.* forests in the Mediterranean Sea. We are aware that diacritical characters may vary in connection with the environment and thus may be difficult to interpret. Moreover, some taxonomic questions are not yet fully resolved and species assignment can only be achieved through modern molecular methods.

The next step will be the development of an electronic tool to ensure that the identification key always remains up to date.

5. Note Added in Proof

After the revision of this paper, D'Ambros Burchio et al. [45] downgraded *Cystoseira pustulata* (Ercegović) Neiva & Serrão to the rank of variety, proposing the combination *Cystoseira compressa* (Esper) Gerloff and Nizamuddin var. *pustulata* (Ercegovic) D'Ambros Burchio & Falace.

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Glossary

Adventitious	A branch arising out of the normal position
Aerocysts	Air-filled vesicles aiding buoyancy
Alternate	Branches on opposite or nearly opposite sides of an axis but at different levels
Anchorage structure	Encrusting or discoid holdfast, with or without haptera
Antheridium	Male reproductive cell, producing male gametes
Apex	The tip of the axis
Axis (cauloid)	The main stem of the thallus
Bifid	Divided into two for about half the length
Bifurcate	More or less equally divided into two branches
Branchlets	Lateral ramuli
Caespitose	Thallus with several axes arising simultaneously from the anchorage structure, giving a tufted or clumped appearance
Circalittoral	Zone extending from the lower limit of Infralittoral to the maximum depth which photosynthesis is possible
Clavate	Club-shaped, narrow at the base and widening gradually to the apex
Compressed	Flattened but not strongly so, with an ovate cross-section
Conceptacle	A flask-shaped cavity, opening to the surface, containing reproductive cells and paraphysis
Coralloid	Coral-shaped
Cortex	The outer layer of small isodiametric cells covering the medulla and sometimes covered by the meristoderm
Cryptostomata	Flask-shaped cavities opening to the surface and containing hair; when prominent they give rise to a pustulate appearance
Diacritical characters	Key distinguishing features used in taxonomy
Digitate	Possessing finger-like lobes
Diploid	Phase with two sets of chromosomes in each nucleus
Distichous	Branching arranged in two opposite rows and thus lying in one plane

Flattened	Strongly compressed, leaf-like
Fusiform	Spindle shaped, thicker centrally and tapering to both ends
Haptera	A root-like portion of the anchorage structure
Hemitophule	A slight basal swelling of the primary branch, resembling a reduced tophule
Holdfast	A basal attachment structure
Infralittoral	Zone from the lowest low-tide level up to about 35–40 m (lower limit of *Posidonia oceanica*)
Intercalary	In between two cells or cell layers
Irregularly branched	Branches appearing in no regular or consistent pattern
Life cycle	The sum of reproductive phases of an organism
Medulla	The central region of the thallus with irregular arrangement of the cells, internal to the cortex
Meiosis	Nuclear division in which the chromosome number is reduced from 2n to n
Meristoderm	External meristematic layer responsible for increasing thickness
Midrib	A rib-like structure running up the middle of a frond or a compressed branch
Moniliform	Appearing cylindrical and contracted at regular intervals like a necklace
Multifid	Cleft into many branches or segments
Non-caespitose	Thallus with one axis arising from the anchorage structure
Oogamous	Fertilisation of a large nonmotile egg with a small motile sperm
Oogonium	Female reproductive cell containing a single egg
Paraphysis	Sterile filament, pluricellular and simple, within conceptacles
Pleustophytic	Unattached, free-floating form
Prostrate	Lying on the substrate substrate
Pseudocaespitose	Thallus with a single extremely short axis (generally <1 cm) that branches immediately, looking like a thallus with multiple axes
Pustulate	With small bumps
Radial	Branching arranged all around the axis
Receptacles	Fertile modified branchlets (often spindle-shaped, tuberculate or spiny) which bear the reproductive structures (conceptacles)
Spine-like appendages	Slender, rigid, pointed projections arising from various parts of the thallus (e.g., apex, axes, and branches)
Spinose	Bearing spines, sharp-pointed projection
Spinose branchlets	Short, spine-like lateral ramuli
Stolon	A prostrate or creeping axis
Stoloniferous	Stolon-like
Subterminal	Occurring or attached just below the terminal part
Tophules	Swollen storage structures at the base of primary branches
Trifid	Divided into three
Tuberculate	With small swellings
Verrucose	Warty aspect
Warty	Covered with wart-like protuberances

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