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## Taxonomic revision and systematic notes on some *Halecium* species (Cnidaria, Hydrozoa)

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### Abstract

Although the genus *Halecium* is easy to recognize, identifications at the species level are often difficult, this even for quite common and supposedly well-known species of the north-eastern Atlantic. This paper revises and re-describes some *Halecium* species which resemble each other closely and which are not easy to distinguish. Additional information on a few rare species is also provided. The study is based on material collected from the North Atlantic, Mediterranean, South Africa, and New Zealand. *Halecium scutum* Clark, 1877 is recognized as a valid species and distinct from both *H. beanii* and *H. halecinum*; colony form and microscopic characters allow a distinction. The pinnate colony form of *H. halecinum* is a characteristic trait, but not all colonies show this growth form. *Halecium beanii* can occur in monosiphonic and polysiphonic colonies. Monosiphonic colonies of *H. beanii* have probably been misidentified by some authors as *H. lankesterii*. The differences of *H. lankesterii* to *H. beanii* and *H. petrosum* are discussed. The South African population of the reportedly cosmopolitan *H. beanii* has distinct gonothecae and could belong to a separate species. The Mediterranean *Halecium mediterraneum* is hardly distinguishable from the New Zealandic *H. delicatulum*, but it is kept separate mainly for biogeographic reasons. The rare Mediterranean *Halecium banyulense* is re-described based on a second find from Naples. The male gonothecae of *Halecium corrugatissimum* are described for the first time.

**Keywords:** BIOFAR, BIOICE, Cnidaria, Haleciidae, *Halecium*, Hydrozoa, Iceland, Mediterranean, New Zealand, north-eastern Atlantic, revision, South Africa, species identification, The Faroes, variation

### Introduction

The genus *Halecium* comprises currently about 120 valid nominal species (Vervoort and Watson 2003). They often form large, conspicuous colonies and can be found in all oceans. The genus is also well represented in shallow waters and therefore regularly mentioned in faunal synopses and ecological surveys. Due to the characteristic short hydrothecae, it is quite easy to recognize members of the genus. However, many nominal *Halecium* species are very difficult to distinguish and the status of a considerable number of them is still unclear. Species identification relies mostly on microscopic characters and due to the

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relative simplicity and morphological variability it is sometimes quite a cumbersome task. Taxonomically, the shape of the female gonothecae is certainly the most important character. Several species are currently only reliably distinguishable if female gonothecae are present. For these species, it is therefore impossible to identify immature or male specimens, at least if they are not part of a series that also includes reproductive female colonies. Although it has been known for quite some time that single, immature colonies are often not identifiable, many authors nevertheless continued to do so. These insecure identifications contributed largely to the difficult taxonomic situation of the genus *Halecium*. Many of its nominal species are indeterminate and dubious.

Some characters rarely used in *Halecium* systematics could improve the problem. Cornelius (1998) found some important differences in the living hydranths. Unfortunately, these traits are mostly impossible to study in preserved material and material from deeper waters is usually dredged and therefore often moribund or dead once it reaches the surface. Other largely unexploited characters are the nematocysts and zooxanthellae, which to some degree can also be observed in preserved material. The colony form and the branching pattern are other important characters that have unfortunately been neglected too often.

Another important aspect of the hydrozoans is their large number of cosmopolitan or circumglobal species (cf. Boero and Bouillon 1993). Some *Halecium* species are also reportedly cosmopolitan. That such broad distributions can also be the result of overconservative systematics has been shown for other lower invertebrates (e.g. Klautau et al. 1999), and sibling species in the sea could be much more common than previously thought (Knowlton 1993). Many cosmopolitan hydrozoan species could thus turn out to be complexes of several biological species.

The present publication therefore aims at revising taxonomic errors, at providing a discussion on how to distinguish closely similar species, and to show that some circumglobal species nevertheless show some regional differences. Only species for which new material was available are treated here.

## Material and methods

The material used for this study is based on material of the Natural History Museum of Geneva (MHNG), which also includes recent collections made by the author in New Zealand, South Africa, and the Mediterranean. Some new material from Iceland collected by the BIOICE programme and not yet reported in my earlier publications (Schuchert 2000, 2001) was obtained from the Zoological Museum in Copenhagen. The majority of this material is now in possession of the Icelandic Museum of Natural History in Reykjavík. Material from the Faroes was obtained through the BIOFAR collection. The BIOFAR programme was a predecessor programme of BIOICE and intended to survey the benthic fauna of the Faroe Islands (Nørrevang et al. 1994). The hydroids of the BIOFAR programme are now held by the Kaldbak Marine Laboratory, The Faroes. Some slide material of the BIOFAR and BIOICE collections is also kept by the Natural History Museum of Geneva (MHNG). For more details on methods see Schuchert (1996, 2001). Technical terms are explained in Millard (1975) and Cornelius (1995).

### *Halecium scutum* Clark, 1877

(Figures 1, 2)

*Halecium scutum* Clark 1877, p 14, Plate 4 Figures 13, 14; Broch 1918, p 39, Figures 14; Calder 1970, p 1509, Plate 2 Figures 2, 3.

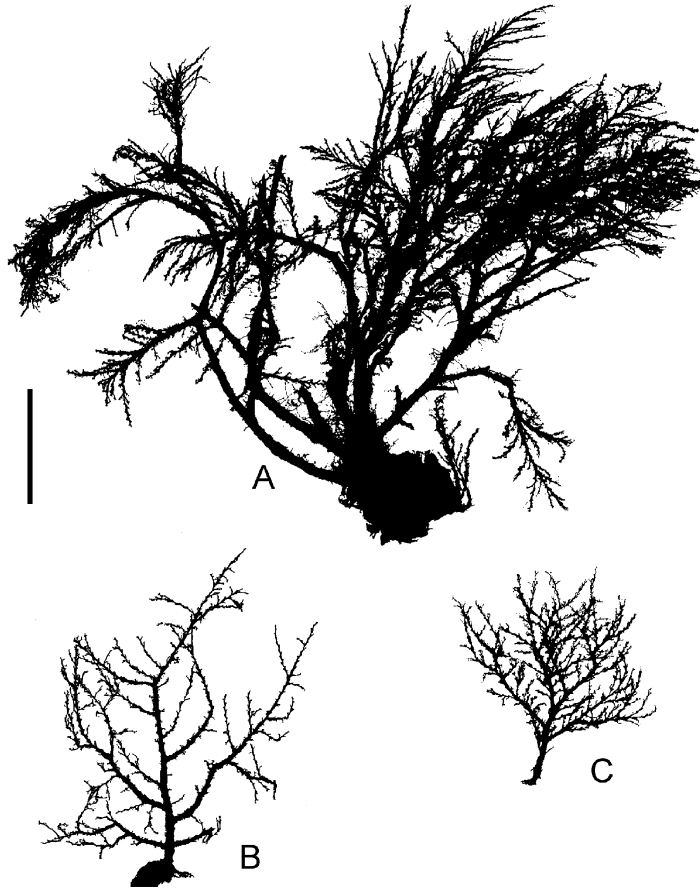


Figure 1. *Halecium scutum* Clark, 1877; colony silhouettes of material from The Faroes. (A) MHNG INVE 33550; (B) BIOFAR station 699; (C) BIOFAR station 459. Scale bar: 2 cm.

*Halecium boreale* Lorenz 1886, p 26, Plate 1 Figures 1, 2.

*Halecium halecinum*: in part Broch 1910, p 144, Figure 4 I–VIII (not others).

*Halecium beringi* Naumov 1960, p 449, Figures 337, 338; Naumov 1969, p 484, Figures 337, 338; Antsulevich 1987, p 107.

*Halecium beanii*: Naumov 1969, p 483, Figure 336; in part Schuchert 2001, p 73, Figure 59A–D.

[not *Halecium beanii* (Johnston 1838).]

#### *Material examined*

MHNG INVE 28450, Greenland, Holsteinsborg, 66.93°N, 53.68°W, 165 m, 8 July 1971, with female gonothecae. MHNG INVE 28731, Greenland, Augpilagtoq, 60.14°N, 44.31°W, 50–60 m, 30 July 1970, on rock, with male gonothecae. MHNG INVE 33550, BIOFAR station 111, The Faroes, 62.11°N, 6.5°W, 50 m, 25 July 1987. BIOFAR collection station 556, The Faroes, 61.97°N, 6.54°W, 41 m, 22 September 1989, on barnacles. BIOFAR collection station 699, The Faroes, 62.12°N, 6.83°W, 72 m, 10 May

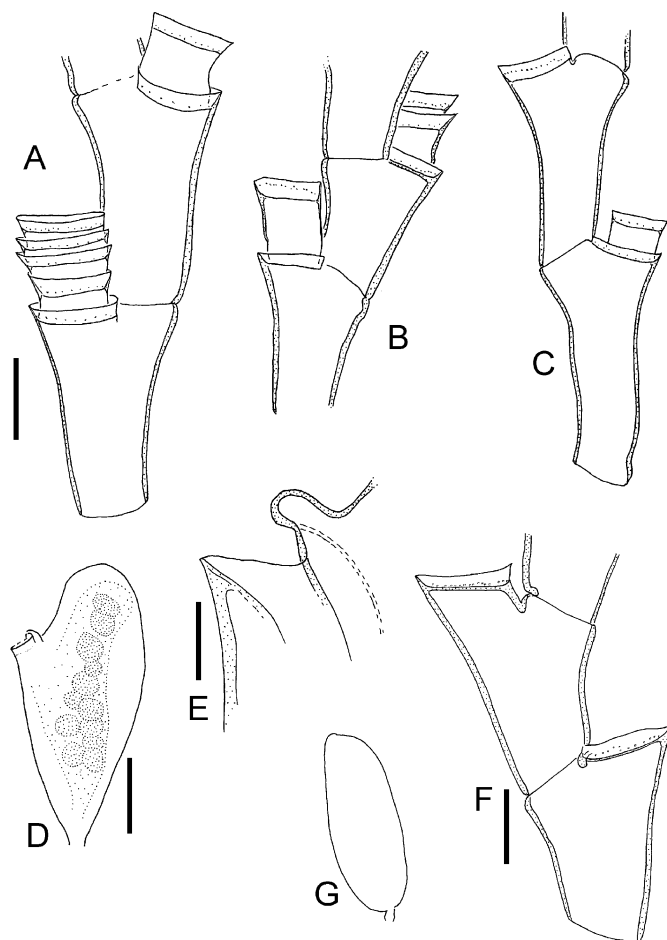


Figure 2. *Halécium scutum* Clark, 1877. (A) From BIOFAR 699; (B) BIOFAR 556; (C–E) Holsteinsborg, Greenland; (F, G) Augpilagtoq, Greenland. (A–C, F) Segments from monosiphonic parts with primary and sometimes secondary hydrothecae (scale bar: 0.2 mm); (D) female gonotheca in side view, eggs stippled (scale bar: 0.2 mm); (E) higher magnification of gonothecal opening, side view (scale bar: 0.1 mm); (G) male gonotheca (same scale bar as D).

1990, on *Tubularia indivisa*, with gonothecae. BIOICE collection, Iceland, 65.78°N, 14.22°W, 28–60 m, 24 July 1991. BIOFAR station 459, The Faroes, 63.00°N, 6.96°W, 910 m, 4 June 1989.

### Description

Colonies erect, up to 10 cm (reportedly up to 30 cm), imperfectly pinnate to shrubby, some colonies perfectly planar. Stem sometimes covered by bark-like overgrowth of anastomosed stolons. Main stem and branches polysiphonic, thinning out to monosiphonic ends. Internodes roughly equal in length; nodes oblique, sometimes indistinct. Hydrotheca sitting at the end of segment like a prolongation of it, not or only slightly inclined, slightly overtopping distal node of segment. Hydrotheca very shallow, walls straight, diameter at

base 0.18–0.25 mm, depth 20–40  $\mu\text{m}$ , with desmocytes, without pseudodiaphragms, rim of hydrotheca often damaged. Secondary hydrothecae on short hydrophore, the latter usually shorter than 1.5 times the diameter. Male gonotheca club- to oblong sac-shaped, 1.4 mm long. Female gonotheca club-shaped, up to 2 mm long and 0.8 mm broad, straight, somewhat flattened, distal end rounded, opening at side at approximately middle of gonotheca on a distinct shoulder; opening partially covered by a characteristic hood-like process, two protruding polyps, 10–20 eggs per gonotheca. Nematocysts: two types of capsules, type I  $(9\text{--}10) \times (3.5\text{--}4) \mu\text{m}$ ; type II  $(5.5\text{--}7) \times (1.5\text{--}2.5) \mu\text{m}$ .

### Distribution

Circumpolar in the Arctic Sea, in the North Atlantic south to Cape Farewell in Greenland, Iceland and Faroe Islands. Type locality: Clark (1877) gives several localities in Alaska.

### Remarks

The trophosome and male gonothecae of *Halecium scutum*, *H. halecinum* and *H. beanii* can resemble each other closely and it is difficult to identify immature or male specimens. In contrast, their female gonothecae are quite distinct and allow a relatively secure identification (compare Figures 2D, 4D and 5G). The female gonotheca of *H. scutum* has a characteristic lip or hood above the hydrothecae on its side wall (Figure 2E). Unfortunately, the shape of the female gonotheca of *H. scutum* can occasionally be so variable as to make it resemble that of *H. halecinum* (Broch 1918, Figure 14). It is therefore not surprising that Broch (1910, as *H. halecinum* forma *gigantea*) considered *H. scutum* as an arctic form of *H. halecinum*. Later, Broch (1918) revised his opinion and kept both species distinct. Calder (1970) likewise regarded *H. scutum* as valid and distinct from *H. halecinum*. Naumov (1969) synonymized *H. scutum* and *H. beanii*, a view later hesitatingly adopted by, for example, Cornelius (1975) and myself (Schuchert 2001).

Examination of material from the Faroes and Greenland, however, convinced me that *H. scutum* is clearly distinct from both *H. beanii* and *H. halecinum*. Although my material from the Faroes did not contain female gonothecae, there were many large infertile and male colonies that agreed well with female colonies from Greenland and with the description of Broch (1918).

Mature colonies of *H. scutum* are larger and considerably more robust than those of *H. halecinum* and especially *H. beanii* (compare Figures 1A–C, 3A–C and 5A–C). The best character, to distinguish *H. scutum* from *H. halecinum* and *H. beanii*, apart from the female gonothecae, is the relative shortness of the secondary hydrophores (Figure 2A–C). These secondary hydrophores are maximally as long as 1.5 times their diameter, but normally much shorter. In *H. halecinum* and *H. beanii*, they are longer, the ratio of length to diameter being in the range of 2 and more (compare Figures 2A–C, 4A–C and 5D, F). *Halecium scutum* also lacks the characteristic pinnate growth often found in *H. halecinum* and its hydrophores are in line with the main axis of the internode. In *H. halecinum* the hydrophores are inclined (Figure 4A, B). In *H. beanii*, the diameter of the hydrotheca is distinctly smaller (0.12–0.16 versus 0.18–0.25 mm), the hydrotheca is usually held oblique relative to the internode axis, and the size of the type I nematocyst capsule is larger.

In the material from the Faroe Islands, one large colony of *H. scutum* was overgrown with several other hydroids, among them were female and male shoots identified as *H. beanii*. The differences in the microscopic structure were quite evident. This syntopic occurrence

is further evidence for them being separate species. For further details see below under *H. beanii*.

Another peculiarity of most large colonies of *H. scutum* is a bark-like covering of the stem by a layer of tightly anastomosed stolons. A similar, but less anastomosed formation may occur in some larger colonies of *H. halecinum*.

Another European species that can be confused with the species discussed above is *Halecium sessile* Norman, 1867. According to Cornelius (1995), this species has very short secondary hydrothecae without distinct hydrophores. This trait may allow a reliable distinction.

*Halecium boreale* Lorenz, 1886 is likely a synonym of *H. scutum*. Lorenz (1886) described *H. boreale* as devoid of female gonothecae and the eggs are reported to develop in the gastric cavity of the feeding zooids (sic!). The males have normal gonothecae. Lorenz depicts a male colony that is indistinguishable from *H. scutum*. The feeding zooid of this colony contains spherical bodies. It seems to me that Lorenz misinterpreted food items, perhaps even eggs of another animal, as the eggs of his *Halecium boreale*. Although it is thinkable that there exist *Halecium* species without gonothecae, I am not aware of any other such species. Moreover, the presence of normal male gonothecae and the position of the eggs within the gastric cavity make Lorenz's assertion improbable.

*Halecium beringi* Naumov, 1960 was synonymized with *H. scutum* by Antsulevich (1987).

Clark's publication with the original description of *H. scutum* was apparently published in 1877 and not 1876 (Cornelius 1982, p 129).

***Halecium halecinum* (Linnaeus, 1758)**

(Figures 3, 4)

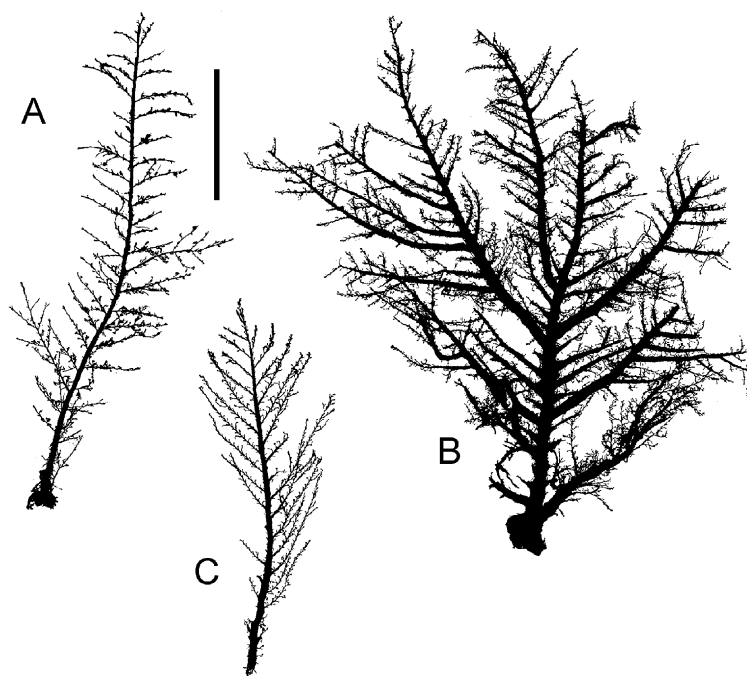


Figure 3. *Halecium halecinum* (Linnaeus, 1758); colony silhouettes, note variation of shapes. (A) Canary Islands; (B) The Faroes (BIOFAR station 111); (C) The Faroes (BIOFAR station 554). Scale bar: 2 cm.

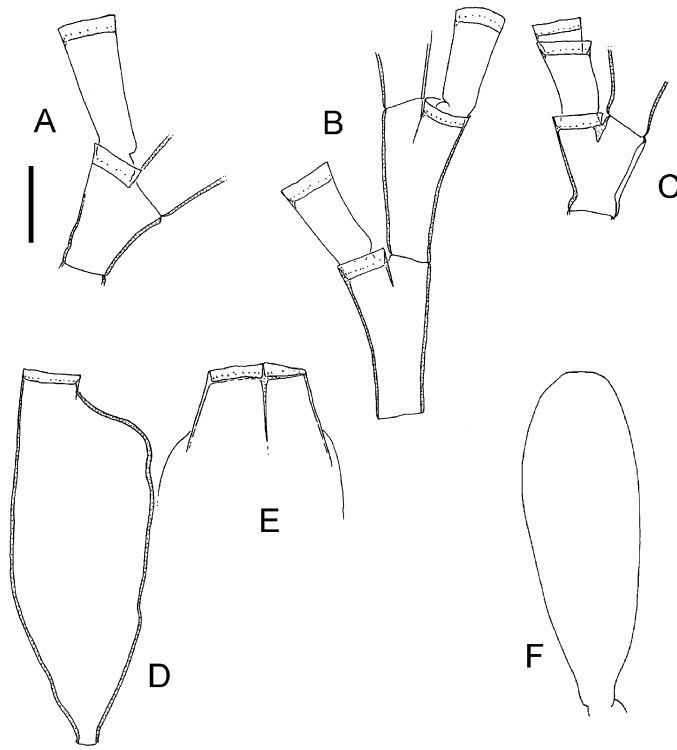


Figure 4. *Halecium halecinum* (Linnaeus, 1758). (A–C) Segments of monosiphonic parts, with secondary hydrothecae, note length variation of internodes, BIOFAR station 350, 205 and 351; (D) BIOFAR 351, female gonotheca in side view; (E) as in (D), but seen from anterior side, note bipartite hydrotheca; (F) BIOFAR 597, male gonotheca. Scale bar: 0.2 mm.

*Sertularia halecina* Linnaeus 1758, p 809.

*Halecium geniculatum* Norman 1867, p 205.

[Not *H. geniculatum* Nutting 1899=*H. tenellum* Hincks 1861.]

*Halecium halecinum*: Broch 1911, p 22, Figure 22; Broch 1918, p 36, Figures 11, 12; Naumov 1969, p 482, Figures 16K, 335, Plate 17 Figure 3; Vervoort 1972, p 25, Figure 3a; Cornelius 1975, p 393, Figure 6, synonymy; Millard 1975, p 150, Figure 49A–H; Cornelius 1995, p 279, Figure 63; Medel and Vervoort 2000, p 14, Figure 2, bibliography; Schuchert 2001, p 78, Figure 64A, B.

Not *Halecium halecinum* var. *minor* Pictet 1893, p 20, Plate 1 Figures 14, 15; Schuchert 2003, p 153.

#### Material examined

MHNG INVE 34732, France, Baie de Seine, 17 September 1987, dredged at 25 m depth, female and male colonies. MHNG INVE 26671, France, Brittany, Roscoff, Roscoff Bretagne, coll. September 1995. MHNG INVE 27667, Canary Islands, Lanzarote, 23 September 1999, coll. A. Faucci. MHNG INVE 33575 (BIOFAR station 205), 62.06°N, 5.89°W, 160 m, 11 May 1988, with female gonothecae, colony form atypical. MHNG INVE 33580 (BIOFAR station 402), the Faroes, 62.1°N, 8.14°W, 121 m, 30 May 1989,



with male gonothecae. MHNG INVE 33582 (BIOFAR station 350), the Faroes, 62.26°N, 7.99°W, 107 m, 22 July 1988, typical female colonies. MHNG INVE 33587 (BIOFAR station 554), 61.94°N, 6.49°W, 62 m, 22 September 1989, no gonothecae, typical colony form. BIOFAR station 111, 62.12°N, 6.50°W, 50 m, 25 July 1987, one female gonotheca present. BIOFAR station 351, 62.26°N, 7.77°W, 102 m, 22 July 1988, with female gonothecae. BIOFAR station 597, The Faroes, 62.17°N, 6.22°W, 100 m, 11 April 1990, male gonothecae present.

### Description

Colonies erect, stiff, up to 10 cm high, colony form often regularly pinnate, sometimes irregular or with several pinnate side-branches. Side-branches alternate, straight, evenly spaced, at constant angle of 40–60° to main axis, secondary branching possible. Stem and main branches polysiphonic, thinning out to terminal monosiphonic branches. Segments of similar length within a region of the colony, segment length much variable among colonies, nodes approximately transverse. Hydrotheca sitting on a shallow hydrophore which is oblique to main axis of internode, opening plane inclined. Hydrothecae alternate, walls straight, with desmocytes, hydrotheca diameter at base 0.12–0.14 mm, depth 30–50 µm. Secondary hydrothecae frequent, on a long hydrophore, the latter at least twice as long as diameter, secondary hydrophore near base usually with a kink. Male gonotheca club-shaped, length about 0.9 mm, aperture terminal. Female gonotheca paddle-shaped, tapering below, distally having a terminal aperture on one side and with right-angled “shoulder” on other side, aperture formed by a fused pair of hydrothecae that overtops gonotheca like a chimney, one or two polyps protruding from aperture, one to four eggs. Nematocysts: two types, type I (8–9.5) × (3.5–4) µm, type II (5–6) × (1.5–2) µm.

### Distribution

East and West Atlantic, Mediterranean, South Africa, Pacific, Arctic Seas. Type locality: Whitstable, Kent, England.

### Remarks

As discussed under *H. scutum*, this species can be difficult to distinguish from *H. scutum* and *H. beanii*. In waters around the British Isles and continental Europe, *Halecium halecinum* often forms quite regular, pinnate colonies (Figure 3A, C). Cornelius (1995) considers this an important diagnostic trait of the species. In the material from the Faroes, the colonies were often quite irregular (Figure 3B). The pinnate colony form, however, is also found in Faroese waters (Figure 3C). Also some of the colonies examined from the English Channel were not so obviously pinnate. Hincks (1868, Plate 42, Figure a) depicted a colony originating from the British Isles which also deviates somewhat from the strictly pinnate form shown in the same plate. The colony form of *H. halecinum* is therefore not always regularly pinnate. But if present, the pinnate colony form is certainly a diagnostic trait of *H. halecinum*. Infertile or male colonies with atypical colony form can be impossible to identify if they are not part of a larger series that also includes fertile females.

Broch (1918) thought that the shape of the secondary hydrothecae in *H. halecinum* differs from those of *H. beanii* in having an asymmetric adcauline wall. Such a difference was not

found in the material examined here and neither was it mentioned by Cornelius (1995) (compare Figures 4A–C and 5D, F). Millard (1966, 1975) also found that only the female gonotheca allows a reliable identification. Medel and Vervoort (2000) found that side-branches arise frontally or at the rear in *H. halecinum*, while in *H. beanii* they arise laterally.

***Halecium beanii* (Johnston, 1838)**

(Figures 5, 6)

*Thoa beanii* Johnston 1838, p 120, Plate 7 Figures 1, 2.

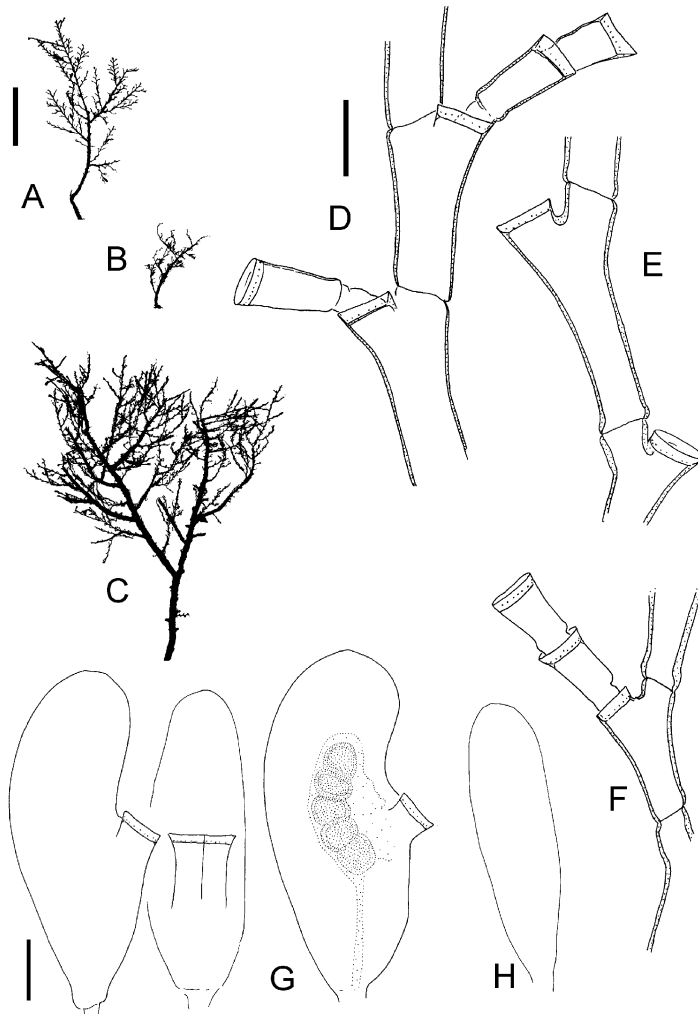


Figure 5. *Halecium beanii* (Johnston, 1838). (A, D) From Roscoff; (B, C, E–H) from The Faroes. (A–C) Colony silhouettes (scale bar: 1 cm); (D–F) subterminal portions of branches (scale bar: 0.2 mm); (G) female gonotheca, middle one seen from side of hydrothecae, right one shown with developing embryos (scale bar: 0.2 mm); (H) male gonotheca (same scale bar as G).

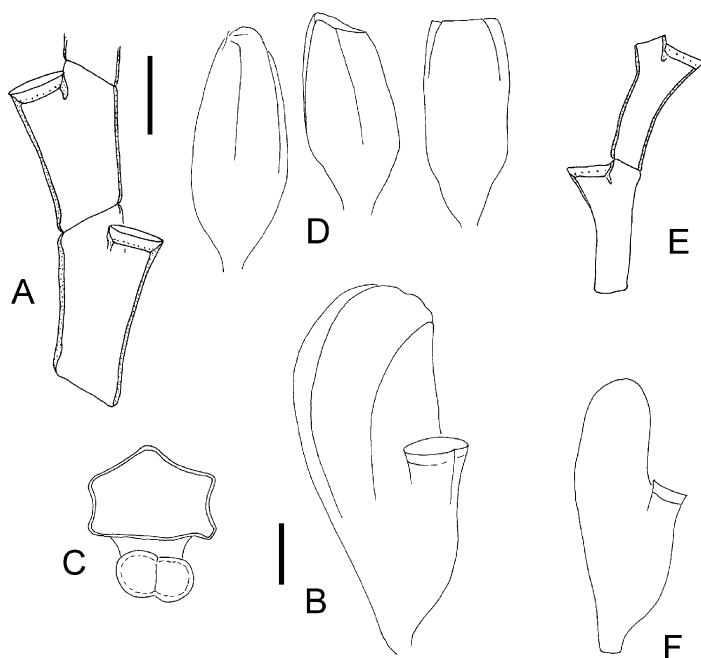


Figure 6. *Halecium beanii* (Johnston, 1838). (A–D) After material from South Africa; (E–F) after material from New Zealand. (A) Two internodes (scale bar: 0.2 mm); (B) female gonotheca in oblique view (scale bar: 0.2 mm); (C) cross-section of female gonothecae in about the middle of its height, note polygonal outline (same scale bar as B); (D) three male gonothecae, note variability (same scale bar as B); (E) two internodes (same scale bar as A); (F) female gonotheca (same scale bar as B).

*Halecium beanii*: Broch 1918, p 38, Figure 13; Millard 1975, p 144, Figure 47A–E; Cornelius 1995, p 276, Figure 62; Hirohito 1995, p 17, Figure 3d–f, Plate 1 Figure A; Medel and Vervoort 2000, p 8, Figure 1, bibliography; Vervoort and Watson 2003, p 86, Figure 15D–H.

In part *Halecium beanii*: Ralph 1958, p 332, Figure 10a, b, e–k; Naumov 1969, p 483, Figures 19G, H, 336; Schuchert 2001, p 73, Figure 59A–D.

? *Halecium lankesterii*: Hamond 1957, p 302, Figures 9, 10; Vervoort 1959, p 221, Figures 3–5; Cornelius 1995, p 285, Figure 65.

#### Material examined

MHNG INVE 33451, France, Brittany, Roscoff, between Islets Astan and Ty Saozon, 24 May 1910, leg. M. Bedot, with female gonothecae. MHNG INVE 33556 (BIOFAR station 193), The Faroes, 62.41°N, 6.91°W, 10 May 1988, 108 m, with female gonothecae. MHNG INVE 33593 (BIOFAR station 111), The Faroes, 62.11°N, 6.50°W, 50 m, 25 July 1987. MHNG INVE 32968, Mediterranean, France, off Banyuls-sur-Mer, 62 m, 15 May 2002, on shell debris, with typical female gonothecae, polysiphonic. MHNG INVE 34011, South Africa, Simon's Town, Boulder Beach, coll. P. Schuchert, 11 January 2003, 1–2 m depth, several female and male colonies. MHNG INVE 25068, New Zealand, Devonport, Cheltenham Beach, coll. P. Schuchert, 14 October 1998, preserved as three slides, with female gonothecae.

*Description of European material*

Colonies 1–10 cm, irregularly branched, varied in appearance. Fertile colonies polysiphonic, thinning out to monosiphonic. Internode length of one colony relatively homogeneous, variable between colonies. Nodes alternately oblique. Hydrotheca sitting on a shallow hydrophore, the latter held oblique to main axis of internode, opening plane of hydrotheca inclined. Hydrothecae alternate, not adnate to internode, rim not overtopping level of distal node. Hydrotheca with straight walls, walls not much diverging, diameter at level of diaphragm 0.12–0.16 mm, depth 25–45  $\mu\text{m}$ . Secondary hydrothecae frequent, their hydrophores long, length two to four times longer than diameter, often with basal kink. Female gonotheca 1–1.2 mm long, curved, approximately kidney-shaped, in middle of concave side two fused hydrothecae, in side-view held oblique, without hood-like cover, normally with two hydranths (may be reduced), convex side of gonotheca without longitudinal crests or crease-lines, four to six eggs per gonotheca, develop in situ into planulae. Male gonothecae club-shaped with terminal aperture, length up to 1 mm, breadth up to 0.25 mm. Nematocysts: two types of capsules, type I is a heteroneme  $(13\text{--}15) \times (6\text{--}6.5) \mu\text{m}$ ; type II  $(5.5\text{--}6.5) \times (1.5\text{--}2) \mu\text{m}$ .

*Characteristics of South African material*

Like European material, but hydrothecae adnate; female gonotheca with polygonal cross-section and with five to six longitudinal crease-lines or shallow ridges, egg number 8–20. Male gonotheca also polygonal in cross-section, but more irregular, distal end often wedge-shaped, aperture terminal. Nematocysts: two types of capsules, larger one is a macrobasic eurytele  $(11\text{--}12) \times (4\text{--}5) \mu\text{m}$ ; smaller one as above.

*Characteristics of New Zealand material*

Like European material, but hydrothecae adnate and smaller, diameter 0.10 mm, depth 25–30  $\mu\text{m}$ . Female gonothecae also identical to European population, with four to five embryos or eggs.

*Distribution*

Considered to be nearly cosmopolitan, found in mostly shallow to moderately deep waters (0–150 m). Type locality: near Scarborough, Yorkshire, England (Cornelius 1975).

*Remarks*

The examined fertile female colonies from the northern Atlantic and Mediterranean were all rather small and delicate (see Figure 5A–C). One sample (MHNG INVE 33593) was particularly confusing as it was growing on a large colony of *H. scutum*. There were female as well as male stems present, although in different regions. The host had therefore been colonized by several, independent colonies (genets). The gonothecae bearing shoots included typical, polysiphonic ones, but also many monosiphonic ones. These monosiphonic colonies were thus hardly distinguishable from *H. lankesterii* sensu Cornelius (1995), a species closely resembling *H. beanii*. The principal difference between *H. lankesterii* and *H. beanii* according to Cornelius (1995) are the monosiphonic stems in the former versus polysiphonic stems in the latter. *Halecium lankesterii* is, however, doubtless a valid species and comparison with

material from Brittany showed that it is distinct from *H. beanii*. I suspect that at least some material identified as *H. lankesterii* by Hamond (1957), Vervoort (1959) and Cornelius (1995) was in fact monosiphonic *H. beanii* (see under *H. lankesterii*).

The microscopic structure of *Halecium beanii* is almost identical to that of *H. halecinum* (cf. Millard 1966, 1975). Both species can only reliably be distinguished by comparing the female gonothecae. *Halecium halecinum* additionally forms often quite regularly pinnate colonies, which helps to distinguish it from *H. beanii* and *H. scutum* (compare Figures 1A–C, 3A–C and 5A–C).

Naumov (1969) synonymized *Halecium scutum* Clark, 1877 and *H. beanii*, a view later hesitatingly adopted by, for example, Cornelius (1975) and myself (Schuchert 2001). However, examination of the material described in this report convinced me that *H. scutum* is a distinct species. The female gonothecae of the two species allow a distinction. There are also significant differences in the colony size and details of the hydrotheca (see under *H. scutum*). The occurrence of *H. beanii* on a colony of *H. scutum* described above strongly argues in favour of them being distinct. Vervoort (1972) and Hirohito (1995) also thought that they are separate species.

The material of *H. beanii* from New Zealand described above was in no significant way different from European specimens, confirming the reports of Ralph (1958). However, part of Ralph's material allocated to *H. beanii* has recently been attributed to a new species, *Halecium ralphae*, by Watson and Vervoort (2001). The female gonothecae of this species is strongly curved, forming nearly a complete circle. Watson and Vervoort (2001) postulated also that *H. beanii* has female gonothecae with one hydrotheca only. This is evidently not the case, as also all here examined female gonothecae had a pair of fused hydrothecae.

The material from South Africa deviated in several aspects from European specimens. Especially the female gonothecae with their polygonal cross-section and the longitudinal ridges or crease-lines rendered it distinct. Also the increased egg number per gonotheca is a significant difference. Following the general practice in current hydrozoan systematics, all these differences would justify the postulation that the South African population belongs to a different species. Because the limited number of examined colonies does not allow the variability of the South African population to be assessed, no new name is proposed here.

### ***Halecium lankesterii* (Bourne, 1890)**

(Figure 7)

*Halecium robustum* Pieper 1884, p 166; Broch 1912, p 14, Figure 1; Babić 1913, p 470, Figures 4–6; Bedot 1914, p 82, Plate 5 Figure 6.

[Not *Halecium robustum* Verrill 1874=*Zygophylax pinnata* (G. O. Sars 1874).]

*Haloikema lankesterii* Bourne 1890, p 396, Plate 26 Figures 1, 2.

*Halecium sessile* var. Billard 1904, p 160.

*Halecium ophioides*: Babić 1910, Plate 1 Figure 1b; Babić 1913, p 469, footnote.

? Not *Halecium lankesterii*: Hamond 1957, p 302, Figures 9, 10; Vervoort 1959, p 221, Figures 3–5; Millard 1975, p 153, Figure 50B–E; Cornelius 1995, p 285, Figure 65.

*Halecium lankesteri*: Bedot 1911, p 213, Plate 11, Figures 1–5; Peña Cantero and García Carrascosa 2002, p 66, Figure 13a–c.

### *Material examined*

MHNG INVE 33471, as *Halecium lankesteri*, France, Brittany, Roscoff, coll. 6 July 1912 by M. Bedot, mentioned in Bedot (1914), with female gonothecae. MHNG INVE 33478, as

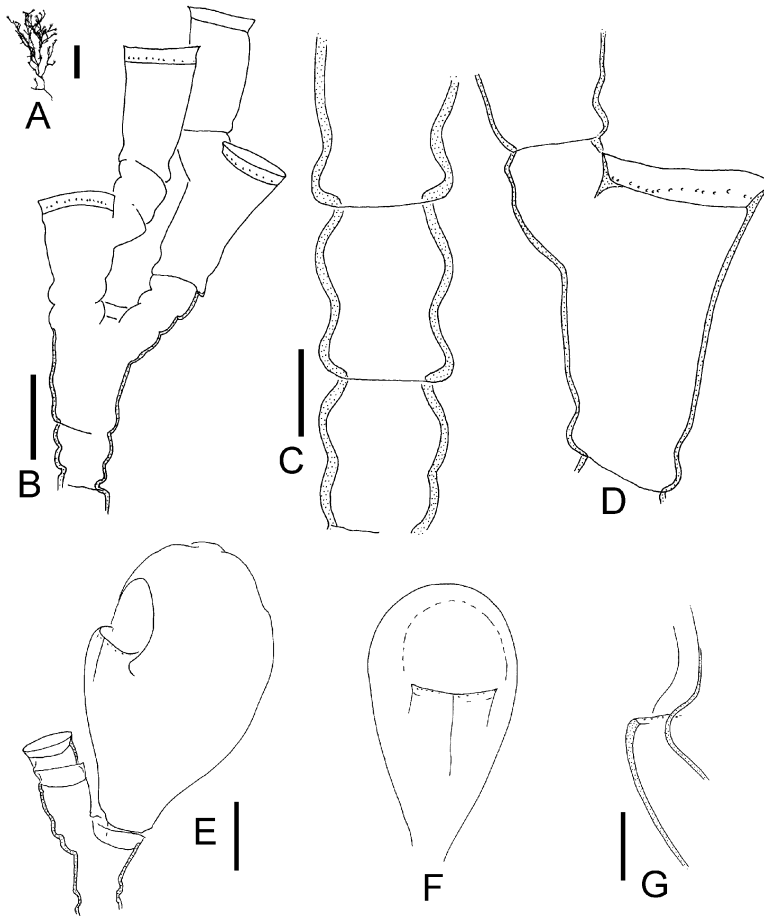


Figure 7. *Halecium lankesterii* (Bourne, 1890); after material from Brittany. (A) Colony silhouette (scale bar: 5 mm); (B) part of stem (scale bar: 0.2 mm); (C) lower part of stem with characteristic ahyrothecate segments with constriction in middle (scale bar: 0.1 mm); (D) hydrothecate segment (same scale bar as C); (E) female gonotheca in oblique view, shown without hydranths (scale bar: 0.2 mm); (F) female gonotheca seen from anterior side (same scale bar as E); (G) lateral view of female gonotheca, higher magnification of opening (scale bar: 0.1 mm).

*Halecium robustum*, Roscoff, 1 June 1910, leg. M. Bedot. MHNG INVE 33479 *Halecium robustum*, Roscoff, May 1910, leg. M. Bedot. MHNG INVE 33480, as *Halecium robustum*, Roscoff, 6 May 1910, leg. M. Bedot.

### Description

Colonies erect, stems unbranched or sparingly branched, up to 8 mm high and with up to 40 hydranths. Stems arise from creeping hydrorhiza. Stems always monosiphonic, irregularly segmented, regularly with intercalated segments without hydrotheca, these internodes short and with two marked bulges at their ends (Figure 7C). Internodes generally short and stout, sides often undulated. Hydrotheca sitting at the end of segment like a prolongation of it, rim perpendicular to segment axis. One or two side-branches, if

present, arising immediately below hydrotheca, angles quite acute (Figure 7D). Hydrotheca with slightly diverging wall, these quite straight, not curved; diameter at level of diaphragm 0.15–0.17 mm, depth 30–45 µm. Secondary hydrothecae present, with hydrophore. Hydranths with 20–24 tentacles, body and tentacles containing zooxanthellae. Gonothecae arising from within primary hydrothecae. Female gonotheca pear-shaped, about 0.8–0.9 mm long, slightly compressed, opening on side, formed by a short, vertical, completely adnate tube with a median septum, opening without distinct hydrotheca, but rim with some desmocytes; opening plane perpendicular to long axis of gonotheca; two protruding hydranths present; about three eggs per gonotheca. Male gonotheca not observed; according to Babić (1913) oblong ellipsoid, 0.68–0.85 mm long, smooth, without hydranths.

### Distribution

Mediterranean, tropical and subtropical eastern Atlantic, English Channel, North Sea, South Africa, Moçambique. Type localities: near Plymouth, England (details in Cornelius 1975).

### Remarks

The type material of Bourne (1890) did not include gonothecae, a character usually indispensable for a correct identification of *Halecium* species. Two other traits, however, allow recognition of the species. This is for one the presence of zooxanthellae, for the other the segmentation pattern with its short, ahydrothecate segments with bulging ends (or segments constricted in the middle). Bourne's material had both characteristics. Babić (1913) and Bedot (1914) described fertile material. Later authors, like Vervoort (1959), Millard (1975) and Cornelius (1995), also included material lacking zooxanthellae and with smooth perisarc. The female gonothecae depicted by Hamond (1957), Vervoort (1959) and Cornelius (1975, 1995) differ from the one depicted in Figure 7E and they appear identical to that of *H. beanii* (Figure 5G). The egg number is also higher than usually found in *H. lankesterii*. These differences prompted Peña Cantero and García Carrascosa (2002) to postulate that the mentioned material of Cornelius and Vervoort actually belonged to a different, so far unnamed species. I concur with Peña Cantero and García Carrascosa (2002). The occurrence of fertile, monosiphonic stems of *Halecium beanii* (see under this species) led me to suspect that the material of Hamond (1957), Vervoort (1959) and Cornelius (1975, 1995) was actually composed of monosiphonic colonies of *H. beanii*. Hamond (1957) acknowledged that *H. beanii* and *H. lankesterii* resemble each other very closely, but he insisted that they are distinct. He kept them apart on account of the sharply curved side-branches. His colony in Figure 9 resembles more *H. lankesterii* and it thus appears that his material contained indeed some *H. lankesterii* besides monosiphonic *H. beanii*.

*Halecium lankesterii* also occurs in the Mediterranean and can be confounded with *H. petrosum* if no female gonothecae are present. The presence of zooxanthellae, the wider hydrothecae and the characteristic ahydrothecate segments of *H. lankesterii* help to distinguish them (compare Figures 7 and 8).

*Halecium nanum* Alder, 1859 resembles closely *H. lankesterii* as described above. Both have zooxanthellae in their tissue. The female gonotheca of *H. nanum* has two hydrothecae that reach to the distal end (Calder 1991), while they end roughly in the middle in *H.*

*lankesterii*. Their different ecology additionally suggests that they are likely separate species. *Halecium nanum* is usually epiphytic, mostly occurring on pelagic *Sargassum* sp. in warmer waters of the Atlantic. Cornelius (1995) thought that it might be wider spread and occur on a wider range of substrata.

***Halecium petrosum* Stechow, 1919**

(Figure 8)

*Halecium robustum*: Motz-Kossowska 1911, p 346, Figure 14; Neppi 1921, p 13, Figures 4, 5.

[Not *Halecium robustum* Pieper 1884, p 166.]

*Halecium petrosum* Stechow 1919, p 36, new name; Coma et al. 1992, p 162, Figure 1A; Peña Cantero and García Carrascosa 2002, p 69, Figure 14a–c.

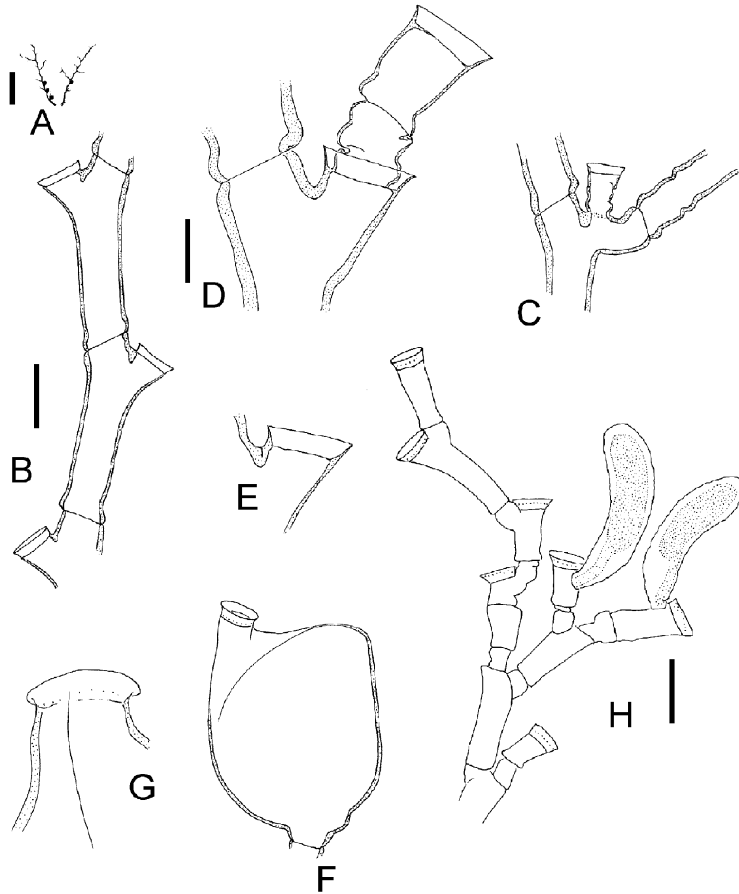


Figure 8. *Halecium petrosum* Stechow, 1919; after material from Banyuls-sur-Mer. (A) Colony silhouette (scale bar: 5 mm); (B) two internodes (scale bar 0.2 mm); (C) branching point (same scale bar as B); (D) hydrophore, primary and secondary hydrothecae (scale bar: 0.1 mm); (E) hydrotheca with straight walls (same scale bar as D); (F) female gonotheca in side view (same scale bar as B); (G) hydrotheca of female gonotheca in anterior view (anterior side in F is directed towards left) (same scale bar as D); (H) part of male colony, sperm masses stippled, note that this sample shows signs of multiple re-growth and regeneration, its identity is not entirely secure (scale bar: 0.2 mm).



*Material examined*

MHNG INVE 26665, Anse de Troc, Banyuls-sur-Mer Pyrénées Orientales, France, 2 m, coll. P. Schuchert, 23 June 1997, fertile female. MHNG INVE 29763, Spain, Mallorca, Cala Murada, coll. P. Schuchert, 23 August 2000, 0.5 m, on rock and red algae, shows signs of multiple re-growth and regenerations, identification not entirely secure.

*Description*

Colonies erect, branched, shoots 5–15 mm, monosiphonic, composed of main axis and shorter side-branches. Erect parts segmented by alternately oblique nodes; nodes distinct, internodes about 0.5–0.6 mm long, diameter 80–90 µm. Perisarc smooth. Side-branches originate from hydrophores. Hydrotheca near segment end, on very short hydrophore; hydrotheca does not reach beyond level of node. Primary hydrotheca with straight or slightly curved walls, basal diameter 0.10–0.12 mm, depth 20–30 µm, desmocytes present. Hydrophore without pseudodiaphragm. Secondary hydrotheca on corrugated hydrophore of variable length, several times longer than primary hydrophore. Gonothecae on main stem. Female gonotheca 0.6–0.7 mm long and about 0.5 mm broad, main body ovoid, bilaterally symmetric through a lateral hydrotheca that overtops gonotheca body, with crease-line running from hydrotheca along gonotheca body. Male gonothecae without hydrotheca, club-shaped, slightly curved or not, length 0.5–0.55 mm.

*Additional information*

Stems may reach 3 cm in height. Female gonotheca with two hydranths (Motz-Kossowska 1911).

*Biology*

Depth range 1–200 m, grows on a variety of solid substrata. Fertile colonies observed from June to October (Peña Cantero and García Carrascosa 2002). Ecological aspects were investigated by Coma et al. (1992).

*Distribution*

Mediterranean. Type localities: Cap Béar and Cap Abeille near Banyuls-sur-Mer, France, Mediterranean.

*Remarks*

Motz-Kossowska (1911) identified abundant material from Banyuls as *Halecium robustum* Pieper, 1884. The latter name was recognized by Bedot (1912, p 14) as a synonym of *H. lankesterii* (see also Hamond 1957 for more invalid homonyms of *Halecium robustum*). Because Motz-Kossowska's material had female gonothecae that differed from typical *H. lankesterii*, Stechow (1919) attributed it to a new species with the name *Halecium petrosum* (compare Figures 8F and 7E). Also the trophosomes of *Halecium lankesterii* and *H. petrosum* are quite distinct (compare Figures 7B and 8B, and remarks under *H. lankesterii*).

***Halecium labrosum* Alder, 1859**

(Figures 9, 10)

*Halecium labrosum* Alder 1859, p 354, Plate 13; Hincks 1868, p 225, Figure 27, Plate 44 Figure 1; Levinsen 1893, p 204, Plate 8 Figures 8, 9; Broch 1910, p 148, Figures 7, 8, Plate 2 Figure 4; Broch 1918, p 45, Figure 19; Naumov 1969, p 489, Figures 16B, 343, Plate 16 Figure 2; Calder 1970, p 1506, Plate 1 Figures 6–8; Cornelius 1975, p 396, Figure 7; Cornelius and Garfath 1980, p 282; Cornelius 1995, p 282, Figure 64; Schuchert 2001, p 79, Figure 65A–D.

*Halecium crenulatum* Hincks 1874, p 150, Plate 8 Figures 21–23; Levinsen 1893, p 204, synonym.

? Not *Halecium reflexum* Stechow 1919, p 37, Figures G, H.

*Halecium schneideri*: Leloup 1952, p 144, Figure 78A1–A3.

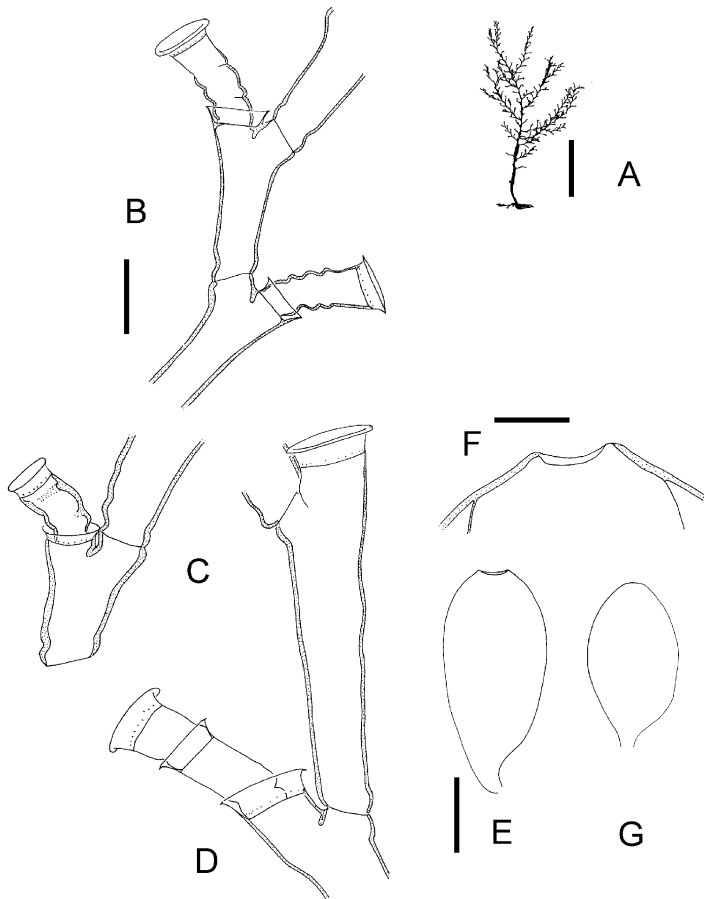


Figure 9. *Halecium labrosum* Alder, 1859. (A, B) From Roscoff; (C, D) from The Faroes, MHNG INVE 33524 and 33581; (E) MHNG INVE 25337, Iceland; (F) MHNG INVE 26684, Iceland; (G) MHNG INVE 28451, Greenland. (A) Silhouette of infertile colony (scale bar: 1 cm); (B–D) internodes and secondary hydrothecae (scale bar: 0.2 mm); (E) female gonotheca (scale bar: 0.5 mm); (F) distal opening of female gonotheca (scale bar 0.1 mm); (G) male gonotheca (same scale as E).

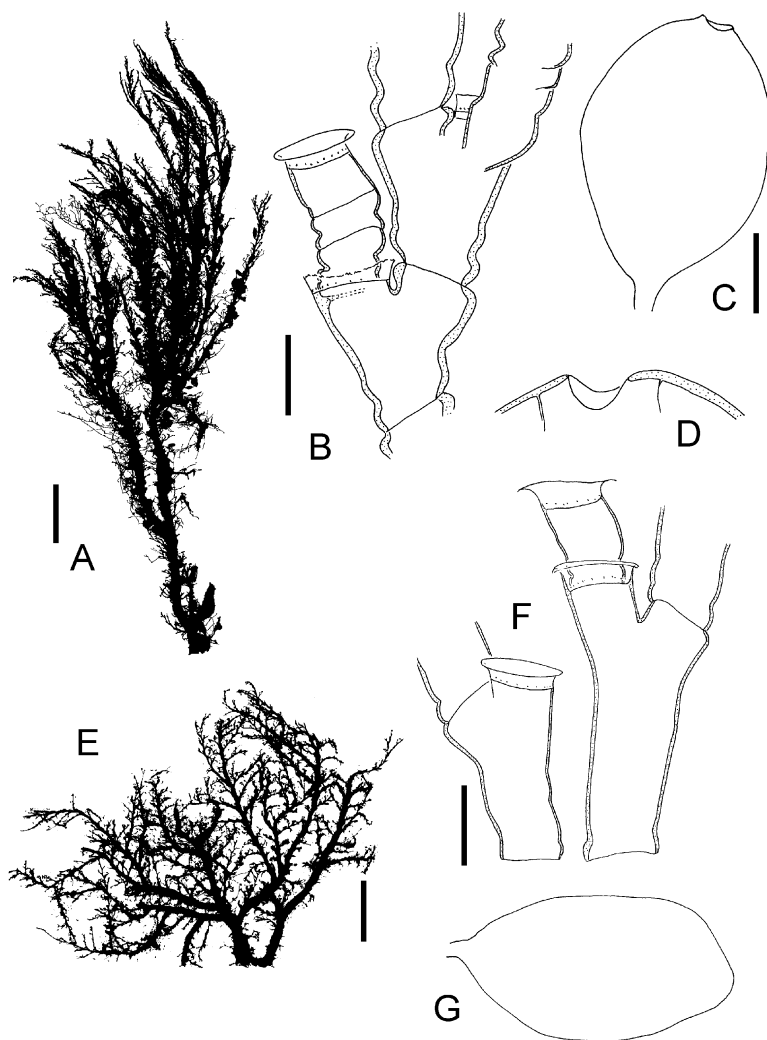


Figure 10. *Halecium labrosum* Alder, 1859. (A–D) MHNG INVE 33563, Iceland; (E–G) MHNG 33583, The Faroes. (A) Colony silhouette (scale bar: 1 cm); (B) segments of distal branch, note short internodes (scale bar: 0.2 mm); (C) gonotheca (scale bar: 0.5 mm); (D) distal opening of gonotheca (scale bar: 0.2 mm); (E) colony silhouette (scale bar: 1 cm); (F) segments of distal branches, note variability of internode length; (G) gonotheca (scale bar: 0.5 mm).

*Material examined* (see also Schuchert 2001)

MHNG INVE 28451, Greenland, Holsteinsborg, 19 July 1953. MHNG INVE 34235, France, Brittany, Roscoff, between Islands of Astan et Ty Saozon, depth 5–10 m according to map, 21 April 1910, ? leg. M. Bedot, juveniles up to 2 cm, no gonothecae. MHNG INVE 33581 (BIOFAR 350), The Faroes, 62.26°N, 7.99°W, 107 m, 22 July 1988. MHNG INVE 33583 (BIOFAR 553), The Faroes, 61.83°N, 6.32°W, 92 m, 22 September 1989. MHNG INVE 33524 (BIOFAR 106), The Faroes, 62.28°N, 6.8°W, 70 m, 24 July 1987. MHNG INVE 33563 (BIOICE collection), Iceland, 65.78°N, 14.22°W, 28–60 m,

24 July 1991. MHNG INVE 26684 (BIOICE station 2099), Iceland, 66.62°N, 18.24°W, 112 m, 4 July 1988.

### Description

Colonies up to 10 cm, arborescent, irregularly branched, predominantly in one plane, stem and some branches polysiphonic. Internodes of unequal length within and between colonies, perisarc corrugated or smooth. Nodes alternately oblique. Hydrotheca on short hydrophore at distal end of internode like a prolongation of it, hydrophore not delimited by node, rim of hydrotheca reaching just to level of distal node of segment, sometimes overtopping it. Hydrotheca short, wall distinctly recurved. Renovations frequent, secondary hydrotheca on hydrophore that is several times as long as depth of hydrotheca, walls usually corrugated. Primary hydrophore often with adcauline semi-circular perisarc thickening (pseudodiaphragm), sometimes at adcauline base of hydrophore a projecting perisarc fold (Figure 9B–D). Hydranths with 20–24 tentacles. Gonothecae without hydranths, females ovoid, compressed by about a factor of two, with short pedicel, distal end with oval opening that may be on a shallow neck-like process. Male gonothecae similar but smaller.

### Typical dimensions

Internode lengths 0.35–1.05 mm, diameter of internodes 0.16–0.26 mm, diameter of diaphragm of primary hydrotheca 0.14–0.21 mm, depth of hydrotheca 40–90 µm. Female gonotheca 1.5–2.1 mm long and 0.8–1 mm broad, male gonotheca 1–1.2 mm long.

### Distribution

Arctic-boreal species, in the North Atlantic reaching south at least to Brittany and North Sea, perhaps even Spain and Azores (Cornelius 1995). Also Northern Pacific and Japan. Type localities: Northumberland coast, Shetland, Moray Firth, UK (Cornelius and Garfath 1980).

### Remarks

*Halecium labrosum* has very variable internode lengths, so much so that this variability itself becomes a diagnostic character. The lengths are variable within and between colonies. In his key to the British thecate hydroids, Cornelius (1995) characterizes *H. labrosum* as having a wrinkled or corrugated perisarc. While some colonies indeed have such a corrugated perisarc, especially the secondary hydrophores, there were also regularly colonies with smooth perisarc among the examined material from the North Atlantic (compare Figures 9B, C and 10B).

Broch (1918) considered *Halecium labrosum* to be an Arctic or northern Atlantic species. Likewise, Cornelius (1975) considered the English Channel as its probable southern limit. As already mentioned by Broch (1918), it is likely that at least some Mediterranean records of *H. labrosum* are due to a confusion with other *Halecium* species, notably *H. mediterraneum*. *Halecium mediterraneum* (see below) is by no means easily separable from *H. labrosum* and in fact might represent a southern form of the latter. The differences between the two forms are only gradual. It differs from *H. labrosum* in forming smaller, mostly monosiphonic shoots (but some are weakly polysiphonic!), the long hydrophore which makes the hydrotheca always overtop the distal node of the segment, the smaller diameter of the hydrotheca, and the smaller diameter of the segments (internodes).

The growth forms are also different, with *H. mediterraneum* tending to form bushy, tangled masses, while *H. labrosum* is always arborescent (compare Figures 10A, E and 11A).

***Halecium mediterraneum* Weismann, 1883**

(Figure 11)

*Halecium tenellum* var. *mediteranea* Weismann 1883, p 160, Plate 2 Figures 5, 6.

*Halecium gracile*: Motz-Kossowska 1911, p 335, Figures 7, 8.1, Plate 18 Figure 2; Neppi 1921, p 12, Figure 10, Plate 1 Figure 10.

*Halecium flexile*: Müller 1914, p 288, Figures 1–3, Plate 10 Figures 1–7.

*Halecium mediterraneum*: Stechow 1919, p 34; Gili and Garcia Rubies 1985, p 41, Figure 2K.

*Halecium tenellum*: García Corrales et al. 1978, p 9, Figures 1, 2.

[Not *Halecium tenellum* Hincks 1861.]

*Halecium delicatulum*: Patrìti 1970, p 23, Figure 20; Ramil Blanco and Iglesias Diaz 1988, p 72, Figure 2; Ramil and Vervoort 1992, p 82, Figure 20a–c. A; Medel and Vervoort 2000, p 12, bibliography; Peña Cantero and García Carrascosa 2002, p 63, Figure 12a, b.

*Material examined*

MHNG INVE 26664, Anse de Troc, Banyuls-sur-Mer, France, Mediterranean, coll. P. Schuchert, 12 July 1999, fertile female colony. MHNG INVE 26666, under raft, beach of Banyuls-sur-Mer, coll. P. Schuchert, 4 September 1996, fertile male colony. MHNG INVE 31115, Anse de Troc, Banyuls-sur-Mer, coll. P. Schuchert, 23 June 1997, infertile. MHNG INVE 32955, between Laboratoire Arago and Anse de Troc, Banyuls-sur-Mer, coll. P. Schuchert, 11 May 2002, male and female colonies, mass occurrence, examined alive. MHNG INVE 34233, Santa Lucia, Naples, Italy, 1 m, coll. 14 April 1911, fertile male. MHNG INVE 34232, Nisida, Naples, Italy, 1 m, 28 February 1902, fertile male. MHNG INVE 34230, Nisida, Naples, Italy, 1 m, 14 February 1911, fertile female. MHNG INVE 34229, Nisida, Naples, Italy, 1 m, 7 April 1911, fertile female. MHNG INVE 34437, Calanque du Port d'Alon, Bandol, France, Mediterranean, 24 April 2003, 1 m.

*Description*

Colonies growing on rock, algae and hydroids, occasionally mass occurrence covering areas of square metres forming a lawn or tangled mass of stems. Stolons tubular, creeping, ramified. Individual shoots 1–3 cm in height, irregularly branched, usually monosiphonic, occasionally weakly polysiphonic, bushy, limp when out of the water, distal parts often geniculate, with regular succession of alternately inclined nodes, nodes distinct. Each internode with a distal hydrophore, oblique, alternately pointing left or right, long and distinctly surpassing level of distal node, hydrophore not delimited by a node. Length of internode 0.4–0.6 mm (mode 0.5 mm), diameter 0.10–0.14 mm, internode length quite homogeneous. Perisarc of internodes smooth, near nodes somewhat bulging, relatively thin. Primary hydrotheca gradually widening and rim somewhat everted or rolled, diameter at base 70–125 µm (mode 80 µm), depth 20–40 µm (mode 30 µm), ring of desmocytes present. Sometimes below diaphragm a semicircular thickening on adcauline side (pseudodiaphragm). Secondary or higher hydrothecae often present, length of their hydrophores as in primary one or longer, often corrugated. Ramification of stems originate from primary hydrophores or from below them; branching usually dichotomous,

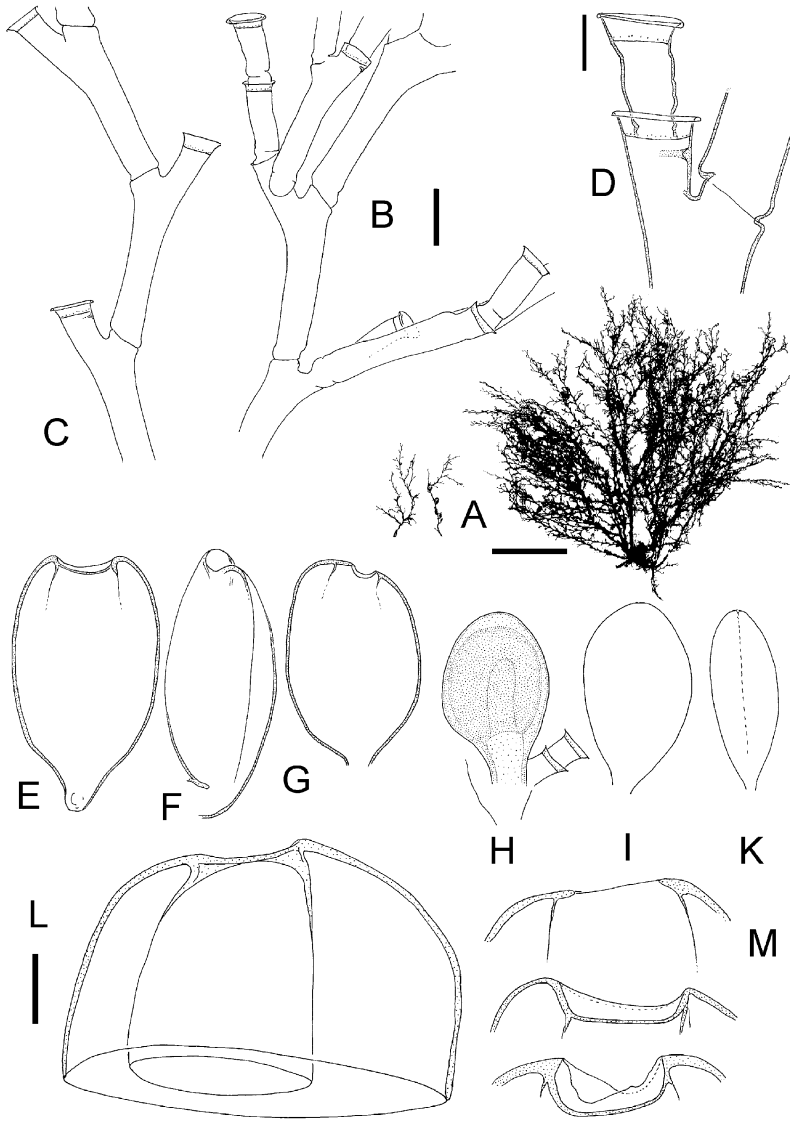


Figure 11. *Halecium mediterraneum* Weismann, 1883; after preserved Mediterranean material. (A) Silhouettes of three fertile colonies showing variability of growth (scale bar: 1 cm); (B) branching pattern of stem (scale bar: 0.2 mm); (C) distal part with geniculate segments (same scale bar as B); (D) primary and secondary hydrotheca (scale bar: 0.1 mm); (E–G) female gonothecae (same scale bar as B), (E) in frontal view and with broad opening, (F) in side view, (G) most commonly found opening size; (H–K) male gonothecae (same scale bar as B), (H) with soft tissue, (I) empty, (K) in side view; (L) empty female gonotheca cut apart to demonstrate secondary capsule within outer capsule (scale bar: 0.1 mm); (M) range of variation of distal openings of female gonothecae (same scale bar as L).

occasionally trichotomous. Hydranth with 18–20 tentacles. Gonothecae arise in upper axils of branching points and hydrophores; gonothecae dimorphic, the two sexes on separate shoots. Gonothecae of both sexes without protruding hydranths. Female gonothecae smooth, ovoid to rectangular, length 0.7–0.8 mm, breadth 0.5 mm, always compressed but

degree variable, along sides a crease-line, distal end obtuse, with or without curved notch-like opening of variable breadth and depth (Figure 11L, M), without distinct lateral ears. Mature female gonothecae have a thin perisarc capsule on inside (Figure 11L). This secondary capsule envelops the gonangium, towards the opening its wall gets thicker. Gonangium oblong, surface epidermis with numerous nematocysts, without hydranth, 6–13 eggs embedded in tissue of ovoid shape, egg diameter about 0.1 mm. Development to planula takes place within gonotheca (larviparity). Male gonothecae smaller, ovoid, length up to 0.7 mm, compressed, sides with crease, distal end rounded, without notch or inner secondary capsule, opening slit-like. One oblong sperm mass. Living colonies have a characteristic yellow-brown colour; the pigment is extracted in formalin fixative.

### Biology

Mature colonies were observed from April to November (Motz-Kossowska 1911; Peña Cantero and García Carrascosa 2002; own observations). Depth range 0.5–145 m (Peña Cantero and García Carrascosa 2002).

### Distribution

Mediterranean, perhaps also adjacent Atlantic Ocean from Morocco to Galicia. Type locality: Naples, Italy, Mediterranean.

### Remarks

Upon closer examination of mature female gonothecae, I noted that there is a delicate tube-like inner capsule enveloping the gonangium. This secondary capsule attaches to the outer capsule along its distal opening (Figure 11L). Such a secondary capsule was also found in *H. delicatulum* and in *H. labrosum*, although in the latter it is very thin and difficult to see. Ralph (1958) also found this inner capsule in *H. delicatulum*.

*Halecium mediterraneum* is almost indistinguishable from *Halecium delicatulum*. *Halecium delicatulum* was first described by Coughtrey (1876) based on colonies found in Dunedin Harbour, New Zealand. Ralph (1958) re-described and revised it and she synonymized several similar nominal species. She also suspected that *Halecium mediterraneum* might be conspecific with it. Rees and Vervoort (1987) agreed and formally synonymized both names. Subsequent studies dealing with Mediterranean collections (e.g. Ramil and Vervoort 1992; Peña Cantero and García Carrascosa 2002) continued this usage. Vervoort and Watson (2003), however, did not synonymize it.

*Halecium mediterraneum* was initially described by Weismann (1883) as a variant of *H. tenellum* Hincks, 1861. Because it is clearly distinct from *H. tenellum*, Stechow (1919) raised it to full species level.

Comparison of *H. mediterraneum* from the Mediterranean and *H. delicatulum* from New Zealand showed that at least the microscopic structure of their trophosomes is very similar. There were differences in the shape of the female gonotheca (compare Figures 11 and 12). Ralph (1958) documented the variability of female gonothecae and her figures also show shapes as found here in *H. mediterraneum*. Therefore, the differences apparent in Figures 11 and 12 are perhaps not really representative. There remain only some slight differences in egg numbers per gonotheca, colony colour and colony form. Because of the slight differences, and mainly for biogeographic reasons, both nominal species are here kept

separate, although it is acknowledged that they are very similar. Genetic methods might hopefully clarify whether they really belong to the same biological species.

Among the European *Halecium* species, *H. mediterraneum* is uncomfortably intermediate between *Halecium labrosum* and *H. tenellum* and it is not always easy to draw a dividing line. This may have led García Corrales et al. (1978) to synonymize *H. tenellum* and *H. delicatulum*. This proposal has been rejected already by other authors (e.g. Ramil and Vervort 1992) and also the present author agrees that they are distinct. *Halecium tenellum* is more gracile and forms smaller colonies, it is sparingly branched only, the internodes appear more elongate, and it never forms polysiphonic colonies. Fertile *Halecium labrosum*, in contradistinction, are always polysiphonic, their gonothecae are about twice as large and their shape differs slightly (compare Figures 10E, F and 11E–G). *Halecium labrosum* often also has a characteristically undulated perisarc (Cornelius 1995), but this is not a diagnostic feature as the perisarc can be entirely smooth. These differences are valid for European populations only. *Halecium mediterraneum* may occasionally have been misidentified as *H. labrosum*. Colonies growing epizoically on dead stems of *Eudendrium* sp. can feign a strong polysiphonic stem and are prone to be confounded.

Another species within this species cluster is *Halecium textum* Kramp, 1911 (see below). The main trait to distinguish *H. textum* from *H. mediterraneum* is its undulated or corrugated perisarc. There are also differences in its branching pattern (frequent trifold branching) and the more pointed gonothecae. The distributions are disjunct. *Halecium textum* is an arctic or northern boreal species. Although I am convinced that they are good species, the diagnosis of the limits of all four species remains difficult due to the absence of clearly apomorphic characters.

***Halecium delicatulum* Coughtrey, 1876**

(Figure 12)

*Halecium delicatulum* Coughtrey 1876, p 26, Plate 3 Figures 4, 5; Ralph 1958, p 334, Figures 11e, h–n, 12a–p, synonymy; Vervoort 1972, p 27, Figures 4, 5; Watson 1973, p 166; Millard 1975, p 145, Figure 47F–L; Stepanjants 1979, p 105, Plate 20, Figure 4A, B; Rees and Vervoort 1987, p 25, Figure 5, synonymy;

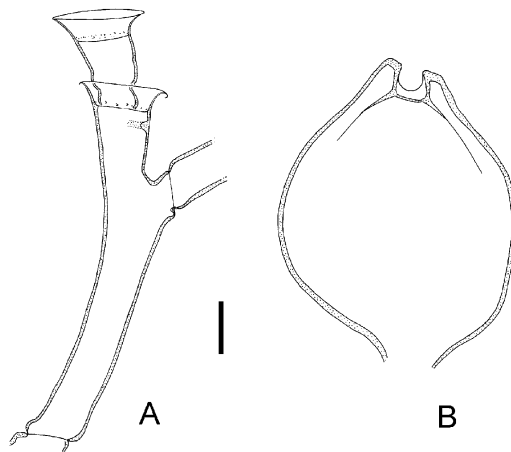


Figure 12. *Halecium delicatulum* Coughtrey, 1876, after preserved material from New Zealand. (A) Segment with primary and secondary hydrotheca; (B) female gonotheca, broad view. Scale bar: 0.1 mm.



Genzano 1990, p 38, Figure 2–5; Hirohito 1995, p 20, Figure 5a–c, Plate 1 Figure c; Migotto 1996, p 30, Figure 6d, e; Vervoort and Watson 2003, p 88, Figures 15I–L, 16A–E.

*Halecium gracile* Bale 1888, p 759, Plate 14, Figures 1–3.

[Not *Halecium gracile* Verrill 1874.]

*Halecium parvulum* Bale 1888, p 760, Plate 14 Figures 4, 5; Millard 1957, p 189, Figure 4A; Vervoort 1959, p 227, Figure 7.

*Halecium flexile* Allman 1888, p 11, Plate 5 Figure 2.

Not *Halecium flexile*: Fraser 1914, p 165, Plate 20 Figure 71; Fraser 1937, p 104, Plate 21 Figure 111; Fraser 1944, p 192, Figure 169 [= *Halecium fraseri* Ralph 1958].

*Halecium balei* Fraser 1911, p 46, new name.

*Halecium flexile* var. *japonica* Leloup 1938, p 4, Figure 1.

Not *Halecium delicatulum*: Leloup 1960, p 218, Figure 1B.

Not *Halecium parvulum* f. *macrothecum* Leloup 1960, p 218, Figure 1B.

Not *Halecium parvulum* var. *magnum* Millard 1957, p 190, Figure 4B–O.

### Material examined

MHNG INVE 26669, New Zealand, Wellington, Te Raekaihau, coll. 1994 by P. Schuchert, fertile female.

### Characteristics

Colony 1.5 cm, monosiphonic, morphology and dimensions of trophosome indistinguishable from *H. mediterraneum* described above. Female gonotheca slightly larger (1 mm), body more rounded, distal opening on a distinct protrusion, notch of opening narrower, 20–22 eggs, egg diameter about 0.09–0.12 mm. Colour of colonies according to Coughtrey (1876) pale and transparent.

### Distribution

Reportedly cosmopolitan (Peña Cantero and García Carrascosa 2002), not in Arctic regions (see below). Type localities: *Halecium delicatulum*, Dunedin Harbour, New Zealand; *Halecium gracile*, Port Stephens and Port Jackson, Australia; *Halecium parvulum*, Bondi Bay, Sydney, Australia; *Halecium flexile*, Marion Island, southern Indian Ocean; *Halecium flexile* var. *japonica*, Sagami Bay, Japan.

### Remarks

See discussion under *H. mediterraneum*. *Halecium delicatulum* has been reported to occur in nearly all oceans and is thus considered cosmopolitan (Peña Cantero and García Carrascosa 2002). The descriptions of some records, however, are quite distinct and suggest that some belong to different species. *Halecium parvulum* var. *magnum* Millard, 1957 forms large, stiff, highly polysiphonic colonies. The dimensions of the hydrothecae and gonothecae are significantly larger. The female gonothecae have a different shape and contain a reduced hydranth. Mature gonothecae have only three to four large eggs. Because both morphotypes occur sympatrically in South Africa, *Halecium parvulum* var. *magnum* should be regarded as specifically distinct from *H. delicatulum*.

The infertile material from the Arctic Sea described by Leloup (1960) is very unlikely to be *H. delicatulum*. Better guesses may be *H. minutum* Broch, 1903 or *H. textum* Kramp, 1911 (see below).

***Halecium textum* Kramp, 1911**

(Figure 13)

*Halecium textum* Kramp 1911, p 368, Plate 21 Figures 5, 6; Schuchert 2001, p 85, Figure 71A–G, 72A, B.

*Halecium tenellum*: Jäderholm 1909, p 27, Plate 4 Figure 12; Fraser 1944, p 201, Figure 179 [not *Halecium tenellum* Hincks 1861].

In part *Halecium tenellum*: Broch 1918, p 46, Figures 20, 21; Kramp 1932, p 19; Kramp 1938, p 8; Kramp 1943, p 32.

? *Halecium undulatum* Billard 1922, p 137, Figure 3.

*Halecium undulatum*: in part Calder 1970, p 1510, Plate 2 Figures 5–8, not 9 [?= *H. minutum*]; Hamond 1957, p 304, Figures 12, 13; Cornelius 1995, p 198, Figure 70.

*Material examined*

MHNG INVE 33592 and 33574 (BIOICE collection), 65.78°N, 14.22°W, Iceland, 28–60 m, 24 July 1991, on bryozoan and on *Sertularella polyzonias*, with female gonothecae. BIOFAR station 402, 62.10°N, 8.14°W, The Faroes, 121 m, 30 May 1989. BIOFAR station 554, 61.94°N, 6.50°W, The Faroes, 62 m, 22 September 1989, on hydroid.

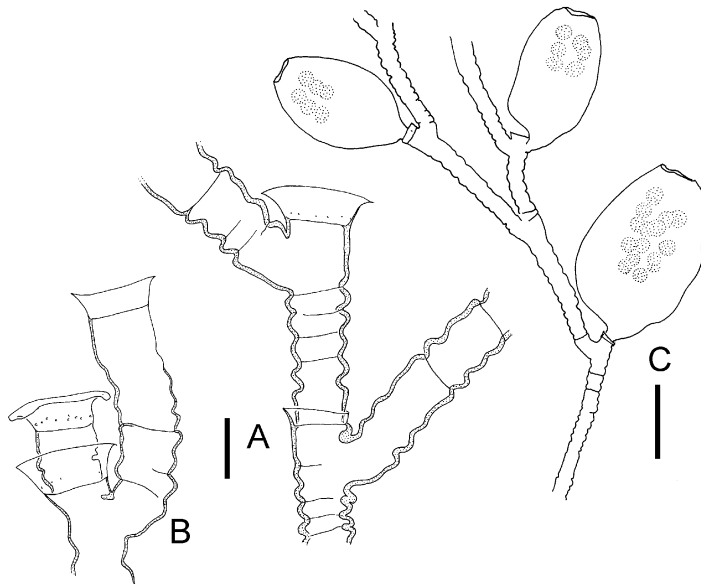


Figure 13. *Halecium textum* Kramp, 1911; after MHNG INVE 33592, Iceland. (A, B) Hydrothecae and internodes, note strong corrugation (scale bar: 0.1 mm); (C) part of colony with three female gonothecae, eggs stippled (scale bar: 0.5 mm).

*Description*

Colonies reaching 2 cm in height, stems irregularly branched, polytomies frequent, branches not in one plane. Larger colonies form a tangled mass. Branches curving sharply upwards, with irregularly occurring nodes. Perisarc strongly undulated or corrugated over stretches, but smooth stretches can also occur. Hydrotheca on hydrophore of about equal length as hydrothecal depth. Hydrotheca diameter at base 0.1 mm, depth 30–50  $\mu\text{m}$ , upper part distinctly everted or even rolled-in, diaphragm fine, desmocytes present. Below diaphragm frequently a pseudo-diaphragm, variable in form and position, either formed as a horizontal or oblique annular thickening or as a mere process at the origin of the apophysis. Gonothecae borne on branches, dioecious. Female gonotheca about 1 mm long, oblong, in side view only half as thick, narrow truncated end with oval aperture. Male gonotheca slightly smaller, spindle-shaped, not much flattened, shape somewhat variable, gonad fills gonotheca nearly completely (after Schuchert 2001).

*Distribution*

Boreal-arctic species; known from Greenland, north-eastern Canada, western and eastern Iceland, Faroes. Some records of *H. undulatum* from the British Isles, the North Sea, Sweden, and Norway could also be *H. textum*. Type locality: Maroussia, eastern Greenland, 160–180 m (Kramp 1911).

*Remarks*

This species has recently been re-described by Schuchert (2001) and several records previously attributed to *H. tenellum* or *H. undulatum* could be referred to it. The newly examined material from eastern Iceland, from where it has not been recorded so far, is especially notable for the strongly corrugated perisarc (Figure 14A, B).

***Halecium banyulense* Motz-Kossowska, 1911**

(Figure 14)

*Halecium muricatum* var. *banyulense* Motz-Kossowska 1911, p 338, Figures 10, 11.

*Halecium banyulense*: Stechow 1921, p 253.

*Material examined*

MHNG INVE 34237, Mediterranean, Italy, Island of Capri, coll. 22 January 1892, two colonies, one with gonothecae, one overgrown by *Lafoea dumosa*.

*Description*

Colonies erect, up to 8 cm high and 6 cm broad, much branched, branches strictly in one plane, branching pattern quite regular, stem and branches polysiphonic, thinning out to monosiphonic terminal regions. Monosiphonic parts segmented through weak nodes, these alternately oblique. Segments elongate, about 1 mm long, with a subterminal apophysis for the next segment and a hydrophore overtopping node of segment, at junction of apophysis and hydrophore a tongue-like process projecting into lumen of internode. Hydrotheca shallow, basal diameter 0.15–0.17 mm, depth 20–40  $\mu\text{m}$ , walls everted,

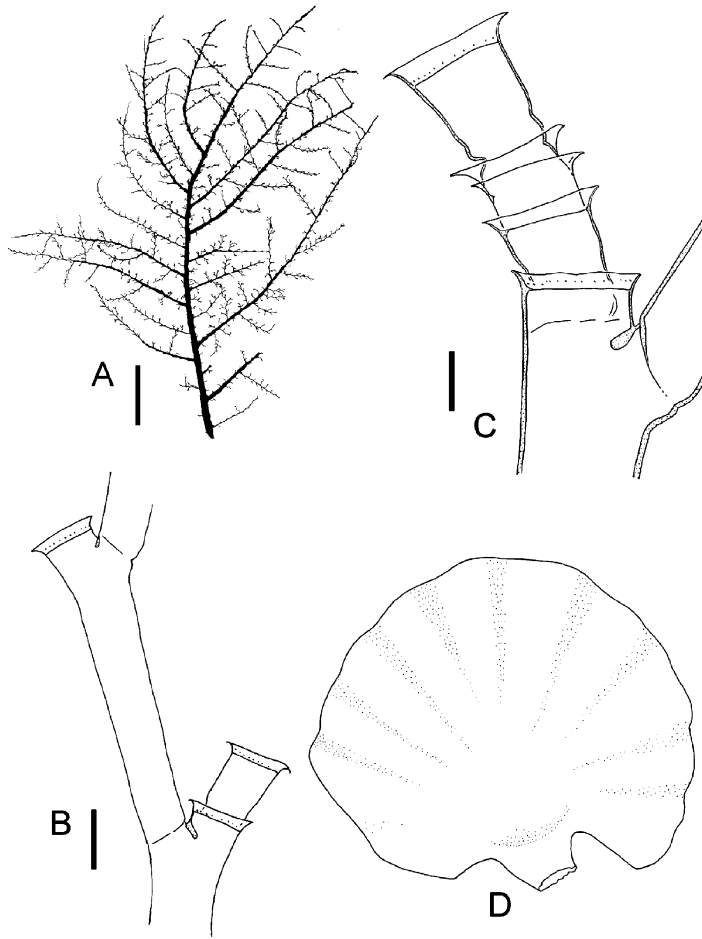


Figure 14. *Halecium banyulense* Motz-Kossowska, 1911, after MHNG INVE 34237. (A) Colony silhouette (scale bar: 1 cm); (B) internode from monosiphonic part (scale bar: 0.2 mm); (C) hydrothecae with regenerated hydrothecae of second and higher degree (scale bar: 0.1 mm); (D) female gonotheca, drawn opaque to visualize radiating depressions (same scale bar as B).

sometimes rim rolled-in, desmocytes present, opening plane of hydrotheca tilted, secondary hydrothecae frequent, first one with hydrophore (length up to twice the diameter), tertiary or higher hydrothecae with short hydrophore (Figure 13C). Hydranth with about 22 tentacles. Gonothecae on stem and branches, only female ones could be identified, diameter 1.1 mm, shape resembling a *Pecten* shell (scallop) through nine or 10 radiating depressions and elevations, these elevations and depressions rounded and without crease-lines, rim of gonotheca slightly undulated.

#### *Further data*

Motz-Kossowska (1911) describes the colonies as hermaphroditic, with male and female gonothecae occurring on the same stem. Female gonothecae contain four to six eggs. Male gonothecae are smaller, either smooth or also with ribs.

*Distribution*

Mediterranean. Type locality: Banyuls-sur-Mer, France.

*Remarks*

The characteristic female gonotheca (Figure 13D) leaves no doubt that the present material belongs to this rare species. The material differed from Motz-Kossowska's description (1911) only in the more everted hydrothecae (Figure 13C).

Motz-Kossowska (1911) described this species as a variant of *H. muricatum* var. *banyulense*. *Halecium muricatum* (Ellis and Solander, 1786) has gonothecae bearing numerous spines. The gonothecae are not dimorphic as in Motz-Kossowska's variant. The microscopic structure of the trophosome *H. muricatum* is also different (cf. Cornelius 1995; Schuchert 2001): the hydrophores are much longer and they have a basal node. *Halecium muricatum* is a northern boreal to arctic species. The southern limit in Europe is the British Isles. The morphological and geographical differences of *H. muricatum* and Motz-Kossowska's variant are evidence enough to regard both as distinct species. The combination *Halecium banyulense* was used in the species list of Boero and Bouillon (1993).

The female gonothecae of *Halecium banyulense* and of the arctic *Halecium birulai* Spassky 1929 resemble each other (see Schuchert 2001 for re-description of *H. birulai*). The female gonotheca of the latter species, however, has radiating keels that form more or less sharp crease-lines. Additionally, the hydrothecae are much deeper. It is a purely arctic species and therefore it is very likely distinct from *H. banyulense*.

*Halecium banyulense* seems to be a particularly rare species. This report is apparently the second record only, but I suspect that infertile material has occasionally been identified as *H. liouvillei* Billard, 1934. The latter species was originally described as monosiphonic, but some authors also included polysiphonic colonies in that species (see Medel and Vervoort 2000 for references).

***Halecium corrugatissimum* Trebilcock, 1928**

(Figure 15)

*Halecium corrugatissimum* Trebilcock 1928, p 7, Plate 3 Figure 1; Ralph 1958, p 329, Figure 9c-f.

Not *Halecium corrugatissimum*: Patrity 1970, p 25, Figure 24 [= *H. pusillum* (M. Sars 1857)].

*Material examined*

MHNG INVE 26670, New Zealand, Wellington, coll. P. Schuchert, 1 November 1993, several male and female colonies. MHNG INVE 29460, New Zealand, Devonport, Cheltenham Beach, coll. P. Schuchert, 27 July 1991, on seaweeds, fertile male.

*Description*

Stems small, up to 5 mm high, arising from creeping, ramified stolons. Stems unbranched or sparingly branched, usually less than 10 hydranths per stem, monosiphonic, nodes irregular. Perisarc with strong, regular annulation or irregular corrugation. Hydrotheca sitting at the end of segment like a prolongation of its axis, not or only slightly inclined, wall straight and not everted, a small part near the rim can be recurved, desmocytes present.

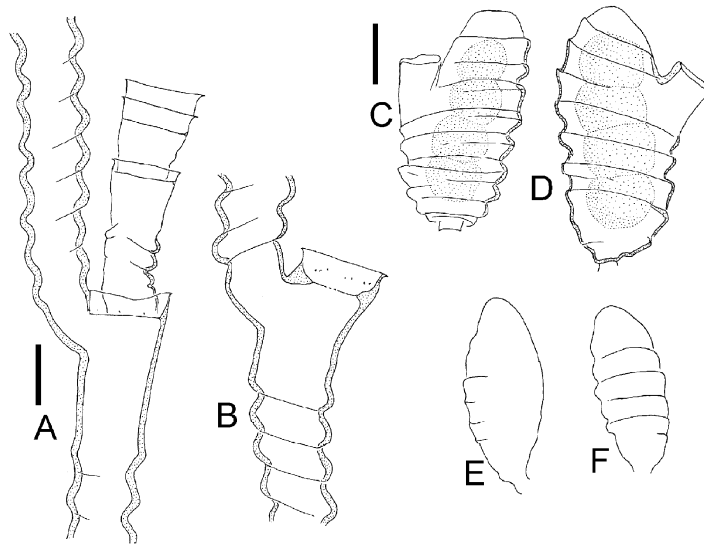


Figure 15. *Halecium corrugatissimum* Trebilcock, 1928. (A) Part of stem with hydrotheca and secondary hydrothecae (scale bar: 0.1 mm); (B) same as (A), note distance of hydrotheca from side-branch and apophysis; (C, D) female gonothecae with eggs (stippled) (scale bar: 0.2 mm); (E, F) male gonothecae (same scale bar as C, D).

Diameter of hydrotheca base 0.12–0.13 mm, depth 30–50  $\mu\text{m}$ . Side-branches originate immediately below hydrothecae, curved steeply upwards. Gonothecae on stems and sometimes stolons, dimorphic, the two sexes on separate stems. Female gonothecae ellipsoid, straight, length 0.7–0.85 mm, diameter 0.35 mm, strongly sculptured by up to 10 transverse ridges, chimney-like opening in middle on side, short, formed by two fused tubes, with median separation line, two hydranths protrude from this aperture, four to five eggs that develop in situ. Male gonothecae, without lateral opening, straight, spindle-shaped, smaller than female, 0.6 mm long and 0.25 mm diameter, less corrugated than female gonotheca, variable within the same colony. Vegetative propagules unknown.

#### Distribution

New Zealand, North and South Island. Type locality: St Clair, Dunedin, New Zealand.

#### Remarks

The male gonothecae of this species have not been described so far. As for many other *Halecium* species, their morphology differs from the female ones.

Patrity (1970) identified closely similar colonies from Morocco as *H. corrugatissimum*. The hydrothecae of her material were clearly everted and therefore her material was more likely *Halecium pusillum* (M. Sars, 1857), a well-known Mediterranean species. *Halecium pusillum* is very similar to *H. corrugatissimum*, but usually has everted hydrothecae (see Broch 1912 for re-description of the type material; Babić 1913 for figures of gonothecae). Motz-Kossowska (1911) attributed similar, but infertile, colonies to *H. pusillum*, despite the hydrothecae having straight walls. Stechow (1919) therefore considered this material to belong to a separate species which he named *Halecium annulatum*. Because this name was

preoccupied by *H. annulatum* Torrey, 1902, Leloup (1938) changed it to *Halecium stechowi*. Peña Cantero and García Carrascosa (2002) also attributed the records of Motz-Kossowska (1911), hence *H. stechowi*, to *H. pusillum*. The presence of the characteristic vegetative propagules in the material of Motz-Kossowska (1911) makes this quite reasonable, but allowing also straight hydrothecae for *H. pusillum* narrows uncomfortably the gap to *H. corrugatissimum*.

Another nominal species in this complex is *Halecium speciosum* Nutting, 1901, a species originally described from Alaska (see also Fraser 1937). Considering their climatic and geographic separation, it appears unlikely to me that *H. corrugatissimum*, *H. pusillum* and *H. speciosum* belong to the same biological species.

These three nominal species are likely another example of the limitations we must be aware of when we attempt to discriminate biological species by morphological characters.

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