

Demosponges of the genus *Hymedesmia* (Poecilosclerida: Hymedesmidae) from Rathlin Island, Northern Ireland, with a description of six new species

CLAIRE E. GOODWIN* and BERNARD E. PICTON

Zoology Department, National Museums Northern Ireland, 153 Bangor Road, Cultra, Holywood, County Down, Northern Ireland, BT18 0EU

Received 8 February 2008; accepted for publication 30 June 2008

Six new species of *Hymedesmia* (Hymedesmiidae, Poecilosclerida) are described from Rathlin Island, Northern Ireland: *Hymedesmia cohesibacilla* sp. nov., *Hymedesmia umbelliformis* sp. nov., *Hymedesmia cratera* sp. nov., *Hymedesmia rathlinia* sp. nov., *Hymedesmia stellifera* sp. nov., and *Hymedesmia crami* sp. nov. Additional descriptions are provided of the poorly known species *Hymedesmia hibernica* Stephens, 1916, *Hymedesmia peachii* Bowerbank, 1882, and *Hymedesmia primitiva* Lundbeck, 1910. The specimens were collected by scuba diving, and digital photographs were taken *in situ*; notes on external morphology are given, in addition to information on internal morphology and ecology. The majority of North-East Atlantic *Hymedesmia* species have been described from deep water, whereas this study sampled the little-researched circalittoral depths (30–50 m). Using scuba diving allowed us to take specimens from habitats such as crevices and bedrock, which, in this depth range and geographical area, have not previously been extensively sampled.

© 2009 The Linnean Society of London, *Zoological Journal of the Linnean Society*, 2009, 156, 896–912.
doi: 10.1111/j.1096-3642.2008.00498.x

ADDITIONAL KEYWORDS: circalittoral – digital photography – *Hymedesmia hibernica* – *Hymedesmia peachii* – *Hymedesmia primitiva* – North Atlantic – sampling – scuba – taxonomy.

INTRODUCTION

The genus *Hymedesmia* Bowerbank, 1864 is large, with 118 species currently known from the North-East Atlantic and Mediterranean, and with 169 species worldwide (Van Soest *et al.* 2005). They are characterized by an ectosomal skeleton of, usually smooth, thin spicules, which are arranged in a layer at the surface and may form bundles in the choanosome, and a choanosomal basal layer of one or more sizes of acanthostyles, which stand with their heads on a basal plate of spongin. Microscleres such as chelae, raphides, and sigmas may also be present (Van Soest, 2002). There are two subgenera: *Hymedesmia* Bowerbank, 1864, in which microscleres are present, and *Stylopus* Fristedt, 1885, incorporating species without microscleres. This division is artificial, as the loss of microscleres is not likely to

indicate a close relationship; however, in the most recent classification of this group (Van Soest, 2002), this division has been retained for convenience, as it helps to separate the large number of species in the genus.

The majority of *Hymedesmia* species from the North-East Atlantic have been described from deep water, mainly by Lundbeck (1910) and Topsent (1893, 1901, 1904, 1925, 1928, 1938), but also by Stephens (1916), from the west coast of Ireland. Further species have been described by Alander (1935, 1937, 1942), from shallower depths along the coast of Sweden. However, although he collected from depths as shallow as 50 m, the unusual hydrographic conditions mean that deep-water species are often dislocated upwards in relation to those in the Atlantic (Alander, 1942), and therefore he was essentially sampling a deep-water fauna. A small number of shallow-water species have been described from the coasts of the UK (Bowerbank, 1864, 1866, 1872, 1874, 1882; Burton,

*Corresponding author. E-mail: claire.goodwin@gmail.com

1930), mainly from intertidal and dredged samples, but very little other work specifically targeting sponges has been carried out in the circalittoral; therefore, the *Hymedesmia* fauna from these depths is not well known.

There are two main categories of megascleres present in the *Hymedesmia*: acanthostyles, and a category of usually smooth spicules that form ascending columns in the choanosome, and in an ectosomal layer. There does not seem to be a satisfactory term for these spicules. The term dermal or ectosomal spicules has been used historically by Lundbeck (1910), Stephens (1916), and Topsent (1928), but this does not reflect their choanosomal function. The term tornotes has been used by others (Ackers, Moss & Picton, 1992; Van Soest, Picton & Morrow, 1999; Van Soest, 2002), but this implies that they are isodiametric diactinal megascleres (Boury-Esnault & Rützler, 1997), whereas the majority are asymmetrical, and presumably monactinal. Symmetrical diactines (oxea and tornotes) do occur in some species, but this may be a secondary symmetry of a spicule that is secreted as a monactine, i.e. only from one end (Bergquist, 1978). Here, we have used the term ectosomal spicules, as the form of these is important in identification, and we felt it was important not to infer shape in the name of the category.

MATERIAL AND METHODS

Specimens were collected by scuba diving around Rathlin Island, Northern Ireland. Sponges were selected by eye: the divers attempted to sample species that looked different from those previously sampled. The aim was to sample as many different species as possible, rather than gaining any quantitative information. Once selected, three photographs of each specimen were taken *in situ*, using housed digital single-lens reflex (SLR) cameras (Nikon D70, in Ikelite and Subal housings, with an Ikelite DS125 substrobe and an SB800 flash unit, and a Fuji S2 Pro in a SeaCam housing, with a Nikon SB105 flash unit: all with 60-mm macro lenses). A small sample was then taken (typically 1 cm² of tissue, although more was removed where possible). After collection, the samples were kept in seawater for a few hours before being transferred to 95% industrial methylated spirits (IMS), for storage.

Tissue slides were prepared by sectioning a very thin portion of tissue at a 90° angle through the sample, this was then dehydrated in absolute ethanol for 4 min, and then placed in clove oil for a further 4 min, to clarify the tissue, before being mounted on a microscope slide in Canada balsam. A coverslip was then placed on the slide, and they were then kept at 50 °C for at least 48 h to allow the mountant to dry.

Spicule preparations were prepared by dissolving the tissue in concentrated nitric acid, which was heated slightly in a water bath to aid the reaction. Distilled water was then added, and the preparation was left to settle for 2 h, before the liquid was pipetted off, and then the process was repeated. The spicules were then washed in a series of three washes of distilled water, and two washes of 70% ethanol, being left to settle for 2 h between each wash. Spicules were then resuspended in a few drops of absolute ethanol, and were either mounted on glass microscope slides in Canada balsam, for light microscopy, or mounted on stubs and sputter coated with gold/palladium, for examination using a scanning electron microscope (Jeol 6500 FEG). In either case, prior to coating, a few drops of the spicule solution were pipetted onto the mount, which was then placed on a hot plate at 50 °C to allow the ethanol to evaporate.

The clarified tissue slide, which enabled an examination of the skeletal structure, was used primarily for identification to genus level. The spicule preparations were used to examine the form of the spicules in more detail. For new species, spicule measurements were taken from the spicule preparations: at least 50 megascleres and 20 microscleres of each type were measured, taking care to measure those that appeared near the ends of the size range. Spicule measurements of megascleres are given to the nearest 5 µm, and the measurements of microscleres are given to the nearest 1.25 µm. Means are given in brackets. For other species, at least ten samples of each spicule type were measured, and only the spicule size range is given.

A list of the currently valid *Hymedesmia* species was obtained from the online World Porifera Database (Van Soest *et al.* 2005). Original descriptions of *Hymedesmia* species were examined; this was greatly facilitated by access to the collection of *Hymedesmia* descriptions at the Zoological Museum of the University of Copenhagen (ZMUC), compiled by Ole Tendal (ZMUC) and Shirley Stone (Natural History Museum, London, BMNH). Data on spicule sizes was entered into a Microsoft Excel spreadsheet to allow comparison of the Rathlin material with the numerous extant species. For comparative purposes, species were subdivided by the type of microscleres present (no microscleres, one size class of chelae, two size classes of chelae, sigmas present, chelae of an unusual form), and then by the form of the ectosomal spicules (tornotes or oxea, strongyles, polytylote strongyles, styles). These categories were further subdivided according to whether one or two classes of acanthostyle were present, and if this was the case, species were differentiated by whether the large acanthostyles were entirely or partly spined.

Type specimens were examined from several collections; those examined are listed in the text. The

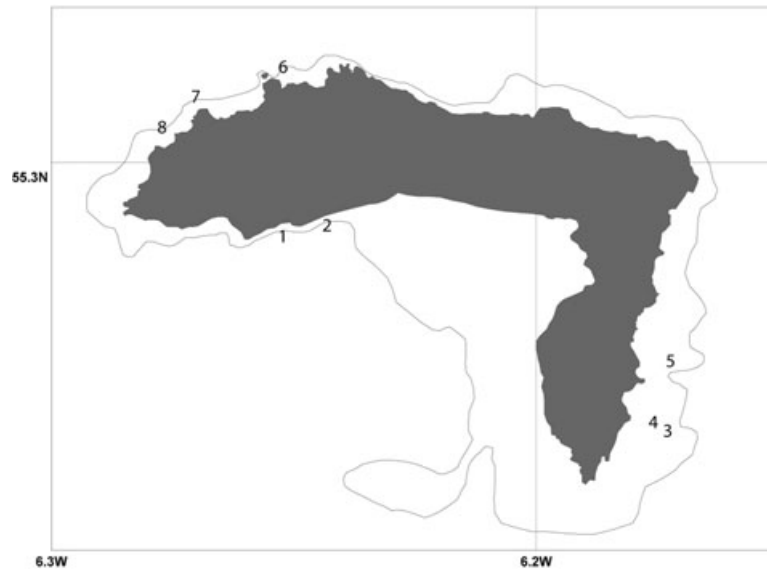


Figure 1. Sampling sites referred to in the text: 1, Damicornis Bay; 2, White Cliffs; 3, Loch Garry; 4, south-east of Doon Point; 5, north-east of Doon Point; 6, Duncan's Bo; 7, Ruecallan; 8, West of Derginan Point. The line around Rathlin Island depicts the 30-m depth contour.

institutional abbreviations used are as follows: BMNH, Natural History Museum, London; MNHN, Muséum National D'Histoire Naturelle, Paris; NMI, The National Museum of Ireland, Dublin; UM, the Ulster Museum, Belfast (National Museums Northern Ireland); ZMUC, The Zoological Museum of the University of Copenhagen.

THE STUDY SITE

The specimens were collected as part of a study of the sponge biodiversity of Rathlin Island, a small island 10 km off the north coast of Northern Ireland. It is characterized by very strong tidal streams and little silt: turbidity is low (the infralittoral zone extends below 20 m), and temperatures are stable (Erwin *et al.*, 1990). Rathlin Island has been noted as being of particular biological importance, with some 530 species (60% of the sublittoral macrofaunal species known from Northern Ireland) recorded from here, including many of particular interest (Erwin *et al.*, 1990). It has been identified as one of the key areas for sponges in Europe (Van Soest *et al.*, 1999), and is designated as a Special Area of Conservation. The area sampled can be divided into three main habitats: the North Wall, a steep sea cliff reaching depths of 200 m; the East Coast, an area of sand and gravel with some boulders, and a small area of rocky reef; and the South Bays, which have a boulder substrate (Fig. 1). Sampling from as many areas of the coast as possible was attempted; however, some areas proved impossible to sample because of the strong tidal streams.

RESULTS

Six new species of *Hymedesmia* were recorded from the survey. Further specimens were obtained of three rarely recorded species: *Hymedesmia peachii* Bowerbank, 1882, *Hymedesmia hibernica* Stephens, 1916, and *Hymedesmia primitiva* Lundbeck, 1910. In addition, many records were obtained of common species: *Hymedesmia paupertus* Bowerbank, 1866, *Hymedesmia jecusculum* Bowerbank, 1866, and *Hymedesmia pansa* Bowerbank, 1882. Several specimens similar to *Hymedesmia brondstedti* Burton, 1930 were obtained, but in view of the confusion in the nomenclature between this species and *Hymedesmia coriacea* Fristedt, 1885 (Van Soest, 1987; Ackers *et al.* 1992), we have refrained from confirming the identification of these samples until closely related species have been examined more thoroughly.

SYSTEMATICS

ORDER POECILOSLERIDA TOPSENT, 1928

SUBORDER MYXILLINA HAJDU, VAN SOEST & HOOPER, 1994

FAMILY HYMEDESMIIDAE TOPSENT, 1928

SUBGENUS HYMEDESMIA BOWERBANK, 1864

HYMEDESMIA (HYMEDESMIA) COHESIBACILLA
SP. NOV. (FIG. 2A, B)

Type material: Holotype: specimen in IMS, section and spicule preparation from tissue sample (Rathlin Island sponge biodiversity project; Damicornis Bay,

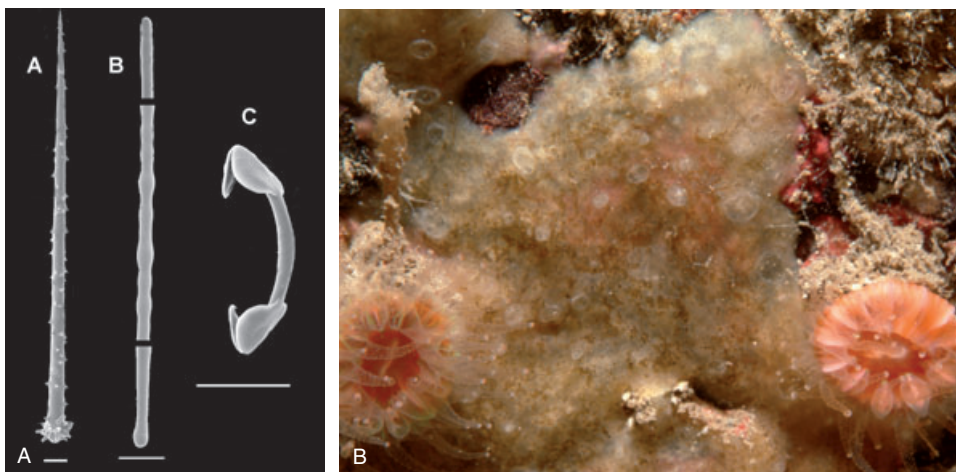


Figure 2. A, *Hymedesmia (Hymedesmia) cohesibacilla* sp. nov. A, acanthostyle; B, ends and middle of ectosomal spicule; C, chelae. Scale bars: 10 µm. B, *Hymedesmia (Hymedesmia) cohesibacilla* sp. nov., surface.

55°17.433'N, 06°15.137'W; water depth, 29.6–32.6 m; Mc2626). Collected by J. Jones and C. Goodwin, 6 July 2005.

Paratypes: Specimen 1, specimen in IMS, section and spicule preparation from tissue sample (Rathlin sponge biodiversity project; Damicornis Bay, 55°17.463'N, 06°15.235'W); water depth, 32–35 m; Mc3189). Collected by J. Jones and L. Scally, 17 August 2005. Specimen 2, specimen in IMS, section and spicule preparation from tissue sample (Rathlin sponge biodiversity project; Damicornis Bay, 55°17.460'N, 06°15.238'W; water depth, 27–32 m; Mc3036). Collected by J. Jones and L. Scally, 10 June 2005.

Etymology: Named from the Latin *cohereo*, meaning connected, and the Latin for stick or shaft, *bacillum*, because of the fusion of the alae to the shaft in the chelae.

External morphology: Patches formed small encrustations on boulders, and were 6–10 cm in maximum diameter. The external appearance is a cream to buff crust, with raised white pore sieves. One of the specimens had a large number of diatoms in its surface tissues, and small numbers of diatoms were present in the other specimens.

Skeleton: Basal layer of acanthostyles with ascending columns of ectosomal spicules, of 6–8 spicules in width. Dense layer of chelae at the surface; chelae also present in small numbers throughout the tissue. Both specimens also had diatoms present in the surface layer, and were 400–600-µm thick.

Spicules: Acanthostyles – two size categories present. Both categories are similar in form, with the head marked by large, dense spines, and a shaft entirely spined with smaller spines.

1. Large acanthostyles: 140–220 µm (180 µm) by 14–16 µm (head), or by 8–10 µm (shaft).
2. Small acanthostyles: 70–95 µm (78 µm) by 10–14 µm (head), or by 6–8 µm (shaft).
3. Ectosomal spicules: 150–240 µm (202 µm) by 3–4 µm, with the majority being between 185 and 210 µm in length; strongylote in form, and often polytylote.
4. Chelae: very abundant chelae are present [17.5–20 µm, (18 µm)]. These are rather palmate in form, the lateral alae coalesce with the shaft over their entire length, and the shaft is only slightly curved, appearing straight under the light microscope. However, the end of the median ala is not widened. There are also occasional normal arcuate chelae of the same size range.

Remarks: Comparatively few species of *Hymedesmia* have chelae in which the lateral alae are fused onto the shaft. Of those that do, *Hymedesmia palmatichela* Topsent, 1928 has similar acanthostyles in terms of size and form, and also has polytylote ectosomal spicules, although these are larger (215–280 µm), and its chelae are of a much larger size (45–46 µm). *Hymedesmia cordichela* Alander, 1942 has spicules of the same size, but the chelae have distinctive 'cordate leaves', and the ectosomal spicules are not polytylote. In *Hymedesmia palmatichelifera* Van Soest, 1984, the primary acanthostyles are larger (293–361 µm), the ectosomal spicules are tornotes rather than strongyles, and the large acanthostyles are smooth at

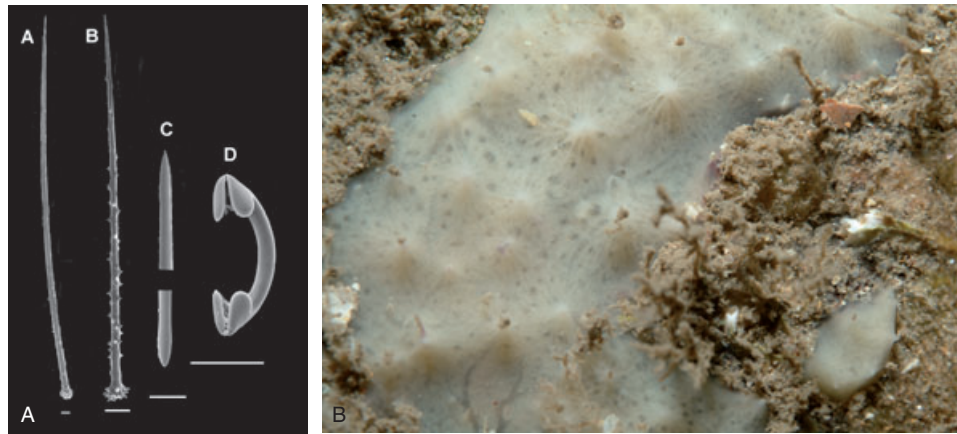


Figure 3. A, *Hymedesmia (Hymedesmia) umbelliformis* sp. nov. A, large acanthostyle; B, small acanthostyle; C, ends of ectosomal spicule; D, chelae. Scale bars: 10 μ m. B, *Hymedesmia (Hymedesmia) umbelliformis* sp. nov., surface.

their tips. *Hymedesmia jamaicensis* Van Soest, 1984 possesses 'whispy' tornotes rather than strongylote ectosomal spicules.

***HYMEDESMIA (HYMEDESMIA) UMBELLIFORMIS*
SP. NOV. (FIG. 3A, B)**

Type material: Holotype: specimen in IMS, section and spicule preparation from tissue sample (Rathlin Island sponge biodiversity project; Loch Garry, 55°15.956'N, 06°10.411'W; water depth, 32–35 m; Mc2645). Collected by J. Jones and L. Scally, 9 June 2005.

Etymology: Named from the Latin for umbrella, *umbella*, in reference to the rays of spongin on the surface, which look rather like umbrella spokes.

Comparative material examined: *Hymedesmia mammilaris* Fristedt, 1885, spicule preparation prepared by Alander (1942), from material from Skagerack station 13, 9 July 1934, and from Skagerack, 5 August 1937 (subspecies).

Hymedesmia simillima Lundbeck, 1910, spicule preparation of specimen from Ingolf expedition station 81. ZMUC.

Hymedesmia proxima Lundbeck, 1910, spicule preparation of specimen from Ingolf expedition station 85. ZMUC.

Hymedesmia basispinosa Lundbeck, 1910, spicule preparation of specimen from Ingolf expedition station 28. ZMUC.

External morphology: This specimen is white, with distinctive rays of spongin showing on the surface, it formed a small (<3-cm maximum diameter), thin encrustation on a boulder.

Skeleton: Basal layer of acanthostyles, evenly dispersed, in which the small acanthostyles are much more abundant than the large ones. Because of the thickness of the sponge, even the largest acanthostyles do not reach the sponge surface. It has ascending columns of ectosomal spicules, of 10–15 spicules in width. Chelae are present throughout the tissue, but are most abundant at the surface, where they form a dense layer. The sponge is 900–1200- μ m thick.

Spicules:

1. Large acanthostyles: 300–525 μ m (434 μ m) by 12–14 μ m at the head, or by 10 μ m on shaft. Long slender acanthostyles that have a well-developed tylote head. The majority are spined only on the head, but in some the shaft is spined with very small spines, which give a roughened texture, for up to half of their length. The spines on the head are rather short, and may have rounded points.
2. Small acanthostyles: 130–210 μ m (167 μ m) by 12 μ m (head), or by 6–10 μ m (shaft). Entirely spined with medium-sized spines. The head is slightly tylote, and is marked by more numerous spines. There is often a small unspined gap on the shaft, just above the head.
3. Ectosomal spicules: 270–380 μ m (336 μ m) by 6–10 μ m. Long tornotes that are style-like in form. The majority are formed into a fine point at one end, with the other end either abruptly pointed or rounded. They are slightly fusiform, and tend to taper towards the more sharply pointed end.
4. Chelae: 20–25 μ m (23 μ m), with a broad shaft; abundant.

Remarks: The size of the spicules roughly equate with those of *H. mammilaris*, which has large acanthostyles (300–400 μ m), small acanthostyles (120–

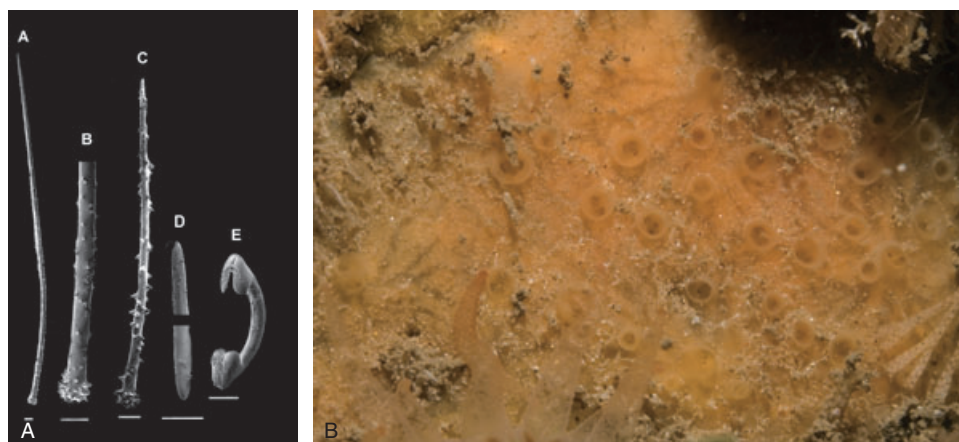


Figure 4. A, *Hymedesmia (Hymedesmia) cratera* sp. nov. A, large acanthostyle; B, base of large acanthostyle; C, small acanthostyle; D, ends of ectosomal spicule; E, chelae. Scale bars: 10 μm . B, *Hymedesmia (Hymedesmia) cratera* sp. nov., surface.

200 μm), oxeote ectosomal spicules (up to 360 μm), and chelae (19–25 μm). However, the large acanthostyles of *H. mammilaris* are shorter, and are spined for at least half of their length, and both the large and small acanthostyles lack a tylote head. Additionally, this species is red when living.

Hymedesmia simillima is also similar. However, its acanthostyles are longer (410–650 μm), the small acanthostyles have more spines, and the ectosomal spicules are true oxeas, tapering to a fine point, rather than being like styles, as in *H. umbelliformis* sp. nov. The chelae are more strongly curved, and are larger in size (28–37 μm).

Hymedesmia proxima can be distinguished from *H. umbelliformis* sp. nov. by its fusiform ectosomal spicules, and by the differences in spination on its acanthostyles: both categories are more spined than *H. umbelliformis* sp. nov., and the spination on the large acanthostyle extends further up the shaft. The larger acanthostyles also reach a greater length (620 μm).

Hymedesmia basispinosa can also be differentiated, as its ectosomal spicules are clearly oxeas, and are often mucronate at the ends, and are longer, reaching up to 500 μm in length.

***HYMEDESMIA (HYMEDESMIA) CRATERA* SP. NOV.**
(FIG. 4A, B)

Type material: Holotype: specimen in IMS, section and spicule preparation from tissue sample (Rathlin Island sponge biodiversity project; Duncan's Bo, 55°18.718'N, 06°15.123'W; water depth, 29–32 m; Mc2897). Collected by B. Picton and C. Goodwin, 6 September 2005.

Etymology: Named from the Latin *Crater*, meaning a bowl, or the crater of a volcano, as the raised rims of the pore sieves give a crater-like appearance.

Comparative material examined: *Hymedesmia proxima* Lundbeck, 1910, spicule preparation of specimen from Ingolf expedition station 85. ZMUC. *Hymedesmia irregularis* Lundbeck, 1910, spicule preparation of specimen from Ingolf expedition station 10. ZMUC.

External morphology: This species has a distinctive appearance, with pore sieves that have high, raised rims. It is a thin peach-coloured crust on bedrock, and has a maximum patch diameter of 3 cm.

Skeleton: Basal layer of acanthostyles, evenly dispersed, in which the small acanthostyles are more abundant than the larger category. It has ascending columns of ectosomal spicules, 10–15-spicules thick, and the orientation of the ectosomal spicules in these columns is not uniform: some point up and others point down. There is a dense layer of chelae at the surface, and chelae are also present in small numbers throughout the sponge tissue. The sponge is 700–800- μm thick.

Spicules:

1. Large acanthostyles: 335–620 μm (452 μm) by 12–20 μm on the head, or by 8–14 μm on the shaft. The majority are between 400 and 500 μm in length. These have a very slightly tylote head, and are spined for about two-thirds of their length with very small spines (much smaller than those on the small acanthostyles). On some, the spines are barely perceptible, giving a roughened appearance. The spines on the head are slightly larger than those on the shaft, and often have rounded tips. The spicules are often curved.

2. Small acanthostyles: 130–220 μm (164 μm) by 14–16 μm at the head, or by 8–10 μm on the shaft. The majority are between 140 and 190 μm long. These are entirely spined, with a slightly tylote head. The shaft is densely set with small recurved spines, on the head, these are slightly bigger, and even more numerous. The spicules are often curved.
3. Ectosomal spicules: 260–350 μm (312 μm) by 6–10 μm . Most of the spicules are styles, in which one end of the spicule is rounded and the other end tapers to a sharp point. However, a few are more tornote-like in form, with the blunter end very slightly pointed, and the other end coming to a more abrupt point. They are very variable in width, and the fatter ones are sometimes fusiform, and occasionally faintly polytylote.
4. Chelae: arcuate chelae are present, and are of 20–27.5 μm (23 μm) in length.

Remarks: *H. proxima* has spicules that are similar in size to this species. However, the ectosomal spicules of *H. proxima* are fatter, 8–12 μm in width, and are uniformly fusiform, rather than variable in form. The small acanthostyles do not have a developed head, or any difference between the spination of the head and the shaft, and the large acanthostyles do not have a tylote head. The chelae are also less robust. Lundbeck also reports that this species is hispid. *Hymedesmia irregularis* has acanthostyles that are more similar in form, with tylote heads; however, these are not divisible into two size categories. Additionally, its ectosomal spicules are always polytylote, and the chelae are much larger (40–50 μm).

HYMEDESMIA (HYMEDESMIA) RATHLINIA
SP. NOV. (FIG. 5A–C)

Type material: Holotype: specimen in IMS, section and spicule preparation from tissue sample (Rathlin

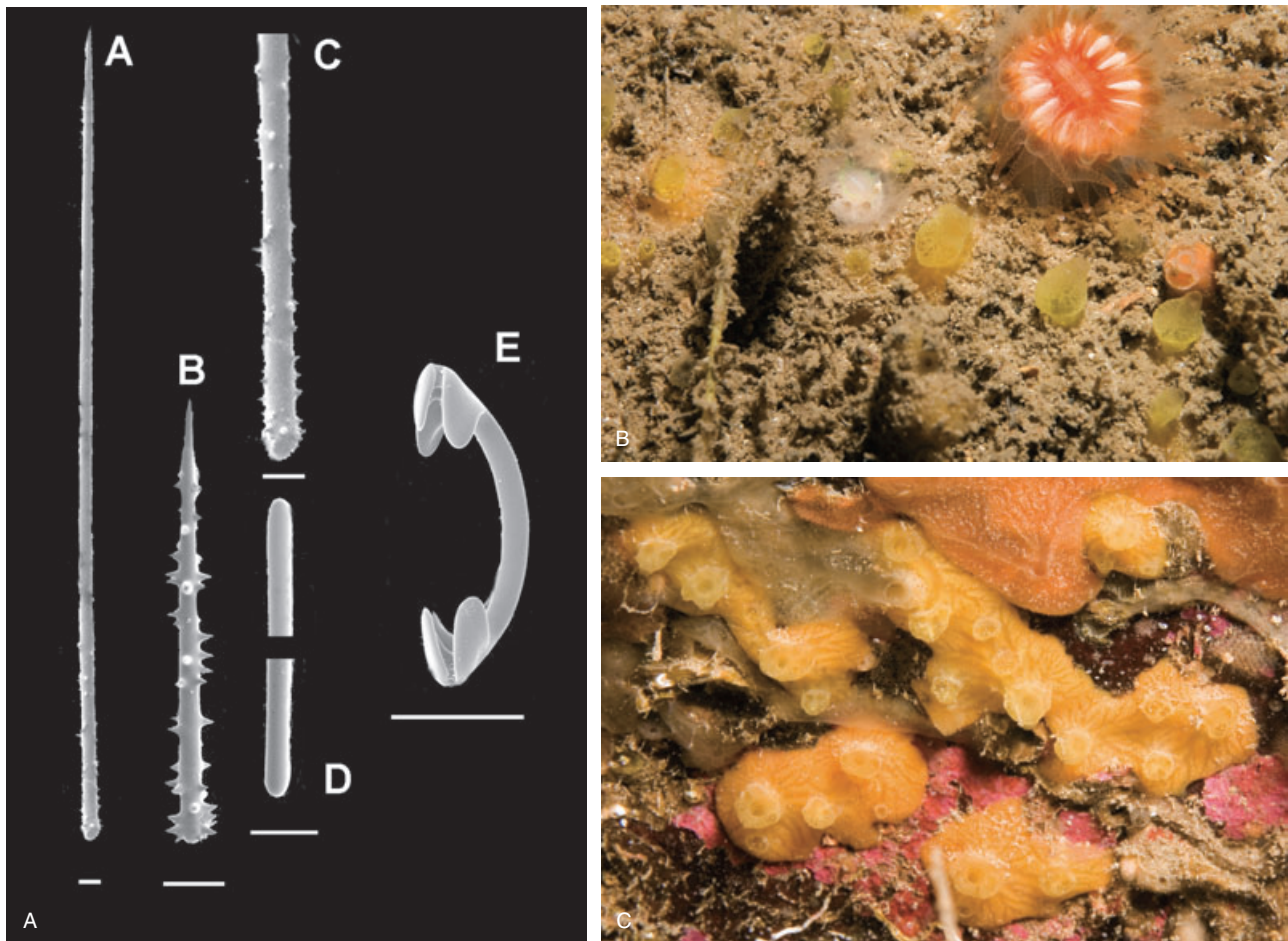


Figure 5. A, *Hymedesmia (Hymedesmia) rathlinia* sp. nov. A, large acanthostyle; B, small acanthostyle; C, base of large acanthostyle; D, ends of ectosomal spicule; E, chelae. Scale bars: 10 μm . B, *Hymedesmia (Hymedesmia) rathlinia* sp. nov., surface, undisturbed, covered in silt. C, *Hymedesmia (Hymedesmia) rathlinia* sp. nov., surface, with silt removed.

Island sponge biodiversity project; Damicornis Bay, 55°17.459'N, 06°15.233'W; water depth, 32–35 m; Mc2792). Collected by C. Goodwin and D. Goodwin, 15 August 2005.

Paratypes: 11 further specimens (specimen in IMS, section and spicule preparation from tissue sample), all from the Rathlin sponge biodiversity project (Mc2399, 2472, 2644, 2692, 2722, 2743, 2810, 2859, 3115, 3147, and 3150).

Comparative material examined: *Hymedesmia versicolor* Topsent, 1893.

DT-86: thick section derived from the holotype. Monaco, 1928, no 42. MNHN.

DT-87: thick section derived from paratype. Station 299, 1908, no. xI 172.19. MNHN.

DT-198: specimen in alcohol. Banyuls. MNHN.

Etymology: Named for Rathlin Island, the type locality.

External morphology: A distinctive sponge, which may be recognised *in situ*. Forms small patches of 3–5 cm in diameter, often with several patches adjacent to one another; each patch bears one or two oscules. The oscules are combined with inhalent pore sieves at the tip of inflated papillae, which project from the sediment that the sponge is frequently covered in. The colour of the sponge is bright yellow, sometimes with darker yellow or orange lines radiating from the papillae. It turns a dark brown/black in alcohol.

Skeleton: Basal layer of acanthostyles, in which the small acanthostyles are very abundant. The larger acanthostyles tend to be surrounded by the columns of ectosomal spicules. It has ascending columns of ectosomal spicules that are variable in thickness: between 5 and 12 spicules in width. Chelae are present in the surface layer, but are not very abundant. The sponge is ~900-µm thick.

Spicules:

1. Large acanthostyles: 175–390 µm (282 µm) by 10–14 µm. Spined for between half and two-thirds of their length, with small straight spines. The head is not tylote.
2. Small acanthostyles: 65–125 µm (103 µm) by 10–12 µm. Spined for their whole length, again the head is not tylote. The spines are very large, and are usually straight (although some are very slightly curved).
3. Ectosomal spicules: tylotes 220–335 µm (280 µm) by 4–6 µm, most with both ends tylote, but in some, only one end is swollen.

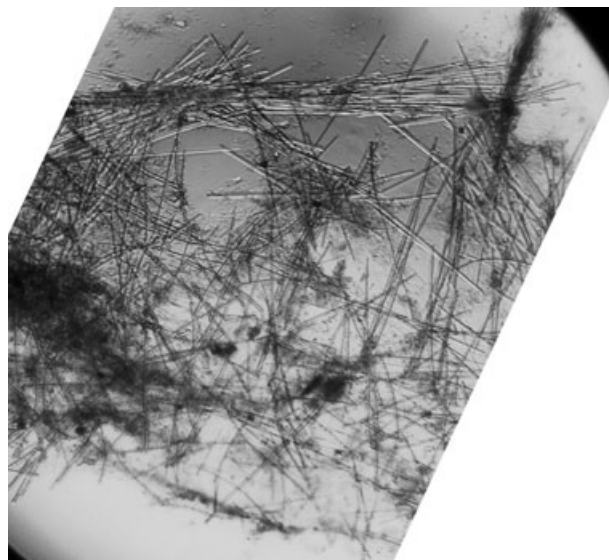


Figure 6. *Hymedesmia (Hymedesmia) versicolor*. Tissue section from paratype (sample XI 172).

4. Chelae: arcuate chelae 22.5–27.5 µm (25 µm) along shaft, with fairly short alae.

Remarks: The spicules are similar in size to *H. versicolor*. *Hymedesmia versicolor* has strongly curved large acanthostyles that have a slightly tylote head, and a largely smooth tip, and are 340–450 µm by 8–11 µm (at the head), small acanthostyles that are 115–180 µm by 7–10 µm (at the head), ectosomal spicules that are 250–325 µm by 2–5 µm, and chelae that are 25–30-µm long. However, we have examined sections from the type of this species, and a paratype and the skeletal structure precludes its inclusion in the genus *Hymedesmia*. It has a reticulate choanosomal skeleton formed of bundles of large acanthostyles, which are echinated with smaller ones. There is also a dense layer of strongyles at the surface (Fig. 6). These characters would indicate inclusion in *Lissodendoryx (Ectyodoryx) Lundbeck 1909*. The skeleton is not described in the original description (Topsent, 1893), or the redescription (Topsent, 1936). However, Topsent originally placed the species in the genus *Myxilla*. Further examination of the numerous paratypes is necessary to fully resolve the taxonomy of this species. Topsent (1893, 1936) notes that the colour and the presence of microscleres in this species is variable, and it is possible that it encompasses more than one species, some of which may be *Hymedesmia*.

Other authors have ascribed specimens to *H. versicolor*, including Sara (1961), Cabioch (1968), and Boury-Esnault (1971), and there may be a *Hymedesmia* with similar spiculation that remains

undescribed. Unfortunately, none of these authors describe the skeleton of their specimens in detail. *Hymedesmia rathlinia* sp. nov. differs in spiculation to *H. versicolor*, in that the spines in the latter are very small, giving the acanthostyles a roughened appearance, whereas the spines in *H. rathlinia* sp. nov. are pronounced, particularly on the small acanthostyles. Both categories of acanthostyles of *H. versicolor* are larger than those found in *H. rathlinia* sp. nov. The ectosomal tylotes of *H. versicolor* are asymmetrical, with one end tylote and the other tapering to a rounded point, whereas both ends in *H. rathlinia* sp. nov. are normally symmetrical, with both ends being tylote.

Since the Rathlin survey *H. rathlinia* sp. nov. has also been found to be present on the Maidens, a group of rocks on the east coast of Northern Ireland.

HYMEDESMIA (HYMEDESMIA) PEACHII BOWERBANK, 1882 (FIG. 7A, B)

Specimens: Specimen in IMS, section and spicule preparation from tissue sample (Rathlin Island sponge biodiversity project; specimen 1, Rucallan, 55°18.473'N, 06°16.206'W; water depth: 29–32 m; Mc2562). Collected by B. Picton A. M. Mahon, 5 July 2005. Specimen 2 (White Cliffs, 55°17.527'N, 06°14.672'W; water depth, 30–33 m; Mc2733). Collected by C. Goodwin, D. Goodwin, B. Picton, 19 August 2005.

Comparative material examined: *Hymedesmia peachii* type specimen, 1877.5.21.1137 (Bk). BMNH.

External morphology: A very thin pale peach to yellow encrustation, with oscules surrounded by radiating veins. Two specimens were taken: one from Rucallan on the North Wall, and one from the White Cliffs on the south of the island (29–33 m). Both formed fairly large patches (with a maximum diameter of < 15 cm) on rock.

Skeleton: Basal layer of acanthostyles, with ascending columns of ectosomal spicules, 3–8 spicules thick. Chelae are present in the surface layer. It is a thin sponge that is 500–600- μ m thick.

Spicules:

1. Acanthostyles: 75–320 μ m by 8–14 μ m; only one size category is present. The smallest acanthostyles are entirely spined, whereas those at the larger end of the size range may be smooth for up to half of their length. The head is not tylote, and the spicules are sometimes faintly or strongly curved. Extremes of this category are shown in Figure 7a; however, there are intermediates in both size and form.

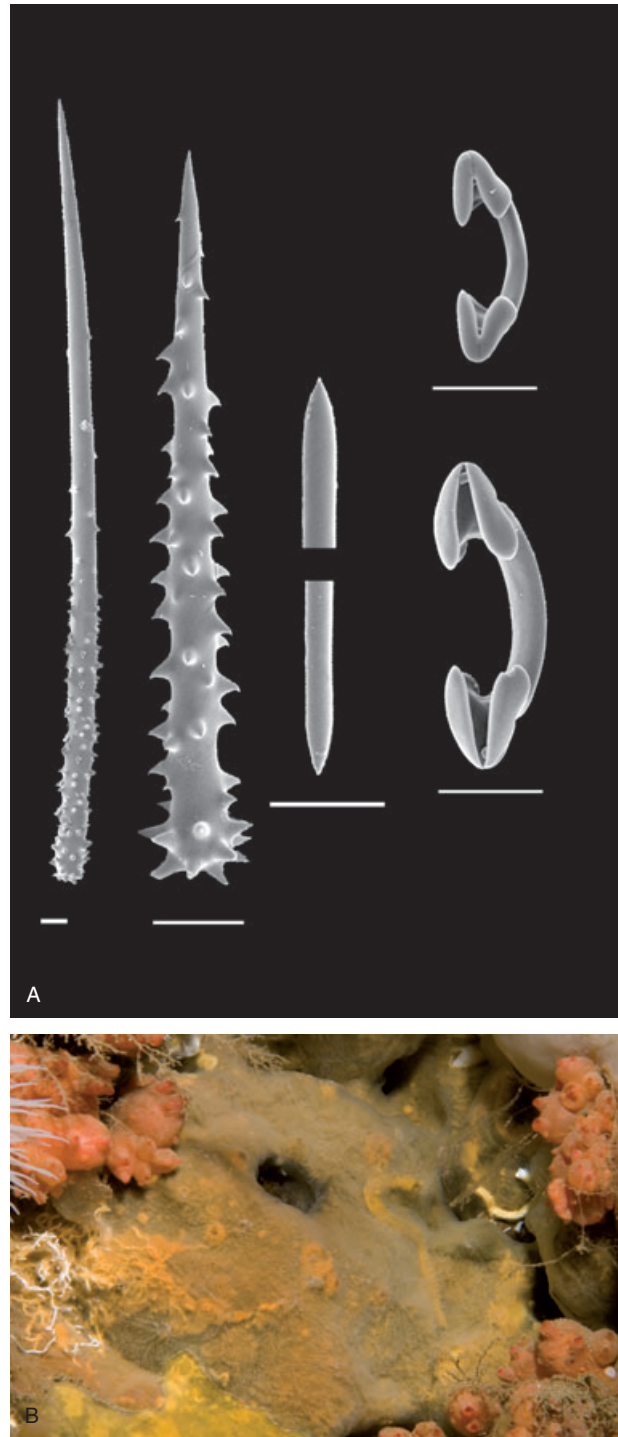


Figure 7. A, *Hymedesmia (Hymedesmia) peachii* Bowerbank, 1882. A, large acanthostyle; B, small acanthostyle; C, ends of ectosomal spicule; D, small chelae; E, large chelae. Scale bars: 10 μ m. B, *Hymedesmia (Hymedesmia) peachii*, surface.

- Ectosomal spicules: 165–225 μm by 4–5 μm ; tor-notes with conical ends.
- Chelae: two size categories of chelae are present. The largest chelae (28–30 μm) have an unusual, broad, flattened shaft, whereas the smaller chelae (20–22 μm) are normal arcuate chelae.

Remarks: The spicules differ slightly from the sizes reported by Bowerbank (acanthostyles up to 379 μm in length, ectosomal spicules 144- μm long, chelae 42- and 13- μm long, respectively), but are the same in form. The sizes agree more closely with those described by Burton (1930), although he stated that the acanthostyles fall into two size classes, and that only large chelae are present.

Hymedesmia peachii was originally described by Bowerbank (1882) from Wick, and can be separated from other *Hymedesmia* by the unusual form of the large chelae. It has also been reported from the Mediterranean (Topsent, 1925; Sara, 1964; Pouliquen, 1972), the Azores (Topsent, 1904), the English Channel (Burton, 1930; Borojevic, Cabioch & Lévi, 1968; Boury-Esnault, 1971), the North Sea (Arndt, 1935), and Sweden (Fristedt, 1885). The reported depths vary, from under 3 m (Sara, 1964) to 1022 m (Topsent, 1904).

HYMEDESMIA (HYMEDESMIA) STELLIFERA
SP. NOV. (FIG. 8A, B)

Type material: Holotype: specimen in IMS, section and spicule preparation from tissue sample (Rathlin Island Sponge Biodiversity Project; Damicornis Bay, 55°17.436'N, 006°15.003'W; water depth, 30–35 m; Mc2606). Collected by B. Picton and A. Mahon, 6 July 2005.

Paratypes: specimen 1, specimen in IMS, section and spicule preparation from tissue sample (Rathlin Island Sponge Biodiversity Project; Damicornis Bay, 55°17.459'N, 006°15.233'W; water depth, 27–32 m; Mc2790). Collected by C. Goodwin and D. Goodwin, 15 August 2005. Specimens 2 and 3: specimens in ethanol, sections and spicule preparations from tissue sample (Sublittoral Survey Northern Ireland Project; Russells Rock, The Maidens, 54°57.291'N, 005°45.008'W; water depth, 25–30 m; Mc3955 and Mc3960). Collected by C. Goodwin and D. Goodwin, 24 August 2007. Specimen 4: specimen in IMS, section and spicule preparation from tissue sample (south-west of Lunga, Firth of Lorne, western Scotland; 56°12.53'N, 005°43.40'W; Mc492). Collected by B. Picton, 31 December 1981.

Etymology: Named from the Latin *stella*, meaning star, and *fero*, meaning to bear, because of the star-shaped pattern on its surface.

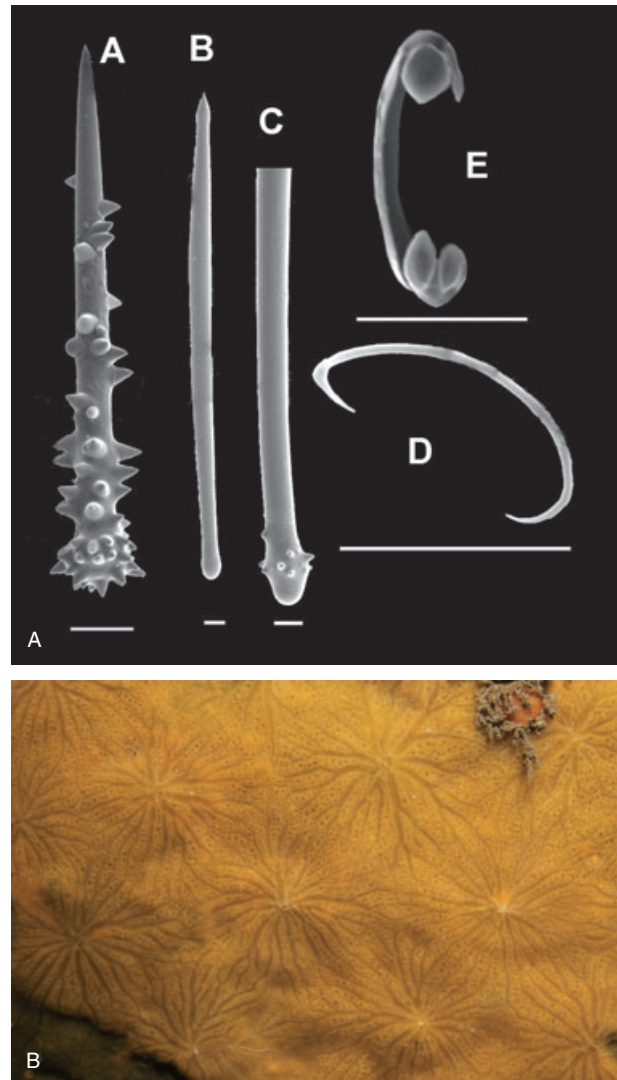


Figure 8. A, *Hymedesmia (Hymedesmia) stellifera* sp. nov. A, small acanthostyle; B, ectosomal spicule; C, large acanthostyle end; D, sigma; E, chelae. Scale bars: 10 μm . B, *Hymedesmia (Hymedesmia) stellifera* sp. nov., surface.

External morphology: Bright yellow/orange sponge forming large patches (over 20 cm in diameter), which are very conspicuous because of their bright colour and oscule form. Prominent oscules surrounded by numerous (10–20) oscular channels, some of which are branched. The oscules are regularly spread over the sponge surface, and are arranged in diamonds. The ends of the oscular channels touch those of neighbouring oscules, giving the surface a regular star-type pattern.

Skeleton: Basal layer of large and small acanthostyles, from which ectosomal spicules arise in columns that are 10–15 spicules thick. The smaller

acanthostyles are more abundant. Sigmas are very abundant throughout the tissue. Chelae are present in certain regions of the sponge, but may not be apparent in some specimens. Where present, they are reasonably common and form a layer at the surface. The sponge is ~800- μm thick.

Spicules:

1. Large acanthostyles: 265–440 μm (358 μm) by 8–12 μm . These are fusiform acanthostyles with a tylote head. The shaft is smooth, and the head is sparsely spined with small, rounded spines. Occasional spicules are present, consisting of two of these acanthostyles fused at the head.
2. Small acanthostyles: 65–95 μm (79 μm) by 8–10 μm . These acanthostyles are very characteristic in appearance; they taper evenly to a sharp point, with no development of the head. The majority of the shaft is spined with large spines, but the last eighth to one-quarter, towards the tip, is smooth, and there are smooth areas on the shaft above the head.
3. Ectosomal spicules: the styles are 210–290 μm (247 μm) in length, with the majority of being 8–10- μm wide, but with some much thinner spicules of 3–5 μm in width. These spicules are fusiform: one end is rounded and tylote, and the other end is pointed; some are mucronate at the tip.
3. Sigmata: 10–12 μm in length.
4. Chelae: 15–18 μm in length. These are small chelae, with leaf-like alae, and are only joined to the shaft by a short section at the top. The alae have a claw-like appearance when viewed under the light microscope.

Remarks: Based on its skeletal structure, this species is in the genus *Hymedesmia*. The smooth, large acanthostyles are unusual for this genus, and are very similar in form to *Lissodendoryx (Ectyodoryx) atlanticus*. However, in the subgenus *Ectyodoryx*, the choanosomal skeleton is composed of either styles or acanthostyles, with a separate category of ectosomal tornotes. The pronounced difference in the form of the acanthostyles is also unusual. The smaller acanthostyles are very similar in form to those of *Hymedesmia zetlandica* Bowerbank, 1864, which is the type specimen of the genus *Hymedesmia*.

Chelae were not visible in tissue sections from either the Rathlin specimens or the Lunga specimen, despite numerous sections being taken from different tissue areas, although scarce chelae were visible in the spicule preparations. However, chelae were numerous in some areas of the surface of two specimens collected from the Maidens: this suggests that

chelae are present only in certain regions of the sponge. It was not possible to determine which precise regions they were associated with.

Embryos were present in the Lunga specimen. These embryos have different spicules to the main tissue: thin, short styles (125 μm by 2 μm), and unguiferous anchorate chelae (20 μm). The majority of the chelae have three claw-shaped alae on each end, but in some individuals there were up to five. In several cases, spines are present on the chelae shaft just below the alae.

SUBGENUS *STYLOPUS* FRISTEDT, 1885

HYMEDESMIA WITHOUT MICROSCLERES

HYMEDESMIA (STYLOPUS) CRAMI SP. NOV.

(FIG. 9A, B)

Type material: Holotype: specimen in IMS, section and spicule preparation from tissue sample (Rathlin Island Sponge Biodiversity Project; White Cliffs, 55°17.542'N, 06°14.507'W; water depth, 30–33 m; Mc2653). Collected by B. Picton and A.M. Mahon, 7 July 2005.

Etymology: Named for the cream colour of the surface, from the Latin *crami* for cream.

Comparative material examined: *Hymedesmia dermatata* Lundbeck, 1910, spicule preparation of specimen from Forsblads Fjord in East Greenland (Amdrup expedition 1900). ZMUC.

External appearance: Thin, cream incrustation on boulder, with a maximum diameter of 5 cm. There are no obvious pore sieves, and the surface appears slightly hispid and is covered in a thin layer of silt.

Skeleton: Basal layer of acanthostyles, sparsely distributed, with a roughly even ratio of large to small acanthostyles. There are ascending columns of ectosomal spicules that are 10–15 spicules thick, which fan out towards the surface, and may adjoin with adjacent columns. The sponge is 900–1000- μm thick.

Spicules:

1. Large acanthostyles: 370–550 μm (436 μm) by 12–18 μm . Head, very slightly tylote; shaft, mainly smooth, with the bottom eighth to one-quarter covered in very small spines, giving it a roughened appearance. The spines on the head may be rounded at the tip.
2. Small acanthostyles: 105–175 μm (136 μm) by 12–14 μm ; the head is not tylote, and is entirely spined with recurved spines, the size of which vary between individual spicules (small–large). In some

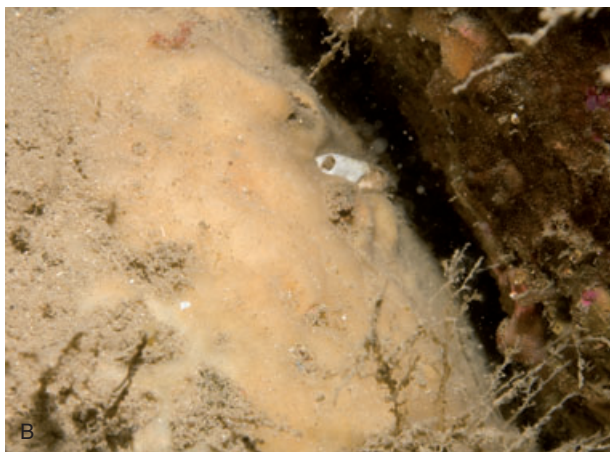
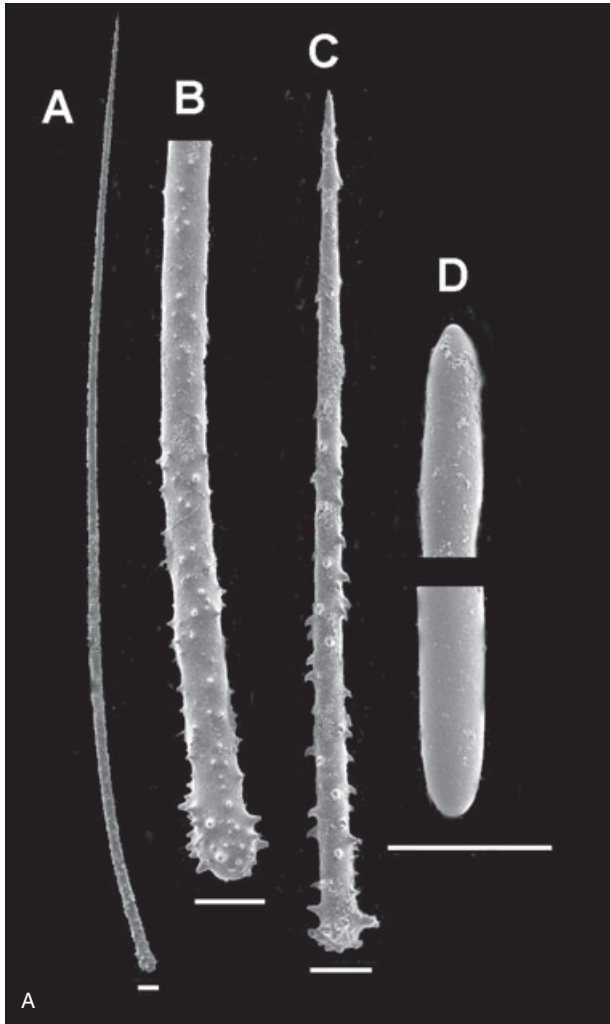


Figure 9. A, *Hymedesia (Stylopus) crami* sp. nov. A, large acanthostyle; B, base of large acanthostyle; C, small acanthostyle; D, ends of ectosomal spicule. Scale bars: 10 μ m. B, *Hymedesia (Stylopus) crami* sp. nov., surface.

individuals the spines on the head are larger, and may have rounded tips.

3. Ectosomal spicules: 290–400 μ m (360 μ m) by 4–7 μ m. These are strongyles in which usually one or both ends are tylote.
4. Microscleres: absent. One arcuate chela was present in the spicule preparation, but is assumed to be contamination, as chelae are not present in the tissue section.

Remarks: *Hymedesia dermatata* has similar spicule sizes. However, it is described as having conical papillae on the surface, and the large acanthostyles are strongly spined, as opposed to the roughened texture of the acanthostyles described above. The strongyles are also thicker (6–10 μ m), and may be polytylote.

HYMEDESMIA (STYLOPUS) HIBERNICA STEPHENS, 1916 (FIG. 10A, B)

Specimens: Specimen in IMS, section and spicule preparation from tissue sample (Rathlin Island Sponge Biodiversity Project; specimen 1, west of Derginan Point, 55°18.283'N, 06°16.774'W; water depth, 28.5–31.5 m; Mc2766). Collected by B. Picton and C. Goodwin, 15 August 2005. Specimen 2: White Cliffs (55°17.546'N, 06°14.518'W; water depth, 32–35 m; Mc2950). Collected by J. Jones and C. Goodwin, 7 August 2005.

Comparative material examined: *Hymedesia hibernica* Stephens, 1916 type (W141 14.1916). NMI.

External morphology: A yellow sponge with large pore sieves, which is slightly translucent in appearance. Both specimens formed thin encrustations on rock: these are very small patches of less than 5 cm in maximum diameter.

Skeleton: Basal layer of acanthostyles, in which the smaller category are more abundant, and in which acanthostyles are spread evenly but fairly sparsely, with some space in between them. The ascending columns of anisostrongyles are 5–8 spicules thick. The sponge is 500–800- μ m thick.

Spicules:

1. Large acanthostyles: 250–325 μ m by 5–12 μ m. These acanthostyles have a slightly tylote head, which is more obvious in thinner specimens, and are spined on the head and up to half of the way up the shaft, although with much smaller spines. The head spines are often strongly curved up towards the shaft.

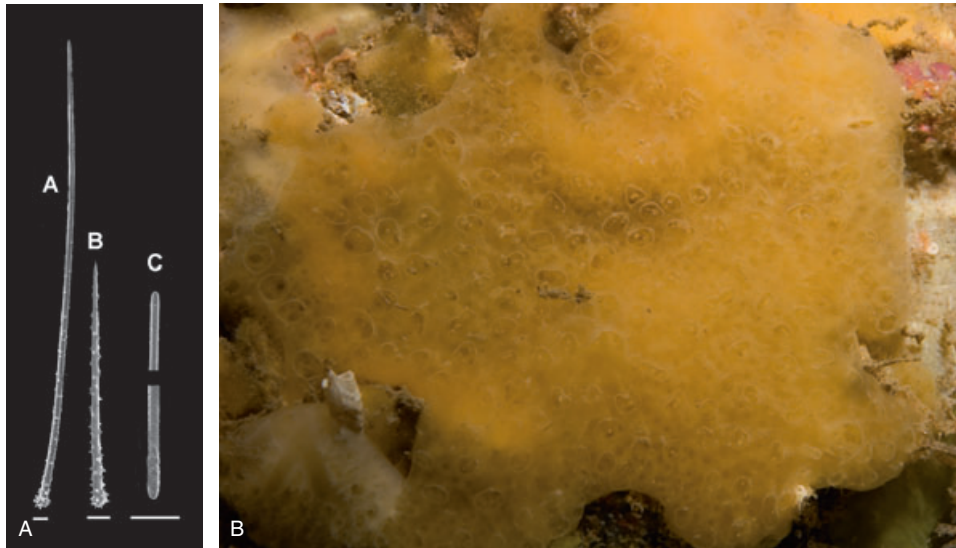


Figure 10. A, *Hymedesmia (Stylopus) hibernica* Stephens, 1916. A, large acanthostyle; B, small acanthostyle; C, ends of ectosomal spicule. Scale bars: 10 μ m. B, *Hymedesmia (Stylopus) hibernica*, surface.



Figure 11. A, *Hymedesmia (Stylopus) primitiva* Lundbeck, 1910. A, acanthostyle; B, ectosomal spicule. Scale bars: 10 μ m. B, *Hymedesmia (Stylopus) primitiva*, surface.

2. Small acanthostyles: 110–130 μ m by 10–12 μ m. These are entirely spined with large recurved spines on the shaft, which become progressively sparser towards the tip; the head is not tylote, but is marked by denser spines that are often curved up towards the shaft.
3. Ectosomal spicules: 200–250 μ m by 2–4 μ m, with thin anisostrogyles. One end is usually thicker than the other, and neither end is tylote.
4. Microscleres: none present.

Remarks: The spiculation agrees almost exactly with that described by Stephens (1916), apart from the tendency for the tylostyles to become subtylote. This

species was originally described from 74 m off Reena-cry Head, County Kerry, Ireland. It has since been recorded from the English Channel, from Roscoff (Cabioch, 1968).

HYMEDESMIA (STYLOPUS) PRIMITIVA LUNDBECK, 1910 (FIG. 11A, B)

Specimens: Specimens in IMS, sections and spicule preparations from tissue samples (Rathlin Island Sponge Biodiversity Project; specimen 1, White Cliffs, 55°17.543'N, 06°14.517'W; water depth, 26.4–29.4 m; Mc2611). Collected by J. Jones and C. Goodwin, 7

July 2005. Specimen 2: White Cliffs (55°17.538'N, 06°14.542'W; water depth, 37–40 m; Mc2981). Collected by B. Picton and C. Goodwin, 7 September 2005. Specimen 3: Damicornis Bay (55°17.429'N, 06°15.098'W; water depth, 30.5–33.5 m; Mc3107). Collected by J. Jones and L. Scally, 16 August 2005. Specimen 4: north-east of Doon Point (55°16.454'N, 06°10.296'W; water depth, 35.7–38.7 m; Mc3132). Collected by J. Jones and B. Picton, 25 August 2005. Specimen 5: Loch Garry (55°15.956'N, 06°10.411'W; water depth, 31–34 m; Mc3161). Collected by C. Goodwin and A.M. Mahon, 26 August 2005. Specimen 6: Loch Garry (55°15.956'N, 06°10.411'W; water depth, 32–35 m; Mc3162). Collected by J. Jones and B. Picton, 26 August 2005.

Comparative material examined: *Hymedesia primitiva* spicule preparation of specimens from Ingolf expedition stations 6 and 89. ZMUC.

External morphology: The sponge is a thin cream crust with large pore sieves; in two of the sponges the area around the pore sieves was yellow from algae in the surface tissues. The sponge formed patches with maximum diameters in the range 4–15 cm.

Skeleton: Basal layer of acanthostyles, in which the smaller acanthostyles are more abundant. There are ascending columns of ectosomal spicules that are 5–8 spicules thick. The sponge is 400–500- μ m thick. Several of the specimens had diatoms present in their surface layer.

Spicules:

1. Acanthostyles: 100–315 μ m by 10–16 μ m on the head, or by 6–10 μ m on the shaft; entirely spined with small, short, recurved spines. The head is slightly tylote, and bears slightly larger spines that often have rounded tips. In the longer spicules the spines may be very sparse towards the tip, and part of the shaft may be smooth.
2. Ectosomal spicules: 200–250 μ m by 2–4 μ m. With tylotes that are usually faintly polytylote.
3. Microscleres: absent.

Remarks: The spiculation broadly agrees with that of Lundbeck's (1910) specimens. However, the strongyles of his specimens have a slightly broader size range (196–280 μ m), and the acanthostyles are also somewhat thicker than the Rathlin specimens, with base widths varying from 14 to 27 μ m. However, Lundbeck states that there is much variation of acanthostyles between individuals in terms of robustness and spination.

This species was originally described from deep water (108–840 m) around Iceland and the Faroe Islands. It has subsequently been reported from the Caribbean (De Laubenfels, 1936) and from Wembury Bay in Devon (Burton, 1957), although it would seem unlikely that the former record is of the same species.

DISCUSSION

There are several factors that may account for the number of new species discovered on Rathlin. Firstly, the richness of the community sampled: the Rathlin Island study site has a particularly rich sponge fauna, and is thought to be one of the best areas for sponges in Europe (Van Soest *et al.*, 1999). Although samples have been collected from this area previously (Erwin *et al.*, 1990), there has never been a survey targeted solely at Porifera, and inadequate resources meant that material collected was sometimes not identified to species level, particularly in groups such as *Hymedesmia*, where this can be time consuming. New records are not solely limited to *Hymedesmia*: of the 128 species recorded from the site, over 30 are believed to be species new to science. New species from several other genera (including *Tethya*, *Eurypon*, *Polymastia*, *Paratimea*, *Axinella*, *Phakellia*, *Halicnemis*, *Spongosorites*, *Crella*, *Phorbas*, *Ectyodoryx*, *Plocamionida*, *Antho*, and *Hymenaphia*) were also collected from the survey (Picton & Goodwin, 2007). The sponge fauna of the UK in general is poorly known, in part because of a lack of taxonomic expertise.

A second factor is the methodology used, which will have resulted in species being overlooked in other surveys. By solely targeting sponges, much more time was devoted to their collection. Photographing, scraping, and bagging the samples was time consuming, and, together with the decompression constraints, this meant that only seven (on average) sponges could be collected per dive. It is not feasible to allocate such time in general marine surveys. This methodology resulted in the sampling of many small crusts that may have been overlooked on other occasions. Additionally, habitats such as overhangs and crevices in bedrock were sampled, which would have been difficult to get specimens from by other methods. Scuba diving surveys have been shown to provide good records of sponge biodiversity (Boury-Esnault, 1971; Wiedenmayer, 1977; Pansini, 1987), particularly in areas where many species are small, and in habitats that are difficult to sample by other means (Vacelet & Perez, 1998).

Sampling by scuba diving resulted in the collection of material from the little-sampled circalittoral depth range (30–50 m): the majority of the currently known *Hymedesmia* species have been described from deep

water (> 200 m), and consequently the *Hymedesmia* of these shallower depths are poorly known. Some species of *Hymedesmia* have a wide depth range: for example, *H. peachii* has been recorded at depths of between 3 (Sara, 1964) and 1022 m (Topsent, 1904). However, other species are likely to be more restricted. In the Mediterranean, a clear distinction between the Porifera species composition of sublittoral (0–40 m), circalittoral (40–120 m), and bathyal (> 120 m) zones has been recorded (Voultsiadou, 2005). Further work is needed before the depth range of many species is understood: many *Hymedesmia* species are currently known from only one or two records. Historically, some circalittoral species may have been assigned erroneously to available species names because of the small interspecific spicule differences. Consequently, the perceived large depth ranges may be inaccurate.

Hymedesmia species appear to be more diverse at higher latitudes, with the majority of the species from the North-East Atlantic described from Scandinavia (Lundbeck, 1910; Alander, 1935, 1937, 1942). Further studies of species from the UK and Ireland have the potential to discover more new species, and to increase our understanding of the distribution and ecology of poorly known species.

Hymedesmia are regarded as problematic to identify because of the large number of species in the genus, and because of the subtle differences between the spicules. The use of *in situ* digital photography in this study greatly aided the identification to species level, as the species often had characteristic external appearances. The presence and form of pore sieves was a particularly useful character. In the future, it should be possible to identify some of the more distinctive species (for example *H. rathlinia* sp. nov.) to species level, largely on the basis of appearance.

We have described *H. cohesibacilla* sp. nov., a species with chelae in which the alae are fused onto the shaft. This is not an example of a true palmate chela in the currently accepted meaning of the word: Boury-Esnault & Rützler (1997) define palmate chelae as ‘An iso- or anisochela in which the lateral alae coalesce with the shaft over their entire length, and the single, median, anterior ala stands free and widens distally’. This chela form is typically found in the Microcionidae Carter 1875 (Hooper, 2002). However, historically, the term palmate has been used in the description of *Hymedesmia* species to encompass a range of forms in which the alae are fused onto the chela shaft (Topsent, 1928; Alander, 1942; Van Soest, 1984). Topsent (1928) erected a subgenus *Holorodesmia* for *Hymedesmia* species with palmate isochelae, and this was given full generic status by De Laubenfels (1936). Van Soest (2002) reassigned the *Holorodesmia* to *Clathria* (*Microciona*) based on an

examination of the type species *Hymedesmia flaccida* Topsent, 1928. However, other species originally ascribed by Topsent to *Holorodesmia* have spicule forms including sigmata- and tornote-form ectosomal spicules, which would preclude inclusion in this genus. It seems likely that where chelae of a palmate appearance are present, these are actually modifications of the arcuate chelae characteristic of the genus *Hymedesmia*. The Microcionidae include species in which the palmate isochelae are superficially modified to arcuate-like or anchorate-like forms (Hooper, 2002), and it appears that the reverse modification also occurs.

The genus *Hymedesmia* currently contains 169 species, several of which are known from only one specimen. It has been suggested that these may in fact not be separate species, but are rather varieties of a few species (Vosmaer, 1935), although this has been disputed by others (Alander, 1942). In the course of preparing this paper, we examined 303 specimens from the Ulster Museum collections, and many more from other museum collections (ZMUC, BM, and MNHN) belonging to the genus *Hymedesmia*, mostly from the North-East Atlantic. We found that species were often separated by small differences in acanthostyle shape, chela shape, and dermal spicule shape, and that these small differences usually correlated with clear differences in external appearance and colour. We support Lundbeck, Topsent, and Alander’s view that this is a very speciose genus in the North-East Atlantic, rather than the view that there are too many names applied to a few variable species. We also found that small differences in size, and size range, in spicules between species were very consistent; thereby refuting the view that spicule size is very variable within each species, at least in areas with similar silica levels. However, where silica levels are low, notably in areas of the Mediterranean, spicule size and shape may be affected (see Uriz *et al.*, 2003; Uriz, 2006 for reviews), and therefore more care may be needed when comparisons are made with fauna from these areas. The examination of external appearance together with internal morphology may assist in determining the level of variation within each species.

It is likely that the large size of the genus may result from a lack of phylogenetic relationships between the species placed in it. The characteristics of *Hymedesmia* are a result of the thin growth form, and are therefore unlikely to be a good indicator of phylogenetic relationships (Van Soest, 2002). The variability of ectosomal megascleres found in the subgenera such as *Stylopus* makes them unlikely to be monophyletic (Van Soest, 1987). Indeed, the genera of *Hymedesmia*, *Phorbis*, and *Stylostichon* may all be artificial, with phylogenetic relationships not corre-

sponding with their architecture (Van Soest, 1987). The increasing use of molecular techniques in taxonomy should help to elucidate these relationships. A revision of the genus *Hymedesmia*, and a re-examination of the type specimens of species currently ascribed to it, is urgently needed. Changes in taxonomy in the past and a lack of description of skeletal characteristics in the original descriptions have resulted in the retention of some species that should probably be ascribed to other genera, as demonstrated in *H. versicolor*.

ACKNOWLEDGEMENTS

The 'Sponge Biodiversity of Rathlin Island Project' was part funded by European Union strategic funds from the EU Building Sustainable Prosperity programme. Subsequent work on the material collected and the collection of additional samples was funded by the Environment and Heritage Service Northern Ireland, as part of the 'Sublittoral Survey Northern Ireland' project. Work in Copenhagen was supported by a grant from the European Commission's (FP 6) Integrated Infrastructure Initiative programme SYNTHESISYS (DK-TAF), and we would like to thank Ole Tendal for his assistance during this visit. The study utilized a collection of literature and information of occurrence of *Hymedesmia* species that was compiled by Shirley Stone and Ole Tendal, and we would like to thank them for allowing us access to this material. The authors would like to thank all of the fieldwork team, particularly Jen Jones, Anne Marie Mahon, and Louise Scally. Samples of other species for comparison were provided by the National Museum of Ireland, the Muséum National d'Histoire Naturelle, Paris, and the Natural History Museum, London. We would like to thank the curators of these collections Mark Holmes (NMI), Isabelle Domart-Coulon (MNHN), and Clare Valentine (NHM) for facilitating access to the material. We would also like to thank three anonymous referees for their helpful comments on the manuscript.

REFERENCES

- Ackers RG, Moss D, Picton BE. 1992.** *Sponges of the British Isles (Sponge V)*. Ross-on-Wye: Marine Conservation Society.
- Alander H. 1935.** Additions to the Swedish sponge fauna. *Arkiv F ur Zoologi* **28B**: 1–6.
- Alander H. 1937.** Sponges from the Trondheimsfjord and Adjacent waters 1. *Det Kongelige Norske Videnskabers Selskab* **10**: 68–70.
- Alander H. 1942.** Sponges from the Swedish west-coast and adjacent waters. Unpublished D. Phil Thesis, Lund University.
- Arndt W. 1935.** Porifera. *Tierwelt Nord-Ostsee* **IIIa**: 1–140.
- Bergquist PR. 1978.** *Sponges*. London: Hutchinson & Co.
- Borojevic R, Cabioch L, L evi C. 1968.** Spongiares. *Inventaire Faune Marine de Roscoff* 1–44.
- Boury-Esnault N. 1971.** Spongiaires de la zone rocheuse de Banyuls-sur-Mer. 2. Syst ematique. *Vie et Milieu* **22**: 287–350.
- Boury-Esnault N, R utzler K. 1997.** *Thesaurus of sponge morphology*. Smithsonian Contributions to Zoology number 596. Washington, DC: Smithsonian Institution Press.
- Bowerbank JS. 1864.** *A monograph of the British Spongiadae, volume I*. London: Robert Hardwicke.
- Bowerbank JS. 1866.** *A monograph of the British Spongiadae, volume II*. London: Robert Hardwicke.
- Bowerbank JS. 1872.** Contributions to a general history of the Spongiadae. 1. *Proceedings of the Zoological Society of London* **1872**: 115–129.
- Bowerbank JS. 1874.** *A monograph of the British Spongiadae, volume III*. London: Robert Hardwicke.
- Bowerbank JS. 1882.** *A monograph of the British Spongiadae, volume IV*. London: Robert Hardwicke.
- Burton M. 1930.** Additions to the sponge Fauna at Plymouth. *Journal of the Marine Biological Association of the United Kingdom* **16**: 489–507.
- Burton M. 1957.** Porifera. In: Russell FS, ed. *Plymouth marine fauna*. Plymouth: Marine Biological Association, 26–32.
- Cabioch L. 1968.** Contribution a la connaissance de la faune de spongiaires de la manche occidentale. Demosponges de la region de Roscoff. *Cahiers de Biologie Marine* **9**: 211–246.
- De Laubenfels MW. 1936.** A discussion of the sponge fauna of the Dry Tortugas in particular and the West Indies in general, with material for a revision of the families and orders of the Porifera. *Carnegie Institute of Washington (Tortugas Laboratory paper No.467)* **30**: 1–225.
- Erwin DG, Picton BE, Connor DW, Howson CM, Gillece P, Bogues MJ. 1990.** *Inshore marine life of Northern Ireland*. Belfast: HMSO.
- Fristedt K. 1885.** Bidrag till K annedomen om de vid Sveriges vestra Kust levande Spongiae. *Kungliga Svenska vetenskapsakademiens handlingar* **21**: 1–56.
- Hajdu E, Van Soest RWM, Hooper JNA. 1994.** Proposal for a phylogenetic subordinal classification of poecilosclerid sponges. In: Van Soest RWM, Van Kempen ThMG, Braekman J-C, eds. *Sponges in Time and Space*. Rotterdam: Balkema, 123–139.
- Hooper JNA. 2002.** Family Microcionidae Carter, 1875. In: Hooper JNA, Van Soest RWN, eds. *Systema Porifera: a guide to the classification of sponges*. New York: Kluwer Academic/Plenum Publishers, 432–468.
- Lundbeck W. 1910.** *Porifera. 3. Desmacidonidae (pars.)*. Copenhagen: Bianco Luno.
- Pansini M. 1987.** Littoral demosponges from the banks of the Strait of Sicily and the Alboran Sea. In: Vacelet JB, Boury-Esnault N, eds. *Taxonomy of Porifera from the northeast Atlantic and Mediterranean Sea*, Vol. 13. Berlin: Springer-Verlag, 149–186.
- Picton BEP, Goodwin CE. 2007.** Sponge Biodiversity of

- Rathlin Island, Northern Ireland. *Journal of the Marine Biology Association of the United Kingdom* **87**: 1441–1458.
- Pouliquen L. 1972.** Les spongiaires des grottes sous-marines de la région de Marseille: écologie et systématique. *Téthys* **3**: 717–758.
- Sara M. 1961.** La fauna dei Poriferi delle grotte isole Tremiti. Studio ecologico e sistematico. *Archivio Zoologico Italiano* **46**: 1–59.
- Sara M. 1964.** Poriferi di acque superficiali (0–3 m) del littorale italiano. *Annali del Pontificio Istituto Superiore de Scienze e Lettere 'S. Chiara'* **14**: 299–317.
- Stephens J. 1916.** Preliminary notice of some Irish sponges. The Monaxellida (suborder Sigmatomonaxellida) obtained by the Fisheries Branch of the Department of Agriculture and Technical Instruction, Ireland. *Annals and Magazine of Natural History* **8**: 232–242.
- Topsent E. 1893.** Nouvelle série de diagnoses d'éponges de Roscoff et de Banyuls. *Archives de Zoologie Expérimentale et Générale* **1**: 33–43.
- Topsent E. 1901.** Éponges nouvelles des Açores. *Mémoires du Société Zoologique de France* **14**: 447–466.
- Topsent E. 1904.** *Spongiaires des Açores*. Monaco: Imprimerie de Monaco.
- Topsent E. 1925.** Étude de Spongiaires du Golfe de Naples. *Archives de Zoologie Expérimentale et Générale* **63**: 623–725.
- Topsent E. 1928.** Spongiaires de l'Atlantique et de la Méditerranée, provenant des croisières du prince Albert Ier de Monaco. *Résultats des Campagnes Scientifiques Accomplies par Prince Albert I. Monaco* **74**: 1–376.
- Topsent E. 1936.** Éponges observées dans les parages de Monaco. 2e partie. *Bulletin de l'Institut Océanographique de Monaco* **686**: 1–70.
- Topsent E. 1938.** Contribution nouvelle à la connaissance des Éponges des côtes d'Algérie. Les espèces nouvelles d'O. Schmidt, 1868. *Bulletin d'Institut Océanographique de Monaco* **758**: 1–32.
- Uriz M-J. 2006.** Mineral skeletogenesis in sponges. *Canadian Journal of Zoology* **84**: 322–356.
- Uriz M-J, Turon X, Becerro MA, Agell G. 2003.** Siliceous spicules and skeleton frameworks in sponges: origin, diversity, ultrastructural patterns, and biological functions. *Microscopy Research and Technique* **62**: 279–299.
- Vacelet J, Perez T. 1998.** Two new genera and species of sponges (Porifera, Demospongiae) without skeleton from a Mediterranean cave. *Zoosystema* **20**: 5–22.
- Van Soest RWM. 1984.** Marine sponges from Curaçao and other Caribbean localities. Part III: Poecilosclerida. *Studies on the fauna of Curaçao and other Caribbean Islands* **199**: 1–167.
- Van Soest RWM. 1987.** Biogeographic and taxonomic notes on some Eastern Atlantic sponges. In: Clifford-Jones W, ed. *European contributions to the taxonomy of sponges*, Vol. 1. Middleton: Sherkin Island Marine Station, 13–28..
- Van Soest RWM. 2002.** Family Hymedesmiidae Topsent, 1928. In: Hooper JNA, Van Soest RWN, eds. *Systema Porifera: a guide to the classification of sponges*. New York: Kluwer Academic/Plenum Publishers, 575–593.
- Van Soest RWM, Boury-Esnault N, Janussen D, Hooper J. 2005.** World Porifera database. Consulted on 2006-10-18. Available online at <http://www.marinespecies.org/porifera>
- Van Soest RWM, Picton BE, Morrow CC. 1999.** Sponges of the North East Atlantic. In: *World biodiversity database CD ROM series. Windows/Mac version 1.0*. Amsterdam: ETI, University of Amsterdam.
- Vosmaer R. 1935.** *The sponges of the Bay of Naples: Porifera: Incalcaria with analyses of genera and studies in the variations of species*. The Hague: Martinus Nijhoff.
- Voultsiadou E. 2005.** Demosponge distribution in the eastern Mediterranean: a NW-SW gradient. *Helgoland Marine Research* **59**: 237–251.
- Wiedemayer F. 1977.** *Shallow-water sponges of the western Bahamas*. Basel & Stuttgart: Birkhäuser.