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Taxonomic characters from the hydranths of live thecate hydroids: European Haleciidae (Cnidaria: Leptothecatae)

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Key words: Haleciidae; *Halecium*; hydroid; hydranth; identification; Leptolida; Leptothecatae; taxonomy.
The hydranths of six species of hydroids of the family Haleciidae from NW Europe are described from life and compared. Notes are given on the hydranths of three other species, and general taxonomic comments on some others. Hydranth character-states are useful in defining and distinguishing *Halecium* species, but the characters may not be useful in routine identification by non-specialists. *Halecium undulatum* is recorded for the first time from Sweden, and from three localities in Norway whence there was just one previous record. *Halecium halecinum* may breed year-round in British waters.

Introduction

The importance of the hydranths of thecate hydroids in biological studies has waxed and waned. At Brighton, SE England, in 1748, the sight of hydranths emerging from a colony of *Sertularella* spec. (family Sertulariidae) gave Abraham Trembley and William Watson support for their view, developed from the work of the Frenchman Jean-André Peyssonnel, that hydroids were animals, not plants (historical accounts in Watson, 1753, and Cornelius, 1996). In August 1752, the Englishman John Ellis visited a shore at Queenborough, in the Thames estuary, and similarly saw hydranths of *Sertularella* spec. Nearby, in 1753, he saw those of *Halecium halecinum* (Linnaeus, 1758), and at an unidentified locality those of *Obelia longissima* (Pallas, 1766). At Brighton, in June 1754, he saw those of several thecate hydroids, and again in the Thames estuary he saw those of further species in the autumn of that year. He took the artists Brooking and Ehret on one or other of his visits, and their illustrations in Ellis's book became the first ever published of the hydranths of thecates (Ellis, 1755).

Detailed study of hydranths under a high-power microscope is not easy. The high magnification required needs bright light. The associated heat, together with the small volume of sea-water in which a specimen is mounted on the microscope stage, typically discourage the emergence of a hydranth, or its adopting a natural posture when it does. Thus the observations of Watson, Trembley and Ellis are the more remarkable.

As a result of these difficulties, taxonomic studies on thecates have had a peculiar limitation. Apart from reproductive structures, almost no attention has been given to the animal itself, and essentially all the taxonomy has been based on the exoskeleton alone. With species from many habitats, especially offshore and deep-water ones which experience the greatest environmental shock when collected, study of hydranths has been difficult. The most painstaking of taxonomists have ignored the hydranths, even of shallow-water and intertidal forms. As a result, remarkably few comparisons have been made between those of any living thecates. Nearly two centuries ago, Lamouroux (1812: 182) had already remarked:

"[Je caractérise l'espèce] d'après la forme du polypier [colony], comme on l'a fait jusqu'à présent. L'étude des animaux qui habitent ces singulières productions de la nature est si peu avancée, qu'on ne peut s'en servir pour les classer."

"[I characterise the species] on the form of the colony, as is customary at present. The study of the animals which inhabit these notable natural productions is so little advanced, that one cannot use them in classification."

Lamouroux was writing about all soft-bodied colonial cnidarians and some other "zoophytes". His warning was little heeded, and in thecate hydroid studies his comment is still valid two centuries later. Hydranths had been a crucial character in the mid-eighteenth century in assigning hydroids to the animal kingdom, but have hardly ever been used for species discrimination in the Leptothecatae.

The present account reports some work done during a survey of hydranth characters I conducted in the early 1980s, comprising visits to several NW European sites. There have been subsequent accounts of several species in the subfamilies Clytiinae and Obeliinae, family Campanulariidae (see Cornelius, 1987a, b; Cornelius & Östman, 1987). In the Obeliinae, hydranth characters proved consistent and useful in species characterisation. And in the Clytiinae, their earlier use would have resolved a long-standing taxonomic problem concerning the validity of *Clytia gracilis* (Sars, 1850). It was eventually resolved by an elegant but more time-consuming approach by Östman (1979; 1987; see also Cornelius & Östman, 1986). Recognition of distinctive hydranth features in this genus later led to the identification of the hydroid stage of *C. gracilis* from several sites in SE England (summary in Cornelius, 1995b), resulting in the recognition of the hydroid of the species as a regular part of the British fauna. Previously only its medusa had been known from British waters, and this only by inference from some data collected by F.S. Russell in the 1930s (Russell, 1953). Indeed, at the time of Russell's work the distinction of the medusa stage was still debated; and the geographical origin of the British-caught medusae that eventually proved to be of this species was unknown.

Reported below are accounts of the hydranths of certain species of *Halecium*, family Haleciidae, from a variety of NW European sites. Although intra-population and inter-population variation have yet to be assessed, some value can still be gained from comparing the data already obtained. The observations reported can be simply made, given an optically good high-power microscope. Low-power, stereomicroscopes do not resolve the necessary detail.

Scientific names of non-haleciid hydroid species incidental to the discussion follow those used in a recent summary (Cornelius, 1995a, b).

Supplementary glossary

The terms used here in the description of hydranths follow a glossary and general description published elsewhere (Cornelius, 1995a, b) with certain additions given below. Related terminology was employed by Bouillon (1995: 33-37, 40-44), who gave a detailed account of the anatomy of hydroid hydranths and tentacles. Detailed histological details and terminology were also given by Harrison & Westfall (1991).

Apical angle - Of the hypostome, the approximate angle made between the two sides as seen in lateral view. Since in many species the sides curve to a greater or lesser extent, the measurement can be somewhat imprecise; but its value can indicate the general shape of the hypostome. In some species the sides of the hypostome are straight, and the angle has a precise value.

Axial cell - In the majority of leptolids the coelenteron does not extend into the tentacles, which are consequently termed "solid". The gastrodermal core comprises a single row of large, conspicuous, cylindrical cells, which when extended are vertically longer than wide. They are here called axial cells.

Bulge (in column of haleciid hydranth) - In all species of *Halecium* studied in the survey the living hydranth had an annular bulge in the column (fig. 1). The bulge was apparent most of the time, but in some species was seen to disappear for irregular periods. Its position had some taxonomic value. In *H. lankesteri* it was recorded as asymmetric.

Extension - The tentacles and hydranths of most, perhaps all, leptolids are extensile and contractile. The hydranths of all the *Halecium* species studied in detail had what seemed to be a normal part-extended condition and posture of both column and tentacles (fig. 1). Hydranths would stay part-extended for minutes or tens of minutes on end. The part-extension seemed to be an innate activity, and was not seen in the hydranths of any other genus studied in the survey. In part-extension the tentacles tended to be thick and parallel-sided, but became delicate and tapered when fully extended. The change in length of the column between the two states was less marked. In the hydranths of all other genera studied, extension was a continual process, with no distinct part-way stage.

Methods

"...it affords us the more frequent opportunities of seeing this animal alive, extending its claws, provided it is immediately, while moist, put into some clean sea-water. In this state it may be kept for some days by renewing the water; we may then cut off small pieces, and put them in a watch-glass full of sea-water, and in a little time they may be examined in the aquatic microscope... This to persons not acquainted with the nature of Zoophytes will appear a most surprising as well as a most agreeable scene of entertainment." [John Ellis, in Ellis & Solander, 1786: 40-41, on *Dynamena pumila* (Linnaeus, 1758).]

In the present study, hydroid colonies were collected intertidally and off-shore by a variety of methods (Cornelius, 1988; Cornelius, 1995a: 48-53). Examination of the material has been described in detail elsewhere and relevant literature cited (Cornelius, 1987a, b; 1995a: 54-57). The procedure is summarised below. Some techniques useful also to high-power study were described by Svoboda (1992) in a paper on low-power microscopy.

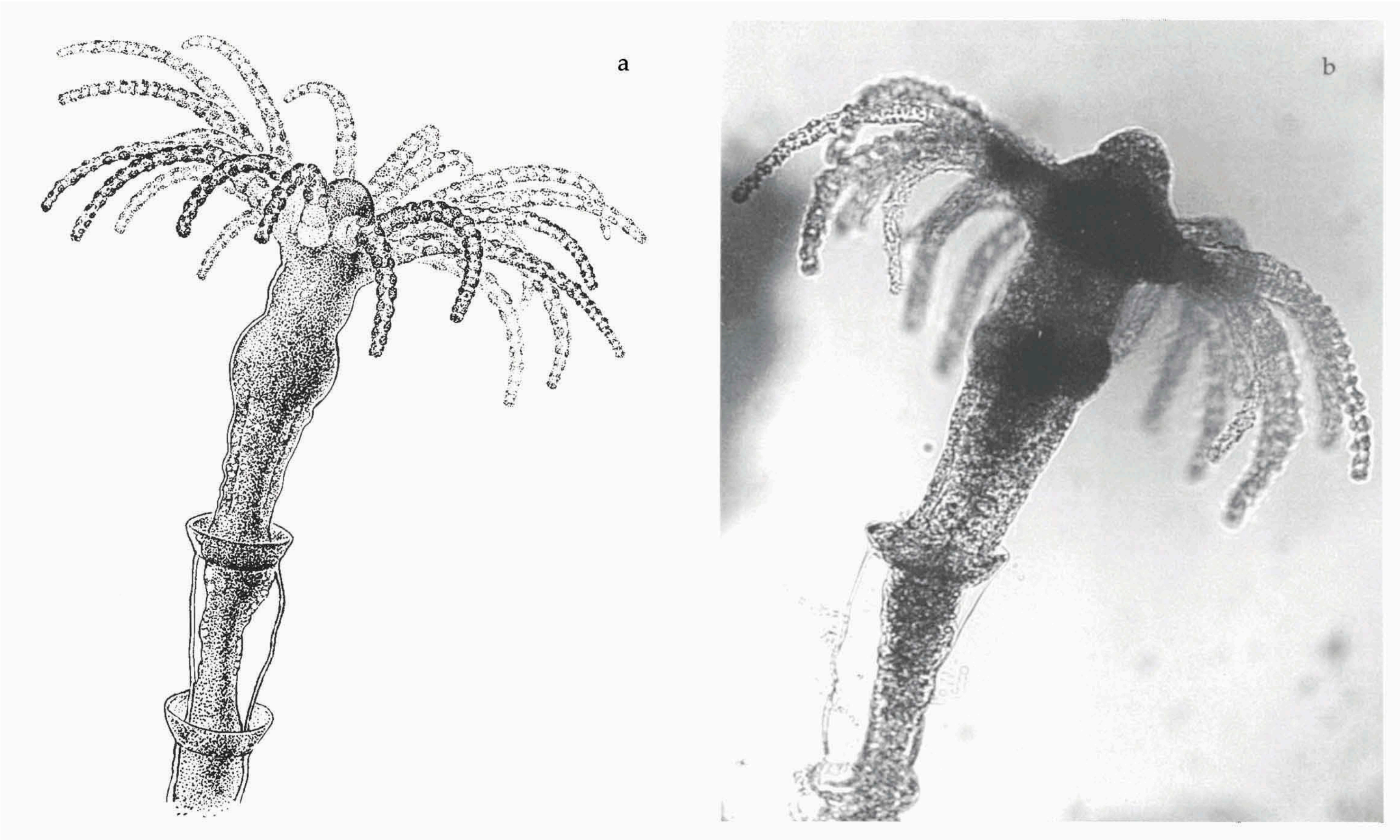

Fig. 1a, b. *Halecium halecinum* (see also fig. 3). Hydranth, partly (1a) and fully (1b) extended. Note that the tentacles appear slightly shorter and thicker when not fully extended; and that the column of the hydranth has an annular bulge. Hydranth column c. 300 μm to base of hypostome. Holme next the Sea, near Hunstanton, Norfolk, England, 29.x.1981 (see text). Fig. 1a drawn by the late Anthony J. Payne, from a photograph.

A 5-7 mm length of 25 mm diameter polythene tube was cemented to a standard microscope slide. The cement used was allowed to dry, and the assembly rinsed to remove possible toxins. This made a convenient cell in which to place a portion of live hydroid colony in sea water. Hydroid colonies were examined by low-power stereomicroscope, and a colony selected in which the hydranths were readily extended. A piece of the colony c. 2.5 cm long was cut off and placed in the sea-water cell. It was convenient if the sample filled the cell, to prevent it drifting around during observation. The specimen in the microslide cell could then be viewed under a high-power microscope. Typically, hydranths would re-emerge after a few minutes on the microscope stage; but after a few minutes of what was judged (from earlier observation under stereomicroscope in the larger volume of water) to be natural extended posture, contraction would set in and further observation become impossible. Details of the extended hydranth had to be recorded swiftly, and photographs taken as an aide-mémoire, typically within 5 minutes. Two, or even three, heat-absorbing filters were, therefore, placed as close as possible to the light source path. Without them, heat from the lamp would quickly cause the hydranths to retract. Each filter absorbed 80 per cent of the heat reaching it, and their successive effect reduced the heat exponentially. Hence full illumination intensity could be used without noticeably affecting the specimen. Plain glass would be almost as effective, but would have to be optically flat and preferably without coloration.

Photographs were taken with a standard Olympus OM2n 35mm camera, which had computerised off-film metering, attached to the microscope. Dedicated electronic flash, providing transmitted substage illumination, was used to obtain correct exposure. Motor-wind film advance and electronic shutter release (via cable) were almost essential to enable observations and photographs to be made quickly. The mechanical disturbance caused by operating manual film-advance and shutter-release caused the hydranths of some species to retract, and also occupied valuable seconds during which observations could be made in the short time available. Due to the narrow nature of the hydranths and the relatively large, pale, transmitted-light background, the camera was adjusted to under expose by two stops. Positive-image colour transparency film of 100 ASA was used since the element of colour helped interpretation of the image: less detail was discernable with black-and-white film. The fine grain of modern 200 ASA film would make it preferable today, but in the early 1980s it was too grainy. Slower film could not be used because the domestic-type flashgun employed scattered the light too widely. A purpose-built microscope flash system, although much more costly, would have enabled use of a slower, less grainy, film. Such equipment was not available to me. Observations were recorded orally onto a tape recorder. This was helpful in the short time that each specimen was extended in a natural posture. Dimensions were measured using a micrometer eyepiece. The microscope used, a standard Zeiss RA, had the advantages of optically excellent lenses and a mechanical stage. Transmitted light was used for initial viewing, cooled as described; and the flashgun introduced into the light path moments before an exposure was made.

Species varied in their readiness to extend. Hydranths of some species would emerge readily on some occasions and not at all on others. A low room-temperature was found essential for the well-being of the material. A high ambient temperature typically resulted in permanent contraction of the hydranths. Other technical details were discussed in the literature cited above.

Although some hydroid species can withstand a long period of transport, the majority extended most readily soon after collection. For this work it was better to collect a drifted specimen from an intertidal pool and take it within minutes to the microscope (Cornelius, 1988), than to employ offshore dredging with unavoidable delay in bringing the material to the laboratory. Speed was useful: but the range of material available intertidally was limited. Some excellent material was collected easily from floating structures, including boating marinas.

The hydranths of some material extended readily only after several days in a cool aquarium. Evidently John Ellis found the same (above quotation).

Most observations were made using the facilities of established marine institutions, but some observations were made in the back of a van using the DC current source of the car battery for the microscope, through a purpose-built transformer; and some in my mother's kitchen in Swanage, Dorset.

Results

The hydranths of six species of *Halecium* were studied in detail. The results are presented as a taxonomic account. See also table 1.

Some species seemed to have two levels of extension of the hydranth, in which the tentacles were either partly or fully extended. All had a bulge in the hydranth column 1/2 to 2/3 from the base. During the survey, these features were seen in the hydranths only of *Halecium* species (see glossary, entries under bulge, extension).

In some species a minute membrane connects the tentacle bases, the intertentacular or basal web. Its extent distalwards along the tentacle is indicated by phrases such as "basal web extending to the 2-cell level", that is, to the level of two axial cells (see glossary).

The term 'amphicoronate' describes the condition common in thecate hydranths, of having alternate tentacles directed upwards and downwards (Cornelius, 1987a, 1995a, b). It may be inherent, that in species having amphicoronate tentacle arrangement their number must be even. Exceptions have been reported, but confirmation seems desirable. Unicoronate indicates a single apparent tentacle whorl.

As in the rest of the Haleciidae, the hydrotheca is very short, recalling a priest's collar. It probably functions only for the attachment of the hydranth to the colony. The ring of c. 15 unusually large desmocytes is attached to the side of the hydrotheca, not to the diaphragm as in most thecates.

Halecium articulosum Clark, 1875
(fig. 2)

Live material.— On rope moored vertically in c. 80 m water depth, Brattholmen Reef, near Bergen, Norway, 10.vi.1983.

Description and measurements.— *Hydranth column* cylindrical, with conspicuous bulge half-way up; 300 μm from diaphragm to tentacle bases; width c. 150 μm, c. 180

μm at bulge but this probably variable; unable to withdraw within the minute hydrotheca. *Hypostome* labile in shape; roughly conical, round at top, to hemispherical; when conical 70 μm high, 130 μm wide. *Tentacles* 28, 280-300 μm when fully extended, c. 200 μm when in part-extended condition; c. 25 μm diameter at base, tapered only slightly to rounded tip; amphicoronate, the lower, horizontal, whorl downcurved distally to point 45° downwards at tip, upper whorl elevated at 45°, only slightly downcurved; nematocysts and their cnidocils conspicuous in distal 2/3, absent from basal 1/3; small basal web extending to 2-cell level.

Readiness to extend.— The hydranths of this material extended readily in the laboratory after three days in an aquarium with running sea-water.

Other published descriptions.— Nutting (1901: 357, fig. 51) stated "hydranths very large, with about 20 tentacles" but also "colony [up to] two feet" [60 cm] in height. He recorded the material as coming from 186 feet [61 m] in Long Island Sound, New York, describing it as "gigantic". The illustrations of both colony and hydranth were poor, and confirmation of both identification and tentacle number would be desirable. The specimen was said to be in the U.S. Fish Commission collections at Woods Hole, so its identity might yet be checked. Jäderholm (1909: 58) cited Nutting's account in his brief synonymy when reporting material as *H. articulosum* from W Sweden, concluding that their identity was the same; and describing the hydranth as thick, with c. 25 tentacles.

Identification.— (see Discussion) The hydranth differed little from that of *H. halecinum*, but the shape of the colony is of course quite different (Cornelius, 1995a).

Remarks.— This seems the first description of the hydranth other than the two comments on tentacle number mentioned above.

Halecium beanii (Johnston, 1838)

Note.— I did not see the hydranth of this common species extended in natural posture. Dalyell (1847: 169, pl. 31 figs 2, 5) recorded a transparent hydranth with 20-24 tentacles. Hincks (1868: pl. 43 fig. 2) provided no textual description, and his illustration of hydranths having only 8 tentacles was diagrammatic. Nutting (1901: fig. 53) similarly provided just a diagrammatic illustration and showed 8-11 tentacles. Vervoort (1946: 161-162) reported that the hydranth resembled that of *H. halecinum* and was colourless.

Halecium halecinum (Linnaeus, 1758)
(figs 1, 3)

Live material.— Strandline, Holme next the Sea, near Hunstanton, Norfolk, England, 29.x.1981 (fig. 1); 80 m depth, NW of I de Batz, Roscoff, NW France, 12.viii.1982 (fig. 3).

Description and measurements.— *Hydranth column* cylindrical, rather wide, often with conspicuous bulge 1/2 to 2/3 from base; 280-430 μm high to base of hypostome (though often not fully extended under laboratory conditions), 100 μm wide; almost entirely projecting beyond minute hydrotheca and never retracted within it. *Hypostome* rounded-conical at rest but sometimes became sub-spherical; when conical, 70-90 μm high, 100-125 μm wide; apical angle 80-110°. *Tentacles* 24-26, 350 μm long when fully extended but often 180 μm or less; diameter 25 μm at base, tapered gradually to

15 μm at tip (appeared untapered when not fully extended); round-ended, fine and delicate when fully extended but often only partly extended when they appeared thicker; amphicoronate; bases of alternate tentacles held 20° above and 20° below horizontal; but when hydranth fully extended, tentacles often more elevated, up to near-vertical and 45° respectively; all tentacles strongly downcurved along whole length, giving reflexed appearance and leaving hypostome clearly visible in lateral view; axial cells large, 16 (Roscoff material) to 25 (Norfolk material); nematocysts irregularly arranged, inconspicuous, sparse in, to absent from, basal 1/4; basal web minute. *Colour* of hydranth column and hypostome in live material pale horn (in Norfolk specimens) and transparent (Roscoff); tentacles transparent.

Readiness to extend.— See under Behaviour, below.

Other published descriptions.— Dalyell (1847: 163, pl. 29, fig. 1) reported 18-22 tentacles. Hincks (1868: pl. 42) diagrammatically illustrated apparently part-extended hydranths with up to 12 tentacles. Vervoort (1946: 146) stated "around the ninepin-shaped hypostome is a ring of approximately ten thread-like tentacles". Nutting (1901: fig. 50) showed passable diagrams of the hydranths with 18-21 tentacles but without natural posture and possibly drawn from preserved material. Cornelius (1975: 395) stated "hypostome conical, tentacles 17-22".

Behaviour.— As indicated in the description, the hydranth seldom extended fully under temporary laboratory conditions. It stayed for long periods incompletely extended, but did this readily.

The hydranth was remarkably insensitive to tactile stimuli. The Norfolk material showed no response when poked with a needle, neither contracting nor changing shape.

The end regions of the tentacles were moved while the basal regions remained still, each tentacle bending sharply at a uniform point mid-way along its length. A single tentacle at a time could be bent in this way. In addition, those of one side of the hydranth were seen bending upwards while those on the other side moved downwards.

The bulge in the column 1/3 to 1/2 way down was usually present. It could slowly change shape to become more or less raised, and it sometimes disappeared altogether.

Identification.— (see Discussion) The hydranth of the samples studied differed little from those of *H. articulosum*, but the skeleton of the two species differs greatly (Cornelius, 1995a).

Remarks.— The Norfolk material, collected live 29.x.1981, had mature, motile planulae in the female gonothecae. The planulae measured 125 × 25 μm. Most had apparently already been liberated, the gonothecae being nearly empty. However, premature, hormetic release may have occurred following removal from the sea (cf. Cornelius, 1992: 252). Other fertile material in British waters was reported from December to the end of August (summary in Cornelius, 1995a). The finding of fertile material in late October suggests the species may be unusual among British hydroids in being reproductive year-round. However, the precise phase reached in the reproductive cycle has not been recorded by all observers when making their dated observations, and detailed data are needed to elucidate the point.

Halecium labrosum Alder, 1859
(fig. 4)

Live material.— Approx. 20 m depth, Vattlestraumen, near Bergen, Norway, on *Modiolus* spec., 20.vi.1983.

Description and measurements.— *Hydranth column* cylindrical, usually with bulge 1/4-2/3 from base; height when fully extended, diaphragm to top of hypostome, 460 μm, diaphragm to tentacle bases c. 350 μm; narrowest width c. 70 μm, varying to up to 120 μm when bulge most dilated; almost entirely outside minute hydrotheca. *Hypostome* hemispherical to bluntly conical with convex sides, with apical angle c. 110°; 100 μm high × 120 μm diameter. *Tentacles* 22, when fully extended 275 μm long, breadth 25 μm at base tapered only slightly distally to c. 20 μm at the blunt tip; tip slightly clubbed when tentacle incompletely extended; total tentacle-span 650 μm; amphicoronate; whorls only shallowly separated, often appeared as single whorl, held either straight or slightly and irregularly downcurved; axial cells c. 20; nematocysts inconspicuous, absent from basal 1/3, irregularly arranged in distal 2/3; basal web to c. 1-cell level.

Readiness to extend.— The hydranths extended readily following collection by dredging and transport to the laboratory, and were still suitable for examination the following day.

Other published descriptions.— Apparently none.

Behaviour.— As in other *Halecium* species, in the laboratory the tentacles remained partially extended for a long time before extending fully.

Identification (see Discussion).— The hydranth column is proportionately long, recalling that of *H. lankesteri*, but that of *H. tenellum* is proportionately longer still. The hydranth column in *H. labrosum* is shorter than that of *H. lankesteri*. But the skeletons of these species are distinctive and it is likely that these would normally prove adequate for identification (Cornelius, 1975; 1995a).

Halecium lankesteri (Bourne, 1890)
(fig. 6)

Live material.— 30 m depth, E of Duke Rock Buoy, Plymouth Sound, Devon, England, 7.vi.1982; 30 m depth, E of Eddystone Rock, 15 km S of Plymouth breakwater, Devon, 9.vi.1982; Sandbanks, entrance to Poole Harbour, Dorset, on drifted *Hydrallmania falcata* (Linnaeus, 1758), 18.x.1982.

Description and measurements.— *Hydranth column* nearly cylindrical, slightly tapered basalwards; height 500 μm to tentacle bases, diameter 80-100 μm; often with slight asymmetric bulge 1/3 up from base, but this disappeared and reappeared across whole colonies from hour to hour; hydranth almost entirely projected beyond minute hydrotheca. *Hypostome* round-conical to n-shaped; when conical, apical angle c. 80°; height 70-100 μm, breadth 100 μm. *Tentacles* 22-24; when fully extended 250 μm long, 15 μm wide, not tapered; amphicoronate; when completely extended, bases of alternate tentacles held horizontal and elevated at 45°; both whorls slightly downcurved, becoming more so when under environmental stress on the microscope stage till lower group bent through 180° and its tips nearly touched column; axial cells c. 15;

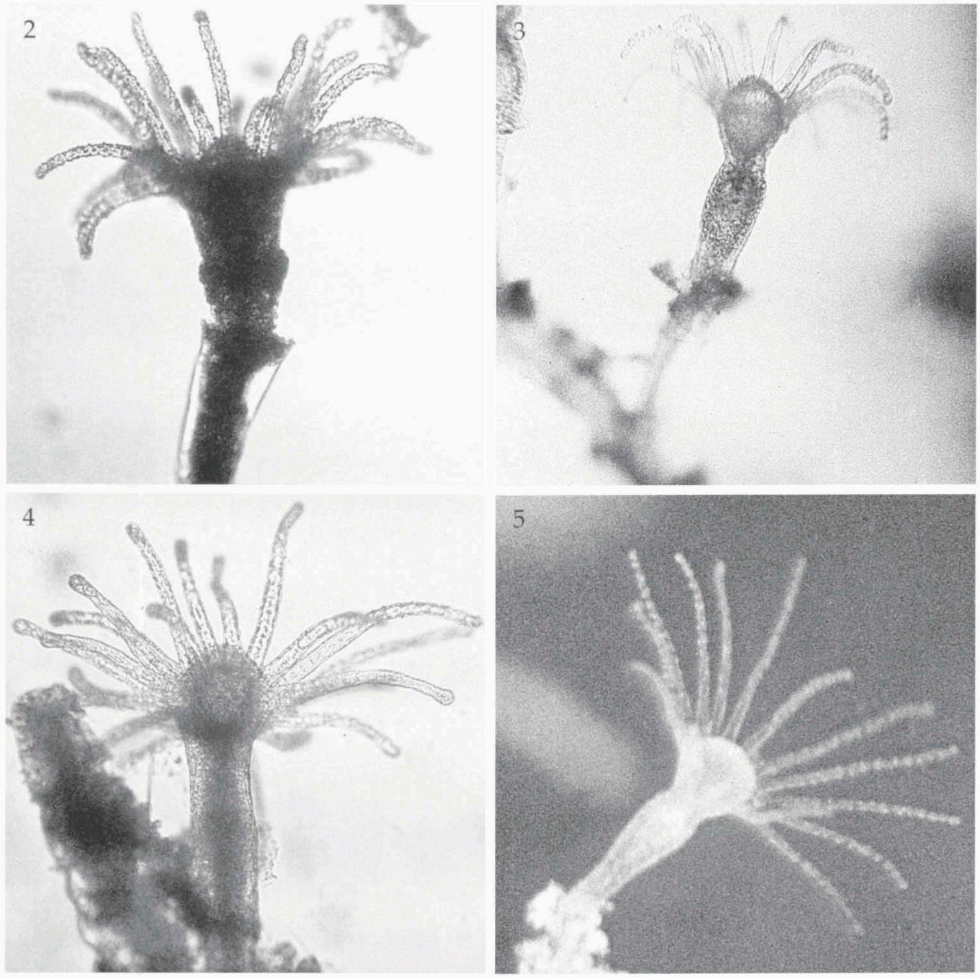

Fig. 2. *Halecium articulosum*. Hydranth. Bergen, Norway, 10.vi.1983 (see text). Column 300 μm to base of hypostome.

Fig. 3. *Halecium halecinum* (see also fig. 1a, b). Hydranth, fully extended. Roscoff, NW France, 12.viii.1982 (see text). Tentacles 180 μm long.

Fig. 4. *Halecium labrosum*. Hydranth, fully extended. Bergen, Norway, 20.vi.1983 (see text). Hydranth column c. 350 μm to base of hypostome.

Fig. 5. *Halecium tenellum*. Hydranth, fully extended. Roscoff, NW France, 25.viii.1982 (see text). Hydranth column c. 750 μm to base of hypostome.

nematocysts conspicuous, irregularly distributed, absent from basal 1/3; basal web absent or minute. *Colour* of column white-translucent, tentacles transparent.

Readiness to extend.— The hydranth seemed not always to extend completely under temporary laboratory conditions, and those of an entire colony sometimes remained partially extended for many hours. However, the hydranth did sometimes extend almost fully; and the Dorset material extended fully almost immediately in a small vessel of static sea-water which was slightly higher in temperature than the local sea.

Other published descriptions.— Bourne (1890) stated "hydranth very large, elongate, fusiform, with a single circlet of sixteen to twenty filiform tentacles, non-retractile...deep brown colour" but the hydranths of the present material were not brown and Bourne's material may have been that colour from their diet. His illustrations showed several hydranths with long, tapering tentacles and a hydranth column with a bulge 1/3 to 2/3 from the base. Hamond (1957: fig. 9) recorded 20-24 amphicoronate tentacles and a column c. 400 μm long (calculated from his illustration).

Behaviour.— The bulge in the hydranth column disappeared from hour to hour in all the hydranths on a colony but would later reappear. When present it tapered away gradually above and below, less abruptly than in *H. halecinum*.

Identification (see Discussion, and the notes under *H. labrosum*).— The skeletal characters of *H. lankesteri* are distinctive (Cornelius, 1975; 1995a) and probably adequate for the identification of all but small colonies in which the distinctive colony form has not yet appeared.

Remarks.— The Duke Rock Buoy locality is that whence part of the type material was collected in 1889 (Bourne, 1890). I collected the species there 2.vii.1973 (Cornelius, 1975), and in 1982 as listed above. No further material was certainly recorded from the area in intervening years (Marine Biological Association, 1931, 1957).

Halecium muricatum (Ellis & Solander, 1786)
(fig. 9)

Note.— I collected this species live from Ramfjord, near Tromsø, Norway, 20-30 m depth, 29.vi.1984, but its hydranths failed to open fully in the laboratory. They had 22 tentacles and a hemispherical hypostome, and were white. Dalyell (1847: 175, pl. 32, fig. 5) recorded the hydranth of some Scottish material as green (!) with 22-24 tentacles. Broch (1911: fig. 18) diagrammatically illustrated a hydranth with 16 tentacles and a conical hypostome.

Halecium sessile Norman, 1867
(fig. 7)

Live material.— Depth c. 40 m, 10 km S of Eddystone Rock, off Plymouth, Devon, England, 22.vii.1983.

Description and measurements.— *Hydranth column* tall, cylindrical, with elongate, gradually sloping central bulge about 1/3 from top; column 450 μm high to tentacle bases, c. 130 μm wide but up to c. 180 μm at bulge; almost entirely projecting beyond minute hydrotheca. *Hypostome* hemispherical to conical, apical angle c. 80°; c. 130 μm high and wide. *Tentacles* 26, probably c. 300 μm when fully extended, c. 20 μm diameter basally; amphicoronate, the two whorls separated by c. 30°; posture when fully extended not seen; axial cells 20-25; nematocysts inconspicuous, in bands (annuli) in distal 2/3, absent from basal 1/3; basal web to c. 4-cell level. *Colour* of all tissues in present material translucent-white in life, but yellow recorded by Storm (1882).

Readiness to extend.— The present colony did not extend its tentacles fully, and did not extend readily even to the 'half-way' stage characteristic of most of the other *Halecium* species studied.

Other published descriptions.— Hincks (1868: 229, pl. 44, fig. 2), whose illustration was based on a drawing by Joshua Alder, recorded A.M. Norman's observation that the hydranths extended to a length up to five times the diameter of the hydrotheca. Hincks diagrammatically illustrated just 10 tentacles, and stated the hydranth to be narrow basally "gradually expanding to the summit;...tentacles long and slender". Cornelius (1975: 408) stated "hydranth long, tentacles 18-25 (after Vervoort, 1941); citron-yellow colour recorded (Storm, 1882) but this perhaps unusual".

Identification. (see Discussion).— In proportions, the hydranth column was typical of several of the species of *Halecium* studied, being about three times as high as broad, but the tentacles were rather longer than in most. On present evidence the high hypostome seems diagnostic.

Remarks.— No other large, distinctive, colonial thecate hydroid from British waters has been so seldom reported as this species. The colony studied resembled the large one described as *Halecium plumosum* by Hincks (1868: 227-228, pl. 64 fig. 1) in the first description of the species. That nominal species was referred to *H. sessile* Norman, 1867, by Cornelius (1975); and a colony essentially similar to that illustrated by Hincks as *H. plumosum* was illustrated by Cornelius (1995a) as *H. sessile*. These large, distinctive, but seldom reported colonies were regarded by Cornelius as conspecific with the much smaller colonies to which the name *H. sessile* has often been applied, on the basis of details of the skeletal anatomy; but confirmation is desirable, perhaps by comparison of the hydranths. Storm (1882) also thought that the two nominal taxa, sympatric and proposed one year apart, might prove conspecific.

Curiously, *H. sessile* is the only *Halecium* species of which the industrious hydroid naturalist Hincks (1868) gave a textual description of the hydranth, but it was apparently transcribed from notes by A.M. Norman (in litt.) to Hincks, since the original description includes no mention of the hydranths.

Halecium tenellum Hincks, 1861
(fig. 5)

Live material.— Depth 70 m, N of Ile de Batz, off Roscoff, NW France, 25.viii.1982.

Description and measurements.— Only one group of living colonies seen. *Hydranth column* narrow, cylindrical, up to c. 750 μm long, 90 μm wide in centre, narrowed near top and broadened out sharply to 200 μm width below tentacle bases; bulge c. 1/3 from top; much too long to fit in hydrotheca. *Hypostome* a very low dome, 50-70 μm high, 200 μm wide, much wider than column; apical angle of hypostome shallow, but measurement of it meaningless since hypostome curved across whole surface. *Tentacles* 16, length not recorded directly from life but estimated 600 μm from photograph; measured from life as 25 μm wide at base, c. 12 μm at tip; delicate and tapering, unicoronate; bases at 20-40° to horizontal; approximately straight for basal 2/3, distal 1/3 downcurved slightly; 15-20 large axial cells; nematocysts irregularly distributed along whole length, moderately prominent. *Colour* of column, hypostome and tentacles pale horn.

Readiness to extend.— The material described was apparently fully extended but the hydranths were more sensitive to disturbance than those of most hydroids studied in the survey. When a test sample was transferred to a microslide cell for study under a high-power microscope (see Methods), the hydranths did not extend. Therefore, it was described and photographed while still under a binocular microscope.

Other published descriptions.— Apparently none.

Identification (see Discussion).— The hydranth differed from those of the other species studied in its proportionately longer hydranth; in its unusually wide, low-domed hypostome, wider than the column and not conical; and in having only 16 tentacles. The exoskeleton of the colony is also distinctive, in having long, narrow internodes; and the colony is much smaller than that of most other *Halecium* species.

Remarks.— Little is known of this unusually small *Halecium* species, despite its having been reported from parts of all major oceans (summary, and caution of accepting unconfirmed records, in Cornelius, 1995a). The slight bulge in the hydranth column was in the upper 1/3 and tapered away gradually above and below: in most *Halecium* species studied it was lower.

Halecium undulatum Billard, 1922
(fig. 8)

Note.— Billard (1922) gave no details of the hydranth, and I was similarly unable to make satisfactory observations on the hydranth of this species. Material I collected 8.vi.1984 by dredging at Vattlestraumen, near Bergen, Norway, had hydranths with c. 20 tentacles but the hydranths did not extend in the laboratory. Material collected 2.vii.1984 from Kval Sundet, near Tromsø, Norway, which did not extend fully, had c. 26 tentacles, a hemispherical hypostome in the contracted hydranth, broadening out to a low mound when partly extended, and a prominent central bulge on the column. Hamond (1957: 304-306, figs 12-13) described briefly and illustrated hydranths c. 350 μm high under this name, with 18-24 tentacles, amphicoronate in arrangement, and with hemispherical hypostome. The length of the hydranth is deduced from his illustration, which is of hydranths apparently part-extended.

The species had been reported from Scandinavia only once before, from Brattholmen Reef, near Bergen (Burdon-Jones & Tambs-Lyche, 1960). I found it in June 1984 at the above localities and also in Porsanger Fjord, N Norway; and in July 1984 (with Dr Carina Östman) at Gasö Ränna, near Kristineberg, Gullmarsfjord, W Sweden, 40 m depth, the first Swedish record. These new Scandinavian records were mentioned in Cornelius (1995a), without detail excepting the comment "common at these localities".

Discussion: hydranths in identification

Little has been published on the hydranths of species of Haleciidae. A few gross anatomical details of possible taxonomic significance have been mentioned in scattered literature and are mentioned under each species above. Of no *Halecium* species is there a satisfactory published description of the hydranth. It is known, however, that the hydranth gastrodermis is divided into a distal digestive region and a proximal non-digestive region (Bouillon, 1995: 334 and fig. 22, which shows a longitudinal section of the hydranth of *Halecium halecinum*). It is unclear whether or not this division corresponds to the position of the externally visible bulge in the hydranth col-

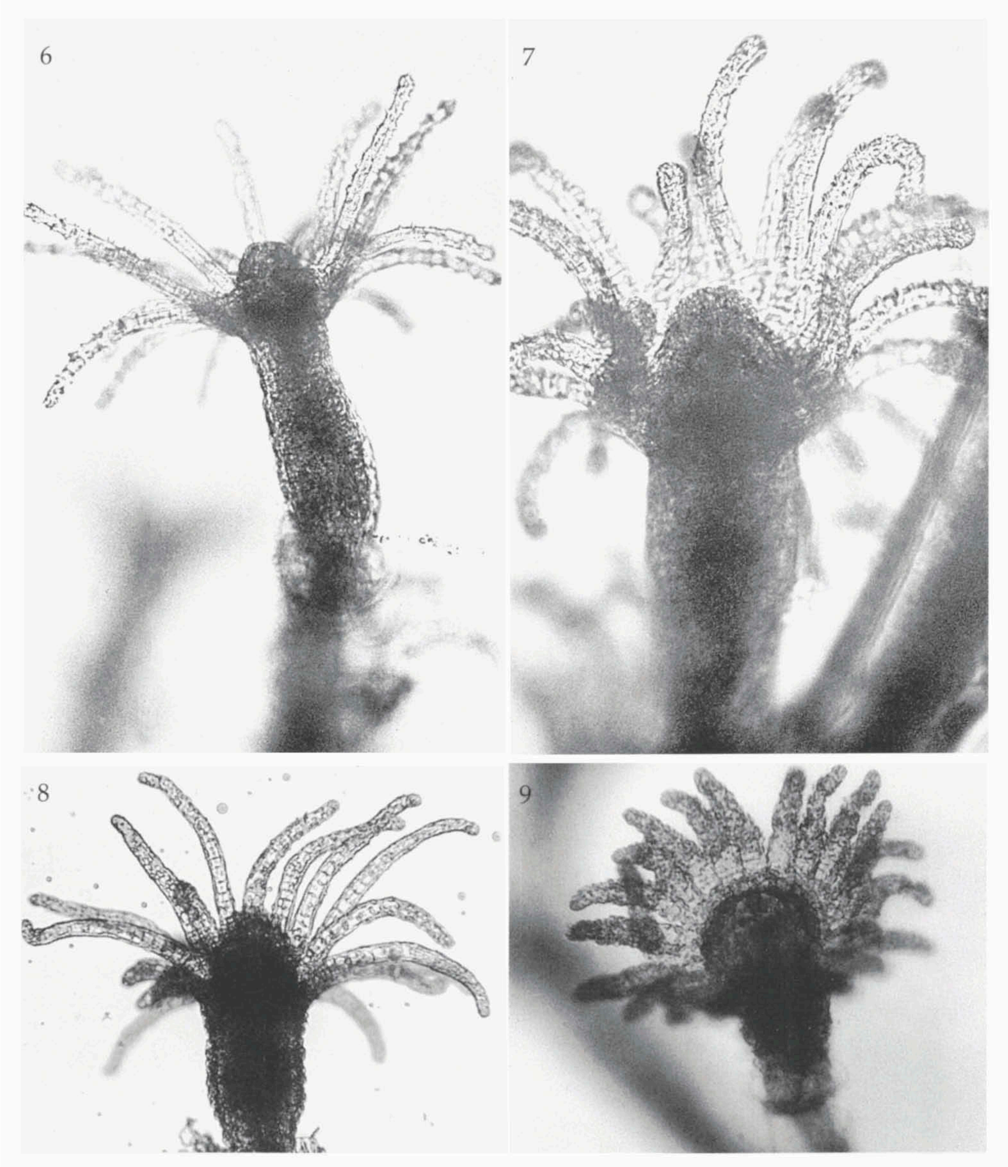

Fig. 6. *Halecium lankesteri*. Hydranth, fully extended. Dorset, England, 18.x.1982; dimensions of photographed material not recorded (see text).

Fig. 7. *Halecium sessile*. Hydranth, partly extended. Devon, England, 22.vii.1983; hydranth column c. 450 μm to base of hypostome.

Fig. 8. *Halecium undulatum*. Hydranth, partly extended. Near Tromsø, Norway, 2.vii.1984; dimensions not recorded (see text).

Fig. 9. *Halecium muricatum*. Hydranth, partly extended. Near Tromsø, Norway, 29.vi.1984; dimensions not recorded (see text).

umn; and whether the essentially non-contractile nature of *Halecium* hydranths makes such a division able to function. The hydranths associated with the gonangium uniquely, or nearly so, in species of *Halecium* have not been studied in detail, and are not considered here.

The hydranths of six NW European *Halecium* species are described above from life (table 1). Their hydranths proved distinctive in the proportion of column height/breadth, tentacle length, hypostome shape, position and shape of the annular bulge, number of axial cells in the tentacles, and upward extent along the tentacles of the basal web. The NW European species not studied alive in natural posture were *H. beanii*, *H. muricatum* and *H. undulatum*, and brief notes on them are included above.

Although distinctive differences were noted between the hydranths of most of the six species that were studied adequately, there was some uniformity. All except *H. tenellum* had rather thick, short, downcurved tentacles and a thick hydranth column issuing from a minute hydrotheca. All had a prominent bulge part-way up the hydranth column during most of the observation period.

Most distinctive within the genus was the hydranth of *H. tenellum*, a minute species. It had an unusually long hydranth, with length:breadth ratio and actual length substantially greater than in the other five species. It had by far the longest tentacles and hydranth column, and proportionately the widest, lowest hypostome. But the distinctiveness of its fully extended hydranth was nullified for use in routine identification by its being extremely sensitive to handling, making it difficult to observe adequately. And since its exoskeleton is one of the most distinctive of the genus in NW Europe, in this region there is little need to use hydranth character-states to discriminate it.

Two other species had a proportionately long hydranth column, *H. labrosum* and *H. lankesteri*, that of the latter being absolutely the longer. In the material studied these two differed also in the level of the bulge on the hydranth column, this being unusually low in *H. lankesteri* compared with its position in the material of all the other species studied in detail.

The three remaining species had hydranth columns just 2-3 times as high as broad when fully extended. Among these, the tentacles of *H. sessile* were very long and the hypostome was as high as wide instead of being proportionately flatter. This species also had the most extensive basal web of all those studied.

The hydranths of the other two species, *H. articulosum* and *H. halecinum*, differed only slightly from each other, but the two could easily be separated on skeletal characters.

Some of the inter-specific differences highlighted may, however, seem subtle to those not familiar with hydranths in the genus. Most of the species have distinctive skeletal characters probably more useful in identification (Cornelius, 1975; 1995a). However, the study of gross hydranth anatomy might confirm species limits in cases in which there is taxonomic debate over skeletal characters. Hence *Halecium* hydranths do seem to provide useful taxonomic parameters. In some circumstances, for example when identification of young or infertile material is essential, the differences between the hydranths of *Halecium* species could prove valuable.

Table 1. Hydranths of six *Halecium* species from western Europe. Dimensions (in μm) and other data.

Species / Character	*H. articulosum*	*H. halecinum*	*H. labrosum*	*H. lankesteri*	*H. sessile*	*H. tenellum*
Column:						
height	300	280-340	350	500	450	750
width	150	100	70	80-100	130	90
Height/width ratio	2	3	5	5-6	3.5	8
Proportionate distance of bulge in column from base	1/2	1/2 - 2/3	1/2 - 2/3	1/3	2/3	2/3
Hypostome:						
shape	conical to hemispherical	round-conical	conical	conical	conical	low dome
height	70	70	100	70-100	130	50-70
diameter	130	100-125	120	100	130	200
Tentacle:						
number	28	24-26	22	22-24	26	16
length	280-300	350	275	250	c. 300	c. 600
Extent of basal web	to 2-cell level	present (not measured)	to 1-cell level	absent/minute	to 4-cell level	?
Axial cells	?	16-25	20	15	20-25	15-20

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