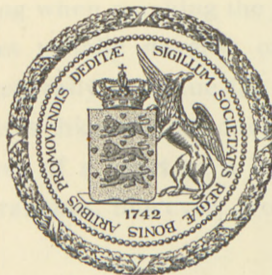


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ON THE GENUS *CODIUM* STACKH.
IN DANISH WATERS

BY

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ON THE GENUS *CODIUM* STACKH.
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SORENSEN



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Of the genus *Codium* two species inhabit the Danish waters: *C. dichotomum* (HUDS.) SETCHELL and *C. fragile* (SUR.) HARIOT, both belonging to the group *Tomentosa* DE TONI. They are characterised by having an erect, cylindrical, ramiferous thallus expanding into a holdfast-cushion at the base. Several erect shoots generally grow from the basal portion. The characteristic feature of the anatomical structure of the erect frond is that it consists of a central part of long hypha-like threads, running lengthwise, branching and interwoven, and a peripheric part of large, serried, cylindrical or club-shaped vesicles (utricles), resembling palisades. The utricles projecting at right angles from the central part are formed at the apices of the pith-filaments (or sometimes laterally?). The latter change the direction of their growth, bending towards the periphery of the frond swelling when reaching the former. The bottom part of the utricles usually develop one or more lateral branches, which generally continue the growth of the pith-filaments, themselves likewise producing utricles at their tips after the course of a short or a long time. In several cases the lateral branches, however, grow directly into new utricles.

The utricles as a rule do not branch off; they contain a number of nuclei and numerous small chromatophores chiefly found at the upper end. Often they bear at the upper end one or more hairs (or the scars from them).

The hairs contain a rather small number of chromatophores.

The reproduction is by motile gametes, which develop in gametangia. The position of these is lateral, on the utricles. In addition, in *C. dichotomum* there is a vegetative propagation by means of vegetative buds.

Transverse walls do not exist. On the other hand, local pad-shaped thickenings of the external walls occur, the so-called plugs. Such bodies are seen between the utricles and the pith-filaments, at the bases of the gametangia and the hairs and in the pith-filaments. In *C. dichotomum* between the utricles and the vegetative buds, too.

Regarding the general structure reference may be made to OLTMANN'S (1922, p. 386) and SCHMIDT'S monography (1923), regarding the taxonomy to the latter treatise.

1. *Codium dichotomum* (HUDS.) SETCHELL.

SETCHELL 1931, p. 357; SUNESON 1939, p. 57, fig. 1 A.

Codium tomentosum (HUDS.) STACKH.; GIBSON and AULD 1900, pl. 1—3, figs. 1—21 (—fig. 13 a, b, e); K. ROSENINGE 1920, p. 129; SCHMIDT 1923, p. 39, figs. 20—21; VAN GOOR 1923, fig. 1 d.

f. *proliferum* KÜTZ.; VOUK 1936, p. 15, Taf. IV, fig. 2, Taf. V, fig. 2.

f. (?) *dichotomum* VOUK 1936, p. 15, Taf. I, fig. 1.

In the attached state this species is noticed in the northern Kattegat only, near Frederikshavn, in which place it grows on wood, stones, shells of *Balanus* and *Modiola*, tubes of worms and the like. It often occurs in the upper sublittoral region, from a little below the surface of the water down to the depth of a few metres. This is the case, for instance, in the harbour of Hirsholmene, where it grows very gregariously, so that there is here a *Codium*-association. However, it may be found at a greater depth, too, having been met with in down to 11 meters' depth.

The colour of living plants is dark green or more or less bright green. The brighter colour is more pronounced in plants, which are exposed to a rather large amount of sunshine and is particularly characteristic of the young shoots. As the latter are most frequently met with in summer, plants from this season are often rather bright. This species, however, taken at large, too, is lighter than *C. fragile*. The Danish individuals are in that respect different from COTTON'S Clare Island plants. Regarding *C. tomentosum* this author writes (1912, p. 114) "Colour dark

green. . . . does not assume a light green colour when growing in sunlight". In contradistinction he says about *C. mucronatum* var. *atlanticum*: "Colour deep green, bright green when growing in sunlight".

The erect part of the thallus consists of branching filaments, of a diameter of about 2—4 mm, the maximum length being up to well over 20 cm. The appearance of the specimens at my disposal is rather varying; nearly all of them are collected in the month of July (a few of them, however, in May, June and August), mainly originating from Hirsholmene. They group round three types, which are to be sure very closely allied.

In one type (plate I), represented by a few plants gathered in May the frond is hardly 20 cm in length by 4 mm in diameter. The ramification is dichotomous, rather scanty. The branches are somewhat squarrose, often curved and bent downwards. The upper segments, of a length of 2.5—6 cm, are rather characteristic, being curved, recurved or incurved. The frond of the greater part of the plant has numerous small warts, often arranged so as to be partly one-sided. On the convex side of the upper segments they have often developed into short lateral shoots, as a rule, however, not exceeding the length of 0.5 cm.

The second type includes a few plants gathered in the month of June. They seem to be consistent with the former except that they have the warts developed into small, short shoots, sometimes attaining the length of more than 1 cm. — The specimen represented in plate II was cast up, but the attached plants looked very much like it, even if the tendency of the upper segments to incurve or recurve is not quite so marked.

The great majority of the plants, however, seem to fall

under the type pictured in plate III. In these plants, mainly gathered in July, the frond reached a length of up to over 20 cm, while the diameter of the branches amounted to about 3 mm. The plants seem to show a distinction between main branches and lateral branches. The former, arisen by dichotomous ramification, are squarrose and curved, recurved or incurved; the lateral branches are mainly found on the convex side. They may, however, be found, too, on the unbranched bottom part of the main shoot. The lateral branches in full-grown plants are generally about the length of 7—10 cm; the ramification is usually regularly dichotomous, in rare cases they develop lateral shoots of their own.

The appearance of a great number of young plants, likewise mainly gathered in July, is similar to that of the latter. The frond of these plants consists of a short main filament, branched or unbranched, often somewhat curved, producing numerous lateral branches particularly on the convex side. In other cases the branching of the young plants is regularly dichotomous throughout the entire plant, without any distinction between main and lateral branches.

The two first mentioned types may presumably be referred to f. *proliferum* Kütz. (see Vouk, l. c.). The third may possibly be referred to f. *dichotomum* Vouk because of the comparatively short, not parallel end segments mainly of equal length. Owing to the distinction, however, between main and lateral branches it is not very much like Vouk's fig. 1. of plate 1. In spite of the morphological difference the three types are presumable nevertheless closely related, perhaps representing different stages of development of the same form. Actually, the only difference between types 1 and 3 is that the warts of the former have

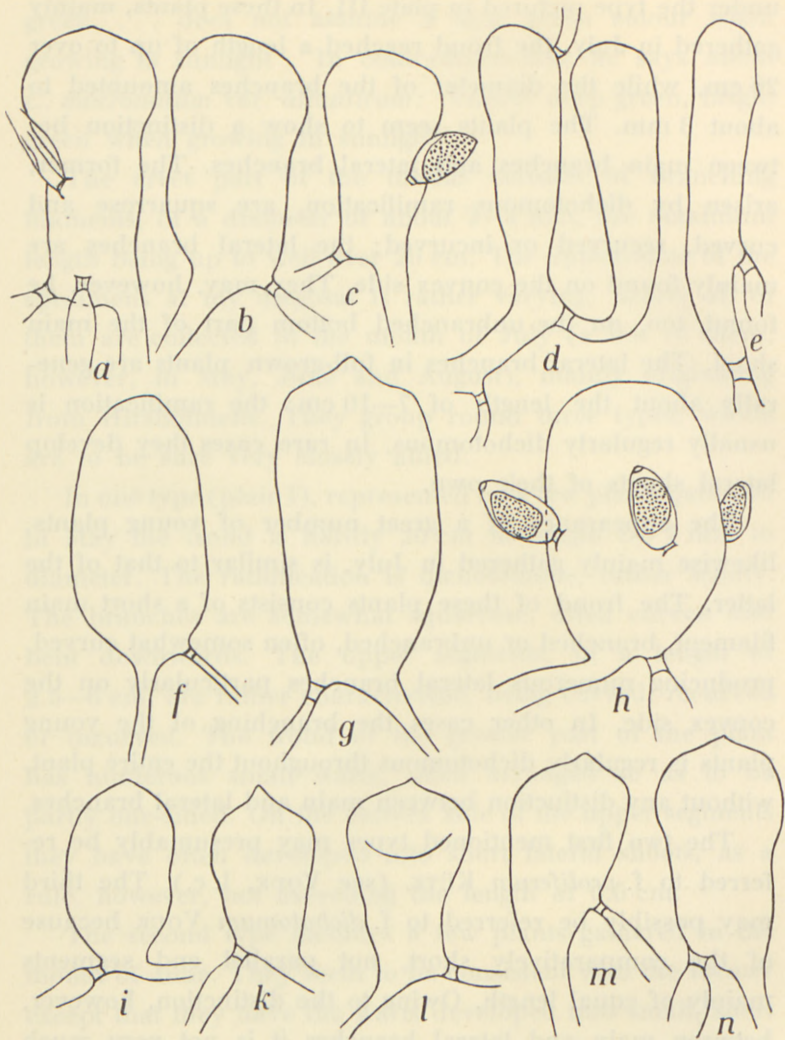


Fig. 1. *Codium dichotomum*. Utricles. *i*, *k*, and *l* from seedlings; *m* and *n* from the apex of a branch. Gametangia with contents are seen in *c* and *h*, a gametangium emptied in *a* and a utricle hair in *d*. — *a-h* and *m*, *n* from Hirsholmene, the harbour; *a-c* and *f-h*, 29-VII-19; *d*, *e*, 23-V-29; *m*, *n*, 10-VII-34. *i*, *k*, from east of Deget, 4-VIII-32. *l* from Holme-havn's Reef, 3-VIII-28. (46:1).

come out as lateral shoots of a considerable length in the latter. The plant shown in plate II represents an intermediate stage. As the three types were gathered in May, June and July, respectively, it is to be presumed that in this species, at the locality mentioned, an abundant production of lateral branches takes place during the summertime.

Nor does the anatomical structure of the three types seem to show any difference. They all have the same types of utricles, and they are subject to the same variation as to the size of the utricles.

As to shape the utricles vary rather much. VOUK (l. c. p. 7) mentions a dimorphism in this species of club-shaped utricles and of utricles of a vesicular shape. A dimorphism like that is not a characteristic feature of the present writer's material, here polymorphism is more pronounced. In addition to club- and bladder-shaped utricles numerous top-shaped and cylindrical utricles appear, and some of still other shapes. In figs. 1, 6, and 7 I have shown different types of utricles.

As to shape the end of the utricles show a fairly great variation. Some of them are rounded, as for instance in SCHMIDT's figures (1923, figs. 20, 21), others are more or less rounded conical, as appears for instance from VAN GOOR's fig. 1 d, the drawing of which is from a specimen from Hirsholmene. Very often they have, however, a more or less marked point, nay, this type seems even often to be the most frequent. Thus this seems especially to be true in the case of the utricles which occur in the young shoots (fig. 1 m, n). This type, for instance, was very common in the lateral shoots of the specimen shown in plate III. In the upper part utricles like these correspond exactly to the

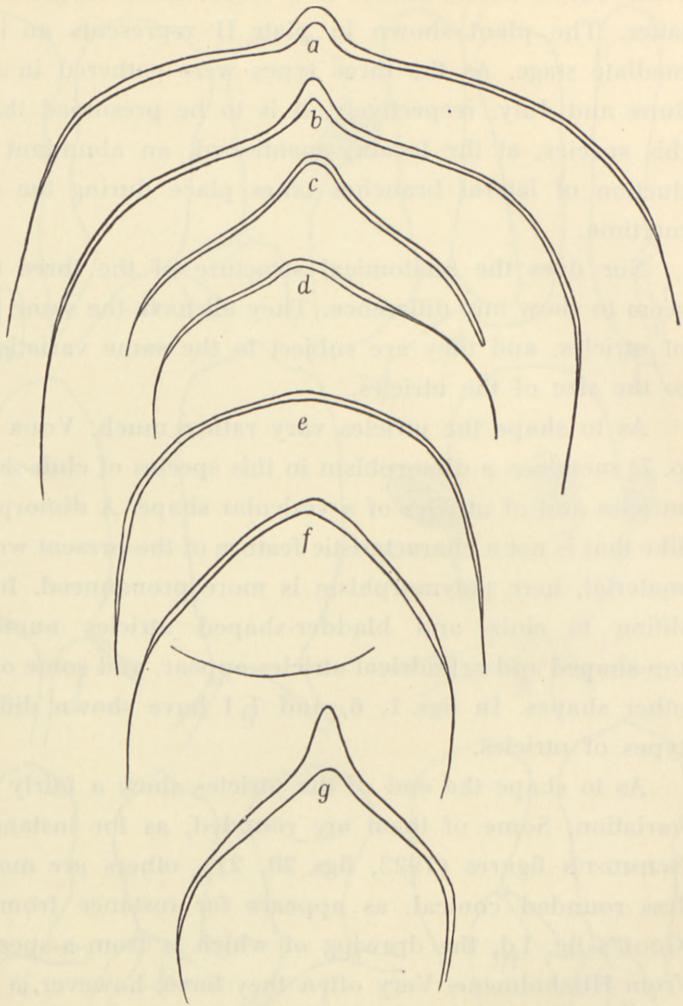


Fig. 2. *Codium dichotomum*. Apices of utricles. *a*, *b*, and *f* from a main filament; *c-e* from a lateral branch, 2 cm from the apex. The apex of utricle in *g* with a marked mucron. — *a-f* from Hirsholmene, the harbour, 29-VII-19; *g* from Hirsholmene 27-VI-19. (173:1).

ends of utricles with point which SUNESON (1939) pictured in his fig. 1 A. In figs. 2—4, 7 I have shown different ends

of utricles, rounded ones as well as some with a more or less marked point.

The wall of the utricle is, as a rule, only slightly thickened at the top. Even in utricles with a point the thickness in this place amounts usually to about 4—12 μ only. However, in some cases, the tip may be developed into a more or

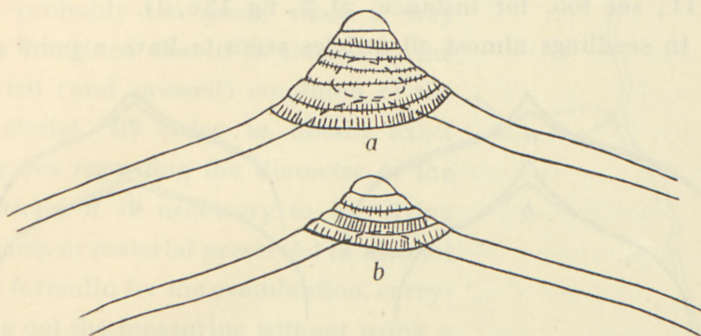


Fig. 3. *Codium dichotomum*. Apices of utricle. Old, thickened apices with longitudinal grooves arranged concentrically in rings (the drawings a little exaggerated, perhaps). In a in addition, a cavity in the thickened apex of the utricle is seen. — From Hirsholmene, 27-VI-19. (355:1).

less marked mucron, as it is found in *C. fragile*, and the thickness may then come to 14—21 μ . Nay, in a single case (the case shown in fig. 2g) a utricle was observed, the thickness of the wall of which even amounted to 50 μ , which, however, probably is exceptional.

If the utricles have a mucron, it is usually rounded. At the tip a number of small, longitudinal grooves may sometimes be detected, arranged in concentric rings (fig. 3). The phenomenon completely corresponds to what SCHMIDT (1935, p. 156) mentioned in *C. fragile*. In addition sometimes in the thickening may be seen cavities (fig. 3a), as also a more or less marked lamination.

Thus it is seen that the ends of the utricle vary rather

much. They may be rounded, or more or less rounded conical; the end may be pointed without any special thickening of the tip or pointed with the tip thickened. The last category leads to *C. fragile*. The fact that *C. dichotomum* may have the tip of the utricle rounded and mucronate as well is evident, too, from the work of GIBSON and AULD (l. c. p. 11; see too, for instance, pl. 2, fig. 13c, d).

In seedlings almost all utricles seem to have a point at



Fig. 4. *Codium dichotomum*. Apices of utricle from seedlings. In *a* and *b* a little mucron is seen. Frederikshavn, the harbour, 28-VII-34. (173:1).

the top (fig. 1 k, l). Generally, however, it is not thickened very much. In some small seedlings, only of a length of 2.5 cm at most, taken by scraping in the harbour of Frederikshavn, most of the tips of the utricles had a small acute mucron, the thickening of which usually amounted to 12–17 μ (fig. 4 a, b). These plants, possibly, belong to *C. fragile*. On the other hand, other tips of utricles had no mucron; they were, moreover, only slightly thickened (fig. 4 c, d); consequently the tips shown in fig. 4 a, b perhaps only denote the variation of the species.

As to size, too, the utricles vary greatly. SUNESON states 480–1000 $\mu \times$ 190–400 μ from his material from the Swedish west coast. These measurements agree fairly well with mine. Only the maximum limits in my material lie still higher, though values over 900–1000 μ are not

very frequent. In bladder-shaped utricles I sometimes noticed a length of up to $1380\ \mu$ and a diameter of over $600\ \mu$, nay, in a single case the diameter even came to $670\ \mu$. The latter extreme value of the diameter is probably too great, since it may be imagined that it is caused by the dried (and pressed) condition of the material. In order to obtain exact figures regarding the diameter of the utricles it is necessary to use living plants or material preserved in alcohol or formalin for the examination, carrying out the measuring without using a cover on the slide. The measurements most frequently found seem on an average to be: the length $500\text{--}700\ \mu$ ($\text{--}800\ \mu$), the diameter about $300\ \mu$.

The formation of utricles in Danish plants takes place (always?) — as in *C. fragile* — in the manner described e. g. by KÜSTER (1898, p. 171) regarding his plants from the Adriatic. This method by which the utricles develop from the pith-filaments by sympodial growth, is widely recorded in the literature and is mentioned in the introduction of this paper.

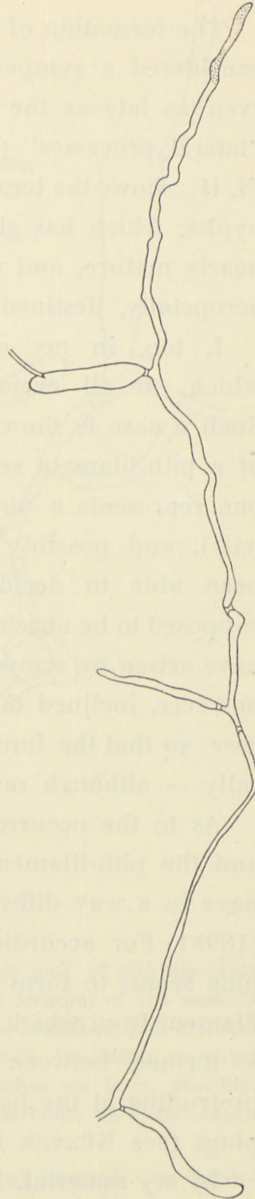


Fig. 5. *Codium dichotomum*. Upper part of a segmented pith-filament with a utricle (carrying a utricle-hair) and two shoots, which possibly will develop into utricles, too. — From Hirsholmene, 29-VII-19. (18:1).

The formation of utricles, however, has not always been considered a sympodial process. Thus GIBSON and AULD even as late as the year of 1900 regarded the utricles as "lateral processes" (p. 11). They write here: "Figure 11, Pl. II., shows the terminal portion of a superficial medullary hypha, which has given off a lateral "palisade cell", now nearly mature, and which is forming two lateral processes acropetally, destined to become "palisade cells"".

I, too, in my material noticed pith-filaments, from which, at all events apparently, lateral utricles project. Such a case is shown in fig. 5, illustrating the upper part of a pith-filament sending out 3 shoots. It is evident that one represents a utricle (which even possesses a utricle-hair), and possibly the others behave alike. I have not been able to decide, whether this utricle and the two, supposed to be utricles, are formed laterally, or whether they have arisen by sympodial growth of the pith-filament. I am, however, inclined to believe that the former was really the case, so that the formation of utricle might take place laterally — although rarely — as well as sympodially.

As to the occurrence of the plugs between the utricles and the pith-filaments the Danish specimens seem to behave in a way different from what is reported by KÜSTER (1898). For according to the description of this writer a plug seems to form first between the utricle and the pith-filament from which the utricle has come out. Later another is formed between the utricle and the lateral branch, protruding at the base. Thus each utricle would have two plugs (see KÜSTER fig. 1c).

In my material, however, a plug seems not always, by far, to appear between the utricle and the pith-filament that has formed it. On the other hand a plug is always

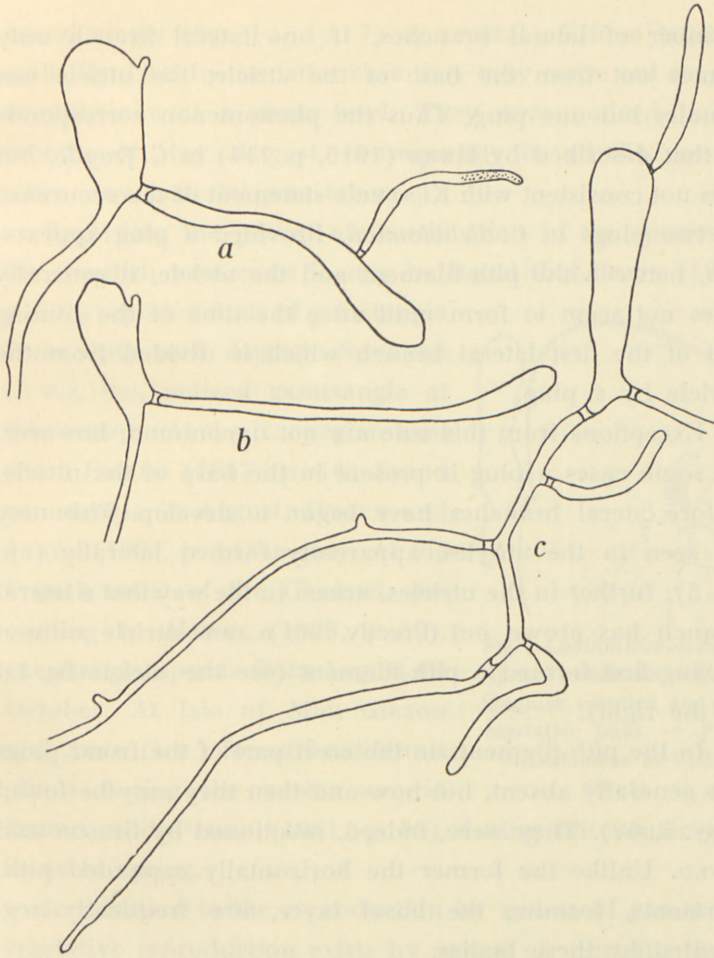


Fig. 6. *Codium dichotomum*. *a* and *b*: the upper part of pith-filaments with utricles, each having one plug only; the location of the same is between the utricle and the lateral branch. *c*: branched pith-filament from the erect frond, showing plugs and a utricle, the latter provided with a utricle hair. The two short lateral branches are later, possibly, developed into utricles. — Hirsholmene, the harbour, 23-V-29. (42:1).

found between the utricle and the lateral branch (or branches) coming out at the base (figs. 1, 6a, 6b). Usually the number of plugs at the base of the utricle is equal to the

number of lateral branches. If one lateral branch only comes out from the base of the utricle, the utricle has usually but one plug. Thus the phenomenon corresponds to that described by HURD (1916, p. 114) in *C. fragile*, but it is not consistent with KÜSTER's statement of the occurrence of two plugs in *C. dichotomum*. Provided a plug appears, too, between the pith-filament and the utricle, it generally does not seem to form until after the time of the coming out of the first lateral branch which is divided from the utricle by a plug.

Exceptions from this rule are not uncommon, however. In some cases a plug is present in the base of the utricle, before lateral branches have begun to develop. This may be seen in the utricles, apparently formed laterally (cp. fig. 5); further in the utricles, arisen in the way that a lateral branch has grown out directly into a new utricle without having first formed a pith-filament (see the utricle fig. 1 d to the right).

In the pith-filaments in the erect part of the frond plugs are generally absent, but now and then they may be found (figs. 5, 6 c). They were, indeed, mentioned by GIBSON and AULD. Unlike the former the horizontally expanded pith-filaments, forming the basal layer, are frequently segmented by these bodies.

The utricles in the upper part often bear hairs (figs. 1 d, 5, 6 c), which are distinctly seen to contain chromatophores, even if scanty only. The plugs between the utricles and the hairs either are unilaterally developed, or they may be more or less all-sided.

Gametangia occur laterally on the utricles, most frequently about the middle part. The length usually is 250—285 μ , the diameter being 100—115 μ (—140 μ). They are

found singly (figs. 1 a, 1 c, 7) or several of them together (—3; fig. 1 h). In the latter case they may come out several or only one at a given level. They were noticed in the months of May—August, consequently in all the months when any material was taken.

Regarding the period of fructification in the species at the Swedish west coast it may be stated that KYLIN (1933, p. 391) reported finds of gametangia from July and August. SUNESON (l. c.), too, noticed gametangia at this season. At the Norwegian west coast EKMAN (1857, p. 16) found gametangia in August, HYGEM and JORDE (1934, p. 14) in July. At the French coast of the Channel, according to HAMEL (1928, p. 89), gametangia appear from August till October. At Isle of Man GIBSON and AULD (l. c.) found fructiferous plants during the winter as did KNIGHT and PARKE (1931, p. 55) during the winter and in early spring.

In addition to the reproduction by means of gametes a vegetative reproduction exists by means of vegetative buds coming out on the sides of the utricles (WENT 1889, p. 443, Pl. VII, figs. 3—9; GIBSON and AULD, l. c. p. 15, Pl. II, figs. 4, 6—9, 12). Vegetative buds like these seem to be frequent in the plants which I examined. In fig. 7 is shown a utricle, on which were found two vegetative buds, both on the point of coming out at the base, as well as an evacuated gametangium. Between the vegetative bud and the utricle a plug is seen.

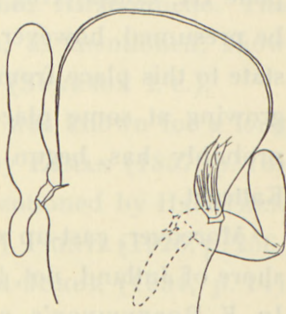


Fig. 7. *Codium dichotomum*. Apex of utricle with a gametangium emptied and two vegetative buds. — From Hirsholmene 27-VI-19. (70:1).

Attached specimens of the species, as mentioned above, are noticed only in the northern Kattegat. But specimens cast up on the shore are found in several places; this was the case at the northern coast of the peninsula of Djursland in the middle part of the Kattegat, where in August 1937 I found a number of cast-up specimens. These plants were consistent with the type from Hirsholmene, pictured in plate III. Considering the abundant occurrence it is not to be presumed, however, that they have drifted in a detached state to this place from Hirsholmene, more likely they were growing at some place near Djursland. Thus the species probably has begun spreading southwards through the Kattegat.

Moreover, cast-up specimens are noticed on the western shore of Jutland, not, however, until after the year of 1929. In K. ROSENVINGE's survey on foreign algae cast-up on the shore of west Jutland (1900, p. 83) it is mentioned no more than is the following species.

The presence of the species was first ascertained in Danish waters in 1919 (K. ROSENVINGE 1920, p. 129), when it was found, partly in an attached state in the harbour of Hirsholmene and in the neighbourhood, partly cast-up in various places at Hirsholmene. K. ROSENVINGE (l. c. p. 130) supposed it to be imported by a ship. In my interpretation it would, however, be as likely to connect its immigration with an importation of drifting, fructiferous specimens deriving from the Norwegian or the British shores. Or is it possible that the vegetative buds be instrumental in its immigration? At any rate there is every reason for presuming that it originates from the same place as the specimens which are cast up on the shore of west Jutland, for these

plants are of the same type as to the utricle as those found at Hirsholmene.

As in the case of Denmark the occurrence of the species in Sweden was ascertained only recently. It was scraped in that country for the first time in 1932 (KYLIN 1933, p. 391), i. e. 13 years after its discovery in this country. The occurrence of the species at the Swedish west coast is possibly due to an immigration from Hirsholmene. The Swedish and the Danish specimens, as mentioned, show much conformity as to the utricles (SUNESON l. c.).

In Norway, on the other hand, it was known for a long time. Thus it is already mentioned by EKMAN (1857, p. 16) from Christianssund. Later it was mentioned by HANSTEEN (1892, p. 355), BOYE (1894—95, p. 45), PRINTZ (1926, p. 256, only drifting, however), HYGGEN and JORDE (1934, p. 14) and LEVRING (1937, p. 34).

Regarding the distribution of the species in north west Europe it may be stated, moreover, that it is common at the French, British and Irish coasts. It has not yet been noticed in Holland (VAN GOOR 1923, p. 133) nor at Heligoland (SCHMIDT 1935, p. 157). The northern limit of its range seems to lie at well over 63° north latitude at the Norwegian west coast.

In the following list of localities of the Danish waters the same designations as to the division of the waters are used as by K. ROSENVINGE (1909, p. 19).

Localities. **Ns**: Vorupør, 1 mile north of the pier, 13-VII-30, length 17 cm, cast-up specimen, not intact, with gametangia (S. Lund). — **Sk**: Kandestederne, 22-VII-34, 29 cm, cast-up, not intact, with gametangia (L. K. Rosenvinge); the Nordstrand of Skagen, a little east of the northernmost point, 15-VII-29, 10 cm, cast-up, not intact (S. L.). — **Ku**: Bunken, the beach, 13-VIII-32, cast-up, not intact, with gametangia (H. E. Petersen); Hulsig Stene, seedlings, 25-VII-33 (L. K. R.); Namands-Reef, seedlings

(Boye Petersen); the extreme verge of Hvidsten Reef, seedlings (L. K. R.), Hirsholmene, the harbour, abundant, seedlings and full-grown plants (Boye P., L. K. R. and others); half-way between Kølpen and Hirsholmene, 7.5 m, seedlings (L. K. R.); Holmehavn's Reef, 5.5 m, seedlings (Boye P.); between Maren's Reef and Borrebjerg's Reef, 7.5 m, seedlings (L. K. R.); Maren's Reef, seedlings (H. E. P.); east of Deget, 11 m, seedlings (H. E. P.); at Syvstenen, 5 m, seedlings (L. K. R.); Frederikshavn, the harbour, the small boats' harbour at the end of the southern pier. 1932. In addition, in 1934 seedlings approaching the habits of *C. fragile* (The Marine Biological Summer course); eastern double broom at Nordre Rønner, 10 m, July 1933 (H. E. P.). — **Km**: Fjellerup, the beach, northern coast of Djursland, 23-VIII-37, numerous cast-up specimens with gametangia, up to at least 14 cm (S. L.).

2. *Codium fragile* (SURINGAR) HARIOT.

var. **typicum** SCHMIDT, 1923, p. 47, figs. 29—31; 1935, p. 156, fig. 3.

Codium mucronatum J. AGARDH 1886, p. 43; HURD 1916, p. 109, pl. 19—24; K. ROSENINGE 1920, p. 131.

Codium mucronatum var. *Tasmanicum* J. AG., l. c. p. 44, Tab. I, fig. 2; COTTON 1912, pl. 8, fig. 7.

Codium mucronatum var. *Californicum* J. AG., l. c. p. 44, Tab. I, fig. 3; COTTON l. c. fig. 8.

Codium mucronatum var. *Novæ Zelandiæ* J. AG., l. c. p. 44; COTTON l. c. fig. 6.

Codium mucronatum var. *atlanticum* COTTON 1912, p. 114, pl. 7, 8, figs. 3—5.

Codium mucronatum var. *tomentosoides* VAN GOOR 1923, p. 136, fig. 1 c.

In the attached state it occurs only in the westernmost and the middle part of Limfjorden. In this water it inhabits the sublittoral region from the upper part to a depth of 11 m. Like the preceding species it is found on stones, wood and shells. The colour is in living plants dark green. The erect frond consists of branching filaments, 3—6 mm in diameter, which may at any rate attain a length of at least 37 cm. Generally the length is not quite so great, though it, however, most frequently seems to be more than 20 cm.

The appearance of the frond does not vary so much as in the preceding species, the branching being almost exclusively dichotomous. Usually the branching of the plants is very regular throughout the entire plant from a little above the basal portion (plate IV). In some cases, however, specimens are found branching richly in the upper part

only. This was the case in some plants, which I secured by scraping at the wharfs at Oddesund Nord on July 4th 1930 (plate V). In these plants the branching was rather scanty in the greater part of the frond. The segments between the levels on which branches developed might even amount to a length of 15 cm. In the upper part, however, dichotomous branching occurred repeatedly, one following the other so closely that the appearance was more or less like a candelabrum.

The different appearance in the two plants pictured is probably due to their environments. In the case of an isolated plant a fairly rich branching begins even a short distance above the basal part. On the other hand, if the plants grow gregariously — as in the case of the plants of Oddesund — the segments become long, giving off few branches only; not until the latter have reached a certain length will the frond branch more abundantly. Such plants, by means of the long segments, secure better conditions of life for a great part of their surface.

In addition to branches, arisen by dichotomous dividing, small lateral branches occur in a few cases. They are, however, not well-grown, but rather like warts only. In a single case such a lateral branch attained a length of 6—7 mm being at the same time very slender.

It is different with a branch that has been injured. Near the injured spot several adventitious branches may project. Some of them become vigorous, continuing the growth of the segments by dichotomous branching.

In cast-up specimens from the Skagerak and the northern Kattegat, however, a rather great number of lateral branches, fairly long, often occur. Not in all the cases, by far, of these lateral branches is it possible to regard their formation as

arising from the injury of the shoot. Their occurrence is perhaps due to an abnormal growth in the plants after their breaking off.

The elongation of the frond, according to SHANNON'S and ALTMAN'S measurements (1930, p. 391) is specially confined to the tips of the branches and to some intercalary zones. In the basal part no growth of length takes place, or it is negligible only, whereas a growth in width goes on.

The basal portion is generally well-grown as in the preceding species. In a specimen, which I gathered at Rønne, north east of the entrance of Lem Vig in Nisum Bredning, the flattened part measured about 20 cm². It was not, however, confined to the shell of a *Mytilus*, which the plant inhabited, it had spread, too, to some pebbles, captured by the byssus filaments of the mussel. It consisted of branching pith-filaments, horizontally expanding and segmented by a rather great number of plugs; at any rate, in many of the pith-filaments chromatophores abounded. The basal portion gave off several vigorous shoots, whereas the pith-filaments frequently had isolated utricles, pointed and mucronate.

Plugs are found in the pith-filaments of the erect frond, too (cp. HURD l. c.). However, they are less abundant than in the bottom part.

As to the occurrence of plugs between the utricles and the pith-filaments, the phenomenon seems to agree with what is stated by HURD (l. c. p. 114) and to what is mentioned by me as to *C. dichotomum*. Between the utricles and the pith-filament, having formed the same, not always, by far, a plug is found — or it is not formed until later. On the other hand, between the utricles and the lateral branches plugs are always present.

The utricles are clavate-cylindrical, nearly always unbranched (fig. 8). Branching utricles of an abnormal appearance, however, are noticed, too. Generally the appearance of the apex of old utricles is different from that of those somewhat younger and of young ones. It is more truncate and, in addition, the mucron is less conspicuous (figs. 8h, 9a).

As to shape the utricles seem generally to agree with those in Irish plants, as described by COTTON (l. c. p. 114). The VAN GOOR's type of utricle, too (l. c. p. 134) — as also transitional forms, are, however, rather frequent. Var. *tomentosoides* VAN GOOR, characterised by the form of the utricles and the mucron besides by the size of the utricle, is considered unmaintenable by SCHMIDT (1935, p. 156, footnote).

Regarding plants from the western North America HURD demonstrated (p. 112, 113) that the utricles in the lower part of the frond as a rule were smaller, having their mucrons developed in a way different from those above. The average size of the utricles increased upwards through the frond, the largest utricles appearing from above the middle up to a few cm from the apex of the shoot.

In Danish plants, too, there was a perceptible difference as to size in the lower part of the thallus and the part above. In the lower part of the frond nearly all the utricles were small and tapering in their upper part, having a conspicuous mucron (fig. 9h—k), whereas those from above were considerably larger. The latter measured, on an average, about 800—1050 μ in length and 225—465 μ in diameter. The dimensions, however, might be much greater. Thus in a plant, gathered in January, the utricles of which most often are 900—1050 μ in length to 300—400 μ

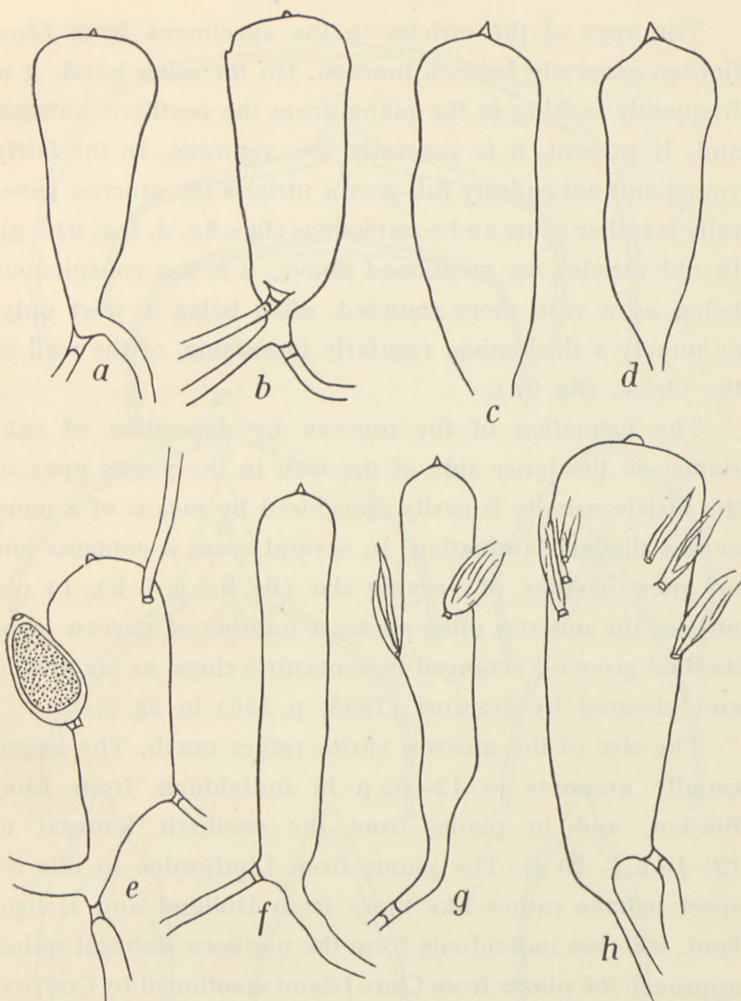


Fig. 8. *Codium fragile*. Utricles. In *h* an old utricle. A gametangium with contents and a utricle hair are seen in *e*, several gametangia emptied in *g* and *h*. — *a* and *c-h* from Limfjorden (*a, f, g*, from Oddesund Nord, 4-VII-30; *c* and *d* from Rønne at Lemvig, 18-IX-39; *e* from Thisted, the harbour, 9-VII-30; *h* from "Limfjorden", January 1921); *b* from inside Maren's Reef at Frederikshavn, 21-VII-34. (173:1).

in diameter, several measured 1400—1600 μ in length and up to 600 μ in diameter.

The apex of the utricles in the specimens from Limfjorden generally bears a mucron. On the other hand, it is frequently lacking in the plants from the northern Kattegat and, if present, it is generally less vigorous. In the fairly young and not entirely full-grown utricles the mucron generally is rather acute and conspicuous (figs. 8 c, d, f, g; 9 b—g). In old utricles, as mentioned above, it is less conspicuous being as a rule more rounded, often being a wart only, or merely a thickening, regularly increasing, of the wall of the utricle (fig. 9 a).

The formation of the mucron by deposition of substance on the inner side of the wall in the young apex of the utricle usually is easily recognised by means of a more or less distinct lamination. In several cases it contains one or more cavities of varying size (fig. 9 e, g, i, k). In old utricles the mucron often shows a number of narrow longitudinal grooves, arranged in concentric rings, as mentioned and pictured by SCHMIDT (1935, p. 156) in fig. 3, 5.

The size of the mucron varies rather much. The length usually amounts to 12—65 μ in individuals from Limfjorden, and in plants from the northern Kattegat to 12—16 μ (—20 μ). The plants from Limfjorden in this respect behave rather like those from Holland and Heligoland, whereas individuals from the northern Kattegat rather approach the plants from Clare Island mentioned by COTTON, in which the mucron is shorter or absent.

As is well known the variation of the mucron has caused the establishment of various varieties; thus the three varieties of AGARDH, mentioned above, and also COTTON's var. *subatlanticum*. While the varieties of AGARDH generally are considered unmaintenable, SCHMIDT (1923, p. 47), however, classifies the variety of COTTON as a subvariety.

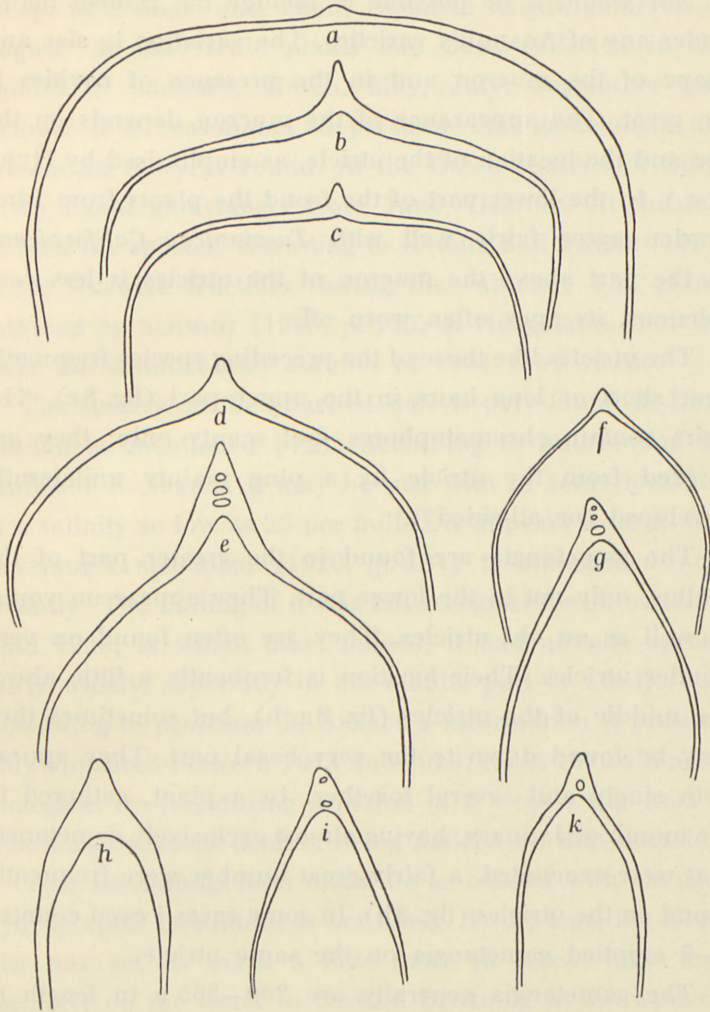


Fig. 9. *Codium fragile*. Apices of utricles from Limfjorden. *a* shows the apex of an old utricule with a mucron not very marked. The apices represented in *b-g* are younger and have a more conspicuous mucron, which in the case of *e* and *g* exhibits cavities. *h-k*: apices of utricles from the basal part of the erect frond. In *i* and *k* cavities are seen in the mucron, which as in *h* is conspicuous. — *a, c, f,* and *g,* from Oddesund Nord, 4-VII-30; *b, d, e* and *h-k* from Rønne at Lemvig, 18-IX-39. (173:1).

Nor would it be possible to include the Danish plants under any of AGARDH's varieties. The variation in size and shape of the mucron and in the presence of cavities is too great. The appearance of the mucron depends on the age and the location of the utricle, as emphasised by HURD (l. c.). In the lower part of the frond the plants from Limfjorden agree fairly well with *Tasmanicum-Californicum*. In the part above the mucron of the utricles is less conspicuous, its apex often worn off.

The utricles like those of the preceding species frequently bear short or long hairs in the upper part (fig. 8e). The hairs contain chromatophores, but scanty only; they are divided from the utricle by a plug mainly unilaterally developed (or all-sided?).

The gametangia are found in the greater part of the thallus, only not in the lower part. They appear on young as well as on old utricles. They are often found on very slender utricles. Their location is frequently a little above the middle of the utricles (fig. 8g, h), but sometimes they may be found down to the very basal part. They appear both singly and several together. In a plant, gathered in the month of January, having almost exclusively gametangia that were evacuated, a fairly great number were frequently found on the utricles (fig. 8h). In some cases I even counted 6—7 emptied gametangia on the same utricle.

The gametangia generally are 200—365 μ in length to 80—160 μ in diameter. Both ♂ and ♀ are demonstrated in the same plant as mentioned earlier by SCHMIDT (1928, p. 627) regarding Danish plants from Limfjorden. Usually my preparations, however, contained chiefly one kind, either prevailingly ♀ + a few ♂ or prevailingly ♂ + a few ♀.

Gametangia occur in all the specimens at my disposal,

except in a single one, about 18 cm in length, gathered in August. As the fertile plants had been collected in the months of January, March, May, July, September and October it is reasonable to presume that gametangia are present all the year round. At the Dutch coasts VAN GOOR (l. c.) found gametangia from June—October. At the Isle of Man the species, according to KNIGHT and PARKE (1931, p. 55) likewise fructifies during the summer. The plants gathered by SCHMIDT (1935, p. 156) at Heligoland, deriving from the summer and autumn of 1934 were sterile.

The species, in the attached state is only found in Limfjorden as mentioned p. 21. According to information by professor R. SPÄRCK it may be met with in some localities of a salinity so low as 25 per mille. As appears from K. ROSENVIINGE's statement (1920, p. 131) it immigrated only recently. The finding of it was not recognised with certainty until 1920, at which time, indeed, it had already spread fairly widely, especially in the middle part of Limfjorden. According to professor R. SPÄRCK's information it presumably appeared between 1913 and 1919; for in 1913 a marine biological course, during a period of 6 weeks, was held at Nykøbing, without *Codium* being noticed on that occasion.

That the immigration might be associated with changed hydrographic conditions is not likely. To be true, the North Sea has set its mark a little more in recent time than formerly on the water in Nissum Bredning in the westernmost part of the Limfjord, owing to a widening of the bed of the Thyborøn canal, but the changes have only been small (LUND 1940). Moreover, the species is most widely distributed in the middle part of Limfjorden, and in this place the change is less than in the western part. Consequently, these circumstances do not seem to indicate that

the species prefers North Sea-water to that of Limfjorden. — In this connection, however, it must be stressed that it is not necessary, as a matter of course, that the conditions of immigration coincide completely with the conditions of a continuous occurrence. The water in Nissum Bredning, in recent time more influenced by the North Sea, may possibly have been instrumental in its immigration; once having entered, it may have become acclimatised, and afterwards it may have penetrated farther into Limfjorden. — The writer thinks it likely, indeed, that its presence — like that of other species immigrated in recent time (LUND, l. c.) — is nothing but the result of a natural immigration.

During recent years (since 1933) loose, fertile plants were repeatedly gathered by scraping in the northern Kattegat near Frederikshavn, and fertile plants cast ashore are likewise noticed in this place. Attached plants¹, how-

¹ After having finished this work I succeeded, however, in finding attached plants, too, in this part of the Danish waters. For, during a visit at the harbour of Hirsholmene on the 19th of Juli 1940, several fructifying specimens of this species were found on the pier at the depth of 1 m. They were growing here, partly together with *C. dichotomum*, from which species they were, indeed, easily distinguished as to habitat, owing to the ramification and the coarser thallus as also to the darker colour. These plants, hence the first attached specimens which have been found in the Danish waters outside Limfjorden, were up to 50 cm in length and 8 mm in diameter. In one of these plants, in addition to dichotomous branching, a few lateral branches occurred, too (one of these reaching the length of about 11 cm). The utricles, being perfectly in accordance with the information given above, as to shape and dimensions, on an average had—like the utricles in loose specimens from the northern Kattegat—but a small mucron or the latter was even frequently absent. Attached plants as well as loose ones from the northern Kattegat thus seem to recall COTTON's var. *atlanticum* more than do the plants from Limfjorden.

The finding of attached specimens of *C. fragile* in the harbour of Hirsholmene is interesting by the fact that the time of the arrival of the species may be fixed with fairly great certainty. For in this locality during many years numerous scrapings have been carried out, by

ever, were not yet noticed with certainty in this water, unless the seedlings mentioned p. 12 might actually belong to *C. fragile*. Cast-up plants, moreover, were found a few times on the shore of western Jutland; not until 1930, however.

K. ROSENVINGE, in this case, as well as in that of the preceding species, in 1920 (p. 132) attempted to show a relationship between the immigration and the importation by ships. After the finding, in 1923, of a cast-up specimen at Büsum in Eiderstedt on the shore of western Schleswig-Holstein K. ROSENVINGE admitted in 1925 (p. 417) that there is some probability that the immigration might have taken place "by means of the coastal current, and not . . . by means of shipping".

I, too, suppose that the immigration is due to an importation of drifting plants. This is also indicated by the plants just mentioned, cast up on the western shore of Jutland. Loose and fructifying plants alive, when entering Nissum Bredning in the western part of Limfjorden, exposed to altered hydrographic conditions (during the summer season to an increase of temperature), might be imagined to begin reproduction, forming gametes.

The occurrence of the species at Heligoland seems, moreover, to support the idea of an immigration by means of drifting plants. In this island none but cast-up plants appeared, according to SCHMIDT (1935, p. 156); later, only (1930), attached plants, too, were found.

As to the distribution of the species in Europe it may be stated that it is known from the British coasts (Scotland, the Orkney Islands, the Isle of Man), the Irish west coast professor ROSENVINGE as well as by the Marine Biological Summer course. As professor ROSENVINGE has been scraping in the harbour so late as 1933 and 1934, the immigration presumably has taken place in the course of these last six years.

and south west coast, Holland, Heligoland as also from the Norwegian south and west coasts. Its northern limit in Europe seems to be at about 60° north latitude on the western coast of Norway, its southern limit at the Dutch and Irish coasts. Whereas its occurrence at the Irish and Scottish coast does not date from recent time (COTTON, l. c. p. 116), the first Dutch specimens were not collected until 1900 (VAN GOOR 1923, p. 133). At Heligoland the species was not noted in the attached state until 1930 (SCHMIDT 1935, p. 156). On the west side of Sylt KÜSTER (1933, p. 335) found it "namentlich im Sommer 1930 . . . überaus reichlich". The plants concerned, however, were probably loose. In Norway the species was first found in the skerries, in 1930, at Mandal by ARWIDSSON (1936, p. 100); later — in 1935 — near Bergen by LEVRING (1937, p. 34). In Sweden no finding of the species has been recorded up till now (SUNESON 1939, p. 57).

Localities. **Ns:** Vorupør, a few places a little north of the pier, 6-VII-30, cast-up plants, not intact, bearing gametangia; plant of greatest length 33 cm (S. L.). — **Sk:** Tversted, 17-VII-35, 1 very vigorous specimen, intact, about 60 cm in length with gametangia, the utricles having a conspicuous mucron (often 40—70 μ in length) (S. L.). — **Lf:** the western and middle part. Particularly common in the middle part. **Kn:** Hirschholmene, August 1934, about 41 cm in length, loose plant, not intact, with gametangia (Glenstrup); Hirschholmene, the harbour, 19-VII-40, several attached plants with gametangia, about 50 cm in length and up to 8 mm in diameter (S. L.); inside Maren's Reef, about 8 m, 21-VII-34, about 9 cm in length, loose plants, not intact, with gametangia (L. K. R.); north of Hjellen, 3-VIII-33, about 18 cm in length, loose plants, not intact, with gametangia (Boye P.); at Syvstenen, 5 m, 7-VII-34, large loose plants, not intact, with gametangia, up to 33 cm in length (L. K. R.); Strandby, cast up (H. E. P.); Rønnerne at Frederikshavn, 6-VIII-33, about 18 cm in length, cast-up plant, not intact, with gametangia (Glenstrup).

Finally, a brief, diagrammatic survey of the chief characteristics, distinguishing the two species in the Danish waters, is given. The diagram concerns attached plants only.

Survey of the Danish *Codium*-species.

	<i>C. dichotomum</i>	<i>C. fragile</i>
Thallus, colour	dark green or a bright green; generally lighter than <i>C. fragile</i> .	dark green.
Thallus, ramification	dichotomous. In addition lateral branches generally very numerous. Branching more abundant than in <i>C. fragile</i> .	dichotomous. Lateral branches rare, rudimentary as a rule.
Thallus, length	up to well over 20 cm; generally not exceeding 20 cm.	up to 50 cm; generally exceeding 20 cm.
Thallus, diameter	2–4 mm.	3–8 mm.
Utricles, size	generally 500–700 μ (–800 μ) \times 300 μ ; some larger.	generally 800–1050 $\mu \times$ 225–465 μ ; some larger.
The apices of the utricle, appearance and diameter	rounded (rounded conical) or with a hollow point, 4–12 μ in diameter; mucron may be found, 14–21 μ in diameter, if any.	Utricles from plants from Limfjorden generally with a mucron, 12–65 μ in length; utricles from the northern Kattegat with a short mucron, up to 12–16 μ (–20 μ) in length or mucron absent. — Old utricles often truncate.
Gametangia, number and location	1—a few (–3), on the middle part of the utricle.	1—a few (–7), a little above the middle of the utricle or on the whole of the lower half.
Gametangia, size	250–285 $\mu \times$ 100–115 μ (–140 μ).	200–365 $\mu \times$ 80–160 μ .
Vegetative buds	frequent.	not noticed.

Summary.

1. A description of Danish specimens of *C. dichotomum* and *C. fragile* is given as also a key for determination. Moreover, the distribution in Danish waters and the adjoining waters is mentioned. The immigration of the species, having taken place recently, presumably has been effected by drifting, fructifying plants.

2. *C. dichotomum* occurs in three types, distinguished by morphological characteristics, nevertheless closely allied, perhaps being stages of development of the same form. As to anatomy they are alike. In *C. fragile* the morphological appearance varies but slightly.

3. The utricles in Danish specimens of *C. dichotomum* in some cases attain considerably larger dimensions than is usually the case in this species. They are rather polymorphous. The ends of the utricles often bear a small point, which is generally, however, but slightly thickened. In some cases, indeed, it may be more thickened, being developed into a mucron, as in *C. fragile*. — The utricles in *C. fragile* generally are cylindrical-clavate. The old utricles are often truncate. In plants from Limfjorden they nearly always have a mucron, rather acute in fairly young and not entirely full-grown utricles, usually fairly rounded in old ones. In plants from the northern Kattegat the mucron is slightly developed only, or absent.

4. In both species the utricles are formed at the apices of the pith-filaments. In more rare cases, too, they may possibly be formed laterally.

5. Plugs occur in both species between the utricles and the pith-filaments, between the utricles and the gametangia, between the utricles and the hairs as also in the pith-

filaments. In *C. dichotomum* between the utricles and the vegetative buds, too. In the pith-filaments they appear mainly in the horizontally expanded basal layer, but they are found, too, in the pith-filaments of the erect frond.

6. The number of plugs at the base of the utricle is in both species as a rule equal to the number of lateral branches coming out from the latter. Between the utricle and the lateral branch(es) a plug is always found, whereas the plug not always, by far, is present in the pith-filament forming the utricle. Provided a plug is present it generally seems to form only after the first lateral branch has come out. In case the plug is formed in the base of the utricle, the utricle still being unbranched, the plugs between the utricles and the lateral branches, if any, as a matter of course do not appear until later.

7. Vegetative buds seem to be common in *C. dichotomum*; they may possibly be of importance for the spreading of the species.

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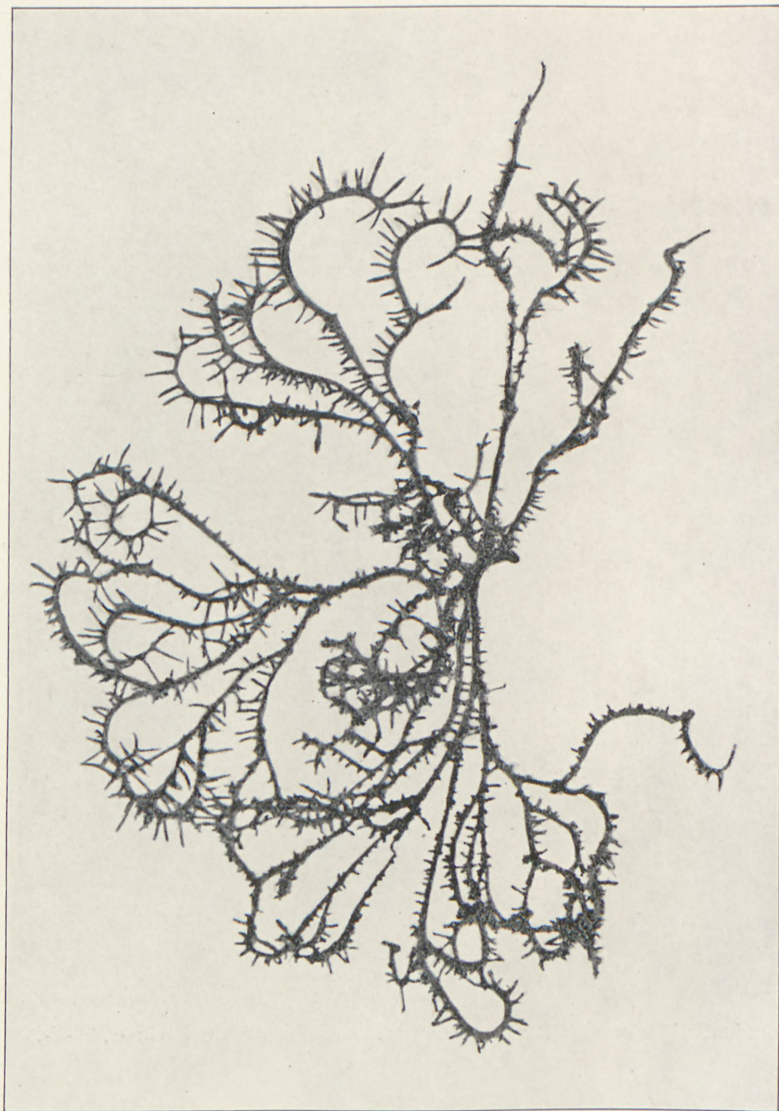
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C. A. JØRGENSEN, photo.

Codium dichotomum (HUDS.) SETCHELL. Hirsholmene, the harbour, 23-V-29
(L. K. R.) (about $\frac{1}{2}$).



Codium dichotomum (Huds.) SETCHELL. Cast up at Hirsholmene, 17-VI-19 (Boye P.) (about $\frac{1}{2}$).
C. A. JØRGENSEN, photo.



C. A. JØRGENSEN, photo.

Codium dichotomum (HUDS.) SETCHELL. Hirsholmene, the harbour,
27-VII-21 (L. K. R). (about $\frac{2}{5}$).



C. A. JøRGENSEN: photo.

Codium fragile (SUR.) HARTW. Rønne at Lem Vig, Limfjorden, 19-V-40 (S. L.). (about $\frac{2}{5}$).



C. A. JØRGENSEN, photo.

Codium fragile (SUN.) HARTW. Oddeund Nord, Limfjorden, 4-VII-30 (S. L.). (about $\frac{2}{5}$).