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THE DANISH

INGOLF-EXPEDITION.

VOL. V, PART 5

CONTENTS:

HJALMAR BROCH: STYLASTERIDAE.

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COPENHAGEN.

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1914.

THE DANISH INGOLF-EXPEDITION.

VOLUME V.

5.

STYLASTERIDAE.

BY

HJALMAR BROCH.

WITH 5 PLATES AND 6 FIGURES IN THE TEXT.

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Stylasteridae.

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Introduction.

The close examination of the Hydrocorallines meets perhaps with more difficulties than the study of the skeleton-bearing Hexacorallia, owing partly to the porous skeleton of the colonies, partly to the delicate nature of the organisms. The characteristics can be determined roughly by means of Dr. Koch's detailed method in which thin sections of the colonies are prepared by grinding with the stained soft parts in situ. The structure of the skeleton can also in part be studied by breaking the colonies as Hickson (1912 p. 891) seems from the following remark to have done. "The way in which it is possible to study the shape of the gasteropore styles is to make a vertical fracture in a plane parallel with the long axis of a branch. In a large percentage of such fractures the whole length of at least one gasteropore with its style will be exposed". It is evident however, that this method is not suited to form the base of a more thorough and systematic investigation of the skeletal parts of the colony. Where it is necessary for the observer to make his results free from chance irregularities he must have recourse to the somewhat slower method of grinding. In the present studies this latter method has throughout been used in the examination of the skeleton. The soft parts are first removed by means of Eau-de-Labarraque, and pieces of the colony have then been ground down on a fine and level whetstone as far as seemed necessary in each single case. For general systematic work it is usually sufficient to grind down a branch to about its median longitudinal plane; in a *Stylaster*, for example, the majority of the gasterostyles will in most cases appear quite free in the middle of the gasteropore. On the finely polished ground surface it will also be possible to study the course of the fine canals. Where there is question of examining the finer structure of the calcareous skeleton, however, this procedure is not sufficient and it is necessary in addition to have thin sections of the same kind as the geologists use in their studies.

Since Moseley's fundamental work on the Hydrocorallines appeared in 1881 investigators have mainly directed their attention towards unravelling the features of the skeleton of the colonies. Excluding a couple of smaller papers on the gonophores of a few species, no observer since that time has sought to penetrate deeper into the organisation and finer structure of the Hydrocorallines. The result is, that we cannot yet be said to have full knowledge of their affinities and thus of their systematic position, a matter I shall return to later. — On studying Moseley's work we see at once, that none of the species hitherto found in the northern seas have been closely investigated; as will be shown in the following; even their specific characters have been more or less imperfectly

studied. It was thus of the highest importance to examine the soft parts of the northern Hydrocorallines more thoroughly; as Pax correctly remarks in a recent work on stony corals (1910 p. 65), "wir dürfen uns nicht verhehlen, dass jede Art, von der nur das Skelett vorliegt, als unvollständig bekannt gelten muss, gleichgiltig, ob ihr anatomischer Bau für systematische Zwecke verwendbar ist oder nicht."

It appears from the investigations, that the least injurious solution with which to remove the calcareous constituents is that recommended by Pax (1910 p. 71): 100 parts 70 % alcohol, 10 parts concentrated nitric acid and 2 parts concentrated, aqueous phloroglucine solution. In small pieces of the colony the calcareous parts are usually completely removed during about 12 hours; larger pieces have sometimes to remain in the liquid up to 48 hours before all the carbonate of lime is removed. The coarser structure is then studied most easily by means of thick celloidin sections, the finer by means of thin paraffin sections. The staining methods depend in part on the fixation. In most cases I have obtained excellent pictures on staining with haematoxylin and counterstaining with eosine or picric-acid-fuchsine (van Giesson's). It is of interest to note, that the structureless organic tissue, which intersects the skeleton in all directions, is coloured very intensely by the eosine and acid-fuchsine in the same way as the supporting lamellae of the zooids, whilst the picric acid does not affect it in van Giesson's staining method. —

I cannot refrain from dwelling a moment here on the mineralogical composition of the skeleton. Pax has investigated the skeleton of *Flabellum inconstans* and found, that it consists of aragonite. He also brings together (1910 p. 70) the results of previous investigations in the same direction. According to his summary calcite has been determined as skeleton in *Corallium, Isis, Tubipora, Cystiphyllum* and *Anabacia*, whilst aragonite has been found in the following genera of Coelenterates: *Heliopora, Montipora, Echinopora, Distichopora, Madrepora, Stylopora, Pocilopora, Millepora, Seriatopora, Goniastraea, Podobacea, Galaxea, Fungia, Dendrophyllia, Porites, Astroides, Hydnophora, Sclerohelia, Cocloria, Pterogyra, Merulina, Favia, Stylaster* and *Trachypyllum*. — At my request the assistant at the Geological Institute of the Polytechnic High School in Trondhjem, Dr. C. W. Carstens, has examined the skeletons of our four northern Stylasterids. Examination by means of Meigen's reaction has shown, that the skeleton in all four is formed of aragonite.

We here face one of the great problems of biology. There can be no doubt, that the power of animals to produce aragonite in the one or the other manner must stand in connection with their power to make use of the magnesium of the sea-water; according to the investigations of mineralogists namely all aragonite contains magnesium. But what makes the matter so puzzling is, that alongside the animals which have aragonite skeletons live some others, which like *Corallium, Tubipora, Cystiphyllum* and *Anabacia* form calcite skeletons. This shows that it cannot depend on a mere chance whether the animal builds its skeleton of aragonite or calcite. It seems more than doubtful that the crystalline system should be of any importance here. Physical characters might probably be found in aragonite, which for most of the marine animals make it biologically more profitable than calcite. Unfortunately the differences between aragonite and calcite in physical regards are still so imperfectly known, that we are unable to form any reasonable supposition as to what part their occurrence plays in the biology of the marine animals.

The Stylasteridae of the North Atlantic.

Pliobothrus Pourtalès

The colonies are branched fan-shaped, often with dichotomously divided branches and branchlets. The gasteropores and dactylopores open irregularly over the surface of the colony and are not collected into cyclic systems. The dactylopores open out on the top of lower or higher tubular projections. The gasteropores are of varying depth, sometimes closed below by one or more tabulae; both the gasteropores and dactylopores sometimes open without distinct ending into the large, irregular, central longitudinal canals of the colony. The gasteropores and the dactylopores have no styles.

With this diagnosis the genus agrees fairly closely with the *Pliobothrus* of Moseley (1881 p. 94). There are a few changes however which require further mention. Moseley included as a generic character in his diagnosis the absence of tentacles in the gasterozooid, in spite of the fact, that his own investigations indicated that *Pliobothrus tubulatus* Pourtalès has 5—6 tentacles on the gasterozooids. When we remember the great variation to which the number of tentacles is subject in other genera, where they have been studied, this character is of extremely problematic value as generic character. The same applies to the form of the polyps, which more than anything else is dependent on the state of contraction and preservation. So long as we are unable to demonstrate more constant peculiarities in the form of the polyps than hitherto, it has no great value even as specific characteristic. The number of the gonophores in the ampullae must also be referred to the specific characteristics and may even here be of subordinate importance.

A close study of *Pliobothrus symmetricus* shows, that the pores of the zooids vary greatly in length and often stand in open communication with the large central canals which appear irregularly in the branches. This blots out the boundaries between *Pliobothrus* and the genus *Steganopora* recently described by Hickson and England (1905 p. 26). Open communications between the gasteropores and the dactylopores may also exceptionally be found in *Pliobothrus symmetricus*. *Steganopora* must therefore be included under *Pliobothrus*. The species *Steganopora spinosa* Hickson and England, the only known species of this genus, stands very near to *Pliobothrus tubulatus* Pourtalès and will possibly on closer examination prove to be identical with the latter.

Pliobothrus symmetricus Pourtalès.

1871 *Pliobothrus symmetricus*, Pourtalès, Deep-Sea Corals p. 57, Plate IV, figs. 7 and 8.
1874 — — , P. M. Duncan, Madreporaria .... "Porcupine" p. 336, Plate 49, fig. 7.
1879 — — , Pourtalès, Corals .... "Blake" p. 211.
1881 — — , Moseley, Stylasteridae "Challenger" pp. 48, 80 and 84, Plate VIII, fig. 2.

The fan-shaped colonies are normally branched in one plane; sometimes a portion of the colony may develop to a new fan, which forms an angle with the primary plane. There is no distinct or prominent main stem. The gasteropores are evenly distributed throughout the colony, somewhat more numerous on the front than on the back. The dactylopores, which open out on low, broadly conical

prominences, are mainly found on the front and lateral sides of the branches and are here irregularly arranged between the gasteropores. The gasteropores are sometimes provided with one or a few tabulae; both the gasteropores and dactylopores are sometimes in open communication with the irregular, large, central canals in the colony, exceptionally also with each other directly. The gastero-zooids have no tentacles. The dactylozooids, which are attached by a narrow base in the pore, have a central lumen. — The ampullae are deeply placed. The male gonophores are composite and are developed singly in the ampullae. — The surface of the colony is smooth, not reticulate.

Colour (in alcohol): yellowish dirty gray.

Occurrence: at Florida and in the Northern Atlantic in depths of 190—700 m.

Material:

"Ingolf" St. 55	63°33′ N.,	15°02′ W.	depth 594 m.	5.9°. C.
— - 57	63°35′ -	13°02′ -	— 658 -	3.4°. C.

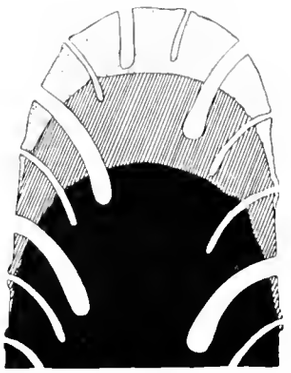
On the Ingolf Expedition some fragments and a complete colony of this peculiar species, which at first sight is all too readily regarded as a Bryozoon, were taken. The intact colony (Pl. I, figs. 1 and 2) shows the marked tendency of the species to branch dichotomously. This characteristic is also clearly seen in Pourtales' and Duncan's drawings. How far this is more than a specific character we are unable at present to determine with certainty, as only a few quite small fragments have been found of the other species of the genus *Pliobothrus*. Pourtalès' drawing of *Pliobothrus tubulatus* (1871, Pl. 4, fig. 9) suggests however, that we have here a specific character, the fragment figured at any rate is not branched dichotomously.

There is in general no very marked main stem in *Pliobothrus symmetricus*, nor do its branches show any regular difference in thickness. In this regard the intact colony of the "Ingolf" differs from those described earlier; the unbranched, basal part of the colony may best be described as a kind of main stem, although its dimensions do not in reality differ obviously from those of the branches. The other, somewhat smaller fragments are not so distinctly and simply fan-shaped. Single branches show a tendency to new fan formations in planes almost at right angles to the primary plane of the colony. As no other difference could be detected between the colonies, however, this must be considered as purely chance variations in the colonial form. — There is a sharply marked difference between the front and back of the colony. On the front the pores are evenly and densely distributed over the whole of the surface and here the dactylopores are present in large numbers; on the back, on the other hand, the dactylopores have practically disappeared and the number of gasteropores is also somewhat reduced. The difference becomes the more pronounced, the nearer we come to the base of the colony, the pores on the hind surface becoming more and more reduced both in number and size. In the above-mentioned, more irregularly branched fragments, all difference between the front and back disappears on the branches which emerge from the primary plane of the colony; the pores are evenly and densely distributed on the whole surface of these branches.

Under a low magnification already (Pl. I, fig. 3) we notice larger and smaller pores, which, however, are not arranged in rows or systems. The larger pores — gasteropores — have their opening plane at the level of the colony surface, whilst the small pores — dactylopores — are found on the top of small, conical protuberances. As mentioned above, the number of the dactylopores especially

is reduced on the hind surface of the colony; what may be the cause of this our imperfect knowledge of the biological conditions of the *Stylasteridae* does not enable us to explain.

If we grind down the branches to about the median longitudinal plane we are able to see the pores in the whole of their length (Pl. III, figs. 19 and 20) and it becomes apparent that these have a typical bend in their course, curving inwards towards the longitudinal axis of the branch and then downwards towards its base. The pores — especially the gasteropores — are of varying length; the terminal pores are, as a rule, quite short and much shorter than those we find further in on the branches. This indicates a terminal and centrifugal growth in the branch and gives us the key to the understanding of the bent course of the pores (Text-fig. A). The pores are first formed at or near the tip of the branch and approximately in its longitudinal direction; during the growth of the branch the pore is gradually moved down on its cylindrical part. The plane of the opening of the pore lies at each place approximately at right angles to its longitudinal axis and the latter will therefore become curved during the growth of the branch, as will be seen from the accompanying diagram.



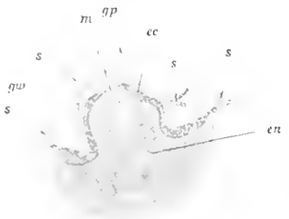
Text-fig. A. Diagram showing the arched development of the pores in *Pliobothrus symmetricus* during the growth of the colony.

A few of the gasteropores open into large, irregular, longitudinal canals, which are formed secondarily in the central part of the branch; often however their base is formed of one or two tabulae. In their original form the gasteropores are cylindrical with a slightly expanded basal part in which the zooid is attached; but during growth the gasteropores often assume a more irregular appearance. The dactylopores also are of varying depth; they are cylindrical, more or less curved and have a slightly constricted opening region; the pore aperture itself, as mentioned, is situated on the top of a slightly prominent, almost wart-shaped protuberance. — The calcareous substance of the colony is penetrated longitudinally and transversely by fine canals in which the stolons lie. No regular arrangement could be noticed in these fine canals, neither in *Pliobothrus symmetricus* nor in our other North Atlantic Stylasteridae.

The connection of the pores and canal system in *Pliobothrus symmetricus* is of special interest, when we compare with the genus *Steganopora* established by Hickson and England (1905, p. 26). The open communication, which is not so very seldom observed between the pores and an irregular central canal system in *Pliobothrus*, is said by Hickson and England to be a constant and always occurring character in *Steganopora* and here also results in an open and direct communication between the gasteropores and the dactylopores. Such a communication also occurs irregularly in *Pliobothrus symmetricus* and we cannot consider this as a fundamental difference between this species and *Steganopora spinosa*, as maintained by Hickson and England. In reality there is here only a gradual difference, which by no means entitles us to make a generic distinction and the last-mentioned species must therefore be referred to the genus *Pliobothrus*.

Moseley (1881) has shown, that the structure of the zooids in *Pliobothrus symmetricus* is very characteristic. The gasterozooid (Text-fig. B) has a fairly broad basal part, from the circumference of

which the stolons emerge. Examination of serial sections seems to suggest, that the endoderm in the basal part itself is strongly vacuolated; but this may also be due to the imperfect state of preservation. The protoplasm is here strongly granulated and all indicates, that the albumen cells (cf. Schneider 1902 p. 579) form the principal mass of the endoderm in the basal part of the polyp, whilst the nutriment cells are in majority in the endoderm of the free wall of the zooid. Apart from this localisation of the cell types the gasterozooid agrees in the whole of its structure with the Hydroid polyp, as is clearly shown by the figures (Text-fig. B, Pl. III, figs. 28 and 29). Whilst the large enidocysts occur in fair numbers in the stolons, the small ones are concentrated in the walls of the zooids. In the gasterozooids (Pl. III, fig. 29) the enidocysts are accumulated densely in the ectoderm near to the mouth of the polyp and entirely disappear further down on the polyp wall; in the dactylozooids they are more uniformly distributed in the ectoderm in the whole length of the zooid, but become however less numerous near its basis. — To judge from Moseley's drawing (1881 Pl. VIII, fig. 2) the gasterozooid should have a wide, cruciform mouth in *Pliobothrus symmetricus*. The mouth of the polyp is closed in all the specimens examined from the "Ingolf" Expedition and is neither larger nor shaped differently from that of the Hydroids generally. The cruciform appearance noted by Moseley is clearly due to chance, for the protruding parts of the endoderm in the numerous sections examined vary greatly in form, size and number.



Text-fig. B. The contracted gasterozooid of *Pliobothrus symmetricus*. *ec* = ectoderm, *en* = endoderm, *m* = mouth, *s* = stolones, *gw* = the epithel of the gasteropore, *gp* = mouth of the gasteropore. ($^{60}/_{1}$).

In their discussion of the family characters of the *Stylasteridae* Hickson and England state (1905 p. 13): "The solid scalariform endoderm of the dactylozooids is another very distinctive feature of the group". This does not hold good for *Pliobothrus symmetricus*; the dactylozooids have a distinct lumen in their centre, as shown in transverse sections (Pl. IV, fig. 34). The authors cited maintain, that "the scalariform tissue is clearly a much more differentiated tissue", — naturally, under the tacit assumption, that the dactylozooid is a reduced polyp. This would suggest, therefore, that Moseley's view of *Pliobothrus* as a primitive genus of the *Stylasteridae* is correct.

There is one condition, however, which seems to point in the opposite direction; this is the male gonophores and their structure. Moseley indicated already, that their appearance differs from that found elsewhere in the *Stylasteridae*. But his drawing (1881 Pl. VIII, fig. 3) is in so far misleading, as it gives the impression, that the difference only consists in a denser accumulation of very small, single gonophores. A series of sections through the male gonophores (Pl. IV, figs. 40—42) shows extremely aberrant features. Each ampulla contains a single, fairly large, globular gonophore, which is composed of a number of follicle-like portions (pseudofollicles); the reproductive cells are in extremely different stages of development in the various pseudofollicles of the gonophore. The spadix as a rule is slightly branched between the pseudofollicles and sometimes we find, that slender connecting bridges lead from the stolons of the ampullar wall over to other parts of the gonophore wall than those where its spadix connects with the stolons of the colony. — Hickson (1891) has demonstrated the formation of a "seminal duct" in *Stylasteridae* where the male gonophores are of primitive structure. Such a formation can certainly not be found in *Pliobothrus symmetricus*. The apex of the compound gono-

phore is prolonged (Pl. IV, fig. 42) but seems never to reach the surface of the colony. To judge from serial sections it opens out into one of the surrounding stolon canals of the calcareous skeleton at the side of and not in the stolon itself. The available material however is not sufficiently well-preserved to enable these conditions to be closely studied, nor does it give any clear picture of the structure or development of the opening of the gonophore.

It would be of great interest to clear up the origin and development of these compound gonophores. Probably we have here a secondary coalescence of the whole gonophore complex which we find collected into the single ampulla in most of the other *Stylasteridae*. The branched spadix and the variating stage of development of the reproductive cells in the single pseudofollicles point in this direction. Investigation of the *Stylaster* species shows, that the male gonophores in an ampulla are in very different stages of development and thus function over a long period; the successive maturation, which obviously must be of great importance for the species, is thus retained in *Pliobothrus symmetricus* after the gonophores have become fused into a single complex. Unfortunately the material has not permitted any close study of the development of the gonophore in the present species. — I was unable to find other developmental stages of the female gonophores than those already known from the work of Moseley. Thus nothing was found which differed from his description. —

Pliobothrus symmetricus was first described by Pourtalès (1871) from the Florida reefs, where it seems to be common between 180 and 300 m. in depth. The species has only once been met with in the Northern Atlantic, where P. M. Duncan (1874) mentions it from the cold area of the Faeroe Channel.

Stylaster Gray.

The usually fan-shaped colonies have the zooids collected into closed cyclosystems, which show no trace of opercula. Both the gasteropores and the dactylopores are provided with styles; the dactylostyles however may be rudimentary.

On the basis of this diagnosis we must also include the genus *Allopora* Ehrenberg in *Stylaster*. Hickson and England (1905 p. 6) rightly point out how small and doubtful the characters are, which are said to distinguish the two genera. In reality there are quite even transitions between the genera. None have shown this more clearly than Hickson and England, who following the proposal of Studer group the species into four divisions: "A. Cyclosystems on lateral sides of branches only; B. Cyclosystems on lateral sides of branches and a few on the surfaces; C. Cyclosystems evenly distributed over the surfaces of the branches, and D. Cyclosystems on the anterior surface of the branches only." The first two groups stand extremely near to each other and should be embraced within one main group or subgenus *Eustylaster*; the last group has just the arrangement of the cyclosystems which is characteristic of *Allopora*; species like *Stylaster divergens* Marenzeller and *Allopora rosacea* Greeff obviously occupy intermediate positions between our northern *Allopora* species with its hardly prominent cyclosystems and those *Stylaster* species which have very prominent, almost stalked cyclosystems. For group D. the old generic name *Allopora* should be retained.

The genus *Stylaster* is represented in the Northern Atlantic by three species, which have been confounded several times. When the ampullae are strongly developed the colonies in our *Eu-*

stylaster species may sometimes become so blown up and deformed that they may easily enough be confused with the *Allopora* species. To facilitate the determination in difficult cases I give in the following table their distinctive features.

	gemmascens	*roseus*	*norvegica*
Cyclosystems	with 12—20, normally 14—18 dactylopores. Wall of gasteropore deeply incised towards the dactylopores.	with 8—16, normally 9—11 dactylopores. Wall of gasteropore slightly incised towards the dactylopores.	with 5—9, normally 6—7 dactylopores. Wall of gasteropore slightly incised towards the dactylopores.
Gasterostyles	conical, twice as high as broad.	almost globular with same breadth as height.	almost globular with same breadth as height.
Ampullae (♀)	near the surface and projecting like a hemisphere; equipped with blunt spines.	near the surface and projecting like a hemisphere; without spines.	deeply embedded, scarcely seen externally on the colony.

Subgenus **Eustylaster** nov.

Stylaster gemmascens (Esper) Milne-Edwards et Haime.

1768 *Madrepora virginea*, Gunnerus, Om nogle norske Coraller p. 56, Tab. VIII, figs. 2—4.
nec 1758 *Madrepora virginea*, Linné, Systema naturae ed. X, vol. I, p. 798.
? 1797 *Madrepora gemmascens*, Esper, Fortsetzungen der Pflanzenthiere, T. I, p. 60, Tab. 55.
1857 *Stylaster gemmascens*, Milne-Edwards, Histoire naturelle des Coralliaires p. 130[1]).
1873 — — , G. O. Sars, Dyrelivet paa vore Havbanker p. 45.
? 1874 — — , pars, P. M. Duncan, Madreporaria .... "Porcupine" p. 332.
1879 — — , Storm, Bidrag til Kundskab om Trondhjemsfjordens Fauna p. 24.
1881 — — , Moseley, Stylasteridae "Challenger" p. 86.
1882 — — , Storm, Bidrag til Kundskab om Trondhjemsfjordens Fauna IV, p. 25.
1910 — — , J. A. Thomson, Note on a Hydrocoralline from Rockall p. 61.
1912 — — , Nordgaard, Faunistiske og biologiske iagttagelser p. 7.
1912 — — , Arndt, Zoologische Ergebnisse, I, p. 122.

The fan-shaped colonies have as a rule a concave front surface and show a distinct difference between stem, main branches and small branches. The cyclosystems are placed laterally and alternately on the outermost small branches and their main axis forms almost without exception a pointed angle of less than 45° with the axis of the branch; they are oval, except those just at the tip of the branch which may be circular, and show from 12 to 20, normally however 14—18 quite separate dactylopores, each provided with a rudimentary dactylostyle. The wall of the gasteropore shows deep incisions towards the dactylopores. The gasterostyle is conical, twice as high as broad. The gasterozooid has 4 quite small tentacles. — The female ampullae project like hemispheres above the surface of the colony and when fully developed are equipped with 1—7, generally 2—4 small, blunt spines. The surface of the colony is smooth and indistinctly reticulated.

Colour: white or faintly rose-red with darker yellowish red gasterozooids.

Occurrence: west coast of Norway, Denmark Strait in 50—560 m. depth, Rockall. (Indian Ocean?)

[1]) This work contains a detailed list of the older synonymy.

Material:

"Ingolf" St. 15	66°18′ N. 25°59′ W.	620 m.	+0.75° C.
West coast of Norway	Hjeltefjord	ca. 150 m.	
	Gidskö (Söndmöre)	?	
	Söndmöre	?	
	Trondhjem Fjord	50—400 m.	6.5—8.5° C.

The form and appearance of the colonies are subject to such great variations in *Stylaster gemmascens*, that we may often be in doubt as to whether one and the same species is before us. The available material was very large, especially from the Trondhjem Fjord, where the species is fairly common and more luxuriantly developed than from any other locality hitherto known; further, I was able to examine a number of colonies from the west coast of Norway and lastly a couple of small fragments from "Ingolf" St. 15. Examination of this very large material shows the relationship of all the many different kinds of variants, partly owing to series of chain-forming variants, partly on account of apparently quite different growth-types being present in different branches of single colonies. Hickson in several of his works has divided up some of the species into a series of different "facies". As the most illustrating examples I may mention his treatment of *Stylaster eximius* Duchassaing et Michelotti (1905) and *Errina nova-zelandiae* Hickson (1912). The deeper meaning of these "facies" is not apparent from his method of treatment; they seem only to illustrate the varying growth modifications of the species; nor do we obtain any information as to the biological conditions under which they appear. In dealing with the present species, therefore, I discard the subdivision into "facies", which only serves to give the misleading impression that the species is divided into distinctly separated growth forms or types.

There is always a distinct difference present between the front and hind surfaces of the colony in *Stylaster gemmascens* and the more or less composite, fan-shaped colony is almost always bent somewhat inwards, so that the front surface becomes more or less concave. To give any explanation of the biological significance of these structural features cannot be done with certainty at present, least of all for our northern species, which only live in great depths. A conclusion by analogy from tropical species is excluded, since, as Hickson and England (1905 p. 4) point out, we lack all knowledge of the biology of these animals. — There is a gradual increase in thickness from the outermost small branches and inwards towards the thick main branches and main stem; the last are almost entirely free of cyclosystems. The small branches may sometimes show coalescences, but this is seldom.

On the outermost, fine branches we see how the cyclosystems arise alternately on the lateral sides of the branch; this is the primary condition in the species. The larger cyclosystems however are not restricted to the lateral part of the branch; they also extend far in over the front surface of this, as can be seen regularly a few millimetres inside the tip of the branch. The increase in thickness of the branch proceeds most rapidly on the hind surface; in this we may have one of the causes of the colony's tendency to bend in towards the front surface. It has the further effect, that the cyclosystems are secondarily moved more and more forwards towards the front of the branches, the nearer we come to their origin; at the same time a few irregularly situated, new cyclosystems arise between the old. Here and there we also find, that cyclosystems appear quite singly on the back of the colony but their number here is always very small.

When the material available only consists of some few fragments of *Stylaster gemmascens*, we may often be inclined to divide it up into several species, as already mentioned. Some pieces (Pl. I figs. 5—6) show a regular aspect with uniformly constructed branches; others on the other hand (Pl. I, figs. 4 and 7) are irregular in their mode of branching and in the arrangement of the cyclosystems. A larger material soon shows however, that there is no justification in creating subspecies on the basis of these variations. Often the appearance of the ampullae may alter the regular structure of the colony, though not quite so much as in the following species, with which it can easily be confounded. The most reliable mark of distinction between the two species is found in their cyclosystems and gasterostyles. But the female ampullae also afford good characters; in *Stylaster gemmascens* they are equipped with a varying number of conical, blunt spines; normally we find 3 or 4 of these on the ampulla, more seldom 2 or 1; often the number may also be larger and once 7 spines were found on a single ampulla. When the ampullae occur in larger number, these small spines appear in quantities between the cyclocystems and make the boundaries and arrangement of these indistinct to the naked eye (Pl. I fig. 7). Closer examination however shows that the cyclocystems are comparatively little affected by the ampullae.

The cyclosystems appear as small, oval, stellate elevations except at the very tip of the branches, where they are still circular in circumference. Even the tops of the septa-like separating walls between the dactylopores project somewhat strongly above the surface of the colony. The number of the dactylopores in the cyclosystems varies from 12 to 20; in general there are from 14 to 18 dactylopores round a gasteropore. The wall of the gasteropore shows a deep incision towards the dactylopore. Any fusion of the dactylopores which lie side by side could not be detected, as is often the case in some tropical species. — Carefully prepared longitudinal sections made by grinding readily show the gasterostyle (Pl. III fig. 21); in *Stylaster gemmascens* it is pointed, conical and almost twice as high as broad. A thin section (Pl. III fig. 24) shows clearly its lattice-work structure. The dactylostyles are reduced to faint, irregular elevations on the outer wall of the pores; they are very difficult to observe. — Thin sections of the stem and main branches show very distinctly, that the growth here as in our other northern *Stylaster* species proceeds centrifugally and periodically; but it still remains to discover, what influences in the sea produce this periodic growth in the colonies.

The gasterozooid has the same structure as the hydroid polyp, when we exclude the secondarily formed gasterostyle (Text-fig. C, Pl. III fig. 25). Partly near to and partly somewhat below the opening of the mouth we find four quite small, almost rudimentary tentacles. The small cnidocysts of the polyp are gathered in these tentacles, though without leading to the formation of a typical, thickened, distal part such as is found on the capitate tentacles of the *Corynidae*; their structure agrees fully with the thread-like tentacles we find in the athecate Hydroids. The ectoderm of the gasterozooid is normally destitute of stinging cells otherwise. The cell boundaries in the ectoderm are very difficult to make out; the whole structure here agrees with that of the Hydroids. Often we can observe outrunners which connect the ectoderm of the polyp wall with the epithelium of the gasteropore wall; these resemble the irregular outrunners, which are often found in the thecaphore Hydroids and which here connect the ectoderm of the hydranth with the hydrotheca outside the true, basal line of attach

ment. — The gasterozooid is provided with a strongly developed, supporting lamella. The endoderm cells are high and show the same cell types that are usually found in the lower Coelenterata; the endoderm continues on to the gasterostyle and forms its epithelial covering. Distinct cell boundaries can in general not be observed in the endoderm of the gasterostyle; the granulated structure shows, that the albumen cells are decidedly in majority here, whilst Schneider's "Nährzellen" (1902 p. 579) compose the main mass of the cells in the endoderm of the free gasterozooid wall.

Text-fig. C. Diagrammatic median section through the cyclosystem of *Stylaster* (*Eustylaster*) *gemmascens*. The tentacles are not represented in this section. *d* = dactylozooid, *g* = free portion of the body-wall of the gasterozooid, *gs* = gasterostyle.

A transverse section of the basal part of the gasterozooid gives an extremely characteristic picture (Pl. IV fig. 32). The tissues collect into separate columns which gradually become smaller in diameter and pass over into the stolons. No lumen could be detected in these columns until they change over into the typical stolons. Nor do they show any sign of differentiation into ectoderm and endoderm like the stolons. The number of columns does not seem to be constant.

The dactylozooids (Pl. IV fig. 33) have a very thick and muscular supporting lamella and show a more marked power of expansion and contraction than the gasterozooid. The thick ectoderm of the free wall of the dactylozooid is densely beset with cnidocysts, but the zooid is not capitate. The endoderm is scalariform and compact and thus the dactylozooid has no central lumen. The endoderm is on all sides surrounded by the supporting lamella and is not connected with the endoderm of the stolons. The nutrition of the dactylozooid from the stolons must therefore take place through its ectodermal wall. —

In spite of the very large material available for investigation I did not succeed in finding the male colonies and determine their number of gonophores in the ampullae. Nor were young stages of the female gonophores found in the numerous sections. The fully developed female gonophores (Pl. V figs. 46 and 49) have a complicated spadix. From a narrow base, where the main stolon enters into the ampullae, the spadix spreads out semispherically; it is formed by numerous, fine, endodermal blind sacs, the narrow and irregular lumens of which radiate out like the rays of a star from the centre of the base of the gonophore. As the single blind sacs as a rule have a twisted course and not seldom branch, the whole picture thus seems very complicated at first sight. The ripe ovum rests on the spadix like one hemisphere on another and the spherical gonophore, which occupies the ampulla, is surrounded by a thin endodermal layer. The colonies are not hermaphrodite and it is a puzzle even how fertilization takes place in these animals with their closed ampullae. — As the ovum gradually develops to a planula larva and grows in size, the spadix atrophies, its large cell material being probably used for the nourishment of the ovum. When the spadix is more reduced (Pl. V fig. 50) its structure becomes more distinct. — Other stolons of the wall of the ampulla may also secondarily come into connection with the gonophore and thus increase the amount of nourishment during the embryonal development.

It has long been an open question whether the larva ruptures the roof of the ampulla when it escapes. A series of sections through a number of large, empty ampullae points in an opposite direction; in spite of the fact, that the larva must just have escaped from the ampullae, their roof is

quite intact. It is probable indeed, that a fairly small opening is simply formed in the roof of the ampulla, through which the larva escapes. This opening is at once closed again and the ampulla persists for some time as a large empty space after the larva has escaped. The further fate of the ampulla has not been observed.

The synonymy of the species offers several difficulties. It is exceedingly doubtful, if it really was this species which Esper (1797 p. 60) described under the name of *Madrepora gemmascens* and the question cannot be settled from the literature. The reason for nevertheless retaining the specific name *gemmascens* here is, that our commonest northern *Stylaster*, wherever it is mentioned in the literature, appears under this name. Esper's specimens came from the Indian Ocean but no one has later found the species there. — The first quite certain and detailed description of the species is to be found in a treatise of Gunnerus (1768 p. 56), who erroneously identified it with Linne's *Madrepora virginea*; his drawings are the best which have ever been given of the species and the identification is all the more certain because his specimens are still preserved in the Zoological Museum of Trondhjem. One of them is reproduced in fig. 4 of Pl. I. Gunnerus examined several colonies of this species from the west coast of Norway, but his work has been passed over by later investigators and thus Esper has erroneously been taken as the first describer. We thus find, that Milne-Edwards (1857) was still unacquainted with the fact, that *Stylaster gemmascens* lives in northern waters. It was reserved for G. O. Sars (1872 p. 45) to point out its existence on the Norwegian coasts and he was the first to refer the northern colonies to Esper's species. In this he is followed by P. M. Duncan, who however in his work on the material of the "Porcupine" (1874 p. 332) confounds it with *Stylaster roseus* and *Stylaster* (*Allopora*) *norvegicus*; on the whole, to judge from his drawings it is extremely doubtful if Duncan has had any specimens at all of *Stylaster gemmascens*. Storm (1879 and 1881) found the species again in the Trondhjem Fjord and points out that it is fairly frequent in its occurrence there. Lastly, we find *Stylaster gemmascens* mentioned from Rockall; through the kindness of Prof. J. A. Thomson I have had the opportunity of examining his specimens, which are typical individuals of the northern species; it is the only certain instance of its occurrence south of the submarine ridge between Scotland—Iceland and Greenland. Excluding Esper's locality the species has not been found outside the North Atlantic and even there it lives within a fairly restricted area.

Stylaster roseus (Pallas) Gray

1766 *Madrepora rosea*, Pallas, Elenchus Zoophytorum p. 312.
1857 *Stylaster roseus*, Milne-Edwards, Histoire Naturelle des Coralliaires T. II, p. 130[1].
1871 — *erubescens*, Pourtalès, Deep-Sea Corals p. 34, Pl. IV figs. 10 and 11.
?1871 — *roseus*, Pourtalès, l. c. p. 83.
1874 — *gemmascens* pars, P. M. Duncan, Madreporaria ... "Porcupine" p. 332, Pl. 49, figs. 13—15.
1877 — *roseus*, Lindström, Contributions to the Actinology of the Atlantic Ocean p. 15.
1878 — *erubescens*, Pourtalès, Corals ... "Blake" p. 210.
1881 — *roseus* + *S. erubescens*, Moseley, Stylasteridae, "Challenger" pp. 86 and 87.

[1]) This work contains a detailed list of the older synonymy.

The fan-shaped colonies are in general branched in one plane and not recurved; they display a marked difference between small branches, main branches and stem. The cyclosystems are placed laterally and alternately on the small branches; their main axis forms an angle of 45° or more with the longitudinal axis of the branch. The cyclosystems are circular except on the thick main branches, where they have a more oval form. The cyclosystem shows from 8 to 17, in general 9—11 quite separate dactylopores, each provided with an almost rudimentary dactylostyle. The wall of the gasteropore has quite a small incision towards the dactylopores. The gasterostyle is almost spherical with the same height as breadth. The gasterozooid has four very small tentacles. — The male ampullae generally contain 4 to 6 gonophores and are scarcely seen on the surface of the colony. The female ampullae appear like hemispheres on the surface of the colony; they are smooth, without spines. The surface of the colony is smooth and faintly reticulate.

Colour: rose with lighter stem and main branches.

Occurrence: Atlantic Ocean in depths from 230 to 1400 m.

Material:

"Ingolf" St. 7	63°13′ N.,	15°41′ W.	1128 m.	4.5° C.
— - 15	66°18′ -	25°59′ -	620 -	—0.75° -
— - 17	62°49′ -	26°55′ -	1400 -	3.4° -
— - 52	63°57′ -	13°32′ -	789 -	7.87° -
— - 94	64°56′ -	36°19′ -	204 -	4.1° -
"Thor" 1904	65°50′ -	26°53′ -	392 -	?
East Greenland Expedition.	Off Angmagsalik		263 -	?

At first glance *Stylaster roseus* is confusingly like the preceding species; it may especially be easily confounded with such colonies of the latter as are represented in figs. 5 and 6 of Pl. I. Closer examination however shows that there are great and constant differences between the colonies, so that they must be taken as representatives of different species. The first mark of distinction apparent on comparing larger colonies is the form of colony itself. In *Stylaster roseus* there is a greater difference between the main branches and the small branchlets than in the preceding species and the colony is more robust; in addition, the branching of the colony in *Stylaster roseus* normally proceeds in a single plane and it seldom shows a slight tendency to curve inwards towards the front surface. When the colonies are in full process of reproduction they are often so swollen also in the outermost small branches (Pl. II, fig. 11) that there is danger of confusing the species with *Stylaster* (*Allopora*) *norvegica*. The position of the cyclosystems in relation to each other on the outermost small branches however shows that the species here dealt with belongs to the subgenus *Eustylaster*. The main axis of a cyclosystem is at right angles to the axes in the inner-lying and the succeeding cyclosystems and this is more obvious than in *Stylaster gemmascens*, where the cyclosystems owing to the smaller angle with the branch axis do not give the small branches such a distinct zigzag form as in *Stylaster roseus*. In addition the number of the dactylopores is on the whole less in *Stylaster roseus*, their number varying between 8 and 17 but in general lying about 9 to 11. Further, the communication of the dactylopores with the central gasteropore takes place through a smaller incision in the gasteropore wall than in *Stylaster gemmascens*.

The most decisive and constant characters however are found in the condition of the gasterostyles and ampullae. Whilst the gasterostyle in the preceding species was conical and twice as high as broad, in *Stylaster roseus* it is almost transformed to a spherical lattice-work (Pl. III, fig. 22), which rests with a broad base on the bottom of the gasteropore. In fertile colonies the female gonophores especially project like hemispheres above the surface of the colony; whilst the female gonophores in the preceding species were equipped with spines, in the present species they are quite smooth. These are important differences, which compel us to consider the colonies as representing quite different species.

Examinition of the structure of the tissues in *Stylaster roseus* reveals such small and unessential differences from *Stylaster gemmascens*, that we can only ascribe them to the bad preservation of the specimens of the present species. It is only represented in the material by dried fragments and colonies, which have been placed directly in 70 % alcohol. The only difference which might possibly prove to have some importance is, that the large stinging cells, which are extremely seldom in *Stylaster gemmascens* and *Stylaster* (*Allopora*) *norvegicus*, are fairly numerous in the stolons of *Stylaster roseus*; they are not found here either in the zooids.

Most of the colonies are fertile. There is nothing to indicate that they are hermaphrodite and the largest specimens, which come from the waters off Angmagsalik (Greenland), are male. The condition of preservation of the material did not permit any exhaustive examination of the gonophores. I shall therefore only refer here to some few features, which have some interest when compared with the few and scattered observations hitherto reported regarding the gonophores of the *Stylasteridae*. —. On young developmental stages of the male gonophores (Pl. IV fig. 36) we see, that the gonophore has a well-developed central spadix, which however does not reach the apex of the gonophore No trace could be found of an endodermal cell layer under the ectoderm, which according to Hickson (1891 p. 392) surrounds the spermarium of the gonophore in the *Stylasteridae*. Nor did I succeed in finding indications of such a cell layer in the later developmental stages. — When the sexual cells approach maturity we still find a distinct spadix (Pl. IV fig. 39) which extends into the spermarium towards the centre of the gonophore. During the transformation of the spermatocytes to spermatozoa the spadix atrophies and disappears in gonophores with fully developed spermatozoa.

During the last transformation we should expect to find the development of the seminal duct, which according to Hickson is characteristic of the *Stylasteridae*. Fig. 43 of Pl. V shows the condition in *Stylaster roseus* at a spot where the seminal duct should be expected; the picture is of a gonophore with the spermatozoa almost fully formed. A slight thickening of the ectodermal epithelium can be detected both in the gonophore and on the adjacent part of the roof of the ampulla; but a comparison with other gonophores indicates that this is merely a chance. Even at this place, where the spermatozoa would very soon escape, we find no trace of the formation of a seminal duct. The apex of the gonophore points towards a neighbouring stolon canal and at other places also the conditions suggest, that the gonophores of the ampulla empty their ripe sex cells into adjoining stolon canals and not directly out through the roof of the ampulla. The conditions seen cannot be explained by the state of preservation, for they are the same in all the cases, where the course of the cell layers can be determined with certainty.

The female gonophore in its fundamental features is constructed as in *Stylaster gemmascens*. But its spadix is simpler in structure (Pl. V figs. 47 and 48); it is bowl-shaped. Whilst the spadix in *Stylaster gemmascens* develops blind sacs in the direction towards the central parts of the gonophore, all the blind sacs in *Stylaster roseus* lie along the periphery of the gonophore. The structure may here be said to be more primitive than in *Stylaster gemmascens*.

The synonymy of the species is not easily determined with certainty from the literature. No differences between the available colonies and the old descriptions of *Stylaster roseus* can be found. As the species is the commonest Stylasterid in the Atlantic north of the equator, it is probably the same form that served as a basis for Pallas' description of *Madrepora rosea*; the name also agrees with the colour as noted by the collectors of the present material. The only disagreement to be noticed between these colonies and Milne-Edwards' description (1857 p. 130) is, that the small branches seldom show coalescences; but this character is of little importance and can scarcely be considered sufficient as a specific distinction. Pourtalès (1871 p. 34) under the name of *Stylaster erubescens* describes a species from the deeper layers at Florida; his excellent figures show at once, that it cannot be specifically distinct from the North Atlantic *Stylaster roseus*; on the other hand, it is exceedingly doubtful if it is this species which he (l. c. p. 83) with doubt refers to Pallas' species as *Stylaster roseus*. P. M. Duncan (1874 Pl. 49 figs. 13—15) figures the species from the Faeroe Channel, but refers it erroneously to *Stylaster gemmascens*. *Stylaster roseus* is common in the northern Atlantic south of the submarine ridge between Scotland—Iceland and Greenland.

Subgenus Allopora (Ehrenberg)

Stylaster norvegicus (Gunnerus)

1768 *Millepora norvegica*, Gunnerus, Om nogle norske Coraller p. 64, Tab. II figs. 20—22.
1873 *Allopora norvegica*, G. O. Sars, Dyrelivet paa vore Havbanker p. 45.
1874 *Stylaster gemmascens* pars, P. M. Duncan, Madreporaria ... "Porcupine" p. 332, Pl. 49 figs. 1—3.
1881 *Allopora oculina*, Moseley, Stylasteridae, "Challenger" p. 85.
1882 — *norvegica*, Storm, Bidrag til Kundskab om Trondhjemsfjordens Fauna, IV, p. 26.
1888 — *oculina* + *A. norvegica*, Hickson, On the maturation of the ovum and Development of Allopora p. 595.

The fan-shaped colonies are generally branched in one plane; they are not recurved and show no distinct division into stem and branches. The cyclosystems are arranged irregularly; they are most numerous on the front surface of the colony. They are circular or more rarely somewhat oval and have from 5 to 9, in general 6—7 quite separate dactylopores, each with a faintly developed dactylostyle. By means of a shallow incision the gasteropore stands in communication with the dactylopore. The gasterostyle is approximately spherical, of the same height as breadth. The gasterozooid has from 5 to 7, in most cases 6 quite small tentacles. — The ampullae are deeply imbedded and are hardly seen on the surface of the colony. The male ampullae contain in general 3, seldom 2 or 4 gonophores. The surface of the colony is smooth, not reticulated.

Colour: white or faintly rose with strongly yellowish red gasterozooids.

Occurrence: North Atlantic and west coast of Norway at depths from 100 to 1400 m.

Material:

"Ingolf" St. 15	66°18′ N., 25°59′ W.	620 m.	−0.75° C.
— - 17	62°49′ - 26°55′ -	1400 -	3.4° -
— - 52	63°57′ - 13°32′ -	790 -	7.87° -
— - 55	63°33′ - 15°02′ -	594 -	5.9° -
"Thor" 1904	65°50′ - 26°53′ -	392 -	?
	Hardanger Fjord	?	?
(G. O. Sars leg. 1871)	Storeggen (at Aalesund)	?	?
	Trondhjem Fjord	100—400 -	6.5—7.5° C.

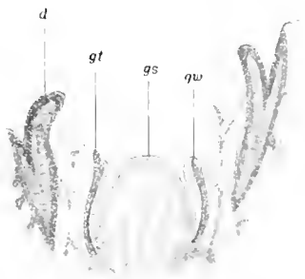
Stylaster norvegicus is of coarser make than the preceding species (Pl. II figs. 12—15) and shows no distinct main stem. Even the outermost tips of the branches may often be very thick (Pl. II fig. 15) and the cyclosystems show no regular arrangement as in our *Eustylaster* species. Nevertheless superficial observation may easily confuse the species with colonies of the preceding species which are deformed by the numerous ampullae (cf. Pl. II, fig. 11). — The branches in *Stylaster norvegicus* are often flattened in the transverse plane of the colony. There is a marked difference between the front and back, the number of cyclosystems being very greatly reduced on the back of the colony (Pl. II figs. 13 and 14).

The cyclosystems are very regular in their formation in *Stylaster norvegicus*. They are almost circular and surrounded by a slightly raised ridge, which continues out into the septa between the dactylopores. As the ampullae are very deeply immersed, their development causes no disturbance of the regular form of the cyclosystems. In general there are 6 or 7, more rarely 8 quite separate dactylopores round the open and deep gasteropore. The wall of the gasteropore shows an incision not specially deep towards the dactylopore. — The short and broad gasterostyle is very characteristic; it is approximately spherical and has almost the same breadth as height (Pl. II fig. 23). The dactylostyles are a little more prominent than in the two previous species, but they are also rather difficult to observe in *Stylaster norvegicus*.

The ampullae are deeply imbedded in the branches and in general cannot be seen externally on the colony; but branches with ampullae are on the whole thicker than sterile branches. — The growth of the colony proceeds after the same type as in the *Stylaster* species already dealt with; the concentric layers, which indicate a periodic growth in the colony, are also distinct here on thin transverse sections of branches of the colony and are also readily seen in transverse series of sections of branches which are freed from their calcareous substance.

Whilst in the two preceding species we constantly find four tentacles on the gasterozooids the number varies in *Stylaster norvegicus*. As a rule the gasterozooid has 6 quite small tentacles, but sometimes their number is reduced to 5 or increased to 7. The tentacles (Text-fig. D, Pl. III figs. 27 and 31) are also very small here; we might be inclined to call them rudimentary. They are also here the seat of the small enidocysts, which the gasterozooid is on the whole provided with. There is no reason

whatever here or anywhere else to call the tentacles capitate; they are formed quite like the thread-like tentacles in the athecate hydroids. — Further, the gasterozooid shows in its finer structure no difference from what has been described in *Stylaster* (*Eustylaster*) *gemmascens*. In the present species it is also broken up at the base into a circle of columns, the number of which seems mostly to be about 6. — The structure of the dactylozooid also agrees with that in the other northern species of *Stylaster*; but the dactylozooids are somewhat larger in *Stylaster norvegicus* than in the previous species. The large enidocysts are found in extremely small numbers in the stolons.



Text-fig. D. Diagrammatic median section through the cyclosystem of *Stylaster* (*Allopora*) *norvegicus*. *d* = dactylozooid, *gt* = tentacle of the gasterozooid, *gs* = gasterostyle, *gw* = free part of the body-wall of the gasterozooid.

Whilst the preceding species was only represented by specimens not very well-preserved, the opportunity was taken to obtain fresh material of *Stylaster norvegicus* from the Trondhjem Fjord, in the outer part of which the species is fairly common in suitable localities. Both male and female colonies could be examined and even if most of the questions concerning the development of the gonophores must still remain unanswered, yet the investigation contributes a good deal to the understanding of the nature of the gonophore in *Stylaster*.

The sexual cells are already present in the youngest developmental stage of the male gonophore which was found (Pl. IV fig. 35) so that their origin cannot be settled. The gonophore shows clearly, that Hickson (1891 p. 384) was wrong in maintaining, that "the spermarium is covered by a double sheath of very thin ectoderm and endoderm". Neither at this stage or later can anything be seen in the numerous gonophores examined (Pl. IV, fig. 37), which could be taken for an endodermal layer between the ectoderm and the generative cells. — Hickson (l. c. p. 390) maintains as a typical difference between the gonophores in *Allopora* and *Distichopora* that the latter genus has no spadix, whilst *Allopora* has a strongly developed spadix. In *Stylaster* (*Allopora*) *norvegicus* the spadix is strongly developed in the young gonophores but atrophies during the transformation of the sperm cells (Pl. IV fig. 38) and lastly disappears entirely in the mature gonophore as is the case also in *Stylaster roseus*.

The present species forms in part the basis for Hickson's studies on the seminal duct. Unfortunately I did not succeed in finding all the developmental stages of it and it is remarkable that it is not always to be found in almost or quite ripe gonophores in spite of the fact, that the preservation of the material is excellent. It seems doubtful, if under all conditions it comes to development even in all gonophores within the same colony; its importance therefore must be reduced in the general considerations on the group. — The youngest developmental stage found (Pl. V fig. 44) appears as a collection of somewhat higher and lighter-coloured cells at the apex of the gonophore. The rudiment is distinctly double, for under the thickened ectoderm cells there is a collection of inner cells (I), which have a characteristic, almost fibrillar protoplasmic structure; these fairly large and light-coloured cells are separated from the outer ectodermal layer by a very fine lamella. At a more advanced stage, when the seminal duct is almost fully formed (Pl. V fig. 45) the inner cells push the thin lamella in front of them into a conical point, which is surrounded by the more deformed ectodermal cells. The

fibrillar protoplasmic structure of the inner cells is still more marked at this late stage than before and is most distinctly seen in the distal part of the developing organ. — I did not succeed in finding a fully formed seminal duct.

We have now the question: from which cell layer arise the inner cells of the duct, are they ectodermal or endodermal? The question cannot be answered on the basis of the present investigations If Hickson's view were correct, that the spermarium of the gonophore is surrounded by a thin endoderm layer, their origin from the endoderm would be a consequence. But the investigations give no support to this view and it is contradicted by Hickson's own figure (1891 Pl. 30 fig. 15) of the yong gonophore in *Distichopora*. The endodermal layer round the spermarium might be a later formation, but this theory does not find any support either in the present investigation. Provisionally therefore the question of the origin of the inner cells in the seminal duct must remain unanswered.

The female gonophores agree down to the smallest detail with those of *Stylaster gemmascens*. The mature egg is surrounded by an ectodermal layer and in *Stylaster norvegicus* no indication can be found either of an endodermal layer between the egg-cell and the ectoderm, as Hickson (1891 p. 390) has found to be the case in *Distichopora*. During the development of the egg the spadix atrophies and the pictures obtained of the condition in *Stylaster gemmascens* (Pl. V figs. 46. 29 and 50) are fully illustrative of the conditions in *Stylaster norvegicus*. Here also I did not succeed in finding the young developmental stages of the female gonophore.

The first description of the species is found in a paper of Gunnerus (1768 p. 64), who calls it *Millepora norvegica*. In an appendix (l. c. p. 67) he states that the species is identical with *Millepora aspera* which Linné described somewhat later in the 11th edition of the Systema naturae. The original specimens of Gunnerus are preserved in the Zoological Museum of Trondhjem; one of them is represented in fig. 12 Pl. II. — It is doubtful if it really is the same species which is described by Ehrenberg under the name of *Allopora oculina*. In Milne-Edwards' diagnosis of the latter species (1857 p. 132) we find: Coenenchyme très-developpé, couvert de points très-serrés, visible seulement avec des verres grossissants . This does not agree with the quite smooth surface, which is characteristic of *Stylaster* (*Allopora*) *norvegicus*. On the other hand, the specimens which are sometimes referred to in the literature from the Norwegian west coast under the name of *Allopora oculina* are undoubtedly identical with *Stylaster norvegicus*, the only *Allopora* met with in the northern Atlantic. It is this species which formed the basis of G. O. Sars' classical investigations (1873 p. 45), in which he restores the specific name of Gunnerus but refers it to the genus *Allopora*; he is of opinion that the species is identical with Ehrenberg's *Allopora oculina*. G. O. Sars was the first to describe the conditions in a living Stylasterid, after studying colonies of *Stylaster norvegicus* out on Storeggen on the west coast of Norway. He was in doubt as to the coralline nature of the animal, as he never succeeded in observing the extended polyps, when the colonies were at rest in sea-water, as is the case in our northern corals otherwise, and when he later studied the preserved animal somewhat more closely he expressed his opinion (l. c. p. 46): though I am far from considering this [1]) as completed, yet I have already learnt this much, that the animal is essentially different from the other corals and probably does not belong at all to the *Anthozoa* but rather to the *Hydrozoa* . As is well-known, Moseley a year later (1878)

[1]) i. e. the investigation.

confirmed the correctness of Sars' supposition. — Since Storm (1882 p. 169) some years later mentioned the occurrence of the species in the Trondhjem Fjord, we find little or nothing in the literature regarding its occurrence on the west coast of Norway.

The species has been figured however by P. M. Duncan (1874 Pl. 49 figs. 1—3) from material from the Porcupine.; the identity of the colony from the figures given cannot be doubted, though the author refers it erroneously to *Stylaster gemmascens*. Moseley (1881 p. 85) notes the species under the name of *Allopora oculina*; Hickson (1888 p. 594) mentions the species from the Hardanger Fjord as *Allopora oculina* and from the Triton Expedition as *Allopora norvegica*. Apart from the doubt whether the two species belong together, the present species must in any case under the international rules of nomenclature retain the specific name which was given it already by Gunnerus in the year 1768.

Remarks on the affinities and systematic position of the Hydrocorallines.

After L. Agassiz in 1859 had pointed out the Hydroid nature of the *Millepora* and Moseley in 1878 had indicated, that the organisation of the Stylasterids also characterised them as *Hydrozoa*, no one has doubted that the Hydrocorallines are most nearly related to the Hydroids and in reality must be regarded as highly specialised Hydroids, whose main characters are the power of the colony to form a skeleton of calcium carbonate and the polymorphic development of their polyps. These are thus the main characters which mark off Moseley's order *Hydrocorallinae*.

Closer consideration of these characters entitles us to doubt, however, whether on such a basis we are justified in raising the Hydrocorallines to the rank of a special order. If we compare them for example with the large order of corals, we see how the greater or less ability of the colonies to separate out carbonate of lime — as for example in the *Umbellula* species — is only regarded as a specific character and is not even sufficient for a generic separation of the species, unless the lime-excreting function is combined with distinct morphological changes in the individuals or colonies. It is thus a question, whether the latter is the case or not when we compare the Hydrocorallines with the Hydroids. We must therefore in the first place endeavour to ascertain, to which of the Hydroids the Hydrocorallines are most closely related.

The first hint is obtained from the tectonic structure of the colony itself. The fine anastomosing canals of the decalcified Hydrocoralline are quite homologous with the stolons of the Hydroid colony; we thus remark a conspicuous resemblance between the *Stylasteridae* and the *Hydrocorallinidae* [1]). Even the structure of the colony agrees exactly in *Clathrozoon Wilsoni* Spencer and the primitive *Stylasteridae*, only the chitin of the skeleton being replaced in the *Stylasteridae* by a thick layer of calcium carbonate. Another Hydroid group also, *Solanderiinae* (family of *Corynidae*, cf. Kühn 1913) shows the same structure of the colony and can be imagined as standing near the parent stem of the Hydrocorallines.

The structure of the polyp will perhaps show the further line of connection. Most Hydroid investigators lay great stress systematically on the form of the tentacles and consider them one of the principal phylogenetic characters. Moseley (1881 p. 46) maintains, that the tentacles of the Hydro-

[1]) By Kühn (1913 p. 228) the *Hydrocorallinidae* are considered a subfamily of *Bougainvilliidae*.

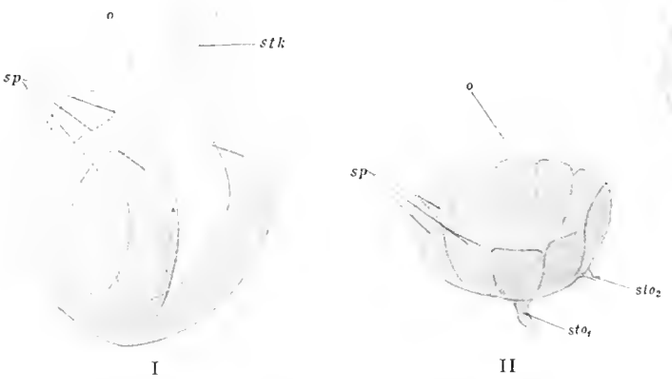
corallines, where they occur, are capitate or rather knobbed at their tips. Closer comparison of his drawings and of the figures later authors have given indicates, however, that the *Stylasteridae* do not have capitate tentacles like the *Corynidae*, even though the cnidocysts are accumulated more densely in the distal part of the tentacles. It has been pointed out several times in the foregoing, that the tentacles in the northern *Stylasteridae* fully agree in their structure with the thread-shaped tentacles of the *Bougainvilliidae*. On the other hand, the *Milleporidae* have typical, capitate Corynid tentacles. This suggests that the Hydrocorallines have a diphyletic origin and that the excretion of a calcareous skeleton in the two groups is purely a character of convergence. This witnesses further to the correctness of the separation of the Hydrocorallines into two families, as is done by Hickson and England (1905 p. 1.). On the other hand, we are not entitled to regard the two groups as sub-orders we should rather consider them as two highly specialised Hydroid families. Hickson and England take the *Milleporidae* as Hydroids, whilst they regard the *Stylasteridae* as most nearly related to the *Trachomedusae*; what support they may have for this last view, does not appear anywhere in their works; the consequence is, that Hickson in his contribution to The Cambrigde Natural History (1906) discusses the two families at widely separated places. — The structure of the gasterozooid in the Stylasterid genera as in *Sporadopora* and still more *Errina* agrees fully with the polyp of the *Bougainvilliidae*; excluding the gasterostyle, which phylogenetically must be of fairly recent origin and which does not occur either in all Stylasterids, the gasterozooids of the *Stylasteridae* fully agree with the polyps of *Clathrozoon*. This indicates, that the latter genus contains the nearest allies of the *Stylasteridae* among the Hydroids.

The second main character, the polymorphic development of the polyps in the *Stylasteridae*, we find already indicated in such *Bougainvilliidae* as *Hydractinia*; in several species of these we find tentacle-less »feelers« and tentacle-bearing nutritive individuals. In the *Hydractinia* species this distinction is not considered a useful mark of generic separation, nor can it be considered so important a feature in the *Stylasteridae*, that it can form the basis for a separation of the group into a special order, even if the dimorphic development of the somatic individuals has become a constant character.

We have hitherto directed attention exclusively to the somatic individuals, assuming that they give the most important supports in judging of the phylogenetic conditions of the Coelenterates. — Hickson (1891) through his evidence of a medusa generation in *Millepora* has produced the last incontrovertible proof of the Hydroid nature of this genus; the medusa seems to be an undoubted *Anthomedusa* and thus shows clearly the close relationship with the *Corynidae*. On the other hand the *Stylasteridae* have sessile gonophores. Moseley (1881 p. 93) maintains that the gonophores of the *Stylasteridae* are »adelocodonic«; but he regards the spadix of the female gonophores as an organ (the trophodisc) special to the *Stylasteridae*. Hickson later (1888 and 1891) has examined the gonophores more closely and supports Moseley's view, that the trophodisc is a special formation in the *Stylasteridae* which is no direct parallel to the spadix of the hydroid gonophores.

If we consider the manifold nature of the development and organisation shown by the gonophores of the Hydroids, the special character of the trophodisc and gonophores of the *Stylasteridae* becomes extremely doubtful. In his excellent studies on the hydroid gonophores (1910) Kühn has shown, that the medusa reduction may be so complete, that even the endocodon may disappear; thus

only the manubrium remains as spadix. In his figures (1888 Pl. 38 figs. 4 and 6) Hickson has shown cases of such reduced gonophores in *Distichopora* and the northern *Stylaster* species also have similar gonophores. Even though such a gonophore structure has not yet been shown in the *Bougainvilliidae*, yet it is not without a parallel in the athecate Hydroids. In *Eudendrium racemosum* (Cavolini) the spadix is bifurcated into two or often three branches, which claw-like embrace the egg-cell (Text fig. E). This is in fact a simplified trophodisc; an increase in the number of the spadix branchings would very soon lead to the condition we have found in *Stylaster roseus* and the step from this to the condition in *Stylaster gemmascens* and *Stylaster norvegicus* is also short. There is thus no fundamental difference present, which justifies the raising of the *Stylasteridae* to a special order.



I II

Text-fig. I: Female Gonophore of *Eudendrium racemosum* (Cavolini) from the Adriatic ($^{05}/_{1}$)[1]. II: semidiagrammatic figure of the female gonophore of *Stylaster roseus*. *o* = ovum, *stk* = stalk of the gonophore, sto_1 = main stolon of the gonophore, sto_2 = secondary stolon of the gonophore, *sp* = blind sacs of the spadix.

There is one condition however to which Hickson ascribes even greater weight. In his work on the gonophores in *Distichopora* and *Allopora* he states (1891 p. 392): Comparing the adelocodonic gonophores (fig. 4) with the male gonophores of Allopora (fig. 5), two points of difference may be observed. In the first place the endoderm completely surrounds the gonad in the latter, excepting at a small aperture at the distal pole, where it forms the inner wall of a seminal duct. Secondly, there is no layer of ectoderm between this endoderm and the gonad of Distichopora. In the adelocodonic gonophore there are two layers of ectoderm between the gonad and the wall of the gonangium .

Quite apart from the disagreements between Hickson's results and the present studies on the gonophore structure in the *Stylasteridae*, his argumentation is hardly maintainable in the light of later studies on the gonophores of the Hydroids. In a species such as *Coryne fruticosa* Kühn (1910 p. 65, Taf. 6 figs. 25—27) has shown, that the gonophores have just the structure which Hickson gives as characteristic of *Distichopora* and *Allopora*. It is thus not without a parallel in the Hydroids. Much more rare then is the still simpler gonophore type in the Hydroids, where the endodermal cell-layer has also disappeared; nor is this without a parallel however; according to Kühn (1912 p. 199) it has been found in *Gymnogonos crassicornis* and in *Eudendrium simplex*.

The only gonophore type in the *Stylasteridae*, which in reality differs greatly from the known conditions in the Hydroids, is the male gonophore in *Pliobothrus symmetricus*. With its follicular structure this shows a higher stage in the gonophore structure than any other gonophore we as yet know from the lower Coelenterata. In reality we have here striking evidence of the fact, that the gonophore structure has been greatly overestimated in judging of the phylogeny of the Hydrozoa; one of the most primitively organised Stylasterids has the most highly organised gonophore type of all.

[1]) After specimens from Triest kindly sent me by Hr. Dr. C. Lehnhofer (Innsbruck).

In its structure *Pliobothrus* shows several features which indicate, that it stands nearer to the origin of the *Stylasteridae* than most of the other Stylasterid genera. In the first place, the zooids are not yet collected into distinct cyclosystems but are irregularly scattered over the colony; no regularity in the occurrence of the gasterozooids and dactylozooids can be detected. In the second place, the dactylozooids are less reduced than in the other *Stylasteridae*, as they still retain their inner cavity; nor do they show the marked division between an expanded basal part attached to the skeleton and a distal tentacle-like part, which is inserted obliquely on the basal part, as in most of the other *Stylasteridae*. Lastly, the gasterozooids lack a gasterostyle. These features show, when taken together, that *Pliobothrus* occupies a primitive position. *Pliobothrus* shows further, that the conservative, somatic parts of the colony are less exposed to the influence of the surroundings, to adaptive tendencies, than the generative parts, the power of which to change plastically in relation to the special biological demands is of vital importance for the existence of the species. In this therefore we also see the reason for the great variety displayed by the hydroid gonophores and in this we have the reason, why the gonophores of nearly allied species may be quite different. Owing to their conservatism in development the polyps are of the most important phylogenetic interest. The gonophores, the generative individuals, on the other hand, might almost be said to be a play-ball in the hands of chance biological conditions and thus phylogenetically have much less interest; they are suited to display the subdivision of the genera into biological adaptive groups and are thus more exposed to the influence of convergence than the other parts of the colonies.

We must therefore not ascribe too great importance to the condition of the gonophores in judging of the affinities of the *Stylasteridae* in relation to the other Coelenterata. Their organisation according to the results of all investigations may well be compared with that of the Hydroid gonophores and even if a single genus shows somewhat special features, they can by no means be used as evidence for the view, that the *Stylasteridae* are more distantly related to the Hydroids than the *Milleporidae*.

Bringing together the main points of the above discussion the result is, that we in reality cannot consider the Hydrocorallines as anything else but two convergent Hydroid families, which are characterised by their power to develop a skeleton of calcium carbonate and by the dimorphic development of their somatic individuals. The family *Milleporidae* traces its origin to that of the *Corynidae*, whilst the *Stylasteridae* is a highly specialised branch which has been derived from the *Bougainvilliidae*. Just as the *Corynidae* are distinguished from the *Bougainvillidae* by their capitate tentacles, the *Milleporidae* with their capitate tentacles are distinct from the *Stylasteridae*, in which the tentacles are constructed like the thread-shaped tentacle type of the *Bougainvilliidae*.

Zoogeographical remarks on the North Atlantic Stylasteridae.

Few animal groups have been so little investigated in our northern waters as the Hydrocorallines. They do not form any prominent faunistic element, it is true, as they are only represented by four species in the northern Atlantic and of these, as known, only two penetrate into the Norwegian Sea. But by contrast these two species at several places form a very characteristic element in the large biocoenosis of the *Lophohelia* reefs and form here a complete and extremely interesting parallel to the numerous Stylasterid species of the tropical coral reefs.

A very speaking example of how little attention has been paid to the Atlantic Stylasteridae on reference being made to the faunistic conditions of this ocean is found in a statement in Parker and Haswell's Textbook of Zoology (1897 p. 147): The Hydrocorallinae occur only in the tropical portions of the Pacific and Indian Oceans, where they are found on the coral reefs partly or entirely surrounding many of the islands in those seas . Nevertheless, some of the oldest, quite identifiable descriptions of *Stylasteridae* are those given by Gunnerus in his work »Om nogle norske Coraller« (1768). His figures leave no doubt as to the identity of the species and his originals, which all came from the west coast of Norway, are preserved in the Zoological Museum of Trondhjem. — The work of Gunnerus has been little known owing to the humble and little distributed journal in which the paper was published. But several papers have also been published later in which the Atlantic *Stylasteridae* are mentioned and here we must place in the first rank Pourtalès' excellent work on the deep-sea corals (1871), in which he describes quite a number of Stylasterids from the American side of the Atlantic, especially from the waters round Florida. Pourtalès described here for the first time *Pliobothrus symmetricus* and also mentions a second of the North Atlantic species, *Stylaster roseus*, under the name of *Stylaster erubescens*. In addition, we have still two other, old records from the North Atlantic. G. O. Sars (1871) has given a classic description of the living *Allopora norvegica* and P. M. Duncan (1874) mentions Stylasterids from the Faeroe Channel. With exception of the work of Gunnerus all these papers are cited in detail by Moseley (1881) in his great work on the *Stylasteridae* of the »Challenger«.

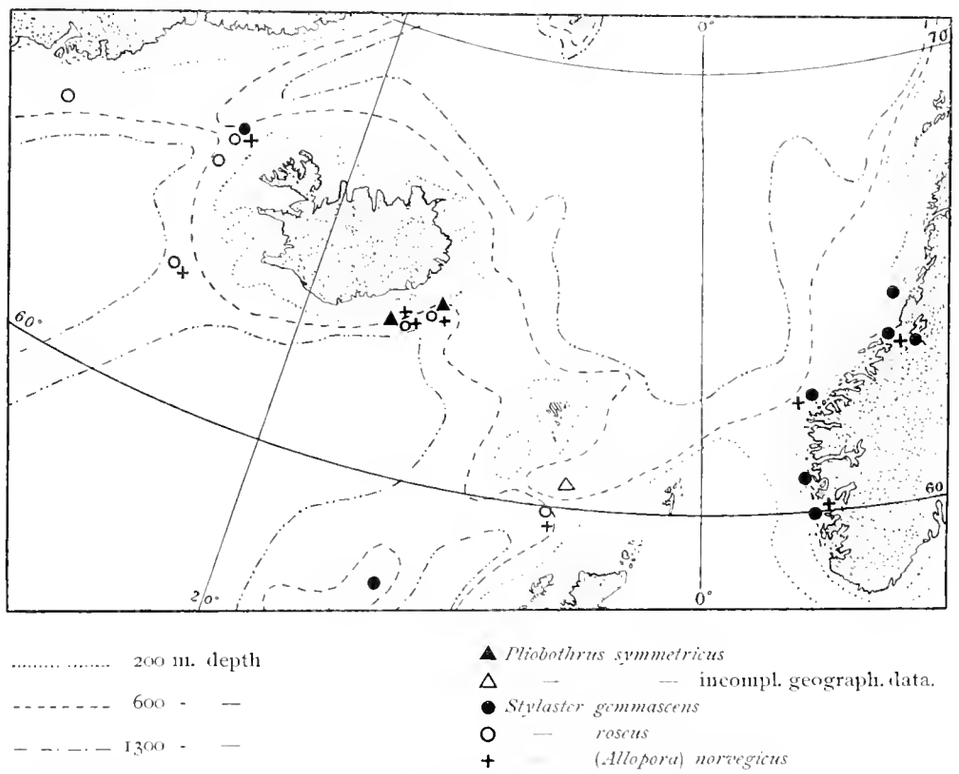
Later information regarding the northern Stylasterids is very meagre. Storm (1882) mentions *Stylaster gemmascens* and *Allopora norvegica* from the Trondhjem Fjord; there is a casual remark by Hickson (1891), that he has had material of *Allopora oculina* from the Hardanger Fjord and of *Allopora norvegica* from the »Triton« Expedition; lastly, J. A. Thomson (1910) informs us, that he has examined colonies of *Stylaster* from Rockall.

On the basis of the literature, therefore, we cannot penetrate very far into the biogeographical conditions of the northern Stylasterids. In this respect the comparatively large material collected by the »Ingolf«, »Thor« and the East Greenland Expedition of 1900 fills up a large gap in our knowledge. Supplementing this material with that preserved in the museums of Christiania and Trondhjem and further with observations from the Trondhjem Fjord we are able to throw a fairly good light on the biogeographical conditions of this enigmatical group in our northern waters.

As already noted, the *Stylasteridae* in the Norwegian Sea are typical coral reef dwellers. Yet at places in the Trondhjem Fjord *Stylaster gemmascens* is able to live in somewhat shallower water, sometimes even in towards a depth of 50 metres. This must depend on the special biophysical conditions of the fjord and it is of interest to note in this connection, that according to the investigations the species is only able to live in the shallower parts at places where projecting, submarine cliffs or barriers force the masses of water upwards which are brought in by the tidal wave. The shallowest occurrence of the species lies near its innermost boundary in the fjord. In the outer parts of the fjord, on the other hand, where the sides of the fjord are steeper and more regular, the species as also *Stylaster* (*Allopora*) *norvegicus* is bound to the *Lophohelia* reefs and both species here as elsewhere

must be regarded as characteristic forms of the large biocoenosis of the coral reefs. This is also strengthened by the single discovery of *Stylaster gemmascens* made in the Hjelte Fjord in the neighbourhood of Bergen, where Dr. O. Nordgaard has obtained two small fragments of colonies from the coral reef there.

We thus see that the two *Stylaster* species which occur on the coast of Norway, form interesting parallels in the animal community of the northern coral reefs to the Stylasterids of the tropical coral reefs. They are thus, like the *Lophohelia* reefs as a whole, bound in their occurrence to those localities with hard bottom, where the Atlantic current makes its influence most felt in the Norwegian Sea.



Text-fig. F. Map showing the localities of the *Stylasteridae* in the North Atlantic and the Norwegian Sea.

The study of the occurrence of the North Atlantic Stylasterids shows several biogeographical features of interest (cf. Chart Text-fig. F). — *Pliobothrus symmetricus* was first described from the waters round about Florida and must be fairly common there between 190 and 300 metres. It has been found by the Ingolf on the steep slope off the south coast of Iceland towards the depths of the Atlantic in 594 and 658 metres. According to Duncan (1874 p. 336) the Porcupine obtained a single specimen in the cold area of the Faeroe Channel; unfortunately he does not state the exact locality. We thus have a species here which belongs to the warm Atlantic waters and normally is not able to penetrate in over the submarine ridge, which towards the south separates the Norwegian Sea from the depths of the Atlantic. The one find in the cold area must be a pure chance and forms a parallel to the single and scattered finds which have been made here and there in the Norwegian Sea of other typical warm water forms among the Hydroids.

Stylaster roseus forms a parallel to *Pliobothrus symmetricus*. It is fairly common between 230 and 620 metres at Florida and on the whole has probably a greater bathymetric distribution than *Pliobothrus symmetricus*. *Stylaster roseus* is much more frequent in its occurrence than the latter form, but is restricted in the Atlantic to the south of the submarine ridges and has not yet been found in the Norwegian Sea. The Ingolf has taken the species at a single place in the Denmark Strait in water of negative temperature; this occurrence is due probably to a submarine wave making the conditions inhabitable for the species when it became attached as larva or that the station at the time of observation was covered by a wave of the cold polar water — In the Norwegian Sea the species is replaced by the nearly allied *Stylaster gemmascens*, which in reality must be ranged with the extremely few animals, which are entirely bound to the warmer layers of the Norwegian Sea. We may feel tempted to consider it a biologically defined, local species, which has divided off from *Stylaster roseus*. The two species have only been found side by side with certainty at the above-mentioned boundary station in the Denmark Strait, where the line of separation must be drawn between the Atlantic deep-water region and the boreal water-layers. This is the only time that *Stylaster gemmascens* has also been found in water of negative temperature. Once the species has been identified with certainty south of the Wyville-Thomson ridge, a couples of colonies being found at Rockall; the fauna at Rockall however has a strong mixture of species, whose chief occurrence is bound to the Norwegian Sea.

Finally, the last species *Stylaster norvegicus* is an Atlantic species which belongs to the North Atlantic and has been able to penetrate into the Norwegian Sea, where it has found a new home in the warmer water-layers there. Its occurrence shows a secondary centre in the Trondhjem Fjord, where along with *Stylaster gemmascens* it is more abundant than anywhere else in the northern parts of the Atlantic. The occurrence of the species in more southern waters cannot be accepted as certain, for its systematic characters have hitherto been too little unravelled; but it can hardly be very common there.

Trondhjem, November 1913.

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EXPLANATION OF THE PLATES

The following letters indicate the same parts in all Plates.

Ae Ectodermal epithelium of the ampulla.
Cn Cnidocysts.
Dp Dactylopore.
Ds Dactylostyle.
Ec Ectoderm.
En Endoderm.
e Ectodermal epithelium of the gastero-
pore wall.
Ge Ectoderm of the gonophore.
Gp Gasteropore.
Gs Gasterostyle.
I The inner cells of the seminal duct.
O egg cell.
Sp Spadix.
s Stolon.
T Tentacle.
t tabula.
W Free wall of the gasterozooid.

Plate I.

Plate I.

Fig. 1. *Pliobothrus symmetricus*; front surface of an intact colony from the "Ingolf" St. 55. Natural size.

— 2. — — hind surface of the same colony. Nat. size.

— 3. — — two ends of branches from "Ingolf" St. 55. 4/1.

— 4. *Stylaster gemmascens*; one of the type specimens of Gunnerus' *Madrepora virginea* from the west coast of Norway. Nat. size.

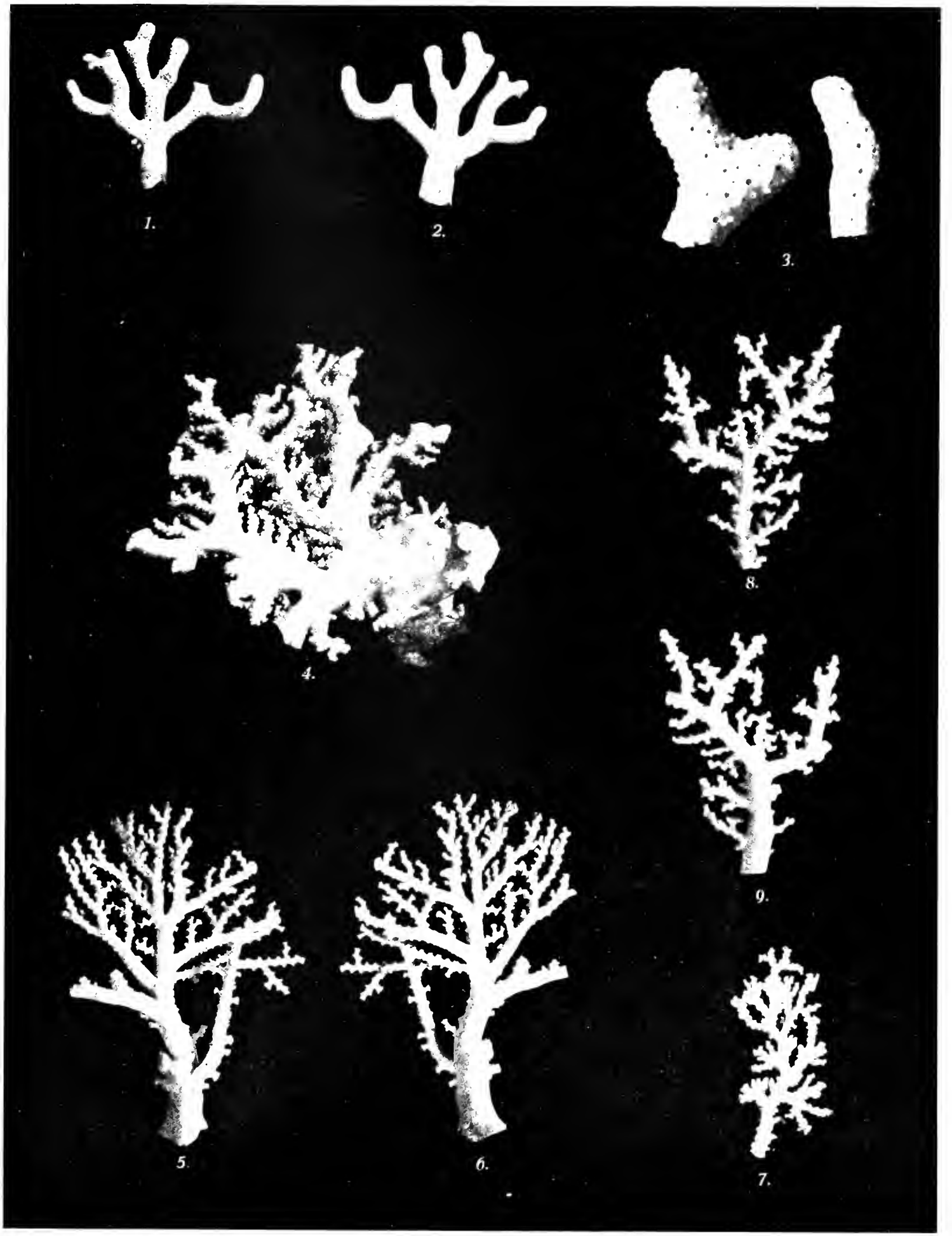
— 5. *Stylaster gemmascens*; front surface of an openly built colony from the Trondhjem Fjord. Nat. size.

— 6. *Stylaster gemmascens*; hind surface of same colony. Nat. size.

— 7. — — front surface of the compact branch of a fertile colony (♀) from the Trondhjem Fjord. Nat. size.

— 8. *Stylaster roseus*; front surface of a fragment of a colony from Angmagsalik with male ampullae Nat. size.

— 9. *Stylaster roseus*; hind surface of the same fragment. Nat. size.



H. Broch, phot.

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Plate II.

Plate II.

Fig. 10. *Stylaster roseus*; front surface of a fragment of a colony with female ampullae; "Ingolf" St. 15. Nat. size.

— 11. *Stylaster roseus*; fragment of a colony which is entirely deformed owing to the development of numerous female ampullae; "Ingolf" St. 7. Nat. size.

— 12. *Stylaster norvegicus*; one of the type specimens of Gunnerus' *Millepora norvegica* from west coast of Norway. Nat. size.

— 13. *Stylaster norvegicus*; front surface of a narrow-branched colony from Trondhjem Fjord. Nat. size.

— 14. — — hind surface of the same colony. Nat. size.

— 15. — — front surface of a broad-branched colony from Trondhjem Fjord. Nat. size.

— 16. — *gemmascens*; ends of two branches of a colony from Trondhjem Fjord. $^4/_1$.

— 17. — *roseus*; end of a branch of a colony from "Ingolf" St. 15. $^4/_1$.

— 18. — *norvegicus*; ends of two branches of a colony from Trondhjem Fjord. $^4/_1$.

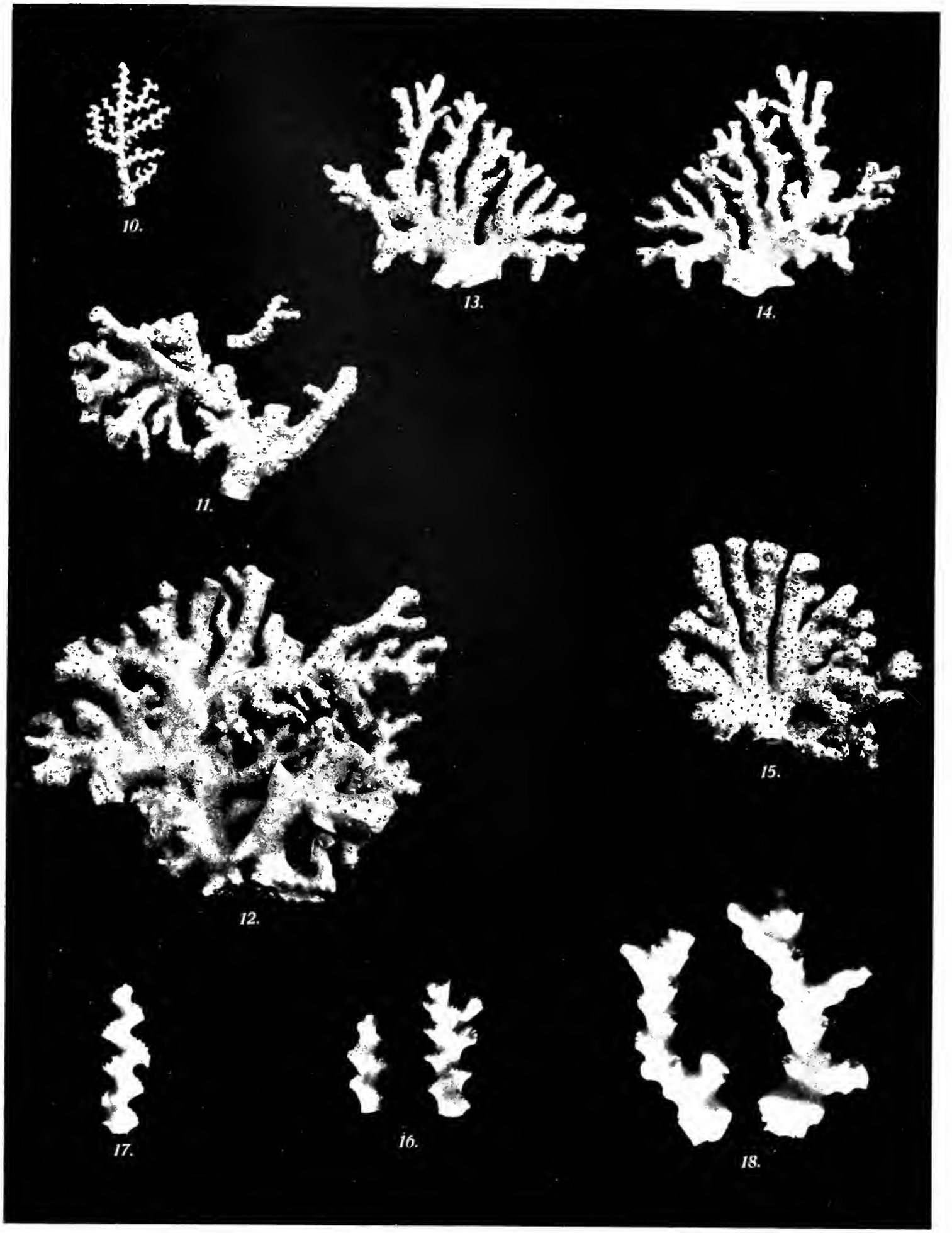

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Plate III.

Plate III.

Fig. 19. *Pliobothrus symmetricus*; median longitudinal section of a branch point. $^{10}/_{1}$.

— 20. — — median section through a gasteropore with tabula. $^{10}/_{1}$.

— 21. *Stylaster gemmascens*; median longitudinal section of a branch. $^{10}/_{1}$.

— 22. — *roseus*; median longitudinal section of a branch. $^{10}/_{1}$.

— 23. — *norvegicus*; longitudinal section through two cyclosystems. $^{10}/_{1}$.

— 24. Median, longitudinal, thin section of the gasterostyle in *Stylaster gemmascens*. $^{90}/_{1}$.

— 25. Longitudinal section of the gasterozooid in *Stylaster gemmascens*. $^{130}/_{1}$.

— 26. Transverse section of the gasterozooid at the base of the tentacles in *Stylaster gemmascens*. $^{300}/_{1}$

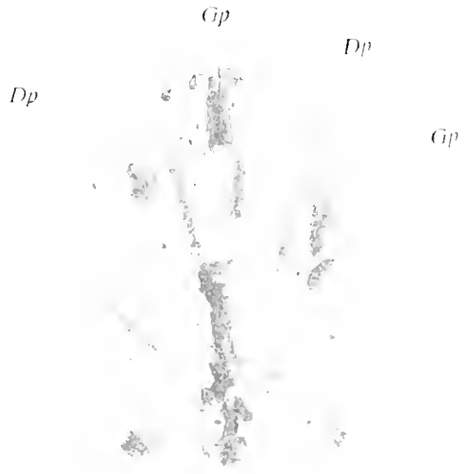
— 27. Oblique transverse section of the gasterozooid at the base of the tentacles in *Stylaster norvegicus*. $^{300}/_{1}$.

— 28. Transverse section of the gasterozooid in *Pliobothrus symmetricus*. $^{300}/_{1}$.

— 29. Longitudinal section through the oral part of the gasterozooid wall in *Pliobothrus symmetricus*. $^{450}/_{1}$.

— 30. Longitudinal section through the oral part of the gasterozooid wall and tentacle in *Stylaster gemmascens*. $^{450}/_{1}$.

— 31. Longitudinal section through oral part of the gasterozooid wall and tentacle in *Stylaster norvegicus*. $^{450}/_{1}$.



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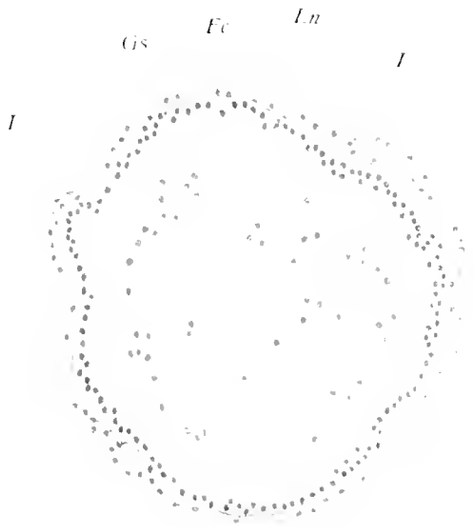

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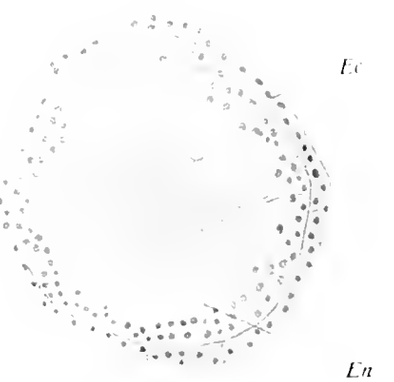

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Plate IV.

Plate IV.

Fig. 32. Transverse section of the gasterozooid at its base near its transition into the stolons in *Stylaster gemmascens.* $^{300}/_{1}$.

— 33. Longitudinal section of the dactylozooid in *Stylaster gemmascens.* $^{300}/_{1}$.

— 34. Transverse section of a dactylozooid in *Pliobothrus symmetricus.* $^{300}/_{1}$.

— 35. Median longitudinal section of a very young gonophore (♂) in *Stylaster norvegicus.* $^{150}/_{1}$.

— 36. Median longitudinal section of a young gonophore (♂) in *Stylaster roseus.* $^{450}/_{1}$.

— 37. Median longitudinal section of an unripe gonophore (♂) in *Stylaster norvegicus.* $^{300}/_{1}$.

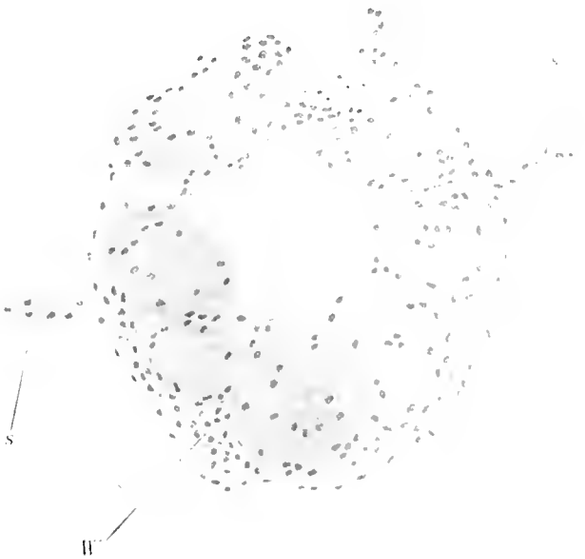
— 38. Median longitudinal section of two gonophores (♂) in *Stylaster norvegicus.* The larger with spadix partially atrophied contains spermatocytes in process of transformation to spermatozoa. $^{130}/_{1}$.

— 39. Median longitudinal section of a gonophore (♂) in *Stylaster roseus*; the spermatocytes in process of transformation to spermatozoa. $^{130}/_{1}$.

— 40. Transverse section of a young gonophore (♂) in *Pliobothrus symmetricus.* $^{300}/_{1}$.

— 41. Median longitudinal section of a gonophore (♂) in *Pliobothrus symmetricus.* $^{300}/_{1}$.

— 42. Median longitudinal section through apex of the fully developed gonophore in (♂) *Pliobothrus symmetricus.* $^{300}/_{1}$.



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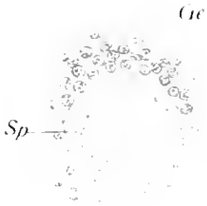

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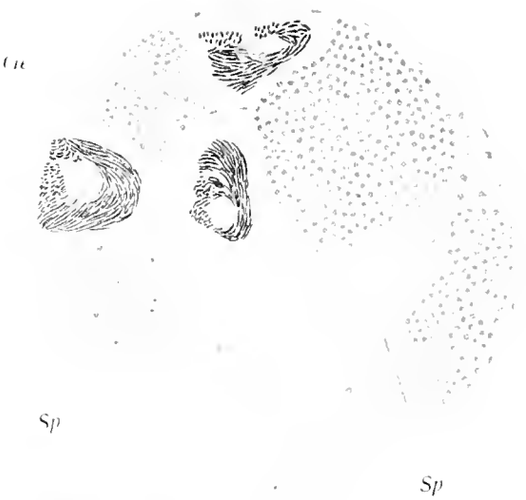

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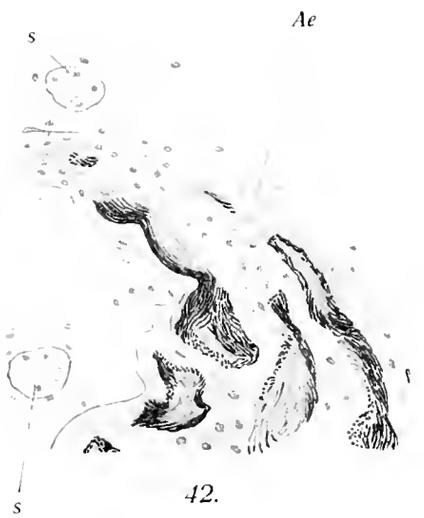

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Plate V.

Plate V.

Fig. 43. Apex of a gonophore (♂) in *Stylaster roseus*, containing spermatocytes in process of transformation. $^{450}/_{1}$.

— 44. Early stage in the development of a seminal duct in *Stylaster norvegicus*. $^{450}/_{1}$.

— 45. Longitudinal section through an almost full-grown seminal duct in *Stylaster norvegicus*. $^{150}/_{1}$.

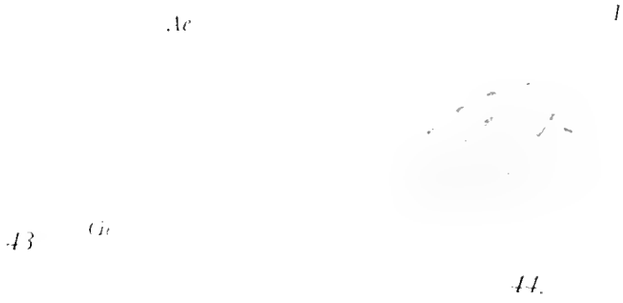
— 46. Median longitudinal section through a gonophore (♀) with ripe ovum in *Stylaster gemmascens*. $^{300}/_{1}$.

— 47. Median longitudinal section of a gonophore (♀) with ripe ovum in *Stylaster roseus*. $^{130}/_{1}$.

— 48. Transverse section of a gonophore (♀) near the distal end of the spadix in *Stylaster roseus*. $^{130}/_{1}$.

— 49. Transverse section of the spadix close beneath the ovum in *Stylaster gemmascens*. $^{130}/_{1}$.

— 50. Median longitudinal section through a gonophore with advanced planula larva in *Stylaster gemmascens*. $^{130}/_{1}$.



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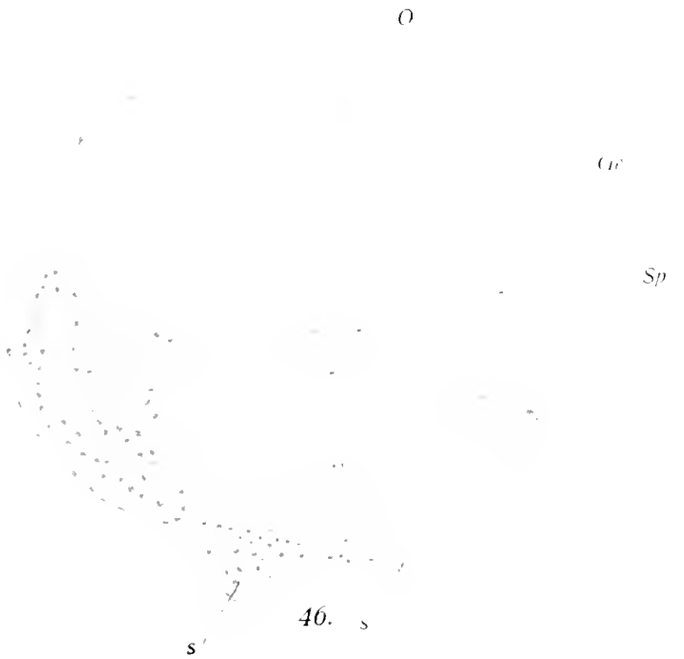

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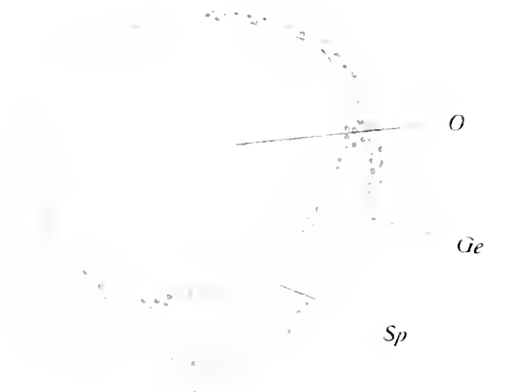

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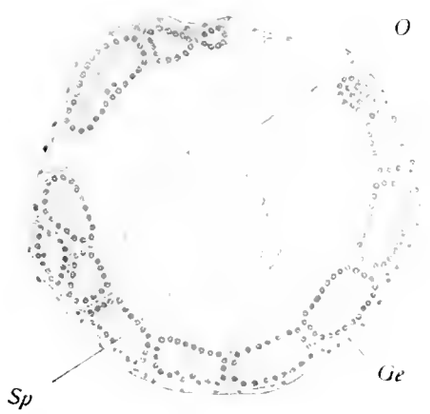

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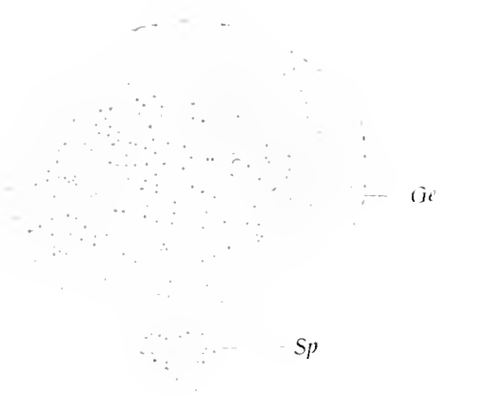

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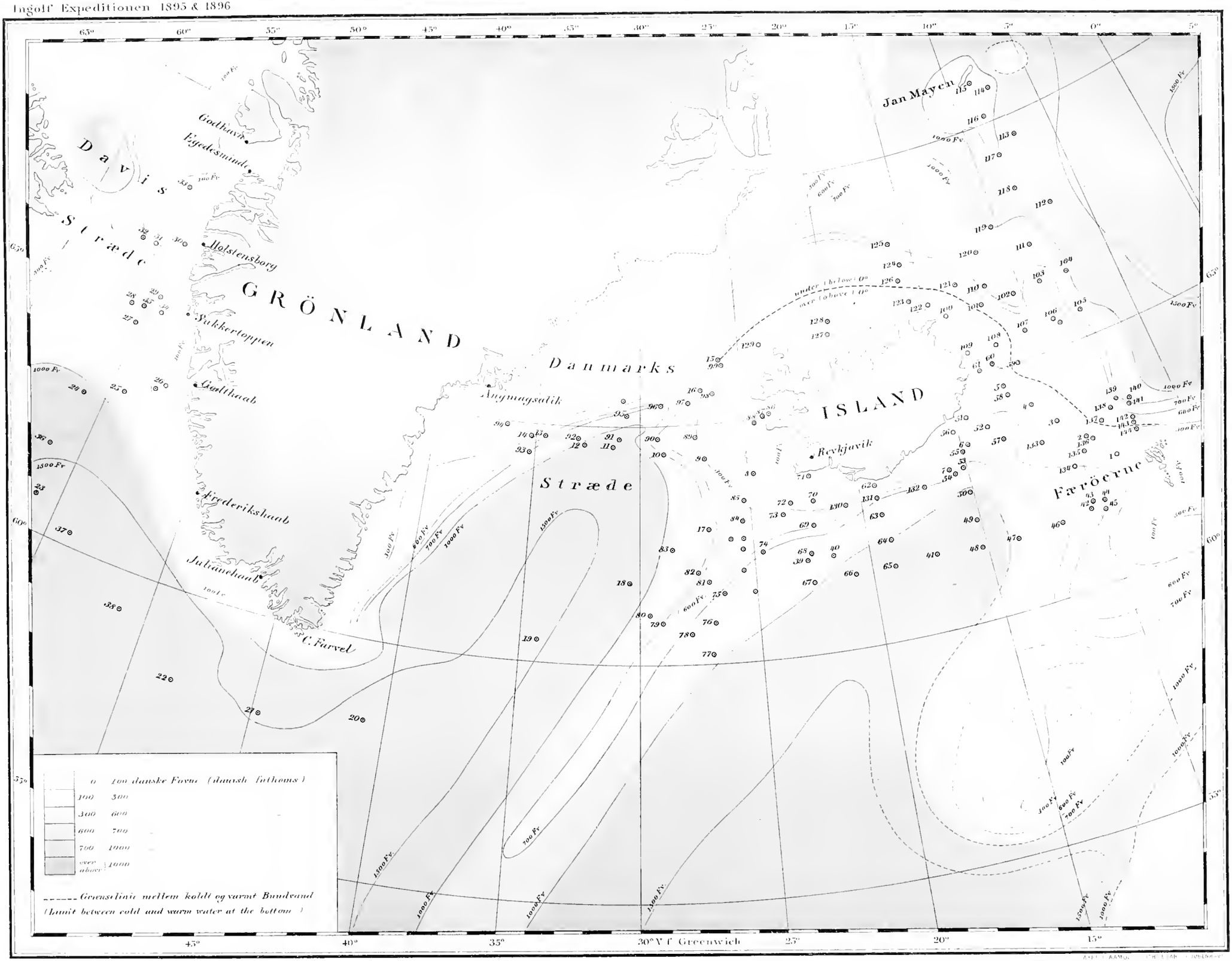
THE INGOLF-EXPEDITION

1895 1896.

THE LOCALITIES, DEPTHS, AND BOTTOMTEMPERATURES OF THE STATIONS

Station Nr.	Lat. N.	Long. W.	Depth in Danish fathoms	Bottom-temp.	Station Nr.	Lat. N.	Long. W.	Depth in Danish fathoms	Bottom-temp.	Station Nr.	Lat. N.	Long. W.	Depth in Danish fathoms	Bottom-temp.
1	62° 30′	8° 21′	132	7°2	24	63° 06′	56° 00′	1199	2°4	45	61° 32	9° 43′	643	4°17
2	63° 04′	9° 22′	262	5°3	25	63° 30′	54° 25′	582	3°3	46	61° 32′	11° 36′	720	2°40
3	63° 35′	10° 24′	272	0 5		63° 51′	53° 03′	136		47	61° 32′	13° 40′	950	3°23
4	64° 07′	11° 12′	237	2°5	26	63° 57′	52° 41′	34	0°6	48	61° 32′	15° 11′	1150	3°17
5	64° 40′	12° 09′	155			64° 37′	54° 24′	109		49	62° 07′	15° 07′	1120	2°91
6	63° 43′	14° 34′	90	7°0	27	64° 54′	55° 10′	393	3°8	50	62° 43′	15° 07′	1020	3°13
7	63° 13′	15° 41′	600	4°5	28	65° 14′	55° 42′	420	3°5	51	64° 15′	14° 22′	68	7°32
8	63° 56′	24° 40′	136	6°0	29	65° 34′	54° 31′	68	0°2	52	63° 57′	13° 32′	420	7°87
9	64° 18′	27° 00′	295	5°8	30	66° 50′	54° 28′	22	1°05	53	63° 15′	15° 07′	795	3°08
10	64° 24′	28° 50′	788	3°5	31	66° 35′	55° 54′	88	1°6	54	63° 08′	15° 40′	691	3°9
11	64° 34′	31° 12′	1300	1°6	32	66° 35′	56° 38′	318	3°9	55	63° 33′	15° 02′	316	5°9
12	64° 38′	32° 37′	1040	0°3	33	67° 57′	55° 30′	35	0°8	56	64° 00′	15° 09′	68	7°57
13	64° 47′	34° 33′	622	3°0	34	65° 17′	54° 17′	55		57	63° 37′	13° 02′	350	3°4
14	64° 45′	35° 05′	176	4°4	35	65° 16′	55° 05′	362	3°6	58	64° 25′	12° 09′	211	0°8
15	66° 18′	25° 59′	330	—0°75	36	61° 50′	56° 21′	1435	1°5	59	65° 00′	11° 16′	310	—0°1
16	65° 43′	26° 58′	250	6°1	37	60° 17′	54° 05′	1715	1°4	60	65° 09′	12° 27′	124	0°9
17	62° 49′	26° 55′	745	3°4	38	59° 12′	51° 05′	1870	1°3	61	65° 03′	13° 06′	55	0°4
18	61° 44′	30° 29′	1135	3°0	39	62° 00′	22° 38′	865	2°9	62	63° 18′	19° 12′	72	7°92
19	60° 29′	34° 14′	1566	2°4	40	62° 00′	21° 36′	845	3°3	63	62° 40′	19° 05′	800	4°0
20	58° 20′	40° 48′	1695	1°5	41	61° 39′	17° 10	1245	2°0	64	62° 06′	19° 00′	1041	3°1
21	58° 01′	44° 45′	1330	2°4	42	61° 41′	10° 17′	625	0°4	65	61° 33′	19° 00′	1089	3°0
22	58° 10′	48° 25′	1845	1°4	43	61° 42′	10° 11′	645	0°05	66	61° 33′	20° 43′	1128	3°3
23	60° 43′	56° 00′	Only the Plankton Net used		44	61° 42′	9° 36′	545	4°8	67	61° 30′	22° 30′	975	3°0

Station Nr.	Lat. N.	Long. W.	Depth in Danish fathoms	Bottom-temp.	Station Nr.	Lat. N.	Long. W.	Depth in Danish fathoms	Bottom-temp.	Station Nr.	Lat. N.	Long. W.	Depth in Danish fathoms	Bottom-temp.
68	62° 06′	22° 30′	843	3°4	92	64° 44′	32° 52′	976	1°4	118	68° 27′	8° 20′	1060	—1°0
69	62° 40′	22° 17′	589	3°9	93	64° 24′	35° 14′	767	1°46	119	67° 53′	10° 19′	1010	—1°0
70	63° 09′	22° 05′	134	7°0	94	64° 56′	36° 19′	204	4°1	120	67° 29′	11° 32′	885	1°0
71	63° 46′	22° 03′	46			65° 31′	30° 45′	213		121	66° 59′	13° 11′	529	—0°7
72	63° 12′	23° 04′	197	6°7	95	65° 14′	30° 39′	752	2°1	122	66° 42′	14° 44′	115	1°8
73	62° 58′	23° 28′	486	5°5	96	65° 24′	29° 00′	735	1°2	123	66° 52′	15° 40′	145	2°0
74	62° 17′	24° 36′	695	4°2	97	65° 28′	27° 39′	450	5°5	124	67° 40′	15° 40′	495	—0°6
	61° 57′	25° 35′	761		98	65° 38′	26° 27′	138	5°9	125	68° 08′	16° 02′	729	—0°8
	61° 28′	25° 06′	829		99	66° 13′	25° 53′	187	6°1	126	67° 19′	15° 52′	293	—0°5
75	61° 28′	26° 25′	780	4°3	100	66° 23′	14° 02′	59	0°4	127	66° 33′	20° 05′	44	5°6
76	60° 50′	26° 50′	806	4°1	101	66° 23′	12° 05′	537	—0°7	128	66° 50′	20° 02′	194	0°6
77	60° 10′	26° 59′	951	3°6	102	66° 23′	10° 26′	750	—0°9	129	66° 35′	23° 47′	117	6°5
78	60° 37′	27° 52′	799	4°5	103	66° 23′	8° 52′	579	—0°6	130	63° 00′	20° 40′	338	6°55
79	60° 52′	28° 58′	653	4°4	104	66° 23′	7° 25′	957	—1°1	131	63° 00′	19° 09′	698	4°7
80	61° 02′	29° 32′	935	4°0	105	65° 34′	7° 31′	762	—0°8	132	63° 00′	17° 04′	747	4°6
81	61° 44′	27° 00′	485	6°1	106	65° 34′	8° 54′	447	—0°6	133	63° 14′	11° 24′	230	2°2
82	61° 55′	27° 28′	824	4°1		65° 29′	8° 40′	466		134	62° 34′	10° 26′	299	4°1
83	62° 25′	28° 30′	912	3°5	107	65° 33′	10° 28′	492	—0°3	135	62° 48′	9° 48′	270	0°4
	62° 36′	26° 01′	472		108	65° 30′	12° 00′	97	1°1	136	63° 01′	9° 11′	256	4°8
	62° 36′	25° 30′	401		109	65° 29′	13° 25′	38	1°5	137	63° 14′	8° 31′	297	—0°6
84	62° 58′	25° 24′	633	4°8	110	66° 44′	11° 33′	781	—0°8	138	63° 26′	7° 56′	471	—0°6
85	63° 21′	25° 21′	170		111	67° 14′	8° 48′	860	—0°9	139	63° 36′	7° 30′	702	—0°6
86	65° 03′0	23° 47′0	76		112	67° 57′	6° 44′	1267	—1°1	140	63° 29′	6° 57′	780	—0°9
87	65° 02′3	23° 56′2	110		113	69° 31′	7° 06′	1309	—1°0	141	63° 22′	6° 58′	679	—0°6
88	64° 58′	24° 25′	76	6°9	114	70° 36′	7° 29′	773	—1°0	142	63° 07′	7° 05′	587	—0°6
89	64° 45′	27° 20′	310	8°4	115	70° 50′	8° 29′	86	0°1	143	62° 58′	7° 09′	388	—0°4
90	64° 45′	29° 06′	568	4°4	116	70° 05′	8° 26′	371	—0°4	144	62° 49′	7° 12′	276	1°6
91	64° 44′	31° 00′	1236	3°1	117	69° 13′	8° 23′	1003	—1°0					


Davis Strædet
GRÖNLAND
Godthaab
Egedesminde
Holstensborg
Sukkertoppen
Godthaab
Frederikshaab
Julianehaab
C. Farvel
Daumarks
Angmagsalik
ISLAND
Reykjavik
Jan Mayen
Færöerne
Strædet
0 100 danske Favne (danish fathoms)
100 300
300 600
600 700
700 1000
over 1000
Grænselinie mellem koldt og varmt Bundvand
(Limit between cold and warm water at the bottom)
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THE DANISH INGOLF-EXPEDITION.

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