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MORPHOLOGICAL STUDIES OF *HALAMMOHYDRA* REMANE (HYDROZOA)¹

By

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ABSTRACT

Species of the interstitial hydrozoan *Halammohydra* REMANE from the west coast of Norway and from Heligoland have been studied morphologically. Of five species encountered two are described as new to science. *H. intermedia* sp. n. is described from the Bergen area, Norway, where it inhabits the medium to coarse shell gravel. It becomes 1 mm long and stands near *H. octopodides* and *H. schulzei*. *H. coronata* sp. n. is described from Heligoland, where it occurs in two forms, the one inhabiting fine and the other coarse sand. It is closely related to *H. adherens*. The number of statocysts and anterior tentacles is reduced, while there is a supernumerary number of posterior tentacles.

INTRODUCTION

Halammohydra is a small and flagellated freemoving hydrozoan living in the marine interstices formed by sand grains or shell fragments. It was discovered in the Kiel Bay in 1924 by REMANE, who also found it the following year at Heligoland and thereafter described two species, *H. octopodides* and *H. schulzei* (REMANE 1927).

A third species, *H. vermiformis*, was described 30 years later from Roscoff by SWEDMARK & TEISSIER (1957b). SWEDMARK & TEISSIER (1959) also announced in the Roscoff area the presence of a fourth species, which they recently have described as *H. (Skodenhya) adherens* (SWEDMARK & TEISSIER 1967). In the same paper also the aberrant *H. vermiformis* is placed in an own subgenus, *Goulvenhydra*.

The known distribution of *Halammohydra* in European coastal waters ranges from the Adria (SALVINI-PLAWEN 1965) to the Barents Sea (MAMKAEV 1962), and recently it has been reported also from the coast of India (CHANDRASEKHARA & GANAPATI 1966).

REMANE considered *Halammohydra* an aberrant medusa and ranged it within the Trachylida in the suborder Narcomedusae.

The extended investigations of the interstitial fauna performed by SWEDMARK & TEISSIER in Roscoff from 1950 onwards yielded more details on the subject, and they also proved that *Halammohydra* has a direct development via an actinula stage. In addition, they discovered a related genus, *Otohydra*, with the same development pattern. A pelagic planula stage is missing in both genera. Their conclusion was that *Halammohydra* as well as *Otohydra* are not modified medusae, but polypoid actinulae with neotenic reproduction. Accordingly they established

¹ Contribution from the Biological Station, Espesgrend, Blomsterdalen, Norway, and from the Zoological Laboratory, Bergen, Norway.

a new order, Actinulida, with the two families Halammohydridae and Otophyridae (SWEDMARK & TEISSIER 1950; SWEDMARK 1957; SWEDMARK & TEISSIER 1957a, b, 1958, 1959, 1966).

Lately WERNER (1965a) has presented a different view as to the nature and systematic position of *Halammohydra*. He could prove that flagellae are a common feature in the hydromedusae. On account of this fact and other details, among which he especially stressed the importance of the cnidome, WERNER was led to consider *Halammohydra* a hydromedusa, constituting an own suborder, Halammohydrina. The diagnosis given by WERNER (l.c.) is: "O. Hydroida, S.o. Halammohydrina, hydromedusae with reduced umbrella and direct development, with outer statocysts with endodermal axis."

In an earlier paper on *Halammohydra* (CLAUSEN 1963) I have mentioned briefly the occurrence in the vicinity of Bergen of two species of *Halammohydra*, which were thought to represent local forms of *H. octopodides* and *H. schulzei* respectively. Both the Norwegian forms differ from the respective type forms in details of the cnidome.

During my continued studies of the interstitial fauna in the Bergen area I found in certain localities a form of *H. schulzei* differing both from the type form at Heligoland and from the presumed local Bergen form. I then tried to find out whether the two Norwegian forms always occurred in isolated populations or not, and succeeded in finding them together in a few places. It appeared from the studies of these mixed populations that the two forms retained their identity, differing from each other in several respects. As a corollary, at least the form differing most from the type form had to be considered a species of its own. I propose to give it the specific name *intermedia*, which suggests its resemblance to both *H. schulzei* and *H. octopodides*.

In 1964 I had the opportunity to visit Heligoland, in order to get material of *Halammohydra* for a comparison with the Norwegian forms. During September I collected in all 69 specimens, comprising six forms, differing as regards either the cnidome or other features.

In my own morphological investigations stress has been laid upon the study of live specimens. Measurements were made by the help of an ocular micrometer. In the study of the nematocysts, which are among the smallest known, I used a phase contrast oil immersion objective (90/1.15 and 90/1.32).

GENERAL ORGANIZATION

As an orientation a brief recapitulation of the morphology, mainly as treated by REMANE (1927) and SWEDMARK & TEISSIER (1957a, b, 1966) is given. Like REMANE and WERNER I am inclined to consider *Halammohydra* a modified medusa; but as long as its taxonomic position is uncertain, I prefer to use neutral morphological terms in the cases where the homology is not clear.

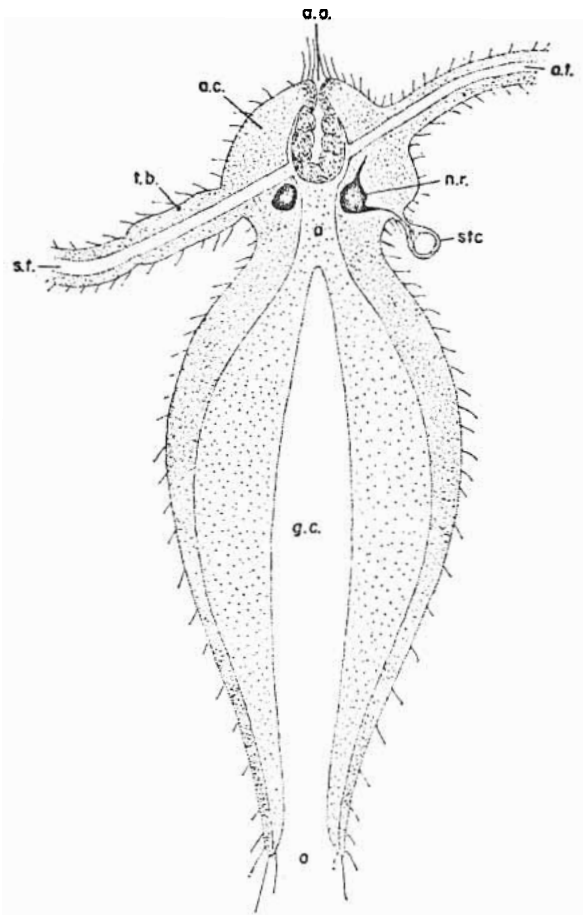


Fig. 1. Organization of *Halammohydra*.
a axial endoderm, *a.c.* aboral cone, *a.o.* aboral adhesive organ, *a.t.* tentacle belonging to aboral whorl, *g.c.* gastric cavity, *n.r.* nerve ring, *o* mouth, *s.t.* tentacle belonging to subaboral whorl, *stc* statocyst, *t.b.* tentacle bulb (from SWEDMARK & TEISSIER 1966).

The lengthened body consists of a smaller, knob-like anterior (aboral) portion, the aboral cone (umbrella?) (REMANE, Kappe; SWEDMARK & TEISSIER, coiffe, aboral cone) and a larger posterior or stomach portion, the gastric tube (manubrium?) (Fig. 1). The latter is more or less compressed and is connected with the aboral cone through a narrow "neck". The stomach ends blindly close behind the neck and opens posteriorly through the mouth. A mouth rim, somewhat narrower than the stomach proper is usually clearly distinguished. The aboral cone, circular in transverse sections, is flattened at its posterior end and more or less rounded anteriorly. It bears up to 32 slender tentacles arranged in an anterior and a posterior, or marginal whorl. The tentacles have a core of endodermal cells. Alternating with the posterior tentacles are the statocysts, which like those of the trachylides have an ectodermal cover and an endodermal axis. A central, usually deep anterior groove in the aboral cone is lined by gland cells and functions as an

adhesive organ. At the base of the second whorl of tentacles is a nerve ring. The entire outer surface bears flagellae, which assist locomotion through the interstices. The sexes are separate, and the gonads, one or two, according to the species, lie in the stomach wall, between the epi- and the gastrodermis.

HALAMMOHYDRA SPECIES FROM THE BERGEN AREA

The material was sampled from various localities in Raunefjorden and Korsfjorden, and from one locality in Lerøyosen. Except for the last place, where the sediments consisted of fine minerogene sand, findings were made in shell gravel ranging in coarseness from fine (practically all fragments less than 1 mm) to fairly coarse (containing fragments or whole shells up to about 10 mm). The depth ranged from 1 to 25 m. At depths down to about 4 m a catcher was applied, at greater depths the sediments were dredged.

Halammohydra octopodides REMANE, 1927

This species has been found in both fine, medium coarse and coarse sediments at depths varying from 1 to 20 m. The localities were:

Visterøy (Biological Station Reference Number 39a—62), Langøy (178—63), Raunane (401—63), Tekslo (517—63), Hundaflesi (432—65), and Lauvholmen (321, 393—67). At the last station a dozen specimens were taken in all, while I got only from one to five at the other stations.

All the specimens examined belonged to one and the same local form, only varying in size (225—380 μ) and in the number of tentacles (10—18). The aboral cone is slightly broader than high, and the adhesive organ is deep and narrow. As in the type form, the anterior tentacles are all about the same length, while the posterior whorl of tentacles contains both the shortest tentacle and the longest one. The endodermal cell strings of both kinds of tentacles meet as usual at the base of the adhesive organ, but contrary to the statement of REMANE (1927), the cells are not narrower in the strings within the cone than in the tentacles, nor has such a tapering been observed in any of the other species studied.

The cnidome consists of two categories of nematocysts, atrichous haplonemes, or isorhizes (c. $4 \times 2.2 \mu$), and stenoteles, according to the nomenclature of WEILL (1934). The latter are of two kinds, macro- and microstenoteles, whereas the type form has only microstenoteles. The macrostenoteles (7—9.2 \times 6—7.5 μ) (Fig. 2) are particularly abundant in the proximal region of the gastric tube and in the distal part of the tentacles. A closer examination showed that the microstenoteles can again be divided into two types, of which the one (5—6 \times 3.5—4.5 μ) has a larger and above all broader capsule than the other (c. 5 \times 3 μ) (Figs. 3 and 4).

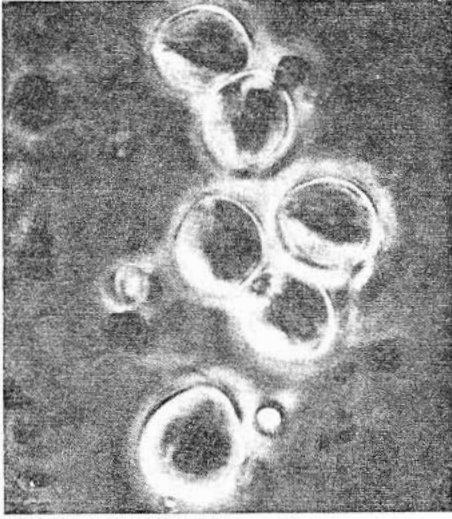


Fig. 2



Fig. 3

Figs. 2 and 3. *Halammohydra octopodides* from Bergen. 2. Undischarged macrostenoetes. 3. Discharged microstenoete of the larger type (below). \times c. 1,750.

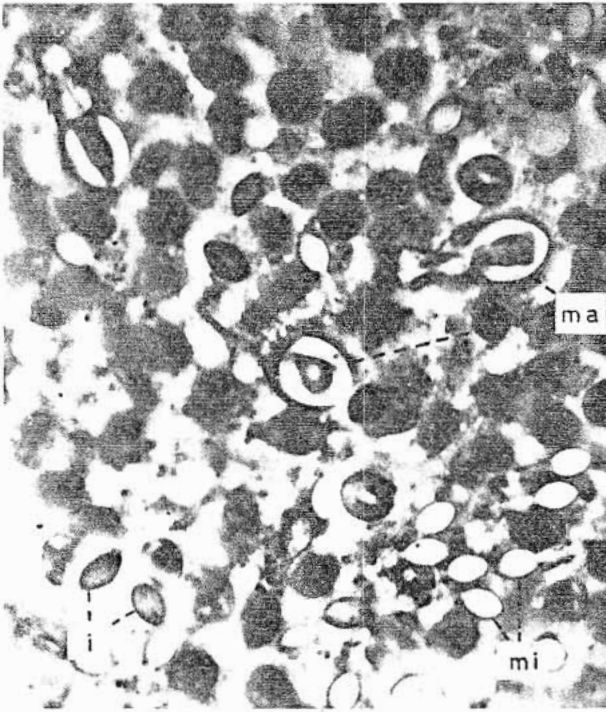


Fig. 4. *Halammohydra octopodides* from Bergen. Nematocysts. *i* undischarged isorhizes, *ma* discharged macrostenoetes, *mi* discharged microstenoetes of the smaller type. \times c. 1,750.

Halammohydra schulzei REMANE, 1927

I have found this species in coarse and medium coarse shell gravel at depths ranging from 2.5–25 m, at the following localities:

Tekslo (517–63, 536–64, 310–65, E of Store Fugløy (80–64), Bondisholmen (82, 107–64), Håkonsund (108–64, 354–65), W of Lille Fugløy (224–64), Donhamna (483–65, 116, 158–66), Kyrkjesusund (224–66), Kyrholmen (245–66), and Lauvholmen (282, 318, 321–66, 18, 55, 55b–67).

H. schulzei like *H. octopodides* has hitherto been found only in one form in the Bergen area. As to outer morphology it seems to agree well with the type form, but with regard to the cnidome, the two forms differ. While the type form has both macro- and microstenoteles accompanying the isorhizes, the Bergen form has microstenoteles only in addition to the isorhizes (c. $4 \times 2.4 \mu$). These are fairly large ($5-7 \times 3.3-4.6 \mu$) and typically oblongish of shape, with the largest diameter nearest the proximal end.

H. schulzei as a rule was very scarce in the samples, and only some 50 specimens have been found in all. A few of the specimens examined had 30 tentacles and 15 statocysts. The largest specimen measured c. 650μ . There are two gonads. The aboral cone is usually markedly broader than long and gently rounded anteriorly (Fig. 7A). It is relatively large in relation to the gastric tube, the proportion being c. 1 to 7 in the largest specimens. The adhesive organ is large, reaching a depth of 65μ and a diameter of $40-50 \mu$. It is fairly distendable, and usually it is broadest in its anterior third, also when the animal moves (Fig. 7A).

The anterior tentacles are more uniform than the posterior ones and on an average longer. One of the posterior tentacles is usually longer than the others, being about the same length as the longest one of the first whorl.

It appears from the description of REMANE that one of the most prominent features of *H. schulzei* is a large thickening of the epidermis in the proximal portion of the posterior tentacles. Such prominent bulbs exist also in the local form, where they attain in large specimens a length of $100-150 \mu$ and a thickness of $35-50 \mu$. The anterior tentacles also have a distinct constriction a short distance from the base, giving the proximal part a bulb-like shape. These small "bulbs" are very uniform and measure on an average $45 \times 22 \mu$. When the anterior tentacles are extended forwards, and their bulbs come in contact with each other, they give the impression of an outspread fan (Fig. 5). When the animal swims freely in the water, the anterior tentacles are kept very straight, bending only quite distally. An annulation of the tentacles, especially distally, is pronounced in both whorls. This is due to the tendency of the nematocysts to be grouped in rings.

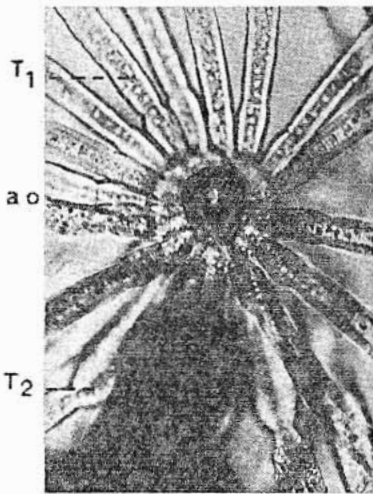


Fig. 5. *Halammohydra schulzei* from Bergen. Anterior part of the body. *ao* adhesive organ, T_1 tentacle of the first whorl, T_2 tentacle of the second whorl. \times c. 200.

Fig. 6. Shell gravel from the type locality of *Halammohydra intermedia*. Natural size. Phot. A. DOMMASNES.

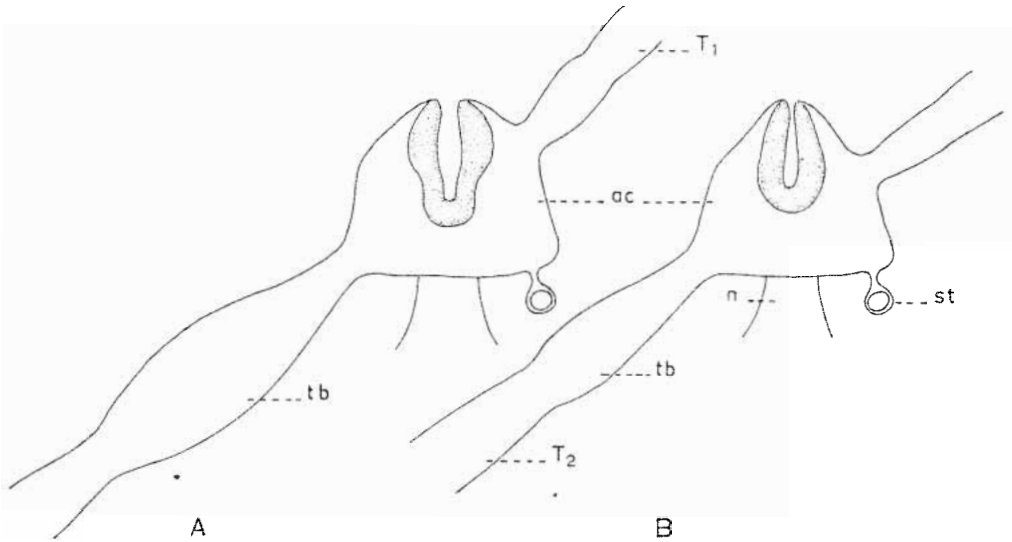


Fig. 7 A. *Halammohydra schulzei*. B. *Halammohydra intermedia*. Longitudinal section through the anterior part of the body. *ac* aboral cone, *n* neck, *st* statocyst, *tb* tentacle bulb, T_1 tentacle of the first whorl, T_2 tentacle of the second whorl. Adhesive organ stippled.

Halammohydra intermedia sp. n.

This is the most common species of *Halammohydra* in the Bergen area. It is typically found in medium to coarse shell gravel (Fig. 6). In Raunefjorden I got it at depths from 2 to 4.5 m, in Korsfjorden from 3 to 15 m. In some of the localities it was very abundant, thus in a quantitative sample from Raunane (395—66), taken with a 120 cm² van Veen grab, I collected 24 specimens in one dig, or 20 per 100 cm². The findings were made in the following localities:

Lauvholmen (83—61, 13, 71, 169, 303, 407—62, 542—63, 20—64, 282, 318, 321, 392, 393—66, 18, 55, 55b, 70—67, Høylandskjær (337—62, 336—66), Langøy (179—63), Store Fugløy (80—64), Bondisholmen (107—64), Håkonsund (108, 167, 168, 169—64, 354—65), Kyrkjesund (244—66), Raunane (283, 395—66, 69—67), and Lille Kinna (394—66).

H. intermedia (Fig. 8) attains a total length of c. 1 mm, of which the gastric tube makes up about nine tenths. The aboral cone is a little broader than long and fairly triangular in outline, as it usually is pointed anteriorly (Fig. 7B). The usually jarshaped adhesive organ reaches little more than half the height of the cone, attaining a depth of 50 μ and a diameter of 25—40 μ .

The maximum number of tentacles is 32, 16 in each of the whorls. The statocysts, to the number of up to 16, alternate as usual with the posterior tentacles, lying in the radial planes through the anterior tentacles. The average diameter of a statolith is c. 11 μ . The tentacles of the first whorl on an average are shorter than those of the second, one or two of which usually are markedly longer than the others.

At a little distance from their base the posterior tentacles have a constriction, so that a kind of basal clubshaped bulb results, but there is no real thickening of the epidermis, as in *H. schulzei*. The bulbs are also shorter than in that species, attaining in large specimens a size of 60—90 \times 22—30 μ . Another difference is that, while the bulbs of *H. schulzei* are thickest in their middle part, those of *H. intermedia* typically are thickest near the constriction. The anterior tentacles either lack a similar constriction, or have a slightly pronounced one (Fig. 7 B). The tentacles may sweep around in all directions, but when the animal is gliding freely forward, the anterior tentacles mostly bend backward and blend with those of the second whorl. *H. intermedia* may be distinguished from *H. schulzei* also by the fact that the tentacles of the former only rarely show an annulation, and never extend completely straight as in *H. schulzei*.

The short and narrow neck is followed by the large and somewhat obliterated stomach portion, which in broad specimens tapers considerably again towards the mouth. As in the other species of *Halammohydra* there are males and females, the males being about ten times as frequent as the females. A notable feature is that specimens with only one gonad and specimens with two gonads occur in the same population. The female gonads lie in the anterior half of the stomach wall, while the male gonads extend the whole length of the stomach. Males with two gonads may reach the considerable breadth of 400 μ .

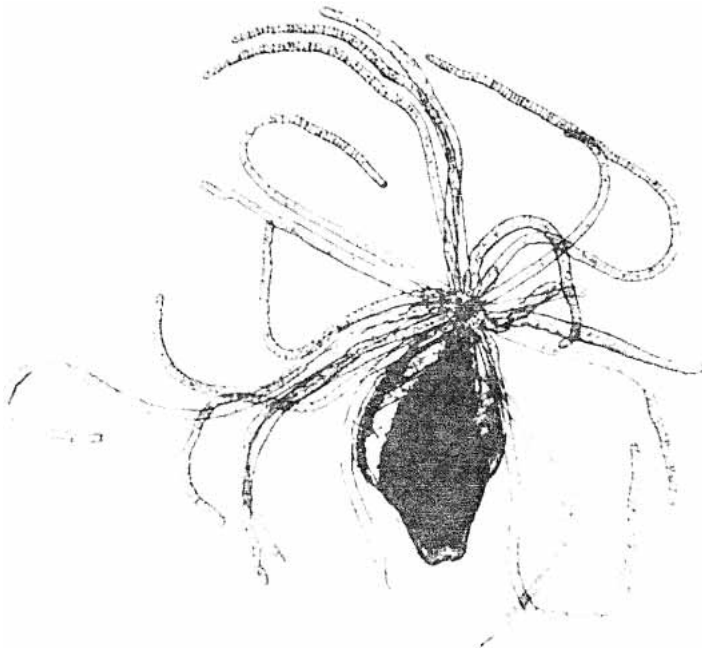


Fig. 8. *Halammohydra intermedia* from Bergen. \times c. 70.

The cnidome consists of isorhizes ($3.2-4.2 \times 2.1-2.7 \mu$) and stenoteles. The latter are rather small and spheric, measuring about $3.6-5 \times 3-4.1 \mu$.

Even though *H. intermedia* prefers the larger interstices, it may occasionally be found in finer sediments as well. Thus it occurs throughout the sound between Bjelkarøy and Lauvholmen, where the fairly coarse shell gravel at the opening of the sound is gradually replaced by finer shell gravel towards the middle. But as the specimens found in the finer sediments were all small and young, it appears that breeding takes place only in the coarser sediments.

The food of *H. intermedia* consists mainly of small copepods, but small nematodes and diatoms have also been observed in the stomach.

Associated fauna

The fauna accompanying *H. intermedia* varies greatly, and only some of the species characteristic for the typical kind of sediment are listed here. Turbellaria: *Plagiostomum torquatum* KARLING; Gastrotricha: *Diplodasys ankei* WILKE; Archiannelida: *Protodrilus rubropharyngeus* JÄGERSTEN, *Nerilla antennata* SCHMIDT, *Nerillidium gracile* REMANE, *Trilobodrilus heideri* REMANE; Copepoda: *Cylindropsyllus laevis* BRADY; Mollusca: *Embletonia pulchra* ALDER & HANCOCK; Echinodermata: *Leptosynapta inhaerens* O. FR. MÜLLER (young), *Leptosynapta minuta* BECHER; Chaetognatha: *Spadella* sp.

Diagnosis

Halammohydra intermedia sp. n.

Body up to 1 mm long, with up to 32 tentacles alternating in two whorls, and 16 statocysts. Posterior tentacles with little pronounced, clublike bulbs at their base. Aboral cone acute, slightly broader than high, small in proportion to the compressed gastric tube. Males and females with one or two gonads. Cnidome consisting of isorhizes and stenoteles.

H o l o t y p e : Specimen 870 μ long, male with two gonads, collected by the author on 15 February 1967. Deposited in the Zoological Museum, Bergen, Catalogue No. 48,366.

T y p e l o c a l i t y : Norway, Raunefjorden, Raunane, 3 m, coarse shell gravel (Biol. St. Ref. No. 69-67).

P a r a t y p e s : 10 specimens, from the type locality, 5 of them deposited in the Zoological Museum, Bergen, Catalogue No. 48,367, and 5 deposited at the Biological Station, Espesgrend.

HALAMMOHYDRA SPECIES FROM HELIGOLAND

During my stay at Heligoland from 2-26 September 1964 findings of *Halammohydra* were made at three places.

1. Outside the mole of the northern bay, near the Youth Hostel. Fine sand (Md 0.2 mm) was there taken with a grab from a depth of c. 10 m.

2. At Skit Gatt, in the northern prolongation of the Düne. The sediments consist, between the under water rocks, of fairly coarse shell gravel (Md 0.7 mm), "Polygordiusschill". Here also sampling was made with a grab. The depth was 5 m.

3. At the "Amphioxus flat", where coarse sand (Md 0.6 mm) was dredged from a depth of c. 15 m.

Halammohydra octopodides REMANE, 1927

REMANE got his specimens of *H. octopodides* from the fine-sand at the Düne. My own search for *Halammohydra* in this area was not successful, but in the fine sand from the locality near the Youth Hostel I collected in all 28 specimens. Only one of these corresponded to the description of *H. octopodides*. It had 9 statocysts and 9 + 9 tentacles, all without bulbs. The cnidome comprised isorhizes and microstenoteles.

Halammohydra schulzei REMANE, 1927

Both in the "Polygordiusschill" from Skit Gatt and in the coarse sand from the "Amphioxus flat" I collected this species, but somewhat surprisingly it was not the type form, as macrostenoteles were missing. Conspicuous proximal bulbs were present on the posterior tentacles (Fig. 9) and also the aboral cone, adhesive organ and gastric tube had the shape typical for *H. schulzei*.

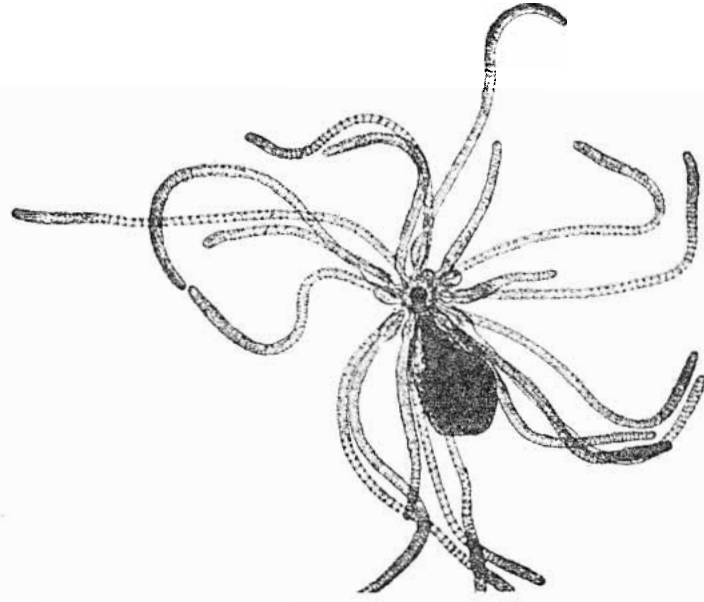


Fig. 9. *Halammohydra schulzei* from Heligoland. \times c. 65.

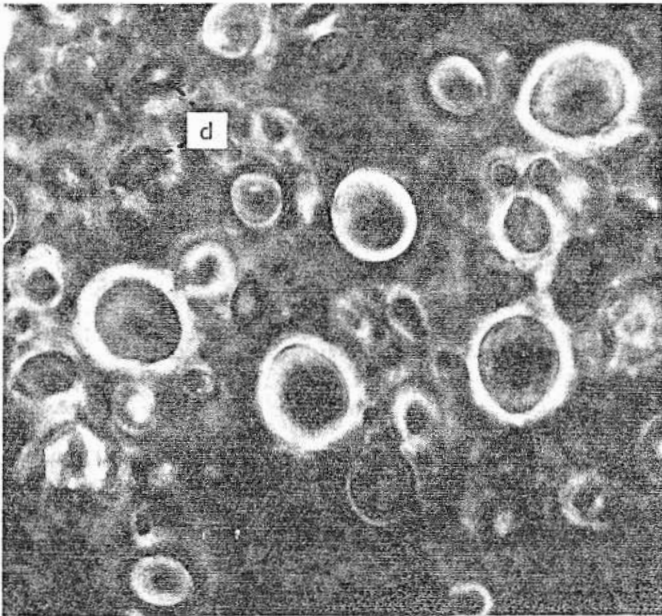


Fig. 10



Fig. 11

Figs. 10 and 11. *Halammohydra intermedia* from Heligoland. 10. Nematocysts, *d* undischarged desmonemes, between undischarged macro- and microstenoteles. 11. Discharged desmoneme. \times c. 1,750.

The cnidome consisted of isorhizes (c. $3.6 \times 2.2 \mu$) and microstenoteles ($5-6 \times 4-4.5 \mu$). The latter were much the same size and shape as those of the local form from Bergen. The largest specimen measured 360μ , and the total number of tentacles varied between 14 and 21. The low maximum number may be due to the fact that only 7 specimens were observed.

Halammohydra intermedia (see p. 356)

Together with *H. schulzei* I found 21 specimens of another *Halammohydra* species, which I hold to be a local form of *H. intermedia*. It resembles the new species from Bergen as regards the shape of the aboral cone and adhesive organ, and the same kind of clublike bulbs were observed on the posterior tentacles in most cases. However certain differences in the respective cnidomes exist. Like the type form the local form has got isorhizes and microstenoteles (c. $5-5.8 \times 3.6-4.4 \mu$), but in addition it possesses macrostenoteles of the usual type (c. $7.4-8.9 \times 6.3-7.2 \mu$) and desmonemes (Fig. 10). The latter are pearshaped and measure only $4-4.5 \times 2.4-3 \mu$. They were found only in the middle region of the tentacles. I observed only two desmonemes in discharged state, and these had a short thread which was coiled up in the usual way (Fig. 11). SWEDMARK & TEISSIER (1957b) claim to have found desmonemes of a larger type in a local form of *H. octopodides*.

Two further specimens of *H. intermedia* were found in the fine sand from the northern bay, together with the single specimen of *H. octopodides*.

The largest of the 23 examined specimens of *H. intermedia* was 430μ long, and the number of tentacles varied between 8 and 18. Also in this case the maximum number of tentacles was low when compared with the type form (32 tentacles).

Halammohydra vermiformis SWEDMARK & TEISSIER, 1957

The major part (22) of the specimens from the fine sand of the northern bay were all very small and without exception supplied with seven tentacles, three anterior and four posterior. One of the latter was two to three times thicker and three to five times longer than any of the others. The statocysts, to the number of four, alternated with the posterior tentacles. The aboral cone was markedly longer than broad; in one case the length exceeded twice the breadth. The adhesive organ was deep and narrow, and the slender neck measured about 10μ .

The specimens ranged in size from 50 to about 350μ , and even if the body could not be said to be really wormlike, the resemblances with *H. vermiformis* are striking.

The extremely long posterior tentacle was either trailing behind the animal, or if contracted, was coiled up in a spiral (Figs. 12, 13).

The nematocysts were of two kinds, isorhizes (c. $3 \times 2 \mu$) and stenoteles (c. $5 \times 3.8 \mu$) (Fig. 14).

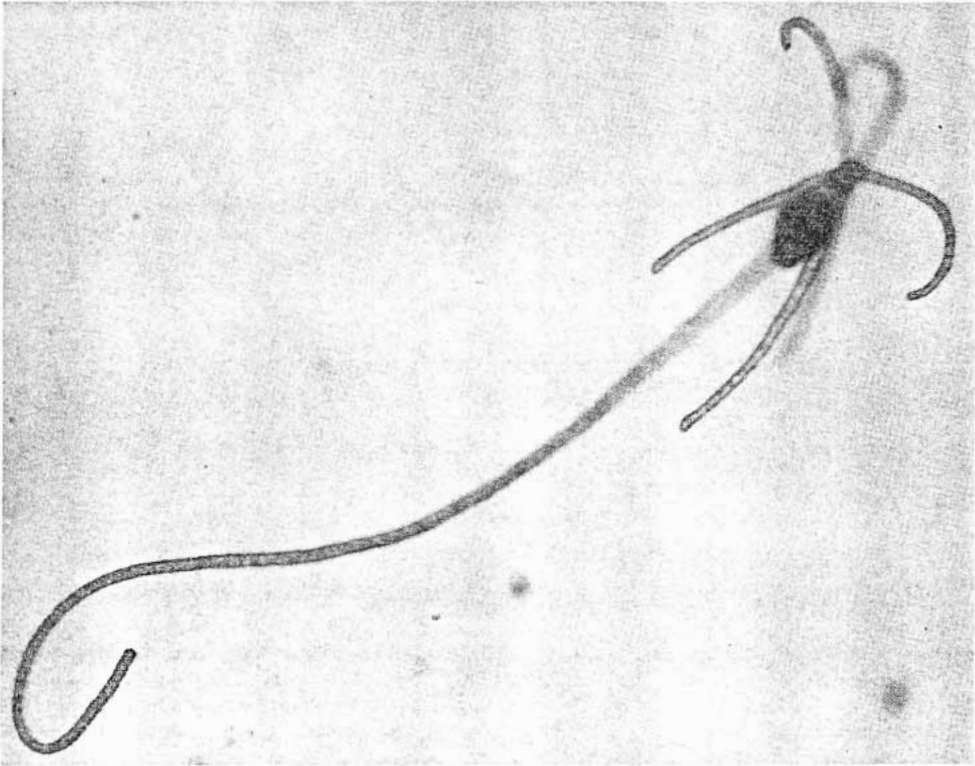


Fig. 12. *Halammohydra vermiformis* from Heligoland. The long posterior tentacle is trailing behind the swimming animal. \times c. 83.

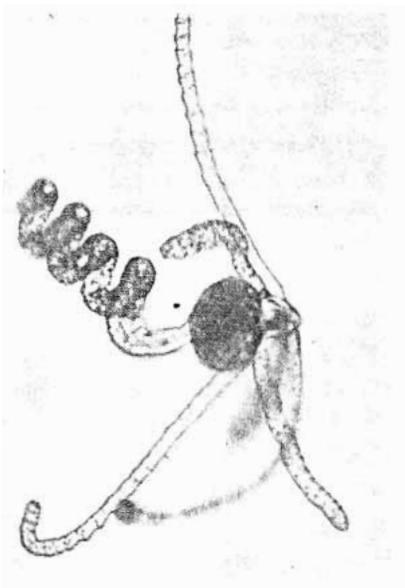


Fig. 13.

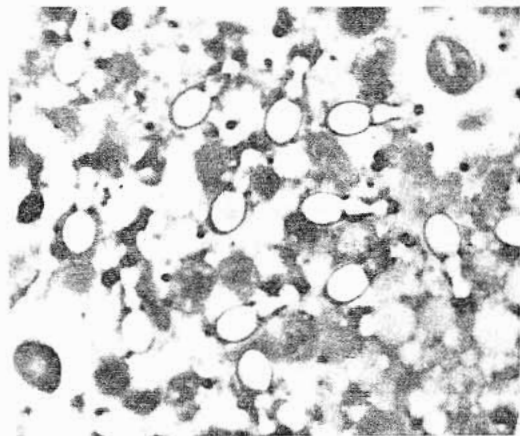


Fig. 14.

Figs. 13 and 14. *Halammohydra vermiformis* from Heligoland. 13. The long posterior tentacle is coiled up in a spiral. \times c. 160. 14. Undischarged stenoteles at the bottom left and above right, discharged stenoteles in between. \times c. 1,750.

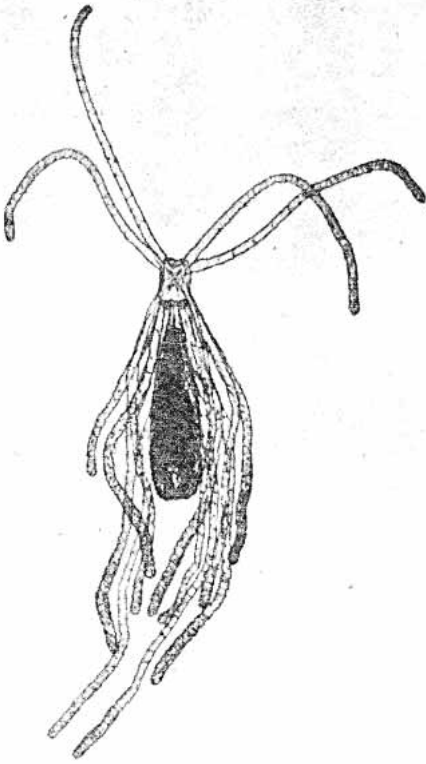


Fig. 15. *Halammohydra coronata* from Heligoland. Smaller form with microeuryteles only. Animal in swimming position. Note the shape of the aboral cone and the shallow adhesive organ. $\times c. 85$.

SWEDMARK & TEISSIER (1957) state indirectly that the larger Roscoff form has only the larger type of stenoteles. The type form inhabits also a totally different biotope, being found in coarse sediments in the tidal zone.

Halammohydra coronata sp. n.

The last one of the four species from the fine sand of the northern bay was unlike all the other species of *Halammohydra* I have studied. What first strikes the eye, is the shape of the aboral cone. This is cylindrical and may even be broadest in the anterior portion. This shape is maintained also when the animal is swimming (Fig. 15). Usually it is a little longer than broad. As in the other species an adhesive organ is present; this is mostly shallow and bowlshaped, occupying only the upper fourth or third part of the cone.

The umbrella had two widely separated whorls of tentacles, the typical total number of which was 14. A remarkable feature was that the number of anterior tentacles was less than half the number of posterior ones. The number of statocysts was also reduced. As these figures apply to sexually ripe specimens, this



Fig. 16. *Halammohydra coronata* from Heligoland, Smaller form with microeuryteles only. Distal end of a tentacle showing undischarged microeuryteles. \times c. 1,100.

indicates that the reduced number of anterior tentacles is a specific characteristic and not due to delayed growth. In the three specimens studied, the numbers of anterior and posterior tentacles and of statocysts were $4 + 10 + 4$, $4 + 10 + 4$ and $4 + 11 + 5$.

The gastric tube was essentially similar to that of *H. schulzei* or *H. intermedia*, but the neck was clearly longer and more slender ($10-14 \mu$). The colour was pale orange or whitish. The total size ranged from 380 to 440 μ .

The sexes are separate. Only one gonad was observed, but the number of animals studied was in any case too small to decide about the sex relations.

As in *H. adherens* only one category of nematocysts is present, the euryteles (Fig. 16). The capsule is a longish ovoid, measuring about $5.5-7 \times 3.2-4.2 \mu$. In the discharged nematocyst the shaft is the same length as the capsule; it bears stylets and apical spines. The nematocysts are similar to the microeuryteles of *H. adherens*, and as in that species atrichous haplonemes are entirely lacking.

So far it was natural to think of a local form of *H. adherens*, the differences between the two not seeming unbridgeable. However, in the coarser sand from the "Amphioxus flat" I later got 9 specimens of *Halammohydra*, differing from the above form only in minor details. This second form has both micro- and macroeuryteles of the microbasic type, both kinds being essentially similar to those figured in the description of *H. adherens* (Figs. 17 and 18). The undischarged

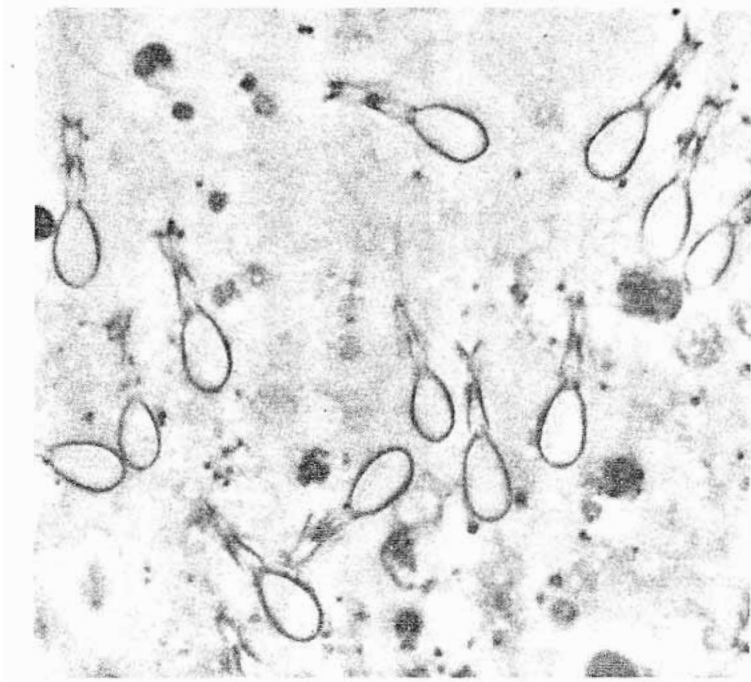


Fig. 17. *Halammohydra coronata* from Heligoland. Larger form with both macro- and microeuryteles. Several discharged and one undischarged microeurytele. $\times c. 1,750$.

microeuryteles measure c. $5.5-8.5 \times 3.0-5.4 \mu$; in discharged state, capsule and shaft together are from c. 10.4 to 12.6μ . The resting capsule of the macroeuryteles measures $12-14 \times 4.5-6 \mu$, the discharged capsule about $10.5 \times 3.5 \mu$ and the shaft about 11μ . The members of this population also attain a larger size and have more tentacles. The largest specimen measured $600 \times 220 \mu$ and possessed four anterior against 18 posterior tentacles. The statocyst number was 4. One specimen had $6 + 16$ tentacles and 6 statocysts. There is of course in this case no regular alternation between the statocysts and the tentacles of the second whorl as in the other species of *Halammohydra*, but as usual, the statocysts are borne on the oral side of the aboral cone, and clearly inside the tentacle whorl. The tentacles are long and slender, in one specimen they reached the considerable length of more than 3 mm, or about five times the body length (Fig. 19). Like those of *H. adherens*, the tentacles of the second whorl taper at their bases. The aboral cone of the larger form has the same cylindrical shape as in the smaller form, the length equalling the breadth. The adhesive organ also has the same simple bowl shape when open, while spheric when closed.

When extended, the tentacles take on a characteristic serrated look, because the euryteles are orientated obliquely to the tentacle axis.

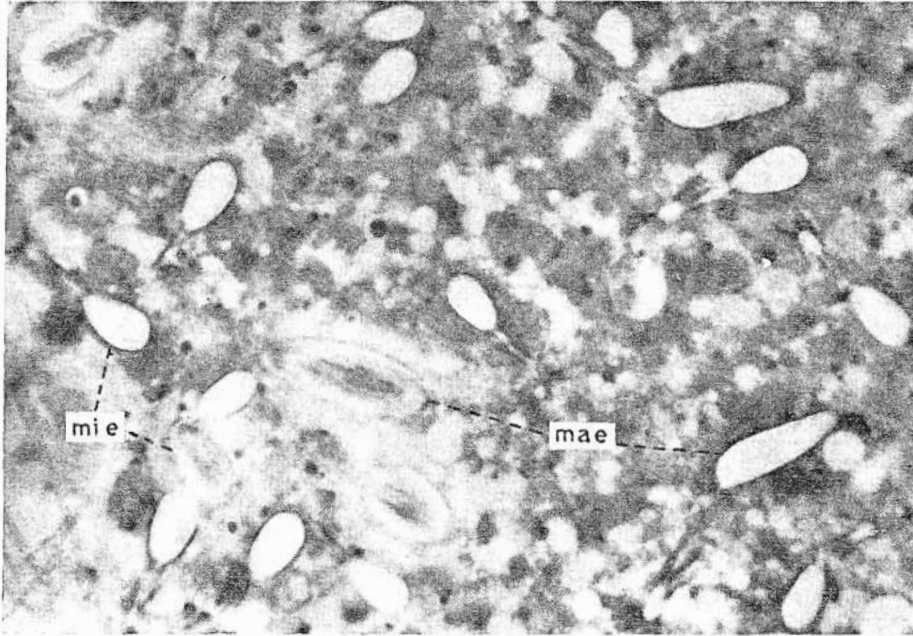


Fig. 18. *Halammohydra coronata* from Heligoland. Larger form with both macro- and microeuryteles. Nematocysts. *mae* discharged and undischarged macroeurytele, *mie* discharged and undischarged microeurytele. \times c. 1,750.

Like *H. adherens*, *H. coronata* is very adherent. In the "Amphioxus sand" it was mostly found with the adhesive organ fixed to a sand grain. It was however not studied over a longer period of time, so that little can be told about its behaviour in the interstices. In a Boverly dish it was once observed swimming freely in the water, and this behaviour has also been observed in all the other species of *Halammohydra* I have studied.

Although nearly related, *H. adherens* and *H. coronata* differ in certain respects, which may be summarized as follows:

1. The relations of the two whorls of tentacles and the statocysts: the three kinds of elements are equal in number in *H. adherens*, while in *H. coronata* the number of anterior tentacles and statocysts is reduced, and the number of posterior tentacles increased.

2. The aboral adhesive organ is much less developed and also shallower in *H. coronata* than in *H. adherens*.

3. In *H. coronata* the aboral cone maintains a cylindrical shape both in fixed and free position of the animal. (The species name *coronata* refers to this characteristic shape of the aboral cone.)

4. The macroeuryteles of *H. coronata* are shorter and broader than those of *H. adherens*.

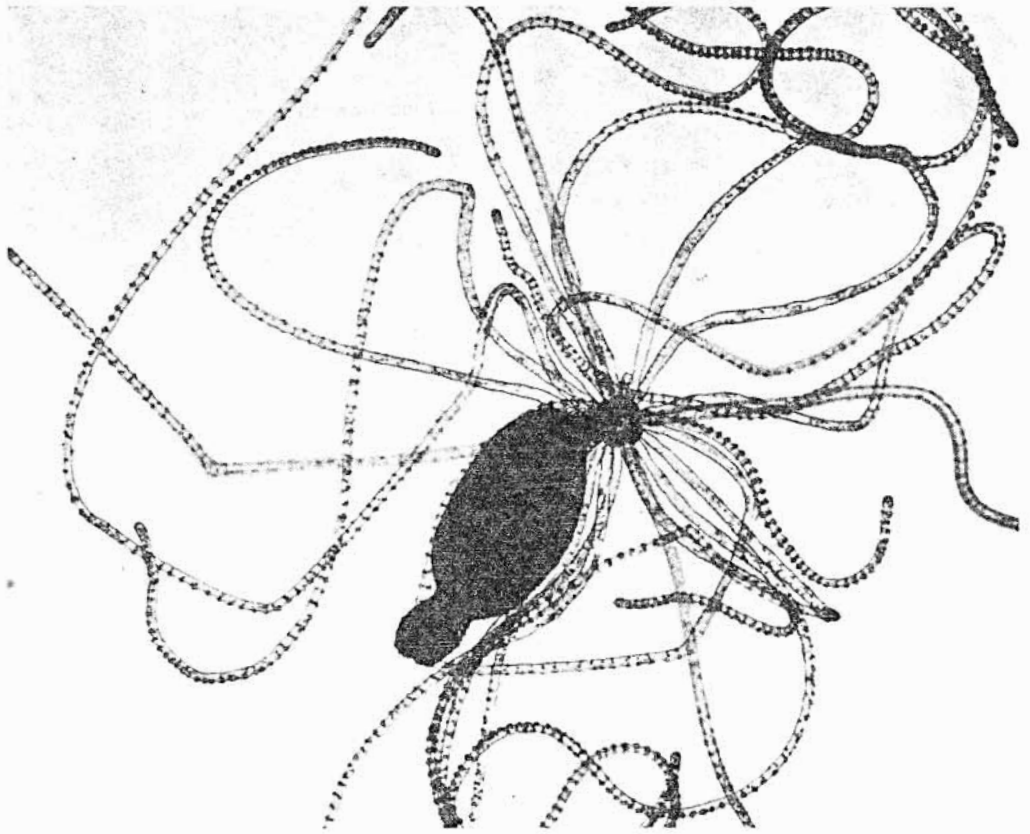


Fig. 19. *Halammohydra coronata* from Heligoland. Larger form with both macro- and microcuryteles.
 × c. 75.

5. While *H. adherens* has a characteristic deep yellow colour, *H. coronata* is either whitish-orange or light yellow.

Associated fauna

In the fine sand of the northern bay the following species were also registered. Gastrotricha: *Aspidiophorus marinus* REMANE, *Neodasys uchidai* REMANE, *Thaumastoderma heideri* REMANE, *Diplodasys major* REMANE, *Tetranchyroderma* sp., *Pseudostomella roscovita* SWEDMARK; Archiannelida: *Diurodrilus minimus* REMANE.

In the "Amphioxus sand" these species were found. Gastrotricha: *Mesodasys* sp., *Lepidodasys martini* REMANE, *Dactylopodalia typhle* REMANE, *Dinodasys mirabilis* REMANE, *Platydasys rarus* FORNERIS, *Ptychostomella* sp., *Tetranchyroderma tribolusum* CLAUSEN, *Tetranchyroderma* sp.; Archiannelida: *Polygordius appendiculatus* FRAIPONT, *Protodrilus* spp., *Trilobodrilus heideri* REMANE; Mollusca: *Caecum glabrum* MONTAGUE, *Microhedyle lactea* (HERTLING), *Philinoglossa helgolandica* HERTLING; Bryozoa: *Monobryozoon ambulans* REMANE.

Diagnosis

Halammohydra coronata sp. n.

Body large, with two whorls of tentacles and one whorl of statocysts. Number of statocysts and anterior tentacles reduced, typically 4–6, number of posterior tentacles c. 3 times greater, typically 10–18. Aboral cone cylindrical, with a shallow adhesive organ. Cnidome consisting of microbasic euryteles in one or two size categories.

Holotype: Specimen 350 μ long, with 4 anterior and 14 posterior tentacles. With macro- and microeuryteles. Collected by the author on 10 September 1964. Deposited in the Zoological Museum, Bergen, Catalogue No. 48,368.

Type locality: Heligoland, "Amphioxus flat", 15 m, coarse sand.

DISCUSSION

Six species of *Halammohydra* have now been described. *H. octopodides* REMANE, *H. schulzei* REMANE, *H. (Gouldenhydra) vermiformis* SWEDMARK & TEISSIER, *H. (Skodenhydra) adherens* SWEDMARK & TEISSIER, *H. intermedia* sp. n., and *H. coronata* sp. n.

SWEDMARK (1957) first noticed that two of the species, *H. octopodides* and *H. schulzei*, are at certain places represented by local forms differing from the type forms. Each time differences are observed the cnidome is involved, but differences are also reflected in such features as size, tentacle number and biotope. As will appear from the present account there exist also two forms of the new species *H. coronata* where the same differences come into play. Also the other new species, *H. intermedia*, is represented by two forms, one having both micro- and macrostenoteles, while the other lacks the last category. Since *H. vermiformis* also, as we have seen, occurs in different forms, it appears that it is a tendency for each species of *Halammohydra* to behave in this way.

SWEDMARK (l.c.) suggested that the evolution of the different forms of *Halammohydra* has been determined by ecological factors, such as the dimensions of the interstitial spaces, and the new findings seems in part to confirm his assumption.

To the extent that the different forms are restricted to special types of sediment, this would in part explain that a varied raiation can take place within the genus. The coarseness of the sediments many places changes rather abruptly, as for instance around projecting rocks or at the openings of sounds, or wherever the water movements act differently upon adjacent areas; isolated patches with special types of sediment may result, some of which may harbour populations of *Halammohydra*.

However, as was mentioned above, a relatively large species like *H. intermedia* may occur also in the finer sediments between its typical habitat of coarser sediments. A certain amount of gene-flow between different populations thus seems ensured, and a multitude of different forms should not be expected to exist.

The cnidome of *Halammohydra* has a certain bearing on the problems of nemato-

cyst classification. WERNER (1965b) stated that only the stenoteles possess stylets, but, as also SWEDMARK & TEISSIER (1967) assert, some of the spines on the shaft of the euryteles of *Halammohydra* are much stronger than the others and deserve the name of stylets. Moreover, RUSSEL (1939) pictures a microbasic eurytele from the siphonophore *Agalma elegans* (M. SARS) with three typical stylets, and he has shown that stylets may be present during a morphogenetic transition from stenoteles to euryteles (RUSSEL 1940). Also in *Craspedacusta sowerbyi* LANKESTER (Hydrozoa Limnohydrina) the proximal spines of the microbasic euryteles have the appearance of slender stylets (see DEJDAR 1934, fig. 39). These nematocysts also in other respects resemble the microeuryteles of *Halammohydra*.

WEILL (1934) defines euryteles as nematocysts with a distally widened shaft, whereas stenoteles have a shaft which is widened at the base. In reality, the shaft of the stenoteles of *Halammohydra* is widened both distally and at the base (see e.g. Figs. 3 and 13) and this fact together with the occurrence of stylets in euryteles, shows that the difference between the two categories of nematocysts is not so marked as generally assumed.

Another aspect, which the presence of euryteles in *Halammohydra* involves, is the systematic position of the group. WEILL (l.c.) has stressed the importance of the cnidome for the classification of the Cnidaria, and WERNER (1965a) arrived at his concept of *Halammohydra* as a group constituting a separate suborder of the Hydrozoa by taking into account i.a. the composition of the cnidome.

The cnidome of *Halammohydra* comprises four types of nematocysts, desmonemes, atriches, microbasic euryteles, and stenoteles. As microbasic euryteles occur within all the three well-established orders of the Hydrozoa — the Hydrozoa, Trachylida, and Siphonophora — it appears that the affinity of *Halammohydra* to any one of these orders has not become greater than to the other two, if the nematocysts alone are taken into account, and when viewed in the light of the new condition which the found of euryteles in *Halammohydra* has brought about.

It seems nevertheless worth while to reconsider the possible affinity of *Halammohydra* to the Trachylida. According to WERNER (1965b), the cnidome of the Trachylida is composed of atriches, microbasic euryteles, and stenoteles. Thus apart from the lack of desmonemes in Trachylida there is conformity as regards the cnidome of the two groups. The already known existing similarities between the Narcomedusae and *Halammohydra* should also be borne in mind: — the presence of solid tentacles and of similarly built statocysts, gonads located in the stomach wall, and direct development. Altogether there are many factors which speak for a close connection between the two groups, and strong arguments are needed to justify a separation.

The mesopsammon is still a promising field, which may possibly supply the details needed to indicate whether it is better to seek for a closer relationship between *Halammohydra* and any already defined group, or establish a separate order, such as attempted by SWEDMARK and TEISSIER.

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