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OBSERVATIONS ON HYDRACTINIA ECHINATA (FLEM.)
AND EUPAGURUS BERNHARDUS (L.)

BY

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INTRODUCTION.

The association of *Hydractinia echinata* (Flem.) and *Eupagurus bernhardus* (L.) has long served as a classical example of symbiosis. From the data in systematic and faunistic literature one gathers the impression, that the Hydroid hardly ever occurs on other substrates than the shell of the hermit-crab (HINGCKS, 1868; MÖBIUS, 1872; SCHULTZE, 1875; DU PLESSIS, 1888; SEGERSTEDT, 1889; DUERDEN, 1897; ALLEN, 1899; BILLARD, 1904; JÄDERHOLM, 1909; BEDOT, 1911; BROCH, 1904, 1911 and 1928a). Moreover *Hydractinia* constantly enlarges the house by building on at the lip of the mouth and "guards the entrance" by a fringe of special defensive spiralzoids. Because of these three facts the association could not be considered as purely accidental and conjectures were made as to the mutual advantages. These were obvious enough -- and have hardly ever been denied -- in the case of *Hydractinia*: a constant supply of food and oxygen as a consequence of being carried about by the hermit and perhaps a share in its meals. But it is rather difficult to demonstrate, where *Eupagurus* profits by this partnership: the hermit-crab is as often as not found in the company of the Hydroid.

These questions have never been treated experimentally and their discussion usually constitutes only a short section in papers dealing more especially with symbiosis of Pagurids with Actinians (e.g., BALSS, 1924). Only AURIVILLIUS (1891) treats more extensively of this matter and bases his views on many observations. According to him both *Hydractinia* and *Eupagurus*

show morphological features, which can only be understood as adaptations connected with their symbiotic association. His views on the structure of *Hydractinia* and on the way in which it profits by this symbiosis, are about the same as have been outlined above and they are not unfrequently quoted in literature (BALSS, 1924). His observations on *Eupagurus*, however, seem not to have been accepted: one never finds them cited in later articles. As a matter of fact all the peculiarities described as adaptations to the company of *Hydractinia*, occur in just the same way in all specimens living without the Hydroid and so BALSS (1924) states, that in the Pagurids there are no morphological adaptations to the association with *Hydractinia*.

The first to point out that *Hydractinia* could occur on different substrates, was AGASSIZ (1862), who collected *Hydractinia polyclina* Ag. (= *Hydractinia echinata* (Flem.)) "in great abundance from rocks in tidepools". Then MARTHA BUNTING (1894), HARTLAUB (1896) and NUTTING (1901) found the Hydroid respectively "on *Limulus* and *Mytilus*", on "*Mytilus* and stones in tidepools (Ebbe-tümpel)" and on "the bare rock and the piles of a wharf". HARGITT (1908) gives a number of instances in which *Hydractinia* was found on different substrates, i.e., the carapace and legs of *Limulus*, the stems of the common rockweed, a piece of waterlogged oak-timber and in immense masses on piles of docks. More recently similar data have been published by DUFRETIN and REY (1926), who found *Hydractinia echinata* (Flem.) on nearly vertical rocks at Portel near Boulogne, and by KRAMP (1933). This author records the occurrence in Danish waters of *Hydractinia* on: *Hyas araneus* (L.), *Balanus balanoides* (L.), *Alcyonidium gelatinosum* L., the haptera of *Laminaria*, fascines, fir poles of a mole, pieces of wood from a submerged forest, and human bones dredged from the bottom of the sea.

So it seems that *Hydractinia* is less exclusive in its choice of a substrate than current opinion would have it and probably many more similar cases would be found if special attention were given to this matter. Because of these occurrences on immovable substrates HARGITT (1908) most emphatically disputes the symbiotic nature of the association between *Hydractinia echinata* (Flem.) and *Eupagurus bernhardus* (L.): "*Hydractinia* has a range of habitat, which is clearly incompatible with the foregoing conception of necessary symbiosis" and "there is probably no

essential advantage to this Hydroid in its habitat on the shell of the crab".

BROCH (1928) draws attention to another fact in the life-history of *Hydractinia echinata* (Flem.) and allied species: "die Symbiose von *Hydractinia* und Gasteropoden ist auch nicht selten in unseren Gebieten. In arctischen Gebieten findet man überhaupt die *Hydractinia*-arten sozusagen ausnahmslos nur an lebenden Gasteropoden, besonders an Buccinidae". It looks as if in regions, where *Eupagurus* is wanting, the Gasteropods – as next best – can take its place, which again is no support for the theory of a truly symbiotic relation between the hermit-crab and the Hydroid. Whether the association with the Gasteropods merits the name of symbiosis, is of course equally contestable.

Though BALSS (1924) and BROCH (1928) still call the association of *Hydractinia echinata* (Flem.) and *Eupagurus bernhardus* (L.) true symbiosis, it seems to me, that general opinion is less positive on this point. The question whether *Hydractinia* must be considered as a symbiont, a commensal or an epizoön of *Eupagurus*, is usually passed over. The present paper is the result of my endeavour to treat this question experimentally and by means of direct observation. It was approached from four different sides:

1. Does *Eupagurus* prefer *Hydractinia*-covered houses to clean ones?
2. Does *Hydractinia* share in the food of *Eupagurus*?
3. How do the planulae of *Hydractinia* locate the shells of hermit-crabs?
4. What is the significance of the spiralzoids?

MATERIAL.

My material consisted of a great number of *Eupagurus bernhardus* (L.), which in Den Helder are available all the year round in practically unlimited quantities from the nets of the fishermen. Nearly all are covered with *Hydractinia echinata* (Flem.), sometimes with other Hydroids or Bryozoa, a.o. *Alcyonidium gelatinosum* L.

The shells of *Natica* and *Littorina*, which serve as houses for young hermit-crabs, and are not covered with Hydroids or the like, generally have been perforated at several places near the top by boring Polychaeta, probably belonging to the genus

Polydora, which have built their tubes of lime and silt-particles in the topwhorls of the shell.

Here follows a list of the localities where my material was collected, completed with some data from the diary of Dr. J. VERWEY, Director of the Zoological Station at Den Helder, which he kindly put at my disposal. Data on depth and bottom-deposits were added as far as they were available.

Localities	Depth in m	Bottom-deposits	Number of specimens	Number of <i>Hydractinia</i> -covered specimens
Harbour of Den Helder	10-16	Very varied: sand, silt and stones	23	16
Zuidwal	2-10	Sand and silt in patches	1 20 43 0 63 102 44 93 (43 young) 3 10 15 23 8	23 30 2 7
Zuidergronden	8-11			
Zuiderhaaks	23-27		67	60
Gully N.W. of Noorderhaaks	23-27	Sand with a little silt?	27	25
Molengat and the prolongation of it	9.5	Sand with much dirt (municipal scavenging)	4	
Schulpengat	10-11	Sand and shells	14	14
Reede van Texel = Texelstroom	3-33		37 68 94	25 54 69
a. Sluice of Prins Hendrik polder	30-33	Clay	16	
b. From same sluice across Texelstroom	14-26	Clay with some sand	32	

Localities	Depth in m	Bottom-deposits	Number of specimens	Number of <i>Hydractinia</i> -covered specimens
c. South of the vlakte van Kerken to Kamp van Oostereind	3-3.5	Silt	1	
d. From south of light-bouy 6 southward	4-10	Sand with silt	1	
e. Along the Eastside of Texelstroom across the mouth of the Scheer	10	Silty?	9	
f. Along the edge of Texelstroom from spherical bouy (= kogelton) 3 to conical bouy (= roode ton) 2	8-8.5	Mud	9	
Texel:				
a. Near 't Horntje E-NE to beacon of De Waard	23-27	Sea-clay	53	
b. 't Horntje near De Mok	23-25	-	11	
c. Eastside of Texel near sluice of Pr. Hendr. polder	17-25	Sea-clay	138	
d. De Mok	4-4.5	Black mud	1	
Topridge of Texelsche Bankje	8	-	12	10
Gully between Fransche Bankje and the beach	5-5.5	Mud	1	-
Between fareway bouy (= verkenningston) Westgat and whistle bouy (= brulboei) of Middelburg	20-21.5	Sand with a little thin silt	36	-
North of Terschelling	-	-	2	-
Near lightschip Borkum	14	-	"a number"	-
Near Petten	18	Sand	29	25

From these data it is evident, that *Eupagurus bernhardus* is found on a number of different bottom-deposits, but very seldom on completely soft bottoms of silt or mud. In this connection it is instructive to compare the catches from the Eastside of Texel, where the firm clay yielded 138 specimens, and from De Mok, where only one hermit was brought up from the black mud. In Texelstroom also the patches of firm sand and clay proved much richer in hermits than the more silty parts. Again the greatly varying numbers of *Eupagurus* captured at different localities along the Zuidwal must be attributed to local differences of the bottom-deposits. When experimenting with *Eupagurus bernhardus* I also could observe on more than one occasion that the hermits are extremely uncomfortable on a layer of silt or mud: they always tried to escape.

Within the limits of the littoral and sublittoral zones depth has little influence upon the distribution of this species. It seems to me that perhaps the young specimens prefer shallower water than older ones.

PREFERENCE FOR HYDRACTINIA-COVERED SHELLS.

It is known of Pagurids, which live in symbiosis with actinians, that they are able to perceive a (hidden) anemone from a distance (probably by means of chemoreception, sometimes with the eyes) – and actively search for it in order to plant the welcome symbiont on their house. Also when they move into another shell, they “persuade” the anemone to shift to the new house (FAUROT, 1910; BROCK, 1927; BRUNELLI, 1910). It is clear that the Pagurids “know” the actinians: these have a definite biological significance for the hermit-crabs. In VON UEXKÜLL’s terminology: the anemone is a “Merkmalsträger” in the “Umwelt” of the Pagurid. If *Hydractinia* has the same significance for *Eupagurus bernhardus*, this ought to express itself in a marked predilection for shells covered with this Hydroid. The first series of experiments served to investigate this point.

LITERATURE.

As far as I can judge there is hardly any literature, which treats of this question in particular, but there are some articles, which touch upon the relation of *Eupagurus* and the shell it chooses for house.

BOUVIER (1892) tried to make out whether *Eupagurus*, in accordance with its dextrally curved abdomen, has a preference for dextral shells. He made his hermits choose between dextral and sinistral shells and concluded that such a predilection does not exist. As I have not been able to procure BOUVIER’s paper, it is only known to me from THOMPSON’s discussion (1904). THOMPSON does not approve of the method, because the animals keep moving from one house into another: they try nearly every shell that they meet, and generally keep a firm hold on their old house, so as to be able to return into it when the new shell does not prove suitable. Consequently a great many shiftings do not mean an actual choice and the observer is confused by those meaningless movings. According to THOMPSON the inspection of the shell only teaches the animal, that it is “hollow, empty and clean”. “Apparently the crab does not perceive either the size or the type of shell until it has inserted its abdomen into the chamber and tested the shell by moving about in it, etc., deciding by actual trial, whether the new house will prove better than the old one”. It is certainly true that in many cases the choice is made by trial, but I do not agree with the view that *Eupagurus* does not perceive anything of the size of the shell it inspects. This is proved by the totally different attitude of diverse objects during my experiments on their moving into clean or *Hydractinia*-covered shells. Moreover there are some investigations by animal-psychologists, which prove beyond doubt that Pagurids are able to discern something about dimensions and structure of the surface of the objects they “finger”. Even some colours are perceived by them. About the perception of forms opinions are divided.

ANNA DRZEWINA (1910) published a contribution to the biology of *Clibanarius misanthropus* (Risso), from which it would seem, that this hermit is able to distinguish between the shells of *Trochus* and *Cerithium* by their form. A number of *Trochus*-shells, securely stoppered with corks, were dropped into an aquarium with several houseless misanthropes. During the first days many floating particles of cork proved, that the animals were continually busy trying to remove the stops. Gradually they left off and after some days there were no corkfragments floating on the water: the hermits had formed an association between the form of the shell and the uselessness of their endeavours. When at this point in the experiment, however, a stoppered *Cerithium* was dropped

into the aquarium, this was inspected again with the same perseverance. On the contrary, to a *Trochus* loosely stopped up with paper – an obstruction, which the animals are perfectly well able of removing and generally immediately do clear away – no more attention was paid than to the corked specimens. According to ANNA DRZEWINA this proves beyond doubt that *Clibanarius* is able to distinguish between the different shapes of the shells by means of tactile perception.

MATHILDE HERTZ (1928), who experimented on practically the same matter with the same species, does not agree with this conclusion. The animals do not discriminate different shapes as long as they have not discovered a hollow in it, but as soon as they have found a cavity, this is inspected and distinguished from others by its depth and size. Different structure of the surface is certainly perceived, for a number of objects, which differ in this respect, can be arranged in a definite order after the length of time that the animal spends on the search for an aperture in it. *Cerithium* is the most favoured object ("Lieblings-object") and it appears that a misanthrope, that has several times been disappointed in its search for an opening in a stoppered *Cerithium*, has not got the slightest interest for a *Trochus* any more. When the experiment is repeated in the way ANNA DRZEWINA did it, but with the difference that now and again the position of the corked *Trochus*-shells is altered, or hermits and shells are moved into another basin, the result is quite different: the interest in the stoppered shells does not wane and every *Trochus* they meet is inspected again and again. Consequently in ANNA DRZEWINA's experiments the animals did not discern the different shapes of the shells but individual shells, which they "knew" by their positions.

MARIE GOLDSMITH (1918) drew a similar conclusion from experiments with *Eupagurus bernhardus* (L.). Several different shapes of modelling-wax, having more or less the same dimensions and the same colour (red), are all inspected by the hermit with the same attention and for the same length of time: the animal was not able to distinguish them from each other. The same result was obtained in a second series of experiments, where the animal had to choose between several objects, a.o., its own house – covered with a thick layer of lime. Similar experiments on the perception of dimensions, however, yielded an affirmative answer: the hermits were able to discriminate two

balls of different sizes, two cones of the same height but with different bases, etc.

The third point she investigated was: can a hermit distinguish rugose and smooth surfaces from each other? In this series of experiments the attention rather than the length of time spent on each object proved a criterion: after contact with the antennae objects with a rough surface were always and thoroughly inspected, whereas smooth objects were often not or only perfunctorily investigated. So perception of different surface-structure is evident, but it is not very keen, for glass and modelling-wax can not be distinguished from each other. As *Hydractinia*-covered shells have a much rougher surface than clean ones, this faculty of *Eupagurus* must be taken into account in experiments on an eventual preference for houses with this covering.

For the sake of completeness I will mention the experiments of KOLLER (1929), who proved that *Clibanarius misanthropus* (Risso) is able to see blue and yellow as colours. Another observation of KOLLER, viz., a preference for dark objects over light ones, was obvious in my hermits too. KOLLER writes: "des öfteren konnte ich beobachten, dass das Versuchstier vor der hellen Schale eine Zeitlang "prüfend" sitzen bleibt um dann in scharfem Winkel von der hellen Schale ab zu biegen und sich der dunklen zu zu wenden". This hesitation was several times visible in my animals, when they came in front of a clean and nearly white shell.

METHOD.

The method used in these experiments was very simple. The bottom of a round glass basin with a diameter of ca 33 cm and a depth of ca 15 cm, was covered with a layer of clean sand and the basin filled with seawater. Then a *Eupagurus*, generally with *Hydractinia*-covered shell, was placed into it diametrically opposite two shells of a suitable size, i.e., a little larger than its own house. One of the shells was clean, the other covered with *Hydractinia*. Of course they were so chosen as to be as similar as possible in every other respect. Special attention was paid to the conformity of the two apertures. Sometimes a third house covered with a dead crust of *Hydractinia* was added, and, when it was impossible to find a pair of shells agreeing sufficiently with

its own house, the hermit was given several different shells to choose from. Originally I presumed that the animals must be induced to shift to another house by compelling them to move into a very unsuitable shell first. To achieve this the hermits were suspended by a (chemically cleaned) horse-hair, which was passed through two small holes drilled in the top of the shell. The greater part of their body was submerged and with their legs they could just reach and "finger" a shell that was much too large for their body-size. Generally they moved into this unsuitable abode within a quarter of an hour in order to regain their liberty. Very soon, however, it appeared, that this procedure was entirely unnecessary. The notion that *Eupagurus* is very reluctant of moving holds no truth. On the contrary the "moving-instinct" is very strong unless the animal has a venerable age. Nearly every house they meet with is inspected and sometimes tried on. Only in 18 out of 87 cases the hermit refused to shift to another shell and besides several movings without connection with these experiments were observed, even in the basin, where the material was stored, and the animals were surrounded by a great many "dangerous" congeners. In the 15 first experiments the hermit had previously been compelled to move into an unsuitable house and among the later experiments there are a few, where the animal was chosen because it found itself in this situation. For the rest spontaneous movings were observed.

As a rule each experiment took less than an hour, often much less, sometimes only a quarter of an hour. When the temperature was noted before and after the experiment, it had hardly or not risen, seldom more than 0,5° C.

This method is as simple as BOUVIERS and it is open to the same criticism. But it seems impossible to me to conceive experiments, in which *Hydractinia* is involved, while the objects are absolutely equal in every other respect.

EXPERIMENTS.

At the beginning of each experiment the hermit was laid into the basin with the aperture of the shell facing upwards, because in this case it immediately shifts to its normal position and begins to walk. Generally the experiment proceeded in the following manner. The animals walk slowly or quickly – ac-

cording to their mood – along the brim of the basin, with which they keep in touch as much as possible. This positive thigmotaxis has also been mentioned by BROCK (1926). Generally the animals do not perceive the shells before they happen to touch them and then their behaviour is very different indeed. Sometimes they climb over the house without taking any more notice of it than of a stone and even when a leg or pincer is inadvertently inserted into the aperture, they will not inspect the shell: evidently their "mind was not open" to houses.

In other cases the animal begins to inspect the house as soon as it feels the aperture. In this moment the attitude of the hermit changes completely: it is suddenly interested and keen, once it has recognised the shell as a house. Sometimes even the first contact with the antennae is sufficient to stimulate the animal to this great activity: evidently the house is recognized as such before the mouth was found. In these cases their "mind was very open" to houses.

Generally contact with the shell is so quickly established, that it is impossible to ascertain whether the hermit had already perceived it from a distance with its eyes, but in a few cases it was obvious that the animal suddenly perceived the house before it could reach it with the antennae: it went resolutely and at a quickened pace right to the shell (left the brim of the basin for it!) and began to inspect it actively. So they are certainly able to recognize a house at sight, at least when their "mind is open" to it.

The way in which the house is inspected, and the nimble movement with which the hermit slips into its new dwelling, are too well known than that they need to be described again. Very often the animals move into the first house they meet and are not interested any more in other shells – a circumstance, which made many experiments valueless. But fortunately others do not tire so quickly of moving: in some cases they moved three or four times either into a new house every time or alternately into a new shell and back into the former again. The old shell is often firmly kept hold of or it is dragged along over a considerable distance. Generally the hermit uses the discarded shell to draw itself up after moving into a new house, which as a consequence of the inspection is lying with its mouth turned upwards.

After moving the hermit nearly always displays this typical

reaction: the antennae are swung backwards and travel over the surface of the shell as if to probe the new situation. Sometimes the third and second pereopoda also grope backwards about the shell and now and again seem to lift it up in order to bring it into the right walking position, especially when the house is a little heavy. More than once it occurred that the animal retired entirely into the new house as if to try whether it was large enough for complete retreat.

As already stated the hermits often would not move or inspect a house more than once, which made many experiments useless, but others were longer inclined to move and inspected several houses. When these animals kept sitting quietly for a long time, they were started again by laying them "on their backs" in front of but at some distance from the houses. They are so little shy (JACKSON calls their usual demeanour as long as they are safely within their shells: "sleek impudence") that this does not spoil the experiment: the hermit walks on quite unruffled along the brim of the basin till it finds the shells and eventually inspects them. When the animal refused to take any more notice of the houses, the experiment was concluded: the choice had been made. It is not often that a shell is accepted at a second encounter, when it has been refused at first.

Here follows a description of some examples, chosen so as to give a fair general impression of the 87 experiments that were carried out in all. (In 18, however, the animal refused to move).

Experiment 43. 22. VI. 1933.

A small *Eupagurus* in a *Hydractinia*-covered *Natica*-shell is given a clean and a *Hydractinia*-covered *Natica* to choose from. It meets the clean shell first and begins to inspect it and finds the umbilicus: that aperture seems too small! So it passes on and climbs over the *Hydractinia*-covered shell without inspecting it. Some moments later it meets the same house again, inspects it and moves into it. Now it pulls itself up at the old shell and inspects it for a moment and drags it along for some time but does not move back into it. Meanwhile it has several times swung back its antennae and felt with them over the surface of the new house. It walks about for some time but is not any more interested in houses.

Experiment 45. 23. VI. 1933, time: 11.10, temp.: 17.3°.

Rather small *Eupagurus* in a clean small *Buccinum* chooses between a clean and two *Hydractinia*-covered *Buccinum*-shells. First it inspects the larger *Hydractinia*-covered shell but does not move into it. Then the hermit meets the clean house and shifts to it. The antennae are swung backwards.

The hermit climbs wildly over all houses. Some moments later it moves

into the smaller *Hydractinia*-covered *Buccinum*, walks on and inspects the clean shell again and moves back into it.

11.20. *Eupagurus* meets the smaller *Hydractinia*-covered *Buccinum* again, inspects it but rolls it aside. It passes on and starts digging with its pincers in the sand.

11.25. I "start" the hermit and put the shells in the animal's place. The larger *Hydractinia*-covered *Buccinum* is turned round and round and once a pincer is inserted for a moment into the mouth but then the shell is rolled aside. The animal is busily digging again on the old spot.

11.30. *Eupagurus* walks along half the circumference of the basin and twice it starts back before the larger *Hydractinia*-covered shell. At last it passes this obstacle and meets its former house, which it only pushes aside in order to dig at that place.

11.45. The hermit finds its old shell again, inspects it for a moment but does not move into it — is not any more interested in shells.

Temperature at the close of the experiment 17.3°.

Experiment 54. 25. VI. 1933, temp.: 17.9°.

10.50. Large *Eupagurus* in a *Hydractinia*-covered *Buccinum* that seems rather small for its inhabitant, chooses between two larger *Buccinums*, one clean and one covered with *Hydractinia* and very well matched in other respects.

Eupagurus walks very slowly along the brim of the basin in the direction of the houses and sits quietly just by their side without perceiving them.

11.00. The hermit is shifted to another position and the shells are laid in its place. Slowly it walks to the houses again, meets the *Hydractinia*-covered *Buccinum*. Two legs are laid upon it and a lengthy "fingering" of the surface "with all legs" follows. Then the animal climbs over it till it reaches the aperture on the other side. Pincers and legs are inserted into the mouth of the shell: a thorough inspection. For some time the hermit sits quietly with its pincers in the aperture, at last it moves into the new shell, draws itself up at the old house and swings its antennae backwards. For some time it keeps sitting with legs upon the old house.

11.10. The old house is inspected again briefly and *Eupagurus* walks on. Presently it sits in front of the clean shell with one pincer in the aperture but it does not inspect the house. The hermit returns to the old house but does not inspect it. A few minutes later it puts two legs on the shell again and proceeds to inspect it. Again it sits quietly for some time with the larger pincer in the mouth of the shell, but passes on. Several times it touches alternately the clean shell and its own old house. At last it seems on the point of inspecting the clean shell, but one leg happens to touch the other house and now the pincers are inserted into this one and the hermit seems to have lost the other. It seems as if the animal hardly distinguishes the two houses from each other and passes from one to the other without noticing it. After a moment it walks away and will not inspect houses any more.

Temperature at the end of the experiment 18°.

Experiment 57. 26. VI. 1933, temp.: 16.9°.

9.40. A middlesized *Eupagurus* without a shell may choose from: one large *Hydractinia*-covered *Natica*, two clean *Buccinums*, one *Hydractinia*-covered *Buccinum*, one *Buccinum* with a dead crust of *Hydractinia*.

First it meets the *Natica* and of course adopts it as a covering. Walking on it finds the smaller clean *Buccinum*, which is seized with the small pincer and dragged along over a considerable distance. At last the hermit proceeds to inspect it and moves into it. The antennae are swung backwards. The *Hydractinia*-covered *Buccinum* is walked over but not taken any notice of. After some time the animal finds this shell again and inspects it very thoroughly – also with all legs round the circumference. For some time it sits quietly with pincers in the mouth of the shell but “decides” not to move.

Eupagurus walks for some time over all houses and once the pincers are inserted for a moment into the *Natica*. Sometimes it clasps all legs round a house so that it seems going to inspect the shell. Only much later, however, it inspects the larger clean *Buccinum*, moves into it and repeatedly swings its antennae backwards. Once it turns the shell with its top perpendicularly upwards.

10.05. *Eupagurus* climbs over the *Hydractinia*-covered *Buccinum* – one pincer even passes into the aperture – but it does not inspect the shell. In this way it touches the shells now and again without inspecting them.

After some time it comes near the *Hydractinia*-covered *Buccinum*, points at it with the antennae (Brock's “Signalreaction”), but does not go to it. Concluded at 10.25 (temp.: 17°).

Experiment 74. 1. VII. 1933.

A small *Eupagurus* without a house may choose between a clean and a *Hydractinia*-covered *Buccinum* and a large *Hydractinia*-covered *Natica*. It walks calmly along the brim of the basin and apparently recognizes the *Hydractinia*-covered *Buccinum* before or at the moment the antennae can reach the shell: it suddenly makes right for the house at a quickened pace. It climbs on the shell, inspects it briefly and moves into it. Several times the antennae are swung backwards. The hermit climbs over the two other houses: the clean *Buccinum* is not taken any notice of; the *Natica* is “fingered” on the outside and then the hermit searches for the mouth: it turns the shell round and round, so it has recognized the shell before the mouth was found. Presently it inspects the inside and moves into it. The antennae are swung backwards several times. After this it walks about for some time but does not move any more.

Experiment 75. 5. VII. 1933.

A small *Eupagurus* in a *Hydractinia*-covered *Buccinum* chooses between a clean and a *Hydractinia*-covered *Natica* and one with a dead crust of *Hydractinia*. Almost at once it has reached the shells, so rapidly, that nothing can be inferred about recognition from a distance. The clean *Natica* is thoroughly inspected: first the inside, then it is turned round and round till some air escapes – again it is turned round and more air escapes. Then the hermit “jumps” into it and swings its antennae backwards.

Later the *Natica* with the dead crust is inspected and twice the *Hydractinia*-covered shell, but *Eupagurus* does not move.

For the third time the *Hydractinia*-covered *Natica* is “fingered” but not accepted.

A smaller clean *Natica* is added and the hermit “started” again. Soon it meets the new shell, inspects it and turns it round and round: air escapes.

The animal moves into the new shell and swings its antennae backwards.

Apparently the hermit is able when inspecting the inside of the shell to perceive the air in it as “something undesirable” and tries to remove it by turning the shell round and round.

Experiment 78. 5. VII. 1933.

Rather small *Eupagurus* chooses between a clean and a *Hydractinia*-covered *Buccinum*. At once it walks over to the shells, touches the *Hydractinia*-covered house with its antennae and at once proceeds to inspect the shell, which it must have recognized before the aperture was found. The hermit moves into the new house and swings its antennae backwards. Also its legs clutch backward round the shell. Then the animal shifts fore- and backwards in its house: air?

For some time the old house is kept hold of; once it is left for a moment but very quickly the hermit returns to it and puts a pincer on it. It keeps sitting beside the shell, always touching it with a leg. Again antennae and legs move backwards over the house. The old house is “fingered” now and again.

The new house is turned with its top perpendicularly upwards: air?

Walking on the hermit comes in front of the clean white house, touches it and turns immediately back: afraid?

Eupagurus is “started” again and several times it approaches the white house, sometimes even touches it with the antennae, but it will not inspect the shell and even seems to avoid it sometimes. So the clean house has practically no chance compared with the other shell.

Experiment 80. 6. VII. 1933.

1.45. A very small *Eupagurus* in a *Littorina* may choose between a clean and a *Hydractinia*-covered *Littorina*. It makes almost a bee-line across the basin to the shells, which it must have recognized from a distance. The *Hydractinia*-covered *Littorina* is reached first and briefly inspected, then the hermit passes on to the clean one. This is thoroughly inspected and then the animal moves into it. The antennae are swung backwards. The hermit keeps firmly hold of the old house, and though sometimes leaving it for a moment, the animal always returns to it quickly. At last, after groping a few times with its legs backwards round the house, *Eupagurus* walks on in the direction of the *Hydractinia*-covered shell, which again it seems to recognize from a distance. It touches the *Littorina* with its antennae but does not inspect it. (The perception of “*Hydractinia*” is not always sufficient to stimulate the animal to inspection of the house). After a few moments *Eupagurus* meets its old house again, inspects it but does not move into it. Now and again the *Hydractinia*-covered *Littorina* is passed over with the antennae but not inspected any more.

Concluded 2.10.

Experiment 81. 6. VII. 1933.

2.20 A rather large *Eupagurus* in a *Buccinum* densely covered with *Hydractinia* is given choice between a clean, and a *Hydractinia*-covered *Buccinum* and one with a crust of dead *Hydractinia*.

At first it keeps walking to and fro at the opposite side of the basin and turns back as if shying at the shells every time it sees them. At last it "collides" with the *Buccinum* with dead *Hydractinia*, climbs over it to the clean shell, which is inspected. *Eupagurus* moves into it and swings its antennae backwards over the new house. Then the hermit retires entirely into the shell and repeats this a few times. Again it moves its legs and antennae backwards over the house. Somewhat later it finds the *Hydractinia*-covered *Buccinum* but only climbs over it. Its own old house and the one with dead *Hydractinia* are rolled aside in order to dig in the sand at that place. Again the antennae are swung backwards and the legs grope about the shell. When two legs touch the *Hydractinia*-covered *Buccinum* this is inspected but the hermit does not move.

2.29. The *Buccinum* with dead *Hydractinia* is inspected and the animal moves into it. After swinging back its antennae the hermit disappears entirely into its new house twice or thrice. Then it is digging in the sand among the houses, which it sometimes pushes aside but does not inspect any more.

A smaller pair of houses – clean and *Hydractinia*-covered – is laid into the basin. The hermit climbs over both shells but does not proceed to inspect them. It keeps walking to and fro at one end of the basin, where perhaps it sees its reflection. So the basin is shifted a little so that the houses are at the side where *Eupagurus* kept going to. Presently it happens to touch the *Hydractinia*-covered shell: it walks on for a moment but suddenly turns back to the house as if it recognized it all at once. *Eupagurus* inspects the shell and moves into it, swinging its antennae backwards and groping with its legs about the new house after the shifting. Then it keeps moving fore- and backwards in the shell: air? Again it retires entirely into the house and feels with legs and antennae backwards.

Suddenly it "sees" the clean shell: in one stride it has reached the shell and puts a pincer on it, yet it does not proceed to inspect the house. Again it retires with a jerk into its shell and keeps shifting fore- and backwards like the piston of a pump till a large bubble of air escapes, which apparently inconvenienced the hermit. Once again it disappears completely into its house and another airbubble is expelled. After this the hermit walks calmly about but does not take any more notice of the shells.

Concluded 2.45.

Experiment 85. 7. VII. 1933.

A clean and a *Hydractinia*-covered *Buccinum* and one with a dead crust of *Hydractinia* are placed at regular distances along the brim of the basin and a large *Eupagurus* is put in the middle of it. The hermit walks slowly to the brim of the basin, "signals" the clean house and gives it a wide berth. Walking backwards the hermit encounters the *Hydractinia*-covered *Buccinum* and climbs on it. At once the animal is more interested: "fingers" the shell and proceeds to inspect it and moves into it. The antennae are swung backwards. The old shell has served the hermit as a support to draw itself up and is dragged along over a considerable distance. Again the animal feels with legs and antennae backwards and once or twice it retires completely into the new house. At last it releases the old shell and walks on. Meeting the clean shell, it touches this house with antennae and a pincer, but does not inspect it. This is repeated twice again. Again and again the animal swings

its antennae backwards or gropes with its legs as if it was not completely at its ease. After a moment it touches the *Buccinum* with dead *Hydractinia* with the antennae but does not proceed to inspect it.

Eupagurus is "started" again from the middle of the basin. It walks to the clean shell, touches it with a pincer but will not inspect it. After a moment it finds the shell with the dead crust and inspects it perfunctorily but does not move. Neither will it inspect its own old house, even though one of the pincers passes into the aperture for a moment.

Experiment 87. 7. VII. 1933.

2.30. A middlesized *Eupagurus* in a clean shell is placed in the middle of the basin, while a clean and a *Hydractinia*-covered *Buccinum* and one with a dead crust of *Hydractinia* are lying at regular distances along the brim. Walking backwards the hermit collides with the *Hydractinia*-covered shell and climbs over it. Then it walks to and fro between the clean and the *Hydractinia*-covered house. Coming to the *Hydractinia*-covered *Buccinum* again, the hermit lays some legs on it and proceeds to inspect it. The shell is turned round and round and inspected again but then it is turned away. The shell with the dead crust is passed by without inspection. Again the animal walks to and fro and seems to start back a little every time it passes the clean shell.

2.40. *Eupagurus* is placed near the clean house: it walks away rapidly. Then the basin is rotated over 120°. Again after some hesitation the hermit now proceeds to inspect the clean *Buccinum* and moves into it. The antennae are swung backwards and the hindlegs grope about the new house. For some moments the animal keeps hold of the old shell, then it calmly walks away. Again the hindlegs grope backwards. Meeting the old house again the hermit climbs over it but does not inspect it, though one pincer is resting for some time on the lip of the aperture. Then *Eupagurus* finds the *Hydractinia*-covered shell, touches it with some legs and seems rather excited: "dances" on outstretched legs. Then the animal walks away but returns immediately, touches the shell again with its legs but turns it aside without inspecting it.

Its own house is turned with the top perpendicularly upwards: air!

Concluded 2.50.

From such observations a conclusion can be drawn only with the utmost caution and absolute certainty cannot be attained, because of a number of unknown and uncontrollable factors. Counting the number of experiments in which the animal finished with settling into the *Hydractinia*-covered shell, this amounts to 41 out of 66 cases. But only in 21 of them both shells were inspected or tried on and in 16 of these the clean house was finally chosen. These numbers certainly do not prove a marked predilection for shells covered with *Hydractinia*.

Something more can be inferred from those 21 cases in which both houses were inspected, though it cannot be denied that several other factors – especially concerning the inside of the

shell – may have influenced upon the choice, for absolute similarity – excepted the covering of *Hydractinia* – cannot be secured. But exactly this importance of the interior of the shell seems to me a matter of great moment in drawing our conclusion.

Several times during the course of these experiments it appeared that the animals recognized the clean shells – especially when they are very light coloured – less easily than those covered with *Hydractinia* and seem less inclined to inspect them. Sometimes they even seem to avoid clean shells or start back before them. Also the less rugose surface often causes that contact with the antennae is not sufficient to stimulate the hermit to inspection of the shell it has just met. This may be the explanation of the great number of experiments in which the *Hydractinia*-covered house was first recognized and inspected, after which the animal was not interested any more in the clean shell. Possibly *Eupagurus* may even have formed an association between the tactile perception of *Hydractinia* and the “idea”: house; in other words: *Hydractinia* means a characteristic (Merkmal) of the house (Merkmalsträger). It is, however, not an all important factor, for in 16 out of 21 cases in which both shells were inspected, the clean one was finally chosen. Also the behaviour of the animals when inspecting the houses, shows clearly, that their exterior is of little importance: it is only perfunctorily investigated. Generally the hermit “fingers” the exterior of the shell only just as long as is necessary to find the aperture. When the mouth is found, all attention is turned towards the interior. Only when there is air or sand in the shell it is turned over and over again to remove these inconveniences. The fact that in many cases a new house is “tried on” and discarded again in favour of the old one, proves that after all the interior of the shell alone determines whether it is better than another.

The demeanor of the animals is very different indeed. It is not often, that they are quickly decided and move without looking back at the old house. Often the inspection is a very lengthy affair, several times interrupted whilst the hermit sits quietly with its pincers in the aperture of the shell and cannot “make up its mind”. The attraction of the new house does not seem very strong!

And very often the animal keeps firmly hold of the old shell

or drags it along for some time. More than once it finishes with moving back into it. All this proves beyond doubt that *Eupagurus* chooses between the shells: a comparison, which is sometimes decidedly in favour of one of the two, but more often uncertain, so that only trying the new shell clinches the matter. So THOMPSON (1904) in general is right, when he says, that the choice is made by “actual trying” but it is certainly not true that previous inspection only teaches the hermit that the shell is “hollow, empty and clean”. Without doubt they also compare the sizes of the two houses, for only very exceptionally a hermit will move into a house that is smaller than its own.

Another point mentioned by THOMPSON in favour of the view that *Eupagurus* has a predilection for dextral shells, seems to apply here. When a single dextral shell is dropped into an aquarium which contains a number of *Eupagurus* and many sinistral shells, this unique house – after some time – will always be found inhabited. THOMPSON explains this in the following way: the animals, moving constantly but shifting back to their old houses when the new one is not suitable, will not abandon the dextral shell once they possess it. Similarly in the basin where my material was stored, the clean houses remained tenanted though there was an ample supply of *Hydractinia*-covered shells: this does not seem to denote a marked predilection for houses with *Hydractinia*.

So the conclusion drawn from these observations on the shifting of houses in *Eupagurus*, may be: psychologically *Hydractinia* has not the same significance for *Eupagurus* as symbiotic anemones have for Pagurids, with which they are associated, for there is no majority of cases in which a *Hydractinia*-covered house is preferred to a clean one. The possibility must be admitted, that *Hydractinia* may have obtained the meaning of a characteristic by which houses can be recognized.

In this series of experiments the hermits so seldom took any notice of the shells with a dead crust of *Hydractinia*, that nothing can be inferred concerning the question, whether they distinguish between living and dead *Hydractinia*, but it would seem – exactly from this almost complete neglecting of them – that for the association with the “idea”: house, a living colony of *Hydractinia* is required.

At the close of this chapter I will describe a typical reaction, which my hermits displayed several times. The animal takes a

firm footing with all legs stretched and turns its abdomen round so that the top of the shell points perpendicularly upwards. In one case air escaped through the holes, which had been drilled in the top of the house, and since it appeared on several occasions that there was air in the shell when the animals displayed this reaction. Under natural circumstances it is hardly possible that air gains entrance into the house, but sand may be scooped into it during the inspection of the shell and indeed sand was in one case observed to be removed in the above described way. Presumably this reaction is a means of removing undesirable matter that was not found and cleared away before the house was adopted. Meanwhile in the given unnatural circumstances it served the same purpose as the air ascended into the upper whorls, where it did not inconvenience the hermit any more.

Moreover *Eupagurus* disposes of another means of expelling air from its house: it shifts quickly and vigorously fore- and backwards in its shell like the piston of a pump till the air escapes through the aperture of the shell. Like the former, this reaction also will be meant to remove other undesirable matter, perhaps a.o. faeces.

DOES HYDRACTINIA SHARE IN THE FOOD OF EUPAGURUS?

The second question concerning the relation between *Eupagurus* and *Hydractinia* was: does *Hydractinia* take its share from the food of *Eupagurus*? Experiments or observations on this point have never been made, but generally it is affirmed in literature as a matter of course.

JACKSON (1913) calls *Eupagurus* an omnivorous feeder, and essentially a scavenger, but he does not give many particulars. Important is his description of the way in which *Eupagurus* scoops up small particles with its left chela and tosses them between the mouthparts, where they are sifted.

ORTON (1927) studied the mode of feeding of the hermit crab more specially. Besides of small worms, molluscs, crustaceans, etc. (probably with much seasonal variation) its food consists for a considerable part of detritus. ORTON enlarges upon *Eupagurus*'s special mode of feeding by scooping detritus-particles with the small pincer to the mouthparts, which are much weaker than those of really carnivorous crustaceans, e.g., crabs. This rather untidy way of feeding would seem to be of

great advantage to the symbionts of the hermit and especially to *Hydractinia*. But also shreds of larger pieces of food, which are torn apart, may easily fall to the share of the symbionts, especially when *Eupagurus* fights with or flees for contesting congeners.

It seems probable to me that the hermit will specially seek for animal particles among the detritus, and ORTON himself used *Pecten*-juice as a means of making them eat again when they had stopped scooping detritus.

BROCK (1926) has also observed this peculiar way of feeding in *Pagurus arrosor* (Herbst) but treats more specially of the manner in which the hermit perceives and finds its food by means of chemoreception. The arising of a "chemosector" (made visible with carmine), within which the animal seeks the food it has scented, was also observed in the course of my experiments.

BROCK noticed the particular behaviour of his animals when the meat, used in the experiments, was not altogether fresh and called it "Vermeidungs-reaktion" (avoiding-reaction): the hermits were chemically stimulated by the food and sought for it but coming nearer they were repelled and gave it a wide berth. This is their reaction to repellent but innocuous matters. It occurred several times during my experiments.

As for the food of *Hydractinia*, next to nothing is known about it. MARTHA BUNTING (1894) states that *Hydractinia* "lives upon animal food" and often captures the young *Eupaguri* as they swim out of the shell.

BROCK (1928) calls Hydroids in general: "arge Raubtiere"; so they are typically carnivorous and presumably *Hydractinia* will not be an exception to this rule.

METHOD.

To ascertain whether *Hydractinia* shares in the food of *Eupagurus*, the latter was fed with coloured food, particles of which would be visible within the hydranths in case *Hydractinia* had ingested them. The food consisted of freshly opened mussel coloured during some hours with methylene blue or carmine in ammoniacal solution. In the latter case it was thoroughly rinsed for some hours in running water to remove each trace of ammoniac. Mussel coloured with neutral red was always promptly rejected.

This coloured food was cut in pieces of a suitable size for the hermit to work upon with its pincers, or it was very finely divided by means of a domestic instrument with six circular rolling knives, so that the food could be handled by the hermit like detritus. Very soon it became evident that not all parts of the mussel were accepted with the same eagerness: liver and kidneys seldom find favour but mantle and muscles generally are readily accepted.

The experiments proceeded as follows. A hermit crab with a well developed *Hydractinia*-colony on its shell was placed in the same basin as was used for the experiments on moving, on a bottom of clean sand, which was rinsed or renewed before each experiment. When the animal sat still or walked calmly, I looked through a binocular microscope in what condition of expansion the hydranths of *Hydractinia* found themselves. At a suitable moment a portion of coloured mussel was brought very cautiously into the basin between two small glass spoons and spread on the bottom at some distance from the hermit, which generally took not the slightest notice of these proceedings. After a shorter or longer time, however, it "smelt" the food and began to walk and seek for it. After some time the mussel was found and eventually eaten.

When the animal had finished, I counted through the binocular microscope how many hydranths of *Hydractinia* contained a particle of the coloured meat. It was not always possible to give exact numbers because often several hydranths had fastened themselves on the same morsel and they were not individually discernible. So the number could be estimated only and it was always kept on the low side. Only the hydranths on the upperside were taken into account, because the lower ones, which were dragged through the food, collected so much of it that their condition seemed unnatural. Nevertheless exactly these lower hydranths, which generally are longer and sturdier than the others, will be of great importance for the collecting of food.

In two or three experiments *Eupagurus* was put upon a layer of silt (which had settled on the bottom of one of the seawater-tanks), in order to observe the scooping of detritus on a natural substrate. This, however, always proved a failure: the animals seemed to be so very uncomfortable on this completely soft bottom that they staggered wildly against the brim of the basin and would not calm down. This tallies with several faunistic

data, which show that *Eupagurus* does not occur on completely soft bottom. Wherever this species was found on silt this was always mixed with stones or shells, which procure a firm hold for the legs.

EXPERIMENTS.

Obviously the course of these experiments depended very much on the appetite of the hermits and it proved rather a handicap that they seemed to like the coloured mussel less than the natural product. Sometimes they refused to eat or they sought eagerly for the food but gave it a wide berth when they came in the neighbourhood (BROCK's "Vermeidreaktion") or recoiled as soon as they touched it. In these cases the meat "smelt" attractive from a distance but repelled when "smelt" (or "tasted") from near by.

Also the curious case occurred that a hermit rejected a morsel after grasping it with its pincers but ate from it when I put the same morsel between its mouthparts. This might indicate that the meat "smelt" bad but "tasted" good (perhaps due to the ammoniac not being entirely washed out). The same thing – but less sharply defined – was visible, when the animal, though eating of the food, meanwhile kept pushing away the sand with its pincers. This pushing away of the sand is a sure sign, that the hermit does not like the "smell" of the meat and curiously enough the movement is the exact reversal of the scooping up of detritus. Pushing away the sand is often accompanied by stroking of the antennae and antennulae as if they needed cleaning.

Here follows a description of some selected examples which represent a fair average of these experiments.

Experiment 3. 23. VI. 1933.

A large *Eupagurus*, densely grown with *Hydractinia*, sits quietly when a portion of finely divided methylene blue mussel is spread on the bottom. The blue colour is drawn to the animal in a "chemosector." After about five minutes, when the colour reaches it, the hermit stirs up and walks almost straight to the food. First it finds a few scattered particles, then the bulk and eats greedily of it. After a while the hermit walks away with quite a lump between its mouthparts from which it eats steadily.

The hydranths of *Hydractinia* are very well expanded and five or six are filled with blue meat.

Experiment 6. 29. VI. 1933.

Time 5.25. Some finely divided methylene blue mussel thoroughly mixed

with sand is spread on the bottom of the basin opposite a large *Hydractinia*-covered *Eupagurus*. Very soon the hermit sits in the middle of the blue patch and starts scooping up the sand with both pincers alternately. Unfortunately it stops very soon.

5.37. *Hydractinia* is well expanded and several hydranths are blue with the coloured meat.

During the meal suddenly a *Nereis fucata* comes out of the shell, creeps along the branchiostegite (just above the coxae of the legs) of *Eupagurus* to the mouthparts, where it takes its share from the food.

Experiment 14. 4. VII. 1933.

A middlesized *Eupagurus*, which refused minced blue mussel mixed with sand, is given a new supply without sand. In a moment it has found the food and greedily eats a great deal of it.

The hydranths of *Hydractinia*, which were rather contracted at the beginning of the experiment, are very well expanded and actively moving but none have caught a blue particle.

Experiment 16. 5. VII. 1933.

4.35. A smallish *Eupagurus* is placed into the basin on clean sand. The hydranths of *Hydractinia* are fairly well and very equally expanded.

Finely minced methylene blue mussel is spread on the bottom of the basin. Very calmly the hermit walks over to it and eats eagerly. It remains in the same place but shifts fore- and backwards in its shell and gropes backwards with legs and antennae. By and by it penetrates farther into the blue area and keeps eating for some time. At last it walks away with a lump of meat between its mouthparts.

4.55. The hydranths of *Hydractinia* are beautifully expanded and actively moving but only two contain some blue meat. The smallness of this number is probably owing to the very calm demeanour of *Eupagurus*, which made but little stir in the water.

Experiment 20. 6. VII. 1933.

3.30. A large *Eupagurus* is placed into the cleaned basin. It sits quietly with moving mouthparts. The hydranths of *Hydractinia* are moderately expanded.

3.35. Finely minced carmine mussel mixed with some fresh musseljuice is spread on the bottom, at some distance from the hermit. After one or two minutes the animal starts walking.

3.40. It has found the food and sits eating at the edge of the red area, but will not penetrate farther into it; at first it even retires a little. The hermit keeps groping for food though its mouthparts are crammed with it. On the whole its demeanour is very calm.

4.25. The hydranths of *Hydractinia* are well expanded and four or five have red contents.

Experiment 29. 8. VII. 1933.

Two rather large pieces of carmine mussel are laid opposite a hermit-crab. Presently the animal finds one of them and starts tearing it up and eating from it. Very soon, however, the animal leaves off and tosses the meat

away. After this the hermit keeps walking round and round, passing several times over the pieces of mussel, which sometimes are brought to the mouthparts but never eaten. It does not seem to like the food very much.

The hydranths of *Hydractinia* are very well stretched but none have caught some red particles.

Experiment 33. 11. VII. 1933.

The basin is rinsed and a large *Eupagurus* placed into it, which sits quietly when the minced carmine mussel is spread on the bottom. After a moment the hermit walks calmly in the direction of the meat, but suddenly it alters its course as if to avoid the red area. Somewhat later, arrived amid the red particles, it pushes the sand away and quickly walks on without eating.

Next time when it reaches the food the animal again refuses to eat. Nevertheless when I put some of the same meat between its mouthparts the hermit accepts it.

The hydranths of *Hydractinia* are well expanded and though *Eupagurus* did not eat, ten or fifteen polyps have caught some red particles owing to its running about.

Experiment 36. 12. VII. 1933.

4.45. After thrice rinsing the sand a hermit is placed into the basin. When it sits quietly, finely minced carmine mussel is added. The animal begins to walk before the particles have completely settled. Presently it runs very excitedly into the red area and eats with much bustling, groping right and left with its pincers and cramming its mouthparts with the meat.

4.50. The upperside of the shell is quite scattered with red particles: at least twenty-five or thirty hydranths of *Hydractinia* are coloured with it.

Quick moving on the part of the hermit apparently favours *Hydractinia*'s chances of capturing something of the meal.

Experiment 37. 12. VII. 1933.

The sand in the basin is rinsed and a small *Eupagurus* placed into it. The animal walks about calmly.

4.55. Minced carmine mussel is spread on the bottom. A "red cloud" is drawn towards the animal and as soon as this has reached the hermit, the mouthparts of the animal start moving actively. After a moment *Eupagurus* walks calmly, now and again "sampling" the sand, and guided by some scattered particles, to the red area, where it keeps eating for some time.

5.10. The hydranths of *Hydractinia* are maximally stretched and actively moving in search of food; eight or nine contain red morsels.

Experiment 46. 19. VII. 1933.

A large *Eupagurus*, densely covered with *Hydractinia*, is placed into the basin on a fresh layer of sand. It sits quietly and the hydranths are well expanded.

Minced methylene blue mussel is laid on the bottom and after some moments the hermit walks in the direction of the food, feeling in front of itself with antennae and small pincer. When it has found the meat it eats calmly for some time. Suddenly it starts pushing away the sand and walks away with its mouthparts crammed with meat. When the lump has been ingested, one hydranth of *Hydractinia* at the edge of the mouth of the shell has blue contents. It is remarkable that all hydranths at the edge of the

mouth are hanging down so as to touch or nearly touch the back of *Eupagurus*. All are maximally expanded and searching actively.

Experiment 47. 19. VII. 1933.

A small hermit is placed into the same basin without altering anything in it. While *Eupagurus* seeks for the meat, the hydranths of *Hydractinia* stretch themselves. As soon as the animal has reached the blue area it turns back and sits quietly with actively moving mouthparts but pushing away the sand with its pincers: a sign that it does not like the "smell" or "taste" of the food.

With a thermometer I "start" the hermit again in the direction of the blue area and again it starts back on reaching the spot. For the third time it is pushed to the very edge of the blue patch and this time it starts eating. Presently it walks away with a lump between its mouthparts from which it eats though it keeps pushing away the sand. It seems that the blue meat "tastes" better than it "smells".

The hydranths at the edge of the mouth of the shell are hanging down. All are very well expanded and four or five have blue contents.

Experiment 49. 19. VII. 1933.

A rather small *Eupagurus* is placed on the rinsed sand in the basin; it sits quietly with moving mouthparts. The hydranths of *Hydractinia* are well stretched.

Minced methylene blue mussel is added. After a moment the hermit makes a bee-line for it and eats greedily, cramming its mouthparts with the meat. The animal shifts fore- and backwards in its house and consequently some blue particles on its back are pushed against the hydranths, which are hanging down from the edge of the shell. The hydranths are very well stretched but only two small groups at the edge of the mouth – obviously the most advantageous position – have caught some blue morsels.

Experiment 55. 21. VII. 1933.

After rinsing the sand a small *Eupagurus* in a *Natica*-shell is placed into the basin, where it walks about very actively. The hydranths of *Hydractinia* are rather well expanded.

When minced carmine mussel is added, the hermit becomes so lively that it has to be checked with a thermometer. When released it walks right into the red area and starts eating voraciously, grasping with both pincers and cramming its mouthparts with the meat. Then – eating steadily – it retires against the brim of the basin. At last it has only a tough piece of muscle left, of which it eats half and drops the rest.

The hydranths of *Hydractinia* are beautifully expanded and the upperside of the shell is entirely scattered with red particles, as a consequence of the hermit's liveliness.

In this way 57 experiments were carried out.

In 6 cases no hydranths contained coloured food.

36	1-10				
4	15-20				
1	25-30				
10	many				

So in the majority of cases (nearly $\frac{2}{3}$) ten hydranths at most had captured a particle of the food of *Eupagurus*. The experiments in which fifteen or more polyps were coloured, do not amount to $\frac{1}{3}$ of the total number.

From these experiments it is evident that:

1. the same chemical stimulus that rouses *Eupagurus*, is also adequate for *Hydractinia*, for whenever *Eupagurus* starts searching for a meal it has scented, the hydranths of *Hydractinia* stretch themselves and move about in search of food. So they consume the same kind of food, which is essential for a "table-partnership".

2. *Hydractinia* certainly profits to some extent by the meals of *Eupagurus*. How much food it collects depends very much from the movements of the hermit. When *Eupagurus* feeds calmly, *Hydractinia* will not have much chance of a considerable share in the meal, but when the hermit is excited and makes quite a stir, *Hydractinia* will generally have many opportunities of catching a morsel. It is immaterial in this connection, whether *Eupagurus* himself is eating or not; only the stirring up of food-particles is essential. Yet it seems to me that the quantity of meat captured during each experiment was not sufficient to justify the view that the meals of *Eupagurus* yield a regular supply for *Hydractinia* on which it can depend for its daily nourishment. Probably the Hydroid profits more, and more regularly, by the wanderings of the hermit, during which it is dragged along over the bottom and has many a chance of capturing small animals, aroused by the passing of the crab. I am the more inclined to this view because I think that *Hydractinia* is a regular carnivore and less of a detritus-eater than *Eupagurus* is said to be.

In this connection the result of a few experiments can be brought forward, which are the counterpart of the foregoing series. Plankton was sieved through plankton-gauze and to the diminished quantity of "crowded" seawater neutral-red (a very strong brownish solution in tapwater) was added till the seawater was coloured about orange. The plankton – especially the Copepods – became dark red in a very short time. It was poured out into a basinful of fresh seawater in which one or two *Eupagurus* were placed and kept during the night. Next morning *Hydractinia* was coloured slightly red and in about ten or fifteen hydranths dark red contents were visible. In another experiment, when *Eupagurus* was kept for two nights and a day in the

solution of neutral red, at least forty or fifty hydranths had caught some coloured plankton-organisms.

Looking through the binocular microscope it was directly visible that *Hydractinia* captures living plankton. Several times I could see how a Copepod swam against the *Hydractinia*-covered shell and almost instantly sank paralysed among the hydranths, which then proceeded to ingest it. Also Megalopas were noticed sitting among the polyps as if unable to get away though they were still moving their legs. On another occasion a small worm, possibly a Nematode, was overpowered by several hydranths notwithstanding its frantic wriggling.

So *Hydractinia* is undoubtedly an eater of living plankton and probably this is its chief source of nourishment, though it takes a share in the meals of the hermit-crab. Especially when *Eupagurus* is consuming animal food *Hydractinia* will be stimulated and stretch its hydranths in search of some stray morsels: its movements and its reaching down to the back of *Eupagurus* are unmistakable in their meaning. Yet I am convinced that *Hydractinia* is perfectly well able of securing enough food without the help of *Eupagurus*, provided that it is living in moving water, which constantly supplies fresh plankton. The great advantage of its position on the shell of the hermit-crab lies in the latter's mobility (which can be substituted for the motion of the water) rather than in the chance of an occasional share in the food of *Eupagurus*.

THE SETTLING OF THE PLANULAE OF HYDRACTINIA.

When inquiring into the nature of the association between *Eupagurus bernhardus* (L.) and *Hydractinia echinata* (Flem.), one of the most important questions will be: in which way is the association established? How do the planulae find the shells of hermit-crabs? Are they attracted either by a chemical stimulus or by water-currents caused by *Eupagurus*, or do some of them happen to be picked up by chance when a hermit-crab crosses their way, while the greater part perishes after some time for the lack of a suitable substrate? The first case would be an argument in favour of the symbiotic nature of the association, whereas the latter agrees better with the view that *Hydractinia* is merely an epizoön on *Eupagurus*.

LITERATURE.

These questions have never been treated from this point of view, but there are a few papers on the development of *Hydractinia*, which furnish some useful data.

MARTHA BUNTING (1894) reared planulae from the eggs of *Hydractinia* and described the segmentation and further development. On the whole I adopted her method. Though the temperature at Woods Hole must have been several degrees higher than at Den Helder during my experiments – BUNTING once mentions a temperature of 24° C. when the eggs were deposited, whereas the average temperature in the Laboratory at Den Helder was 15–17° C. – the development took about the same time in either case: in 36–48 hours the eggs would have developed into mobile planulae. But the time of discharge of the ova seems to be different: BUNTING mentions 9.30–10.30 p.m., but in my dishes the young stages of two and four cells were found at 9.00 or 9.30 in the morning, so the eggs must have been deposited some hours earlier at about 6 or 7 o'clock, at least when we assume, that the first cleavages proceed in the same way. As a matter of fact according to HARGITT (1911), whose paper also contains the useful information that the eggs of *Hydractinia* sink to the bottom and therefore can be kept in running water, the ova can be discharged at several different times of the night, sometimes at midnight, sometimes at 5 or 6 o'clock in the morning.

Curiously enough it took the fixed planulae in BUNTING's experiments twice as long (4 days) to develop into polyps as in mine: after two days two or four tentacles were visible. It is true that I did not look whether the mouth had been formed.

AURIVILLIUS (1891) emphasizes the fact that the colonies of *Hydractinia* always begin their development on the columella lip of the shell's mouth right under the hermit-crab and he regards the choice of this advantageous spot as an adaptation of *Hydractinia* to the symbiotic life with *Eupagurus*. This is not in accordance with the result of my experiments and a different statement is also made by MARGARET COLLCUTT (1898): "a small colony is usually situated near the edge of the shell" (the edge presumably being the outer lip).

METHOD.

With the purpose of experimenting upon this question planulae were reared from the eggs in the following simple manner.

One or two shells covered with pink female colonies of *Hydractinia* (with or without *Eupagurus*) and one or two with pale-coloured male colonies were placed together in a shallow glass dish with a diameter of about twenty cm and a depth of five to seven cm. The dish was filled to the brim with seawater and put under a very feeble jet of seawater, running constantly (night and day) from a tapering glass tube fixed with rubber tubing to the seawater-system. Four experiments could be conducted simultaneously as there were four jets available.

When the dishes were prepared in this way in the afternoon, a great many eggs would have been deposited as a rule by next morning, most of them already cleft in two or four blastomeres. After twenty-four hours these would have developed into planulae, some of them still retaining an oval shape, the more advanced already broadened and truncated at the fore-end. During the next twenty-four hours the planulae stretched themselves to one and a half or twice their original length and became mobile. In three more hours most of them would have fixed themselves to some substrate. So presumably the mobile phase will last for twenty-four hours at least. During the mobile phase the planulae could be used for the following purposes:

A, to watch their demeanour directly through the binocular microscope, the optic part of which was movable along two horizontal axes, so that a moving planula could always be kept within the field of vision.

B, for some experiments concerning their settling on shells.

A. Behaviour of the planulae.

When observing the planulae of *Hydractinia echinata* (Flem.) through a binocular microscope, the first thing that strikes one (and which seems significant for their mode of life) is, that they are never swimming freely in the water but always crawl on the bottom. They glide along in the manner of *Turbellaria*, now and again raising their fore-ends and moving it to and fro, after which they often change the direction of their course.

At the end of the mobile phase the planulae fix themselves with the truncated fore-end to the substrate, while the "tail"

points more or less perpendicularly upwards, so that it looks exactly like a nail standing on its head. After some time the planula contracts to a round shape, hardly bigger than the blastula from which it arose. In due course the little ball stretches itself again and tentacles grow out at the top: the pink planula has developed into a white polyp. The first settling with the fore-end to the substrate, however, need not be conclusive: more than once such a "nail-formed" planula was observed to unfix itself again and crawl along for some time till it settled down once more. Perhaps the planulae "hold on" like this when stimulated by a sudden movement of the hermit or a water-current, which threatens to carry them away.

Several times I watched the behaviour of the planulae when a young *Eupagurus* had been placed into their dish. An actively crawling planula was kept in sight with the purpose of seeing whether it was attracted by the hermit. On the first occasion this seemed indeed to be the case: my first planula was joined by three others and after some time the young *Eupagurus* appeared into the field of vision of the binocular microscope. It sat quietly eating from a piece of mussel. One of the planulae fixed itself on the bottom before it had reached the hermit but three disappeared under the shell of *Eupagurus*.

On every other occasion, however, no trace of a directing influence of the hermit on the course of the planulae was discernible: they crawled in every possible direction, even in the close vicinity of the crab and when a planula was "followed" with the binocular microscope, it hardly ever "guided" the field of vision to *Eupagurus*. As a matter of fact this seems hardly possible in view of *Eupagurus*' mobility: the planulae proceed so slowly, that the hermit will almost always have altered its position before they have reached it.

Neither did the planulae show a very definite reaction when a walking hermit passed them. Only once or twice the movement in the water caused them to contract and alter the direction of their course.

A gathering of planulae just beside a small mussel suggested the thought that this Lamellibranch might be used to test the planulae's reaction to water-currents. Several (six or seven) times I put a small mussel into a dish with planulae and looked after some hours whether the planulae had been attracted by the water-current and had assembled on or near the mussel.

The result was always negative: only once or twice two or three planulae had settled on the shell, which is just sufficient to prove that there is no chemical stimulus, which drives the planulae away from it.

Neither was any directing influence of the water-currents visible when the behaviour of the planulae in the neighbourhood of a mussel was watched through the binocular microscope.

When neither a chemical stimulus from *Eupagurus* nor water-currents have any directing influence on the planulae, it looks as if they must find the suitable substrate purely by chance. So I watched their behaviour when they encountered a shell. One valve of a mussel-shell was laid into a dish with mobile planulae with its convex side upwards. When reaching it, a few planulae stayed huddled against the edge and perhaps these crept upwards later on, but most planulae contracted for a moment and then continued their course in a different direction, usually at about right angles to the former. Generally they altered their course even before they touched the obstacle, so it seems that the shell must be moving and overtaking the planula for the latter to be picked up. And here the profile of the shell probably plays a part. For, when I gently shoved the mussel-valve towards a group of planulae, so that they were just touched by the silt-particles in front of the shell, most of them contracted but directly afterwards raised their fore-ends with searching movements. In the case of the flat mussel-valve they did not find any "foothold" and dropped on the bottom again, but if it had been a Gasteropod-shell, the searching heads would have touched the round overhanging profile and could have fixed themselves to it. It is conceivable, that this is the way in which planulae are gathered upon the shells of walking hermit-crabs. Though more than once a planula was observed crawling upwards along the legs of *Eupagurus*, it is very improbable, that they should ever reach the shell in this way.

There is also a possibility that the planula becomes "aware" of the passing hermit by the shadow the latter casts over it. When a shell is gently pushed across the path of a moving planula so that its shadow does not fall over the larva, the latter will not or hardly react to it. But when the shell casts its shadow over the planula its reaction is definite: it contracts and alters the direction of its course, generally at right angles to the previous. This and the fact that the planulae often gathered

at one side of the glass dish in which they were reared, seemed an indication that they might be sensitive to light. The following series of experiments was carried out to test this point. A glass bell was entirely covered with black paper with the exception of one vertical stripe two cm broad and eight cm long. Under this bell a dish with mobile planulae was placed with its brim against the open stripe, which was directed towards the window. In this way only one comparatively thin beam of light fell into the dish. When after one or two hours the bell was removed, there was usually a gathering of planulae against the "window", which sometimes was quite pink with them. Most of the planulae in the vicinity would be directed with their fore-ends towards the light. The result of these experiments can be seen from the following synopsis.

no.	Under glass-bell from to	Result	Remarks
1	12.30-2.15	Many planulae against the "window"; many moving towards it	Apparently not very mobile
2	3.30-4.30	Several against the "window"	
3	9.00-10.30	Nearly all against the "window" or before it on the bottom. In the vicinity all heads directed to the light	
4	12.30-2.30	No gathering at the "window"	Young <i>Eupagurus</i> in the dish
5	3.00-5.00	"Window" pink with planulae. Several mobile planulae moving in the direction of the light	
6	9.30-11.30	No gathering at the "window"; mobile planulae moving in diverse directions	Young <i>Eupagurus</i> in the dish
7	9.30-11.30	Several against the "window"; some crawling towards it, others in diverse directions	
8	1.00-3.00	Definite gathering of planulae at the "window". Mobile planulae moving in several directions	Young <i>Eupagurus</i>
9	12.00-3.00	Definite gathering of planulae against the "window"; nearly all mobile planulae near it	
10	3.45-5.45	No gathering at the "window"	

no.	Under glass-bell from to	Result	Remarks
11	6.15-8.45 p.m.	Definite gathering of planulae at the "window"	
12	11.00-12.30	No gathering of planulae at the "window"	
13	12.30-2.30	Many planulae at the "window"; the others crawling in diverse directions	
14	10.00(?) - 12.15	"Window" pink with planulae and many assembled in the neighbourhood, though not directed towards the light	
15	10.30-12.30	No planulae against the "window" yet, but a great many moving towards it	
16	9.45-11.30	Definite gathering of planulae on the bottom before the "window"	Mussel in the dish has no directing influence. Perhaps the mobile phase was nearly at an end: many already fixed
17	12.15-2.15	Definite gathering against the "window"	

Only four out of seventeen experiments had a negative result: two (Nos 2 and 15) were doubtful and in eleven the result was positive. So they undoubtedly prove the planulae's sensitiveness to light, though they are insufficient to allow any further conclusions: whether the planulae are positively or negatively phototactic will probably depend on the intensity of the light and on internal and external conditions. Perhaps the intensity of diffuse light is of more importance than the direction of the rays: a lighted area might work as a "physiological trap", the planulae being unable to leave it because they start back at a certain minimal light-intensity. This would explain their crawling in sundry directions though they had assembled near the "window".

One experiment, in which planulae that looked distinctly mobile had hardly moved from their spot, presumably because

the light was intercepted by a screen, suggests that light may be necessary to stimulate them to any activity. To settle these questions, however, other experiments would be required.

In three of these experiments a young *Eupagurus* was put into the dish, because I thought it possible, that the planulae and *Eupagurus* seek the same optimal light-intensity, in which case light could be the agent, which guided the planulae to their suitable substrate. *Eupagurus*, however, was never attracted by the "lighted window" and seems phototactically indifferent. Remarkable is the fact that in all of these three experiments the planulae also failed to gather before the window, which is perhaps due to a disturbing influence of the hermit-crab, though this is puzzling in view of the planulae's indifference to its presence during former observations.

It is impossible to see any biological significance in this positive phototaxis of the planulae beyond the fact, that it prevents their moving into deeper and deeper water and keeps them within the lighted littoral zone.

B. Experiments concerning the settling down of planulae.

The first series of experiments served to ascertain whether a greater number of planulae settles on shells inhabited by *Eupagurus* than on empty ones (conditions being the same in every other respect).

Some young *Eupagurus* in clean shells (mostly *Littorina* or *Natica*) and an equal number of empty shells (if possible of the same kind) were put into a dish with mobile planulae and kept over night under the feeble jet of seawater. Next morning the number of planulae settled on each shell was counted. It is true, that by moving into one of the empty shells the young hermits sometimes spoiled the experiments to some extent. But if this inconvenience should be eliminated by putting the young *Eupagurus* and the empty shells into separate dishes, the objection could be raised, that the conditions, e.g., the number of planulae, had not been the same in either dish. In any case the result in my opinion leaves no doubt as can be seen from the following synopsis.

no.	Objects	Planulae fixed on shells inhabited and empty		Remarks
1	Inhabited and empty <i>Purpura</i> , inhabited and empty <i>Natica</i> , 3 in- habited and 3 empty <i>Littorina</i>	4 0 6 3 2	→ 5 0 1 0 0	One <i>Eupagurus</i> has been moving
2	Inhabited <i>Littorina</i> and empty <i>Natica</i>	25-30	10 and 8 still crawling	
3	3 inhabited <i>Littorina</i> and 3 empty <i>Natica</i>	12-14 15-16 20-22	4 1 1	Perhaps the smooth <i>Na- tica</i> is somewhat less favourable than the more rugose <i>Littorina</i>
4	4 empty and 1 inhab- ited <i>Natica</i> , 3 inhabited <i>Littorina</i>	30-40 30-40 30-40 2	5 6 1 ↔ 52	Probably one <i>Eupagurus</i> has been moving
5	2 inhabited and 1 emp- ty <i>Littorina</i> ; 1 inhab- ited and 2 empty <i>Na- tica</i>	countless countless 1	5 2 ↔ countless	Three shells were pink with planulae One <i>Eupagurus</i> moved?
6	3 inhabited and 2 emp- ty <i>Littorina</i> ; 2 empty <i>Natica</i>	countless countless countless	15 10 42 countless	One <i>Eupagurus</i> moved?
7	Inhabited and empty <i>Buccinum</i>	16-18	0	
8	4 inhabited and 3 emp- ty <i>Littorina</i>	17-18 39-40 30-31 13-14	↔ 56-57 22-23 22-23	<i>Eupagurus</i> been moving?
9	Inhabited and empty <i>Buccinum</i>	countless	25	

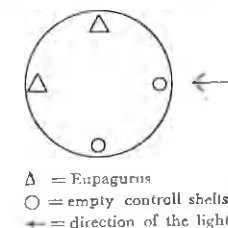
↔ means that *Eupagurus* has moved.

It is evident that generally a greater number of planulae settles on shells inhabited by *Eupagurus* than on empty ones. So a second series of experiments was carried out in order to settle the question, whether this is due to the moving about of the hermit-crabs or to their presence as such. In the first case a higher number of planulae fixed on inhabited shells, could be explained simply by the much greater chance of a planula

meeting with a shell when the latter is moved about. On the other hand, if the presence of *Eupagurus* alone proved to be the cause of the difference in numbers of settling planulae, this would be a strong indication that the planulae are attracted either by a chemical stimulus or by the water-currents caused by the breathing of *Eupagurus*.

When it proved impossible to fix the shells of young hermit-crabs to stones by means of sealing-wax and ceresinum, the animals were "chained" to the glass dish by means of a double or quadruple horsehair, passed through two holes drilled in the shell and fastened to the brim of the basin by means of a clothes-peg. The horsehair was just long enough to allow of the hermit's sitting in a normal attitude against the brim of the dish. Of course the possibility of a little movement remained, but the hermit could not do more than one or two paces in either direction. If the moving about of the hermit is essential, the difference in numbers of planulae settling on their shells and on the empty controls ought to have considerably diminished. In each dish two young hermits were "chained" to the brim with a quarter of the circumference between them and the two controlshells were placed opposite to them. The dish was orientated so, that its division into quadrants (by the four shells) was symmetrical with respect to the direction of the light falling through a window.

Diagram of the arrangement for experiments with fastened *Eupagurus*.



Here again the young hermits sometimes proved themselves up to the situation: they often cut the horsehair with their pincers (before I took the precaution to double or quadruple it) or they left their houses and walked over to the empty controls (which accordingly they must have recognised from a distance). Though a number of experiments were rendered valueless in this way, I think the remainder is sufficient to permit the drawing of a conclusion with at least a passable amount of probability. A synopsis of them is given on the next page.

no.	Planulae fixed on shells			Remarks
	inhabited	empty	never inhab- ited by <i>Eupagurus</i>	
1	15 or 16 4 ← → 15	42-47 15		One <i>Eupagurus</i> has moved into a control-shell and collected 15 planulae. The great number on the other control is perhaps due to the light.
2	23 9	27 6		One <i>Eupagurus</i> has cut itself loose and collected 23 planulae. The control with 27 was a <i>Buccinum</i> larger than the other shells.
3	11 3	10-11 3	16 4	
4	1 2 ← → 10	3 18-20 18-20		<i>Eupagurus</i> has moved from the house with 2 planulae into the one with 10.
5	0 0	7 13-14	2 3	The <i>Littorina</i> with 13 planulae was at the righthand side of the dish: not nearest to the light.
6	2-3 9-10	7-8 8	5 4	<i>Eupagurus</i> has moved from the shell with 2 planulae into the one with 5.
7	0 0	13 8	2 3 on exuvium	
8	0 0	27-28 8-10	0	The shell with 27 planulae was nearest to the light. <i>Eupagurus</i> has moulted, but returned to its own house in both of these exp. <i>Eupagurus</i> with 60 planulae was at the righthand side.
9	33-35 60-70	13-14 21-22	3-4	
10	1 12-13	10-11 6-7	4 8 on stone	

The number of planulae on the shells is so varying, that they seem to have distributed themselves at random, and it is evident that the inhabited shells are by no means always the more favoured. In experiment 3 there is one with a higher and one

with a lower number of planulae among both the inhabited and the empty shells and in experiment 6 the number on all shells are not very different. Probably the light has had some directing influence and as a consequence of the uneven distribution of the planulae on the bottom of the dish, each of the shells may have been reached by a different number of planulae.

In the fourth column of the synopsis are recorded the numbers of planulae fixed on *Littorina*-shells that have never been inhabited by *Eupagurus* and (in experiment 10) on stones. These controls were added because an eventual chemotactical influence might show itself by higher numbers of planulae fixed on shells that had been inhabited by *Eupagurus* than on shells, where only *Littorina* itself had dwelt in. Though the numbers are generally somewhat lower I do not think them conclusive of a chemical stimulus. In experiment 3 the highest number of planulae was fixed on a shell never before inhabited by *Eupagurus*. Moreover in two cases, in which *Eupagurus* moulted, respectively 0 and only 3 or 4 planulae had settled on the exuvia, which certainly is not indicative of a chemotactical influence.

The third series of experiments was the counterpart of the former, in which the inhabited shells were "chained" to the brim of the dish. Now the empty controls were made mobile by tying them with a double horsehair to the shells of the young hermit-crabs. (Of course small holes had been drilled into both shells). So practically every movement of the hermit's shell was imitated by the empty shell it had "in tow" and if the number of larvae settling on a shell is entirely (or chiefly) dependent on the chances of a planula meeting with a shell, the numbers ought to be about equal or at least less different than in the first series of experiments. As immobile controls were added the same number of empty shells that had formerly been inhabited by *Eupagurus* and such as had only belonged to *Littorina*. These controls were filled with ceresinum to prevent the hermits from moving into them. With the "towed" shells this precaution was not taken, because I feared that they would become too heavy. They were chosen so as to be smaller or considerably larger than the shell of the "towing" hermit-crab.

A synopsis of these experiments follows on the next page.

no.	Numbers of planulae fixed on shells:				Remarks
	inhabited	"towed"	formerly inhabited by		
			<i>Eupagurus</i>	<i>Littorina</i>	
1	4 0	1-2 7			One <i>Eupagurus</i> has cut the horsehair, yet the abandoned shell has 7 planulae. Numbers too small.
2	2 1	1 7	3 3	1 0	One <i>Eupagurus</i> has moved.
3	0 0	1 0	0 0	0 0	Numbers too small.
4	9-10 13-14	3 9	0 0	1 1	
5	13 27	30 23	2 9-10	5 2	One <i>Eupagurus</i> has been eaten; on its house are 13 planulae.
6	66-68 47-48 55	62 58-59 26-28	7 7-8	3 0	
7	0 12 12	12-13 14-15 7	3 2 2 1		<i>Eupagurus</i> has moved from the shell with 12 planulae in the one with 2.
8	2 7 1	3 11 6	0 0 0		
9	16 11 29-30	8 26 39-40	17 0 5 6		
10	47 24 26 27-28	95-97 36 48-49 26	17-18 35 35 12-13		

Perhaps the number of experiments is too small and the number of fixed planulae too low for any inference to be made with absolute certainty. Yet in four experiments (no. 5, 6, 9, and 10) the result leaves no doubt that the "towed" shell generally collects about the same number of planulae (and sometimes more!) as the inhabited one. And in three experiments (no. 4, 7, and 8) the numbers are equal enough but somewhat too low to be quite satisfactory. In any case they are higher than the

numbers on the immobile controls in the same experiments. The difference in numbers of planulae fixed on the mobile shells and on the immobile controls is striking in all of these seven experiments. Only two immobile shells in experiment 10 (with 35) and one in experiment 9 (with 17 planulae) have collected an exceptionally high number of planulae, which must probably be attributed to the influence of the light or to some other unknown factor.

From the result of the last two series of experiments it can be inferred with great probability, that the planulae of *Hydractinia echinata* (Flem.) do not actively search for their optimal substrate but arrive there purely by chance when they happen to meet with a hermit-crab. Moreover there is another observation made during these experiments, which fits in with this conclusion. In each experiment a great number of planulae finished with fixing themselves on the bottom of the dish when their mobile phase was at an end. Now in such confined surroundings every single planula ought to have located the shell of a *Eupagurus* if there had been a directing chemo- or rheotactical influence originating from the hermit-crabs.

Incidentally these experiments offered an opportunity to observe, whether the planulae when fixing themselves show any preference for special parts of the shell. The most striking feature seems their gregariousness: whenever a considerable number of planulae has settled on a shell, they are always packed closely together in dense groups in which the individual polyps are hardly discernible. If there is any preference for special places on the shell, it is not very marked. When the shell has a smooth surface, like *Natica*, nearly all planulae gather in the suture, often near the top. On *Littorina*, and especially on *Buccinum*, they are more evenly distributed because the surface of these shells is more or less sculptured. Any unevenness like lines of growth, siphonal canal, umbilicus, cracks, the edge of holes of boring Polychaeta, the circumference of an eventual *Balanus*, etc., are generally used as a "foothold". Also there is often a series of planulae fixed more or less closely along the outerlip and almost invariably one or two or a small group of planulae have settled in the corner of the mouth opposite to the siphonal canal. Another favourite site is the columellar mouthedge right under the mouth and legs of *Eupagurus*. According to AURIVILLIUS (1891) the young colony invariably begins its development at this place

of the shell, but this does not tally with my facts, unless it must be assumed that as a rule most of the young polyps fixed at other points of the shell are rubbed off or perish, while only those right under the protecting hermit-crab have a chance of further development.

Though no special observations were made on this point, I got the impression that the planulae, once they have reached the shell of a *Eupagurus*, settle down for good in a shorter time than they do on an empty shell, where they keep crawling about somewhat longer. This must be due to the movements of the hermit.

THE SPIRALZOIDS.

A special feature of *Hydractinia*-colonies growing on houses of *Eupagurus* is the fringe of spiralzoids along the lip of the shell. By their structure and functioning they are obviously "organs of defence or offence" as their original describer STRETHILL WRIGHT (1857) called them. The only one to take a different view, was AGASSIZ (1862), who simply identifies the spiralzoids with sterile blastostyles and denies their being a special kind of individuals. Because of their special situation the spiralzoids were often considered an adaptation of *Hydractinia* for the benefit of the hermit-crab: they guard the entrance of the house and prevent small animals from entering. So they constitute a strong argument in favour of the view that the relations between *Hydractinia* and *Eupagurus* are truly symbiotic.

Especially AURIVILLIUS (1891) enlarges upon this point (as will be seen later) and similar views have been repeated more recently, a.o. by BALSS (1924), who classifies the association of *Eupagurus* and *Hydractinia* under true symbiosis.

HINCKS (1868) does not call the relations between the two organisms symbiotic ("there can be no doubt that its alliance with the crustacean, though not essential to its well-being, is at least the source of material advantage to it") but he is explicit on the function of the spiralzoids as defensive polyps and especially on the close coördination of their movements. He also remarks that the fringe of spiralzoids is often absent and occurs in mature colonies only.

More recent authors, especially BROCH (1928), generally call the spiralzoids organs of defence ("Wehrpolypen"), but do not commit themselves to any view on their significance for *Eupagurus*.

It is remarkable, that the tentaculozoids, described by STRETHILL WRIGHT (1857) and observed by HINCKS (1868 and 1877), AURIVILLIUS (1891) and COLLCUTT (1898) are never mentioned neither by BROCH (1916, 1928) nor by NUTTING (1901), who like ALLMAN probably regard them as identical with the spiralzoids.

MARGARET COLLCUTT (1898) remarks that they "are principally situated towards the outskirts of the colonies", and believes that they are a special kind of polyps different from the spiralzoids.

So the views expressed of late in literature on the nature of the spiralzoids are not very definite and rather guarded especially concerning their relation to *Eupagurus*.

In order to get an insight into this matter I examined at least eighty shells with living colonies of *Hydractinia echinata* (Flem.) and paid special attention to the borders of the colonies. It is true, that both edges of the mouth – over and under the hermit-crab – are the only places, where the spiralzoids occur almost without exception, but the development of the fringe is very variable. Sometimes there are hardly any spiralzoids, especially on the outer lip. In other cases they stand in a single row and are too short to coil up. Then the fringe thickens to two or three rows but still the spiralzoids are rather short. When maximally developed there are about two or three rows of long spiralzoids. Sometimes the spiralzoids are long but stand in a single row: the fringe seems past its prime. The best developed fringes were always found on mature reproducing colonies, but this may not be reversed into: every mature colony has a well developed fringe of spiralzoids. In one case there was a row of tentaculozoids instead of spiralzoids along the outer lip of the shell. Probably the growing border of the colony had just reached the edge of the shell, for inspection of the margins of many colonies leads to the conclusion, that tentaculozoids generally stand along the young growing borders of the colonies. As in these mature colonies, which entirely cover the shells, the relations between *Hydractinia* and *Eupagurus* must be the same in all these cases, this divergence in the development of the fringe of spiralzoids suggests that they are not a special adaptation for the benefit of the hermit-crab. More probably a special internal condition of the colony – possibly in connection with reproduction – is the cause of their formation.

Moreover there is another fact, which points to this same conclusion. Often the colony does not stop growing at the edge of the mouth but continues its growth on the inside of the lip. In these cases the row of spiralzoids follows the edge of the colony where it curves inwards and part of the mouth-edge is devoid of them. In one shell a separate little colony had developed on the inside of the lip and along its borders there were spiralzoids. At last I found a shell bearing two colonies, and along the line of demarcation, which was at nearly right angles to the mouth-edges, one of them – a ripe male colony – had developed typical spiralzoids over some distance (about 3 cm) across the last whorl, both on the upper- and the underside (as *Eupagurus* wears the shell). Though connected with the fringe along the mouth-edge, this row deviated entirely from the lip. In all these cases the border of the colony and not the lip of the shell was essential for the distribution of the spiralzoids.

When the spiralzoids are short they bear a strong resemblance to sterile blastostyles: the "heads" with their knob-like rudimentary tentacles are just the same and the spiralzoids are only longer and more muscular. When examining the edges of the bare patch on the underside of the shell, where *Hydractinia* is worn away because the shell is dragged over the bottom, one always finds there short sterile blastostyles. But often they are somewhat longer, even so that in some cases one is tempted to call them short spiralzoids. In two or three cases there was hardly any difference and in three or four other cases a few regular spiralzoids were found near the edge of the bare patch. So there seems to exist a very gradual transition from blastostyles to spiralzoids and AURIVILLIUS (1891) is undoubtedly right, when he says: "bei Berücksichtigung der verschiedenen hier angezeigten Merkmale der Spiralpolypen bei *Hydractinia echinata* kann ich schliesslich nicht umhin sie als den Geschlechtspolypen (= Blastostyles) am nächsten verwandte Bildungen anzusehen".

As already stated I looked for spiralzoids along the margins of the colonies. Except in the few cases mentioned above they were never found there, and it is noteworthy that they never occurred in colonies grown on other substrates than the shell of *Eupagurus*. Among my material were twenty-five specimens of *Hyas araneus* (L.) partly covered with *Hydractinia* but on none of them a single spiralzoid could be discovered. But very often

the edges of the colonies were marked by tentaculozoids, which are much longer and somewhat thinner, tapering to a fine point and devoid of rudimentary tentacles. They are less muscular and seem almost entirely passive. I found them:

1. often round the bare patch on the underside of the shell, when the edge seemed well alive and growing.
2. in several cases along the line of demarcation between two colonies, which had developed side by side on the same shell.
3. round the upper-edge of an overgrown *Balanus*.
4. along a line at the hind side of the spire and ending in a tuft on the top of the shell. Probably this was the line, where the margins of the colony growing round the shell had met each other.
5. along the edge of colonies growing on *Hyas araneus* (L.), especially round the eye-sockets, on the articulations of the legs and on the joint between carapax and abdomen.

I got a distinct impression, that the tentaculozoids are best developed along the young growing borders of the colony. Gradually as the colony spreads, they disappear from the older parts but they seem to persist along free edges, e.g., articulations of legs and the like. When the growing border of the colony reaches the edge of the substrate, e.g., the lip of the hermit's shell, its progress is stopped or at least very much slackened and the margin of the colony remains in the same place for a much longer time. Meanwhile the development of blastostyles and sporosacs proceeds from older to younger parts of the colony and in due course must also reach the almost stationary border. Possibly under these conditions the outermost blastostyles take the place of the tentaculozoids, remain sterile and develop into spiralzoids. The correlation of reproduction and the formation of spiralzoids would have found a natural explanation. According to this view the principal condition for the development of a fringe of spiralzoids would be an obstacle, which keeps the growing border almost stationary, and the fact that no spiralzoids occur in colonies growing on *Hyas* and other substrates is readily explained by the circumstance, that in these cases the growing border is not checked by any such impediments. Of course all this is pure hypothesis, but perhaps it is plausible enough to be worth considering, and the fact that STRETHILL WRIGHT found spiralzoids round hollows in the shell, can be adduced in its favour.

To test this hypothesis experimentally I made square holes of about one cm diameter in the youngest whorl of two *Buccinum*-shells densely grown with mature *Hydractinia* and inhabited by *Eupagurus* (23 Aug. 1933). They were then kept for several weeks in one of the large basins of the Zoological Station's aquarium. If spiralzoids developed along the free edges of these gaps, this would be a strong argument in favour of the above hypothesis. The result, however, was not satisfactory. One of the hermits died in less than four weeks and of course on the untenanted house *Hydractinia* did not thrive: there was hardly any trace of regeneration visible at the edges of the hole. The second shell was examined twelve weeks (17 Nov.) after the operation. Though the colony was in good health there were only gastrozoids and no spiralzoids round the hole. Of course no conclusion can be drawn from so small a number of experiments. Moreover in a narrow regenerating margin, quite surrounded by mature parts of the colony, conditions may be different from those in the free growing border.

In order to observe the conditions of the spiralzoids' functioning, I stimulated them in several ways.

1. the spiralzoids themselves, or the border of the colony near them, were touched or even pricked with a needle; the spiralzoids did not lash out but only contracted in some cases.
2. a small piece of the skin of a fish was applied to the spiralzoids. Again the result was negative: no uncoiling.
3. minute crabs (1 or 1½ cm in diameter) were forced to walk along the mouth-edge of the shell, tied to a horsehair or conducted by light touches of forceps or needle. Though this was repeated with different colonies of *Hydractinia* and different crabs, the spiralzoids hardly ever responded with lashing out simultaneously. A few of them contracted and sometimes one or two would uncoil more or less accidentally, but as a rule they did not react. In one colony the spiralzoids reacted properly three or four times, but the movement did not follow instantly every time when the crab touched the edge of the mouth. It may have been caused by my inadvertently moving the shell.
4. when an *Idothea* walked over the shell with *Hydractinia*, the gastrozoids contracted but the spiralzoids did not move.
5. a small *Ophiothrix* was held near the fringe of spiralzoids so that one arm travelled searchingly along the mouth-edge of

the shell. Every time it touched *Hydractinia* the arm recoiled instantly: it seems sensitive to the nematocysts. The spiralzoids did not show any reaction.

6. the same applies to *Asterias*: it avoids the touch of *Hydractinia* and the oral side with the tube-feet seems more sensitive than the aboral side. The spiralzoids never lashed out.

In fact the only stimulus, to which the spiralzoids almost invariably react with lashing out simultaneously, is a movement of the shell (e.g., a rotation round its axis) or the sudden retreat of *Eupagurus* into its house. Perhaps other movements of the hermit-crab can act as adequate stimuli, but I did not record anything of the kind. It is difficult to observe the spiralzoids, when *Eupagurus* is in its normal walking-position: one has to turn the shell with its mouth upwards to see the fringe properly.

These facts do not seem consistent with the view that the spiralzoids are special organs for the defence of the entrance of the shell. Especially one misses the coördination, which HINCKS (1868) emphasizes, when he says: "it has been noticed (STRETHILL WRIGHT) that if any part of the common base be irritated, the spiral appendages uncoil simultaneously and lash themselves violently backwards and forwards and then quickly roll themselves up again. I have seen a whole company discharge themselves with remarkable energy and with the precision of a regiment on drill". Indeed this reaction occurs, but only when the whole shell is moved and not instantly after every tactile stimulus.

Neither can AURIVILLIUS' description (1891) be based on actual observations. According to him the spiralzoids lash out as soon as the colony is touched and so they betray to *Eupagurus* the presence of an intruder long before the hermit could become aware of it. He even describes tactile hairs on the back of the crab as special receptors to be stimulated by the uncoiling spiralzoids.

My observations do not point to such close relations.

They rather lead to the following conclusions: though their structure and functioning obviously denotes the spiralzoids as organs of defence, it is not evident that they are a special adaptation of *Hydractinia* for the benefit of *Eupagurus*: their formation is probably conditioned by internal factors rather than by the association of *Hydractinia* with the hermit-crab.

CONCLUSION.

In the foregoing chapters the following facts have been demonstrated:

1. *Eupagurus bernhardus* (L.) has no marked preference for shells covered with *Hydractinia echinata* (Flem.): psychologically the Hydroid has not the same biological significance for it as symbiotic anemones have for their bearers.

2. though *Hydractinia echinata* takes a (varying) share in the meals of *Eupagurus bernhardus*, this probably cannot be considered to constitute the regular supply of its daily nourishment. *Hydractinia* is mainly an eater of living plankton.

3. the planulae of *Hydractinia echinata* do not actively search for shells carried by hermit-crabs: they reach this optimal substrate purely by chance when a *Eupagurus* happens to cross their way during their mobile phase.

4. though the spiralzoids occur only on *Hydractinia*-colonies fixed on houses of *Eupagurus*, they are not strictly confined to the borders of the aperture of the shell. This, and the fact that they are found only on wholly mature colonies, suggests that their formation depends on internal conditions of the colony rather than on the association of the Hydroid with a hermit-crab. The spiralzoids are organs of defence, but not specially for the benefit of *Eupagurus*.

These four groups of facts all point to the conclusion that the association of *Hydractinia echinata* and *Eupagurus bernhardus* cannot be qualified as true symbiosis: the Hydroid is merely an epizoön, which shares to some extent in the food of the Crustacean, but is not dependent on it.

Considering in this connection the geographical distribution of both animals, (which ought to coincide when their relations are really symbiotic), it must be born in mind that by far the majority of data on the occurrence of *Hydractinia* concern colonies fixed on the houses of *Eupagurus*: these were most likely to be brought up in the nets and it was on these shells that *Hydractinia* was expected to be found and consequently was looked for. So it can hardly be said that the geographical distribution of *Hydractinia echinata* has been sufficiently investigated independently from that of *Eupagurus bernhardus*. Yet there is one point worth mentioning in this connection: *Hydractinia echinata* can live under

truly arctic conditions and *Eupagurus bernhardus* cannot. Accordingly *Hydractinia echinata* has been found on the North-coast of Iceland (on the operculum of *Balanus hameri* (Asc.), WINTHER, 1880, cited by SAEMUNDSSON, 1902 and BROCH, 1916), and on Jan Mayen (LORENZ, 1886, cited by JÄDERHOLM, 1909 and BROCH, 1916), where *Eupagurus bernhardus* does not occur (HANSEN, 1908). *Eupagurus bernhardus* has only been recorded from the West-coast and the western part of the South-coast of Iceland. Perhaps this is due to a branch of the Gulfstream, the Irminger stream, which passes along these shores, while the North- and East-coasts are washed by a branch of the colder Greenlandstream, the East-Icelandstream.

Probably the West-coast of Greenland affords a similar instance. *Hydractinia echinata* was recorded from Upernivik by LEVINSEN (1893) and by BROCH (1916), whereas *Eupagurus bernhardus* has never been found on Greenland (SELBIE, 1921) and though *Eupagurus pubescens* Krøyer occurs there, HANSEN (1908) does not mention its being associated with *Hydractinia* on this coast (SCHELLENBERG's statement (1928): "das von *Eupagurus bernhardus* über sein Zusammenleben mit *Hydractinia* Gesagte, trifft auch auf diese Art zu" seems to apply to more southern regions only). So probably Greenland belongs to those areas, where *Hydractinia* is more often found on the shells of living snails (BROCH, 1928). As a matter of fact LEVINSEN's specimen was fixed on a living *Buccinum hydrophanum* (Hanc.).

From these facts it is evident that *Hydractinia* ranges farther to the north quite independent from the hermit-crabs.

How closely the distribution of *Hydractinia echinata* was connected in the mind of investigators with the occurrence of *Eupagurus bernhardus*, may be illustrated by the following two quotations.

BROCH (1928 a), treating of the bathymetrical distribution of *Hydractinia*, writes: "die Art lebt an Schneckenhäusern, die von Einsiedlerkrebsen (besonders von *Eupagurus bernhardus* (L.)) bewohnt werden; sie ist deswegen in den Küstengewässern Europa's häufig von der Strandregion bis ziemlich tief hinunter" Ought not this to be reversed into: because *Hydractinia* occurs in part of the bathymetrical range of *Eupagurus* it has many opportunities of securing the favourable situation on the shells of the hermit-crabs, which consequently appear to be their usual substrate, especially on sandy coasts and the like, where other

suitable objects for the planulae to settle upon are scarce? Obviously the result is conform to BROCH's statement.

And ALLEN (1899), alluding to *Hydractinia* and two other Hydroids, states: "the distribution of such species depends upon that of suitable hosts and since the hosts are all wandering animals, the nature of the bottom deposits, when it is once sufficiently firm to support them, has little direct effect on their distribution". In the case of *Hydractinia* this can hardly be true, because the eggs sink to the bottom and the planulae remain there, crawling but never swimming freely in the water. The bottom-deposits must be a factor of some importance in the development and consequently in the distribution of *Hydractinia*, for though *Eupagurus* can carry the adult colonies safely over every kind of ground, the Hydroid will not be able to propagate in areas, where the bottom-deposits are unsuitable, e.g., too soft or too badly aerated for the eggs and planulae. *Hydractinia* must invade these regions again and again by means of the hermit-crab.

As a matter of fact from ALLEN's own careful study on the fauna and bottom-deposits near Eddystone (1899) it can be seen that the quality of the bottom is no indifferent factor in the distribution of both *Eupagurus* and *Hydractinia*. The synopsis (of which the part that concerns our objects has been copied on the next page shows that *Eupagurus* is "common" or "present in moderate numbers" only on "fine sand grounds" (grounds I-VIII), whereas on the "coarser grounds" (gravel and shell), which incidentally often contain more mud, only "few" or "no" hermits were found. The only exceptions are ground VIII, a fine sand ground (though containing about 12 % gravel and coarse sand) where *Eupagurus* and *Hydractinia* are both absent, and ground IX, a coarse gravel ground (but with only 1,2 % mud), where *Eupagurus* was "plentiful and associated with *Hydractinia*".

Possibly (among other factors) the amount and the nature of the silt contained in the bottom-deposit determine its suitability as a habitat for *Eupagurus* and *Hydractinia*, for both are notably clean animals. BROCK (1926) remarks on the cleanliness of *Pagurus arrosor* Herbst, which immediately rubs its legs and antennae as soon as some siltparticle adheres to them. *Eupagurus bernhardus* (L.) has the same habit. And BROCH (1928) states: "die Hydroiden müssen als durchaus reinliche Tiere bezeichnet

werden, die durchwegs sauberes Wasser und meist stromreiche Stellen bevorzugen. Schon hieraus erhellt in Bezug auf die Fazies der Hydroiden, dass die weitaus überwiegende Zahl der Arten auf "hartem" Boden angetroffen wird". This applies as well to *Hydractinia* in particular.

Though the data on *Hydractinia* in ALLEN's paper only concern specimens fixed on shells of *Eupagurus* and therefore cannot give complete information on the influence of the bottom on the distribution of this Hydroid, these data clearly show that the occurrence of *Hydractinia* does not run parallel with that of *Eupagurus*. There are several grounds where *Eupagurus* was present (though in some cases scarce) and *Hydractinia* absent, and others where *Eupagurus* was "common" or "present in moderate numbers" and *Hydractinia* scarce or only present in one or two of the hauls. So in the area covered by ALLEN's investigations *Hydractinia* seems to have a more restricted range than *Eupagurus* and, judging from faunistic literature, this applies to other regions as well.

When compiling from faunistic literature data concerning the nature of the seabottom at places from which *Hydractinia* has been recorded, the result is a variety of facts, from which a general rule can hardly be deduced (so probably several other factors play a part). Perhaps this much can be presumed:

1. at many of these localities *Hydractinia* was comparatively scarce, so perhaps it was carried thither by *Eupagurus* but cannot propagate there.

2. at several places, where *Hydractinia* has been found in greater numbers, the seabottom proved to be rocky or consisted of clean firm material, often for the greater part of sand

From ALLEN's synopsis:

	fine sand grounds					coarse grounds mixed with sand and mud					fine gravel		clean shell gr.	stony				
Grounds:	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII	XIII	XIV	XV	XVI	XVII	XVIII
<i>Eupagurus</i> :	P	M	M	P	P	P	F	-	P	Po	F	F	-	F	-	-	F	F
<i>Hydractinia</i> :	P	P	Po	Po	P	P	Fo	-	P	-	-	-	-	-	-	-	-	-

M = many; F = present in moderate numbers; F = few; Po, Fo = resp. present and few in some of the hauls, absent in others.

(AGASSIZ, 1862; DU PLESSIS, 1888: Villefranche; HARTLAUB, 1896: Helgoland; BILLARD, 1904: St. Vaast la Hogue: abondante - lieu de récolte: banc de sable; BROCH, 1905 and 1911: coast of Norway, Laminaria-region at Droebach). These may be localities, where the bottom is suitable for the eggs to develop upon. Of course these points must be more closely studied before anything can be inferred with certainty. Especially comparative data on the abundance of *Hydractinia* and *Eupagurus* at the same locality and records of *Hydractinia* on other substrates than the shells of hermit-crabs would be useful. Probably the result will be this: *Hydractinia* has more special requirements and therefore a more restricted range than *Eupagurus*. As far as their distributions on different bottom-deposits coincide, *Hydractinia* will often fix itself on shells inhabited by hermit-crabs. Subsequently *Hydractinia*'s range can be materially extended by means of *Eupagurus*. On coasts, where the houses of hermit-crabs provide (practically) the only opportunity for the planulae to settle down, the Hydroid will be found (almost) exclusively on this peculiar substrate. On rocky coasts, however, and at places, where piles and moles and the like procure firm substrates for *Hydractinia* to fix itself upon, its independance from *Eupagurus* becomes apparent.

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ACARTIA (ACANTHACARTIA) TONSA DANA EIN NEUER COPEPODE DES NIEDERLÄNDISCHEN BRACKWASSERS

VON

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In einer kürzlich erschienenen Arbeit hat KLIE (1933) den Fund eines ihm bis dahin unbekannten Copepoden aus dem von Bremen bis Bremerhaven reichenden Abschnitt der Weser erwähnt, bei dem es sich alsbald herausstellte, dass es sich um die seinerzeit von JAMES D. DANA beschriebene, bei Port Jackson (Neusüdwaes) gesammelte Art *Acartia tonsa* handelte¹⁾. Das Tier wurde von REMY (1927) zum ersten Mal in Europa gefunden, und zwar in dem von Caen ins Meer führenden Kanal und KLIE selbst entdeckte es zufälliger Weise in einer ihm zur Untersuchung überlassenen Probe aus dem Ringkjöbing Fjord, wo es, wie sich nachträglich herausstellte, schon in Fängen vom Juli 1921 enthalten war.

Die Ausführungen KLIE's haben mich veranlasst, das mir zur Verfügung stehende einheimische Acartien-Material aus früher und später Zeit einer erneuerten Untersuchung zu unterziehen, wobei sich herausgestellt hat, dass *A. tonsa* zum mindesten schon seit dem Jahre 1916 bei uns vorkommt und heutzutage

¹⁾ Die Tiere wurden von Professor STREUER, dem KLIE einige der Bremerhavener Exemplare zur Begutachtung vorlegte, als zu *A. tonsa* gehörig erkannt. KLIE selbst gibt keine Beschreibung; es genügte nach ihm, „unter Hinweis auf die ausführliche Darstellung und die vorzüglichen Abbildungen von REMY festzustellen, dass die in der Wesermündung gefundenen Exemplare genau mit denen aus dem Kanal von Caen übereinstimmen.“ (KLIE l.c., S. 275). Da nun auch die niederländischen Exemplare den französischen sehr ähnlich sind, habe ich kein Bedenken, bis auf weiteres auch jene als zu der Art *A. tonsa* gehörig zu betrachten. Die Möglichkeit scheint mir jedoch nicht ausgeschlossen, dass es sich hier wie dort um eine andere, *A. tonsa* sehr nahe stehende Art, handelt. In einer späteren Arbeit hoffe ich hierüber ausführlicheres mitteilen zu können.