

STUDIES IN THE PHYSIOLOGY OF COMMENSALISM. III. THE POLYNOID GENERA *ACHOLOË*, *GATTYANA* AND *LEPIDASTHENIA*

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(Text-fig. 1)

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INTRODUCTION

Previous experiments (Davenport, 1950; Davenport & Hickok, 1951) gave evidence that in certain echinoderm-polynoid partnerships the specificity in part depended upon a positive response of the commensals to a substance or substances released by their hosts. In the partnership between the starfish *Evasterias troschelii* Stimpson and the polynoid *Arctonoë fragilis* (Baird) the attractant was found to be non-dialysable and relatively unstable; but, as demonstrated by the Y-tube choice-apparatus employed, enough attractant was continuously released by the host to affect the activity of the commensal at a considerable distance.

Experiments with the scale-worm *Halosydna brevisetosa* Kinberg, commensal with the terebellid *Amphitrite robusta* (Johnson), gave no evidence that a chemical attraction plays an important part in governing this association, at least when the partners are adult. However, a single unpublished experiment conducted during the summer of 1952 at the Kerckhoff Marine Laboratory in California showed that the commensal *Hesperonoë adventor*, which lives in the tube of the echiuroid *Urechis caupo*, is effectively 'tied' to its host with a powerful bond. An *Hesperonoë* can unerringly distinguish water in which its host is housed from plain sea water, and will make an active search for its host when separated from it. In this strict association the polynoid is perhaps conditioned to whatever substance it is that gives *Urechis* its familiar, powerful, aromatic smell.

The present work constitutes an effort to elucidate the mechanism of control of additional commensal partnerships.

ACHOLOË ASTERICOLA (DELLE CHIAJE)*Material and Methods*

At Plymouth the partnership between the starfish *Astropecten irregularis* (Pennant) and the polynoid *Acholoë astericola* (Delle Chiaje) is well known (Fig. 1), and the animals are readily available for investigation. In collections regularly brought into the Laboratory from the Eddystone Grounds, at times

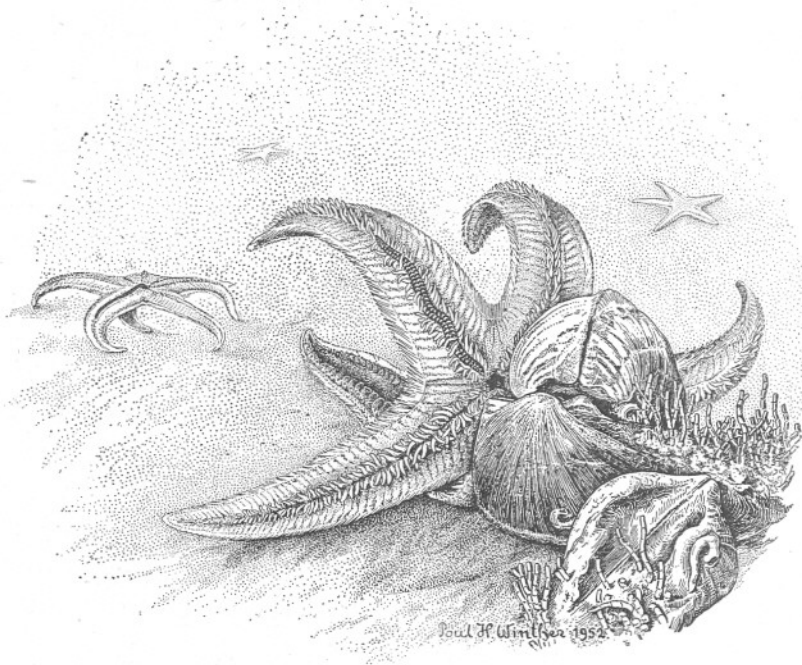


Fig. 1. The host starfish *Astropecten irregularis* showing the commensal *Acholoë astericola* in the ambulacral groove with head directed towards the stomach of the host, into which it may extend when feeding.

(By Courtesy of Gunnar Thorson, from studies made in Dakar, Senegal, April 1952. Drawn by Poul H. Winther.)

as many as 75% of the starfish have the small orange polychaete in the ambulacral groove. Ordinarily only one worm per starfish is found, but very occasionally two are present, which may be markedly different in size and age.

Astropecten is the only known host of *Acholoë* at Plymouth (Marine Biological Association, 1931). In the Mediterranean the polynoid occurs on *Astropecten aurantiacus* and *A. pentacanthus* (McIntosh, 1900). Panceri (1874) records the occurrence of *Acholoë* on the starfish *Luidia ciliaris*

(Philippi) (= *L. fragilissima* Forbes) in the Mediterranean, but no such association is known in Plymouth waters, in spite of the fact that at times *Luidia* is relatively common in the same environment as commensal-carrying *Astropecten*.

At the outset it was obviously important to determine whether the commensal made any constant response to the host. As observed by many workers, if the *Acholoë* were removed from the host and the tip of the arm of the host placed in close proximity to the head, the worms almost immediately became activated and fastened themselves to the host, either climbing quickly on to the aboral surface, or into the ambulacral groove, or wrapping themselves entirely around the tip of the host's arm. Brief experiments indicated that single tube-feet removed from the host would elicit a typical response. If a tube-foot was presented to its head, the *Acholoë* became active and with a twisting motion quickly wrapped itself around the tube-foot and the tip of the holding forceps. This response could only be elicited by contact. In many experiments tube-feet were held within a millimetre or less of the head of the commensal without eliciting any reaction. In addition, several experiments demonstrated that a small quantity of non-circulating sea water which had surrounded two host starfishes in a 200-ml. beaker for 2 hr. had no effect whatever on the behaviour of the commensals when brought near the head by a fine pipette. However, under normal conditions contact of host tissue with the head of the commensal 'triggered' an immediate and typical reaction.

The facility with which this typical and constant response can be evoked from a random sample of worms, and easily manipulatable materials can be presented while the commensals are under observation, has made the partnership particularly productive for investigating the problem of specificity and the nature, source and effect of the attractant.

In the following experiments standard procedure was to isolate six *Acholoë*, selected at random, in shallow dishes of fresh 'outside' sea water. Responses were elicited by presenting materials held in the tip of fine-pointed forceps. An effort was made to keep all materials in one series of tests of approximately the same size. In each experiment materials were presented in rapid order to the six worms and the responses recorded. Between tests of each material the commensals were washed in clean 'outside' water and instruments in alcohol-acetone.

Responses were recorded as follows. If on presentation of the test material the commensal was immediately activated and responded by quickly moving on to or wrapping itself around the material, the response was recorded as +. If a response appeared only after the material had been in contact with the head for several seconds or if the activity produced was sluggish, this was recorded as (+). No response whatever, after insistent presentation, was recorded as o.

Observations

Experiment No. 1. Is the response specific? Single tube-feet from members of the genera of starfish represented in Plymouth waters were presented; and reactions recorded in Table I.

As can be seen, the response is only relatively specific. The majority of *Acholoë* behave consistently in the presence of each starfish presented, but an occasional individual (e.g. A, 3) seems unable to 'tell the difference', a response being elicited by the tube-foot of any starfish.

TABLE IA

Worm	<i>Astropecten irregularis</i> (host)	<i>Asterias rubens</i>	<i>Marthasterias glacialis</i>	<i>Luidia ciliaris</i>	<i>Porania pulvillus</i>
1	+	o	o	+	(+)
2	+	o	o	(+)	(+)
3	+	+	(+)	+	(+)
4	+	o	o	+	(+)
5	+	o	o	+	o
6	+	o	o	(+)	o

TABLE IB

Worm	Host control	<i>Palmipes membranaceus</i>	<i>Solaster papposus</i>	<i>Hemricia sanguinolenta</i> *	<i>Stichastrella rosea</i> *	<i>Asterina gibbosa</i> *
1	+	(+)	o	(+)	o	(+)
2	+	(+)	o	(+)	o	(+)
3	+	(+)	(+)	(+)	o	(+)
4	+	(+)	o	(+)	o	(+)
5	+	(+)	o	(+)	o	(+)
6	+	(+)	o	(+)	o	(+)

* Small size of tube-feet necessitated presentation of tip of arm of starfish.

Unfortunately, because of the limited availability of experimental animals, experiments could not be conducted with a large enough sample of commensals to give a statistically significant quantitative evaluation of the difference of intensity of response to each form. However, from the above data certain conclusions can be drawn.

It can be seen that *Acholoë* respond immediately and with highest intensity to host tube-foot, and with about equal intensity to the tube-feet of *Luidia*. This is of particular interest in view of the absence of *Acholoë* on the *Luidia* of Plymouth waters, where *Luidia* may be taken in the same dredge-haul with *Astropecten*. Curiously, the above-cited reference to the occurrence of *Acholoë* on *Luidia* in the Mediterranean was not found in the literature until after the above experiments had been completed. At the time of writing, *Acholoë* placed on a large *Luidia ciliaris* have lived 5 months in the 'Drake's Island' Tank at Plymouth. The worms do not appear to take up position in the ambulacral grooves, but cling to the sides and aboral surface of the unaccustomed host.

The above data also indicate that the *Acholoë* respond to some extent to all members of the asteroid order Phanerozonia available at Plymouth (*Astro-*

pecten, *Luidia*, *Porania*), to certain *Spinulosa* (*Asterina*, *Palmipes*, *Henricia*), but not ordinarily to *Forcipulata* (*Asterias*, *Marthasterias*, *Stichastrella*). This perhaps indicates some biochemical similarity among these members of the *Phanerozonia* and *Spinulosa*. Evidently the starfish *Porania*, *Palmipes*, *Asterina* and *Henricia*, which elicited a delayed or weak response, either produce a smaller amount of attractant or one slightly different from that of the host or *Luidia*. At any rate their attraction is enough to cause the commensals to become attached to them when contact occurs. The answer to the strict specificity of *Acholoë* and *Astropecten* in Plymouth waters, in view of the attraction which a number of starfish show for this polynoid, can only be sought in further laboratory and field observations.

Experiment No. 2. What can be determined concerning the source of the attractant in the host? Small pieces of host tissue which had been thoroughly washed in clean sea water were presented, with the following results:

Worm	Spine	Aboral integument	Stomach	Gastric caecum	Tube-foot control
1	+	+	+	o	+
2	+	+	+	+	+
3	+	+	+	+	+
4	(+)	+	+	(+)	+
5	+	+	+	+	+
6	+	(+)	+	(+)	+

These clearly show that all parts tested had some attraction for commensals. Again, the sample of worms available for testing was not large enough for a quantitative evaluation of the difference in intensity of attraction of each tissue. It appeared that stomach triggered off the most active and enthusiastic response, but this may have been the result of using slightly larger masses of stomach. However, because of the ready response elicited, a number of subsequent experiments have been conducted with stomach as the source of attractant.

These data also offer rather persuasive evidence that texture or consistency of surface, in which the tissues differed widely, have little to do with the response.

Experiment No. 3. The question was now asked whether the attractant produced by the stomach is released into the stomach cavity, and whether a response can be elicited by the presentation of material that has been soaked in stomach contents.

Small pieces of cotton-wool were introduced into the stomachs of six *Astropecten* and left for 1 hr. They were then presented to six *Acholoë*, whose reactions were:

Worm	Test cotton-wool from stomach	Control cotton-wool	Control stomach
1	(+)	o	+
2	o	o	o
3	+	o	+
4	+	o	+
5	+	o	+
6	(+)	o	(+)

Thus apparently attractant is present in stomach contents. That attractant absorbed on cotton-wool will elicit a response presents additional evidence that surface texture plays little part in the response and provides a tool with which it is possible to investigate the presence of attractant in extracts, etc.

The above results would scarcely have been obtained had there not been a quantity of attractant in the stomach contents. That not enough attractant diffuses from the general surface of the host to affect the behaviour of the commensals at a distance has already been noted. Attractant may collect in the stomach to give a higher concentration than occurs in the water immediately surrounding the host, or in the stomach the attractant may be protected (from oxidation?).

No indication has been given, however, that attractant diffuses from isolated stomach more readily than from other tissues. Although, as noted above, stomach elicits a strong response from commensals, contact still appears to be necessary. This was indicated in the following experiment.

Experiment No. 4. A small bag of 100-mesh bolting-silk was firmly filled with isolated stomach. The bag was presented.

Worm	Bag of stomach	Control stomach	Control bag
1	(+)	+	o
2	o	+	o
3	(+)	+	o
4	(+)	+	o
5	(+)	+	o
6	o	+	o

The results clearly show that when bolting-silk separates the head of the worm from stomach tissue the response is markedly weakened. The weakened responses elicited from four of the worms may have been the result of contact with small bits of stomach protruding through the holes in the silk. One set of experiments has already shown the unimportance of surface texture, and here the failure of the normal response appears to be due to the separation of the head by the bolting silk from the surface of the material to which attractant is closely bound.

These experiments indicate that for normal responses to be elicited contact with a surface to which the attractant appears to be closely bound is necessary.

The effects were then tested of certain physical factors (time duration, temperature change) on the attracting ability of whole isolated host tissue.

Experiment No. 5. Does the passage of some hours decrease the ability of isolated tissue to attract, provided it stays fresh? Fresh stomach pieces elicited a positive response from six commensals. After the passage of 18 hr. in clean sea water at 15° C. the pieces were as effective as ever.

Experiment No. 6. Can a response be elicited to refrigerated whole host tissue? Pieces of stomach were placed in 300 ml. of clean sea water, refrigerated overnight at 1° C. and tested at 2° and 8° C. Worms were tested as usual in shallow dishes of sea water at 15.5° C. The pieces of stomach were

removed from the refrigerated sea water and rapidly presented to the heads of the commensals. Before each worm was solicited, the piece of stomach was briefly put back into the refrigerated sea water to chill its surface again.

Worm	2° C. stomach	8° C. stomach	15.5° C. stomach (control)
1	o	+	+
2	o	+	+
3	o	(+)	+
4	(+)	+	+
5	(+)	+	+
6	(+)	+	+

As can be seen, a weak response was elicited from half the worms at close to freezing temperature, while stomach at 8° C. seemed as effective as controls.

Experiment No. 7. How do high temperatures affect the ability of whole stomach to elicit a response? Pieces of stomach were placed in sea water at 44° and 64° C. for 10 min., then placed in sea water at the temperature of control stomach (15.5° C.) to cool them off, and presented, with results as follows:

Worm	15.5° C. stomach	44° C. stomach	64° C. stomach
1	+	+	o
2	+	o	o
3	+	(+)	o
4	+	+	o
5	+	+	o
6	+	o	o

The data indicate that raising the temperature to 44° C. either slightly alters the attractant or allows just about the quantity to be released which is at the threshold sensitivity of the worms. Temperatures higher than 64° C. either completely destroy or alter the attractant, eliminating all response.

It is apparent, then, from the above experiments that passage of time or reduction of temperature do not markedly alter the attraction of whole isolated host tissue, but that temperatures much higher than 45° C. cannot be used in efforts to extract the attractant factor.

Experiment No. 8. What effect does grinding up the tissue have? About twenty *Astropecten* arms were ground up in a Waring Blendor in 150 ml. of 'outside' sea water. This material was then centrifuged at 1500 r.p.m. for 15 min. Cotton-wool was soaked in the supernatant and presented. No response whatever occurred, while control whole arms elicited typical responses from all six commensals.

Experiment No. 9. Five *Astropecten* stomachs were ground up in 5 ml. of clean sea water and sand and passed through filter-paper. Presentation of cotton-wool soaked in this filtrate resulted in no response whatever. Control pieces of whole stomach elicited typical responses from all commensals.

Experiment No. 10. A large number of tube-feet were rapidly ground up in 5 ml. of clean sea water and sand. This material was centrifuged at 1500 r.p.m. for 15 min. and the supernatant presented soaked in cotton-wool. Again, there were no responses whatever.

Experiment No. 11. What if the ground material is not filtered? Five *Astropecten* stomachs were ground up in 8 ml. of clean sea water in sand and the preparation allowed to stand for a few minutes to settle out, before presentation:

Worm	Control stomach	Control cotton-wool	Cotton-wool soaked in preparation
1	+	o	(+)
2	+	o	o
3	+	o	(+)
4	+	o	o
5	+	o	(+)
6	+	o	o

Here a weak response is occasionally elicited, which may result from contact with minute bits of tissue remaining in the supernatant. Clearly, no very effective amount of attractant remains in the preparation.

The above experiments indicate that grinding obliterates the attraction of host tissue and that the attractant present is rapidly altered or destroyed. Efforts to protect the attractant by introducing a crystal of ascorbic acid in the preparation or by grinding, centrifuging and testing at low temperatures (1-9° C.) resulted in failure.

However, two experiments gave evidence that the attractant is rapidly oxidized.

Experiment No. 12. Five *Astropecten* stomachs were isolated and placed in a test-tube with 8 ml. of sea water and a small quantity of washed sand. Through this preparation nitrogen was bubbled for 3 hr. At the end of this time the stomachs were quickly ground up in the nitrogen atmosphere, the supernatant poured off and tested:

Worm	Control stomach	Control cotton-wool	Cotton-wool soaked in preparation
1	+	o	(+)
2	+	o	(+)
3	+	o	(+)
4	+	o	+
5	+	o	o
6	+	o	+

Here again, as a result of the small sample tested and the appearance of a number of delayed or weak responses, one cannot make a definite statement on the relative effectiveness of the material which had been prepared in nitrogen. Yet the five responses, two of which were typical, appear to indicate that cotton-wool soaked in material prepared in nitrogen was slightly more effective than cotton-wool soaked in material prepared in air (Exp. No. 11).

Experiment No. 13. Finally, cotton-wool soaked in stomach contents and then exposed to air in a moist chamber was found very quickly to lose its attraction. Bits of cotton-wool were placed in the stomachs of hosts for

90 min., quickly removed, placed in a moist chamber in air, and tested. After the passage of 5 min. in air bits elicited normal responses, but others which were tested after they had been in air for 15 min. had lost all their attraction.

GATTYANA CIRROSA (PALLAS) AND *LEPIDASTHENIA ARGUS* HODGSON

The association of these two handsome polynoids respectively with the terebellids *Amphitrite johnstoni* Malmgren and *A. edwardsi* Quatrefages is well known.

In a series of experiments, with material collected at the estuary of the Yealm and at Salcombe, the ability of the commensals to discern the presence of their host terebellids at a distance was tested with the Y-tube choice-apparatus used in the author's 1950 and 1951 experiments. In no tests was it possible to demonstrate that the commensals chose the host-water arm a statistically significant number of times, even when as many as seven or eight host terebellids were placed in the test aquarium, when 'outside' sea water was used and when the commensals were partially protected against the adverse effect of light stimuli by wrapping the Y-tube in red cellophane.

This result strictly accords with that obtained (Davenport & Hickok, 1951) with another terebellid-polynoid association, that of *Amphitrite* (*Neoamphitrite*) *robusta* (Johnson) and *Halosydna brevisetosa* Kinberg of Puget Sound.

Orton and Smith (1935), using *Gattyana* and *Lepidasthenia*, conducted brief experiments which they believed 'appear to indicate... that there is a tropic response on the part of the polynoid, causing it to enter an *Amphitrite* burrow whenever possible.' No data is presented, however, to support this hypothesis. In a personal communication on unpublished work R. Phillips Dales states that he has been able to demonstrate a positive response by *Gattyana* to water from the host, when using only the freshest material and taking the greatest precautions to prevent the disturbing effects of other stimuli (light, contact, etc.). It is clear, however, that while in these terebellid-polynoid associations the commensal's behaviour may be affected by a chemotaxis to the host, certainly not nearly as strong a response can be demonstrated as in the echinoderm-polynoid partnerships. The author has been unable to duplicate, when using *Amphitrite johnstoni* and *Gattyana*, his experiments demonstrating the response to host body wall or tentacle exhibited by *Halosydna brevisetosa*.

Observations made in the field and on material in glass U-tubes indicate that the activity of commensals is perhaps limited more by the powerful thigmotaxis they demonstrate to the wall of the tube and the body-wall of the host than by responses to attractants secreted by the host.

That a chemotaxis may be involved in enabling the young commensals to find their hosts cannot be discounted.

DISCUSSION

In the above experiments the importance of an unstable attractant in regulating the behaviour of the commensal partner in an association has become apparent for a second time. A marked difference exists, however, between the control of the *Evasterias-Arctonoë* partnership of Puget Sound and that of the *Astropecten-Acholoë* partnership of European waters. In both of them the commensal annelid is bound to the host asteroid by a powerful chemotactic response to an unstable substance or substances; but, whereas in the former the attractant will take effect at some distance from the host, in the latter a response can be elicited only by contact with the host. That the response of *Acholoë* may be purely a chemotaxis, in spite of contact being necessary, has been strongly suggested by the tests in which it was elicited by stomach juices soaked on cotton-wool.

Unfortunately in the 1950 Puget Sound experiments no tests were made similar to those in which *Acholoë* was found to respond to several starfish that appear never to be its natural host; however, in the Y-tube choice-apparatus used, *Arctonoë* was found not to respond to water from the star *Pisaster*, closely related to the host *Evasterias* and living in the same ecological niche. The lack of specificity of response in *Acholoë* is difficult to explain in view of the fact that it has been found only on *Astropecten* and *Luidia* in European waters.

It must be kept in mind, however, that under ordinary conditions during adulthood of the commensal, the chemotaxis serves merely to keep the commensal on the surface of the host. In a personal communication, G. Thorson, who has recently made some interesting observations on this partnership and to whom I am indebted for the excellent figure of the animals, says that when *Astropecten* are dying in an aquarium their *Acholoë* will leave them and may visit *Asterina*. This is quite in accord with our observations of the sensitivity of *Acholoë* to *Asterina*, on which the polynoid never occurs in nature. Under natural conditions an annelid during its adult lifetime would seldom be forced to seek a new host when its own is damaged or dying. Such an event is probably too rare to be considered a factor in the evolution of the powerful chemotactic response; but its occasional occurrence could conceivably initiate a new host habit, when the searching commensal finds itself able to 'colonize' a new host species.

Probably no answer will be found to the problems of the observable differences in the distances at which particular commensals respond, of the specificity of their responses, and of their specificity of habit, until the detailed ecology of the developmental stages of the respective commensals is known, including the manner in which the host is sought out and found.

During study of the effect of the host on the early stages of the commensal, Thorpe's (1939) olfactory conditioning factor must be kept in mind as a possible important element in the control of marine associations. In this

work Thorpe demonstrated that in certain insects host selection in part depends upon the conditioning of the parasite's early stages to host substance. For such conditioning to be effective the early stages must obviously spend some time in intimate contact with host tissue. Work at present in progress indicates that the prototrochophore and trochophore stages of *Acholoë* are in the plankton for not less than 10 days. It is a little difficult to see how any conditioning of the early stages can occur in forms with as long a planktonic stage as *Acholoë*.

In considering the evolution of a specific commensal habit it is admittedly dangerous to generalize from an evaluation of the economics of the association based largely on guess-work. It should be possible to determine precisely, in a number of partnerships, just how the commensal is attracted and bound to the host and how the host is forced to tolerate it. Turning to the *consequences* of such an association, the remarks of Maurice Caullery (1952), referring to lichens, are quite as applicable here. He says that we will 'find that the question is really one of analyzing, by precise experiments, the relations' (of the partners) 'and of careful comparison of their behaviour in an isolated state and in association.' Such a careful comparison of the relations and requirements of the partners of specific associations of the type investigated by the author has to his knowledge never been made.

A possible course of evolution of intimate animal associations in general may be suggested. When one animal becomes associated with another to the advantage of the former, then the latter (the host) may have a number of possible fates. It may be able to evolve defences against the partner about as fast as the partner is able to evolve modifications to live at its expense, in which case the association may be considered one of commensalism or balanced parasitism. Or it may not be able, and the association may then be thought of as one of extreme parasitism, internal predatism or disease. Or, again, if *after the association has been unilaterally initiated*, some benefit is thereby given to the host, the host individuals which are best able to take advantage of the situation will perhaps be selected and the association will then tend to become truly mutualistic or symbiotic. However, it is difficult to take any other view than that at the initiation of the association only one of the two associated species is benefited.

With the polynoid-echinoderm partnerships investigated by the author, it appears most unlikely, since such a high percentage of host individuals live quite successfully without commensals, that some selective advantage has accrued to species which developed a substance whereby commensals were attracted. It is most difficult to imagine any way in which the echinoderm benefits from this association and therefore to label the partnership mutualistic. Should not then—the question is often put—these echinoderm-annelid associations be considered parasitic? If commensalism is defined classically as simply 'feeding at the same table', and if it can be demonstrated that no damage is done to the starfish by a commensal that occasionally removes

food from its stomach, the answer is 'no'. Obviously, however, these associations are very close to parasitism and probably are excellent examples of the manner in which truly parasitic associations develop.

In the author's opinion, from the point of view of the evolution of the association, the echinoderm has been passive. It has, in the course of the annelid's adaptation to commensal life, been unable to eliminate the commensal.

On the other hand, an organism that has become physiologically adapted both to finding, by evolving a positive response to a particular chemical secreted by a host, and to successfully 'colonizing' this host, has doubtless been given an advantage of selective importance. The finding itself and the successful 'colonization' must be investigated without undue regard to the economics of the association and with careful consideration of the manner of evolution of sensitivities to specific substances and, undoubtedly, of certain immunities. The author has observed *Acholoë* fully two-thirds within the stomach of the host, and Thorson states that they will keep this position for 10 min. or more. The annelids must be quite immune to host digestive enzymes. It may be that immunological studies will cast light on the apparent anomaly of a commensal that responds positively to a number of starfish (perhaps biochemically related) but is found in nature on only one or two of these.

That various intimate associations among terrestrial organisms (parasitic protozoa, trematodes, insects, etc.) are controlled by chemical sensitivities and immune reactions is well known; so far little attention has been paid to the role of these phenomena in marine associations.

SUMMARY

The commensal polynoid *Acholoë astericola* (Delle Chiaje) exhibits a powerful positive response on contact with its host, *Astropecten irregularis* (Pennant).

This response is only relatively specific, *Acholoë* demonstrating it to a number of starfish that do not serve as host in Plymouth waters.

All living host tissue has some attraction for the commensal; and the attractant is apparently released in quantity in the stomach of the host.

Passage of time (apparently as long as tissue remains alive) and chilling do not markedly alter the attractiveness of isolated host tissue. Temperatures above 45° C. alter or abolish its attraction.

The extreme instability of the attractant has so far made it impossible to demonstrate its presence in extracts.

Evidence is presented that the attractant is rapidly oxidized.

Experiments with the scale-worms *Gattyana cirrosa* (Pallas) and *Lepidasthenia argus* Hodgson, commensal respectively with *Amphitrite johnstoni* Malmgren and *A. edwardsi* Quatrefages, indicate that a chemotaxis to the host may be of relatively minor importance in governing the behaviour of these commensals.

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