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MILNE-EDWARDS AND BOUVIER**

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A SYMBIOSIS BETWEEN *PARACALLIACTIS MEDITERRANEA* N.SP. (ANTHOZOA-ACTINIARIA) and *PAGURUS VARIABILIS* A. MILNE-EDWARDS AND BOUVIER

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SYMBIOSE
COMPORTEMENT
ACTINIES
PAGURES

RÉSUMÉ. - Une Actinie symbiotique recueillie pour la première fois en Méditerranée a été identifiée comme une espèce nouvelle, *Paracalliactis mediterranea*. Elle a été trouvée sur des coquilles occupées par *Pagurus variabilis* A. Milne-Edwards et Bouvier. Aucun comportement orienté vers *Paracalliactis* n'a été observé chez des Pagures hôtes, mais des Actinies détachées de leur hôte se montraient actives, grimpant et se fixant à des coquilles. Au cours d'expériences dans lesquelles on a présenté des coquilles à des Actinies fixées à des roches, environ deux tiers de celles-ci se sont attachées ou ont essayé de se fixer aux coquilles. Il est donc permis de conclure que le comportement de l'Actinie constitue la base de cette symbiose, et que cette dernière est comparable à celle existant entre *Calliactis parasitica* et *Pagurus bernhardus*.

SYMBIOSIS
BEHAVIOUR
ACTINIANS
PAGURIDS

ABSTRACT. - A symbiotic actinian not previously recorded in the Mediterranean has been identified as a new species, *Paracalliactis mediterranea*. It was found on shells occupied by *Pagurus variabilis* A. Milne-Edwards and Bouvier. No activity of the pagurid host towards *P. mediterranea* was observed but the detached actinian showed an active behaviour pattern, clinging to shells and settling thereon. In tests in which shells were presented to actinians on stones, about two-thirds of the actinians transferred or attempted to transfer to the shells. It is concluded that this symbiosis is based on the response of the actinians to shells and is comparable with the symbiosis between *Calliactis parasitica* and *Pagurus bernhardus*.

INTRODUCTION

In studying symbioses between actinians and pagurids at the Laboratoire Arago, Banyuls-sur-Mer, in 1977-78, one of us (D.M.R.) found an association not previously described. A small actinian, whose color ranged from dead white to speckled grey, was collected in

water of several hundred metres depth on shells occupied by specimens of *Pagurus variabilis* A. Milne-Edwards and Bouvier (Plate I, A, B, C). At first, when examined alive, the pagurids were thought to be juveniles of the more common species, *Pagurus alatus* Fabricius, frequently collected at Banyuls with the actinian *Calliactis parasitica* living on their shells (Plate I, D). The two species have often been confused in the past.

With the descriptions of Milne-Edwards and Bouvier (1892), Selbie (1921) and Zariquiey Alvarez (1946; 1968) preserved specimens were positively identified as *P. variabilis*.

There was no record of this symbiosis or of the occurrence of this actinian at Banyuls or elsewhere in the Mediterranean. The examination of living specimens suggested that the anemone might be a species of *Paracalliactis*. The study of preserved specimens confirmed this and it was identified as a new species, *Paracalliactis mediterranea*. It was fortunate that in this case, both of the living symbionts were available for study. This paper reports the results of our observations on both living and preserved material.

MATERIAL AND METHODS

Twenty-three of the symbiotic actinians were collected between November 1977 and March 1978 by the laboratory vessel "Lacaze-Duthiers". These were maintained without loss in aquaria together with their pagurid hosts until the research was completed in May 1978. Pagurids and actinians were both fed small pieces of mussel twice weekly. Most of the actinians were removed at various times from the shells of their hosts and settled on stones or glass. In this state their behavioral interactions with the pagurids and their responses to shells could be studied. Twelve surviving specimens were prepared in 10% formalin in sea water for morphological examination and identification.

19 of the 23 actinians collected were found on 17 shells from various gastropods (e.g. *Nassa mutabilis*) inhabited by *P. variabilis*; 2 more came up on empty shells, which had probably been vacated by their occupants during the trawling. The length of these shells ranged from 18 to 60 mm (measured from the apex to the outside rim of the aperture). 18 of these specimens were taken in two trawls at two locations: 8 anemones on 6 shells (the first specimens obtained) came from one trawl sorted by students from the University of Zurich and said to have been taken about 15 km SE of Banyuls at 200 m depth; the other trawl containing 10 anemones on 9 shells was taken by D.M.R. 25 km ESE of Banyuls at a depth of 400 m. Trawls in other locations over a wide area brought up only 3 more specimens, all on *P. variabilis*. No *P. variabilis* were collected which did not have the actinian on their shells. These data suggest that the symbiosis is a normal feature of *P. variabilis* in this area. The two single trawls that brought up 6 and 9 *P. variabilis* suggested that there are local aggregations of this pagurid at certain places.

The two remaining specimens that bring the total to 23 were found on the shell of a single *Dardanus arrosor* which also carried 4 *C. parasitica*. Since hundreds of *D. arrosor* were collected in the course of the research and only one carried this small actinian, we regard this as a chance occurrence.

RESULTS

Identification of *Paracalliactis mediterranea* n.sp.

When disturbed, our specimens discharged acontia so, in establishing their identity, the Hormathiidae were considered first. This Family includes most of the acontiate actinians that live with pagurids. Not having deformed pedal disks ruled out the genus *Adamsia*, leaving the two genera *Calliactis* and *Paracalliactis* as prime candidates. Carlgren (1949) described the genera *Calliactis* and *Paracalliactis*; Hand (1975) summarized and extended Carlgren's descriptions in his study of two species of these genera in New Zealand; Doumenc (1975) worked on collections of actinians from the North Atlantic including 3 species of *Paracalliactis* which were described in detail.

Absence of cinclides is a fairly reliable means of distinguishing a species of *Paracalliactis* from *Calliactis* (Hand, 1975). In our specimens all the acontia emerged from the mouth when the animal closed tightly under pressure; they never made their exits from the column as in species with cinclides. It is true, as Hand (1975) pointed out, that the presence of cinclides in some of the less well known species of *Calliactis* has not been confirmed but they are very conspicuous in the common *C. parasitica*, *C. tricolor* and *C. polypus*. They are present though much less conspicuous in *C. conchicola* (Hand, 1975). Therefore the absence of cinclides points to *Paracalliactis* as the more likely genus to which these specimens may be assigned.

We thought it possible that our specimens might belong to one of the North Atlantic species of *Paracalliactis* reviewed by Doumenc (1975), *P. stephensoni* Carlgren, *P. michaelsarsi* Carlgren and *P. azorica* Doumenc. Indeed, they shared so many features with *P. stephensoni* that at first we were inclined to assign them to that species. But Doumenc (1975) described *P. stephensoni* as an abyssal species and it seemed from his description that the tubercles were more conspicuous in *P. stephensoni* than in our specimens. Finally data on the cnidom in the anemones in our collection ruled out their identity with any of the North Atlantic species. We therefore assigned our specimens to a new species, *Paracalliactis mediterranea*. The type specimen is deposited in the collection at the Laboratoire Arago, Banyuls-sur-Mer.

Paracalliactis mediterranea sp. nov.

(Fig. 1 and 2. Plate I.)

Nine preserved specimens were used for morphological examination. Their column heights were 1.0-2.5 cm, the diameters of the oral disks, 0.7-2.2 cm and the diameters of the pedal disks, 0.9-2.5 cm.

Column. Divisible into *scapus* and *scapulus*; scapulus translucent and mesenteries visible within; scapus with non-adherent-verrucae irregularly distributed; single co-

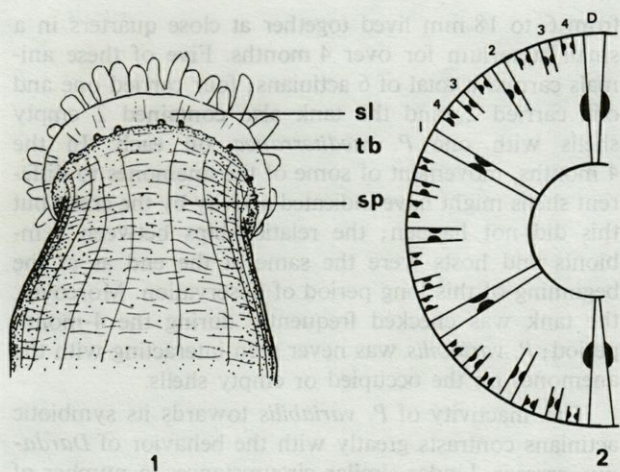


Fig. 1. — 1, *Paracalliactis mediterranea*. Preserved specimen from Banyuls drawn to show rough texture of scapus (sp), smooth, thin translucent scapulus (sl) and small irregularly placed tubercles (tb) at junction of scapus and scapulus. 2, *P. mediterranea*. Diagrammatic half section at level of pharynx to show two pairs of directive mesenteries (D) and examples of the four cycles (1, 2, 3, 4) and their retractor muscles.

rona of tubercles sometimes visible at scapus-scapulus boundary. According to Doumenc (1975) tubercles are a variable feature of *P. stephensoni* which he collected between latitudes 38° and 55° N and longitudes 08° and 13° W in the Atlantic. In our specimens, the tubercles on the corona when present were smaller than those described by Doumenc (Fig. 1). Also in most specimens they did not form a complete corona; in some cases it was difficult to decide whether these structures were tubercles as described by Carlgren (1928) and Doumenc (1975) or outliers of the uppermost series of verrucae found on the scapus. Hand (1975) described "weakly to well-developed" tubercles on *Paracalliactis rosea* which formed a complete corona only in larger animals.

Tentacles. Arranged in 3 cycles and all of same length; numbers approximately 60.

Oral Disk. Virtually colorless; tentacles not invading the central area.

Base. Circular in outline in regions of limbus; tightly adhering mucus often causing base and lower column to assume dark grey color and to feel rough to the touch because of adhering debris.

Pedal Disk. Transparent and revealing arrangement of mesenteries within.

Mesenteries. Arranged in 4 cycles with a total of 48 pairs following the formula 6-6-12-24; Cycle 1 perfect and sterile with 2 pairs of directives; Cycles 2 and 3 imperfect and fertile; Cycle 4 small and sterile (Fig. 2).

Muscles. Retractors diffuse and circumspect; parietobasilar developed and symmetrical; sphincter mesogloal, diffuse and divided into 2 zones, one with large alveoli and spaces for mesogloal tracts and the other with small round alveoli.

Acontia. White, long and coiling on their axes; located on mesenteric Cycles 2 and 3.

Cnidom :

Tentacles :

- 12.4-14.5 μ \times 3.2-9 μ spirocysts
- 21.3-22.5 μ \times 1.8-2.5 μ basitrichs
- 7.4- 8.2 μ \times 2.7-3.2 μ atrichs
- 20.5-22.7 μ \times 3.2-4.2 μ microbasic b-mastigophores

Actinopharynx :

- 10.3-12.5 μ \times 1.9-2.5 μ spirocysts
- 6.3- 7.5 μ \times 2.9-3.5 μ atrichs
- 14.3-16.2 μ \times 2.1-3.0 μ microbasic b-mastigophores
- 24.0-32.0 μ \times 3.4-4.5 μ microbasic p-mastigophores

Column (scapus) :

- 10.0-14.0 μ \times 3.5-4.0 μ spirocysts
- 23.0-25.0 μ \times 2.7-3.2 μ basitrichs
- 8.3- 9.2 μ \times 1.5-3.2 μ atrichs
- 24.0-24.5 μ \times 5.4-6.1 μ microbasic b-mastigophores

Mesenteric filaments :

- 9.4-10.1 μ \times 3.2-3.9 μ spirocysts
- 8.2- 9.1 μ \times 2.2-2.9 μ basitrichs
- 6.1- 6.9 μ \times 5.4-6.1 μ atrichs
- 13.2-14.5 μ \times 5.3-6.1 μ microbasic b-mastigophores
- 23.2-24.5 μ \times 7.6-8.1 μ microbasic p-mastigophores

Acontia :

- 5.4- 5.9 μ \times 3.6-4.2 μ basitrichs

Spirocysts, atrichs and mastigophores were discharged when measured, basitrichs were intact.

In contrast with these data, *P. stephensoni* lacks atrichs and microbasic b-mastigophores, it has basitrichs of two kinds in the actinopharynx, it has no basitrichs in the filaments and few of the capsular dimensions correspond (cf. Doumenc, 1975).

Dechancé and Dufaure (1959) described a small white actinian symbiont of *Anapagurus laevis* in the Western Mediterranean which they named *Paracalliactis lacazei*. But this animal possessed cinclides and also a fosse, features lacking in *Paracalliactis* as defined by Carlgren (1928). For these reasons Hand (1975) doubted that this animal is a *Paracalliactis*.

Behavior of Pagurus variabilis towards Paracalliactis mediterranea

From our collections of *P. mediterranea* in the vicinity of Banyuls we conclude that this actinian is normally a symbiont only on *P. variabilis*. It has not been found on *Pagurus alatus* or on *Paguristes oculatus*, both of which carry *Calliactis parasitica* at Banyuls and only two found on *Dardanus arrosor*. Therefore, if behavioral interactions are to be demonstrated between this pair of species, they should be sought in *P. variabilis*.

We have not been able to demonstrate an active behavior pattern by *P. variabilis* toward *Paracalliactis*. Thus 6 *P. variabilis* whose carapace lengths ranged

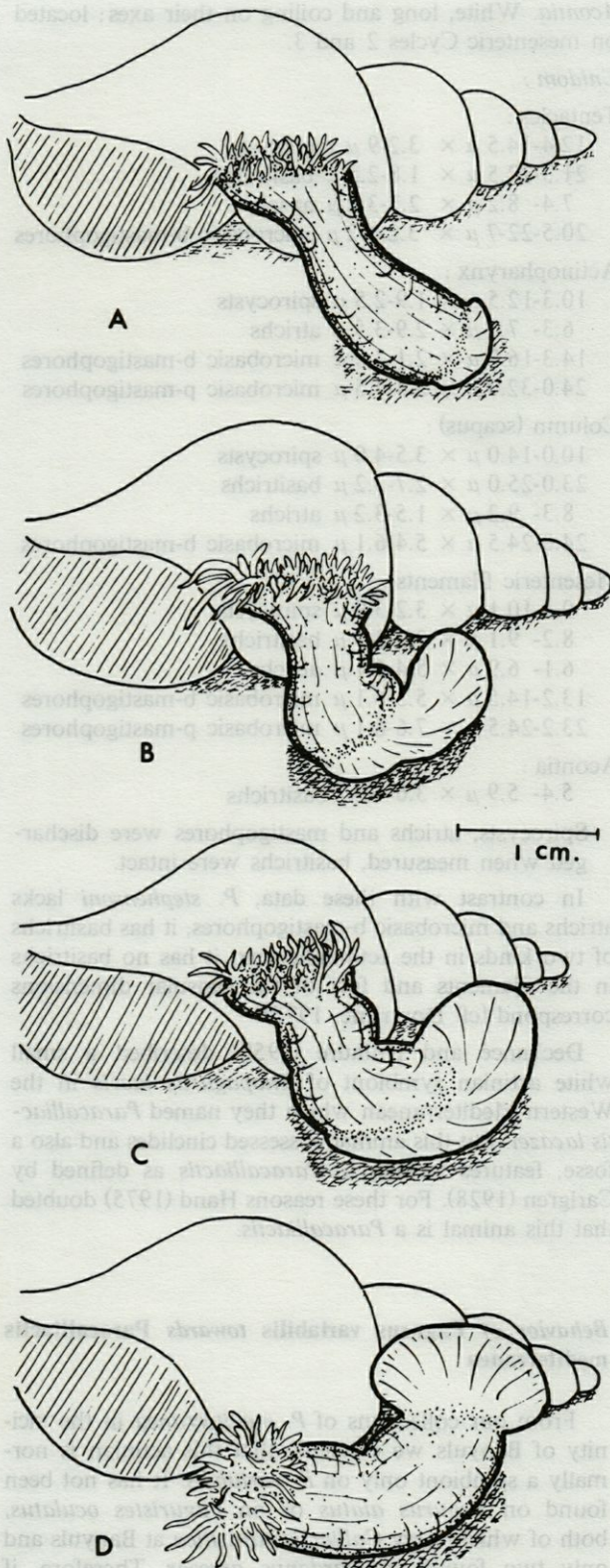


Fig. 2. — Detached *P. mediterranea* climbing on a shell. A, tentacles clinging and pedal disk becoming mobile (4 min). B, pedal disk expanded unilaterally with "tongue" directed towards shell (6 min). C, expanded pedal disk close to shell after two approaches and retreats (15 min). D, pedal disk settling on shell after two more approaches and one retreat; tentacles free of shell and column assuming erect position (32 min).

from 6 to 18 mm lived together at close quarters in a small aquarium for over 4 months. Five of these animals carried a total of 6 actinians; four carried one and one carried 2, and the tank also contained 2 empty shells with one *P. mediterranea* on each. In the 4 months, movement of some of the anemones to different shells might have indicated activity by the crabs but this did not happen; the relationships between symbionts and hosts were the same at the end as at the beginning of this long period of observation. Moreover, the tank was checked frequently during the 4-month period; *P. variabilis* was never seen interacting with the anemones on the occupied or empty shells.

This inactivity of *P. variabilis* towards its symbiotic actinians contrasts greatly with the behavior of *Dardanus arrosor*. Under similar circumstances, a number of *D. arrosor* in a confined space frequently display activity towards their actinian symbionts (*Calliactis parasitica*). They interact with one another to bring about transfers of anemones, especially from empty shells (Ross, 1979).

Ten trials were carried out in which single *P. mediterranea*, living on stones and other non-shell surfaces, were placed in small vessels with single *P. variabilis*. The pagurids encountered the actinians either in moving about or when the actinians were moved into contact with their antennae, chelipeds or pereopods. In these situations, *P. variabilis* either remained in contact and inactive or moved away without reacting in any way. By contrast, when *D. arrosor* encounters *Calliactis* on a stone, it usually begins at once to transfer the anemone to its shell. Other species occurring at Banyuls that carry *Calliactis* on their shells, *P. alatus* and *Paguristes oculatus*, also transfer *Calliactis* to their shells but by special behavior patterns which are less active and less consistent than *D. arrosor* (Ross, unpublished observation).

Behavior of Paracalliactis mediterranea in response to shells

Trials were also carried out in which detached *P. mediterranea* were brought into contact with *Nassa* shells on which our specimens were found. In 8 cases in 10 trials, the detached anemone behaved like most other symbiotic anemones, clinging to the shell and climbing upon it (Fig. 2). In some respects this response of *P. mediterranea* to shells differed from that of *Calliactis* spp. as described by Ross (1974) and from that of *Paracalliactis japonica* Carlgren as described by Ross and Wada (1975). The column of *P. mediterranea* appeared less flexible than in other species and kinks were seen during its flexions. Its distinctive feature was an asymmetrical inflation of the pedal disk producing a tongue-like extension as a means of searching for and adhering to the shell (Fig. 2B). *P. mediterranea*, like *P. japonica*, underwent a series of flexions and inflations, pausing and retreating between each until the extended tongue of the pedal disk contacted and stuck to the shell (Fig. 2 C, D).

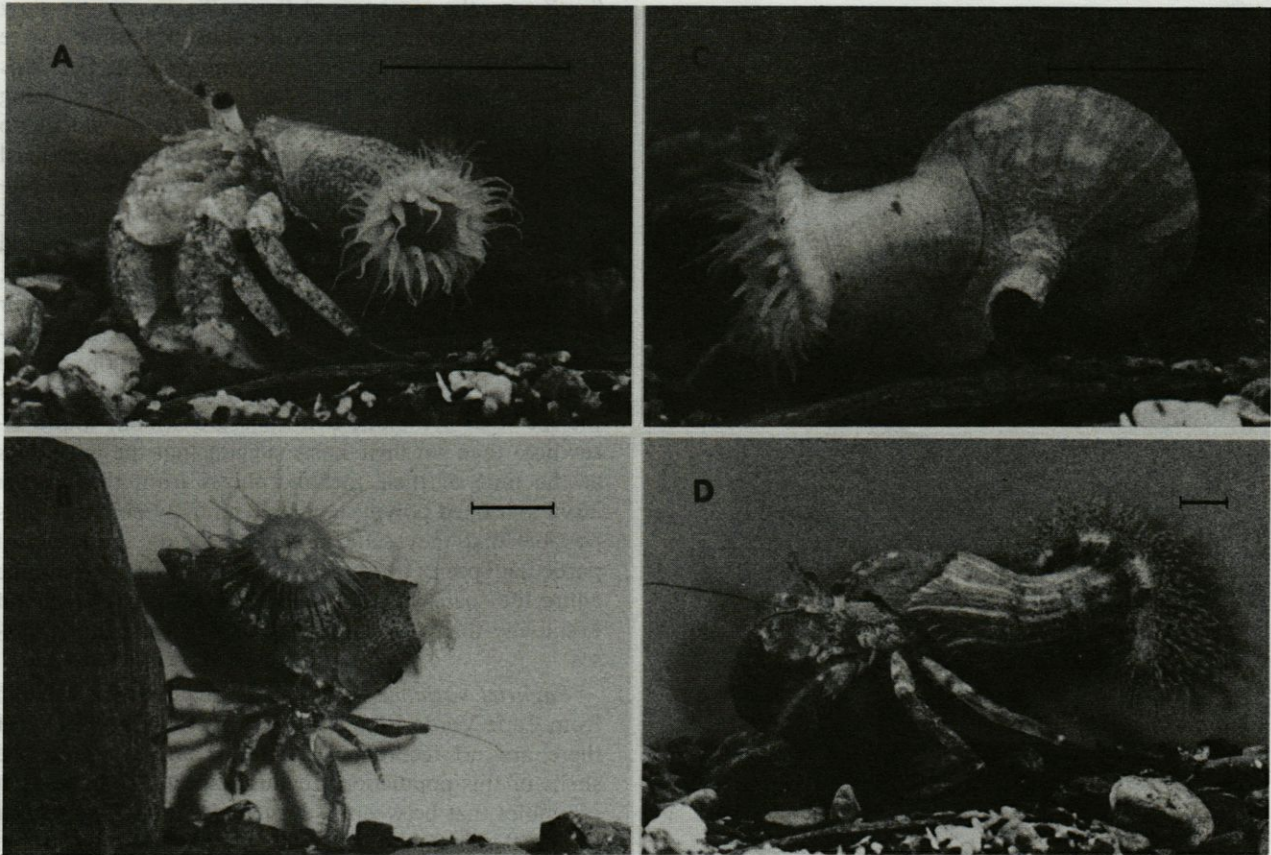


PLATE 1. - A and B, *P. mediterranea* on shells occupied by *Pagurus variabilis*, and C, on unoccupied shell. D, *Calliactis parasitica* on shell occupied by *P. alatus*. Scales: 1 cm.

P. mediterranea on occasion also transferred from other surfaces to shells; in 12 presentations, 5 successful and 3 partial or abortive transfers occurred. In 4 cases, the typical clinging and detachment movements were absent. Fig. 3 shows several stages in one of the transfers. Repeated searching movements by the inflated pedal disk, with changes in direction and in the anchorage on the shell, occurred over a long period (not less than 60 min and in one case 160 min). These observations show that *P. mediterranea*, like most other symbiotic actinians, possesses a behavior pattern by which it responds to shells and settles on them preferentially. The response is more capricious and slower than in the more active *C. parasitica*. Like most of these symbiotic actinians examined so far, *P. mediterranea* shows some features in its shell climbing that are peculiar to this species.

DISCUSSION

This paper reports the occurrence of another actinian-pagurid symbiosis and presents data on the behavioral interactions of the two partners. These data

should be examined against the background of other data which exist already on some 20 symbioses of this type. A number of inferences can be drawn from the information presented above.

Like other symbiotic actinians, *Paracalliactis mediterranea* is not exclusively species-specific in its choice of hosts since it was found also on *D. arrosor*. *P. stephensoni* also has been found on 2 different hosts in the North Atlantic. Even though only a small number of *P. mediterranea* has been collected in the area sampled, it seems from these and other examples that a symbiotic actinian can associate with any pagurid that is suitable in size, habits and location. A pagurid that actively picks up actinians (like *Dardanus arrosor*) can facilitate the establishment of a symbiosis; symbioses of this type are the most widespread and conspicuous. But the symbiosis of *P. mediterranea* with *P. variabilis* presents another case (like *C. parasitica* and the adult *Pagurus bernhardus*) in which the pagurid host is indifferent to the actinian. One must conclude that the actinian establishes the association by settling preferentially on the pagurid's shell. Probably this is a case of phoresy in which the actinian has the advantage of transport and of a firm elevated perch. The pagurid possibly gains some protection from predators but apparently this is

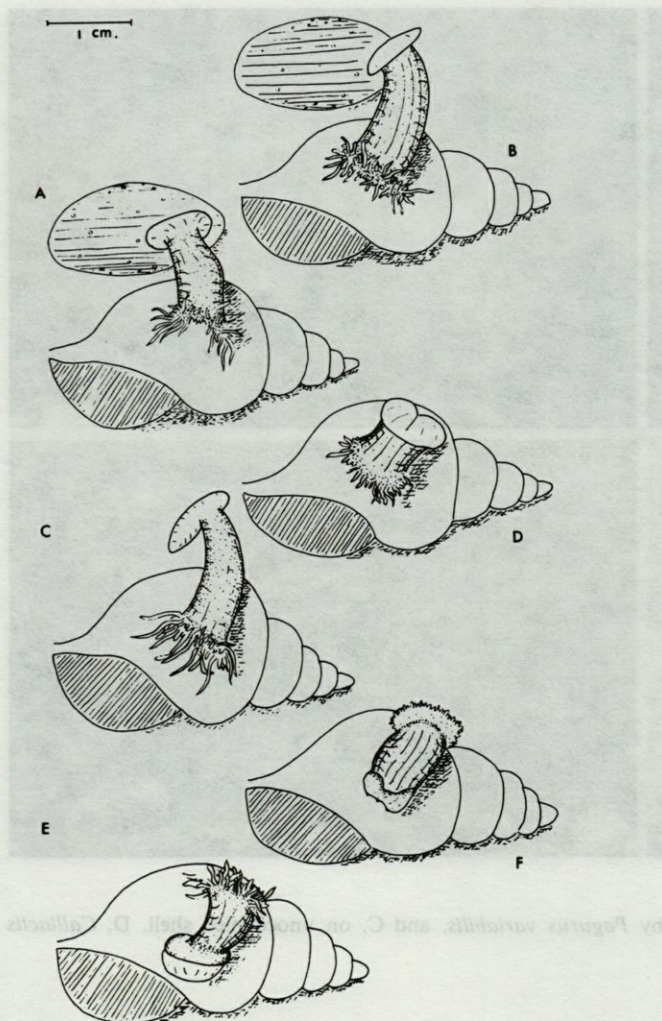


Fig. 3. — *P. mediterranea*. Transfer from stone to shell. A, initial response of tentacles to shell while still firmly settled on stone (3 min). B, pedal disk detached from stone (8 min). C, excentric tongue-like swelling of pedal disk in direction of shell (11 min). D, pedal disk in retreat phase after two approaches to shell failed to make contact; note groove between two swellings on pedal disk (18.5 min). (Two changes of direction and re-siting of tentacles between D and E). E, margin of pedal disk in contact with shell and beginning to adhere (43 min). F, later stage in settlement on shell. One pedal edge adhering while opposite edge curls over after tentacles have released hold and animal begins to assume upright position (63 min).

fortuitous in this case and not due to any action of its own to acquire actinian partners.

This is the third species of *Paracalliactis* whose behavior has been studied in relation to its association with the hermit crab on which it lives. Compared with *Cal-*

liactis spp., the responses of *Paracalliactis* spp. are slow and less well coordinated. None show the same degree of relaxation and flexibility that one finds in *Calliactis* when it responds to the shell or when it is being manipulated by a pagurid. Individual *Paracalliactis* do not relax and detach in response to gentle mechanical stimulation as *Calliactis* does (Ross, personal observation). However, large detached *P. japonica* remain tightly closed and unresponsive to shells except when held and palpated by one of the pagurids, e.g. *Dardanus* spp., that customarily detach and transfer *Calliactis* to their shells. The gap in all these studies is our lack of knowledge of the earliest stages in the formation of the association. Many features of these symbioses (especially the fact that symbiotic actineans are seldom found elsewhere than on their hosts suggest that the anemones at the time of their metamorphosis from the planula larva to a fixed polyp, settle preferentially on the shells of particular species (Ross, 1980). Information covering the entire life spans of pagurid-actinian associations should eventually throw light on these aspects of such symbioses.

Pagurus variabilis is found in the Eastern Atlantic from Cape Verde Islands to Norway (Selbie, 1921). Yet there are no records of symbiotic anemones on the shells of this population. In this respect the association resembles that between *P. bernhardus* and *C. parasitica* in that the anemone lives with the pagurid only in one section of the pagurid's range. This suggests that the symbiosis benefits the pagurid only marginally if at all, a point that is supported by the pagurid's indifference to the anemone in laboratory trials. On the other hand, since *Paracalliactis mediterranea* has not been found living apart from pagurids, it can be argued that the association is beneficial to it and that in this case, as with *C. parasitica*, the anemone's response to shells is the primary factor in establishing the association.

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