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THE LIFE HISTORY OF *LERNAEODISCUS PORCELLANAE* (CIRRIPEDIA: RHIZOCEPHALA) AND CO-EVOLUTION WITH ITS PORCELLANID HOST

*Larry Edward Ritchie and Jens Thorvald Høeg*

**ABSTRACT**

The elaborate life history of the rhizocephalan parasite *Lernaeodiscus* includes a number of counterdefensive measures specifically adapted to circumvent defense systems of the host crab *Petrolisthes*.

*Lernaeodiscus* is dioecious. The externa produces large male and small female cyprids. The female cyprids invade the host by means of a kentrogon stage. The sole site of invasion is the gills. The female parasite later erupts on the ventral side of the abdomen as a virgin externa. This has to be hyperparasitized by a male cyprid in order to reach sexual maturity. The life cycle is completed in about 5 months.

Autogrooming is the crab’s primary defense against infestation and ordinarily only crabs slightly deficient in this regard become infested. Once inside, the parasite gains control of the host crab and induces it to accept the parasite as “self”—in effect, as its own reproductive system. This nullifies all remaining defenses the crab might have against the parasite. In addition, infested male crabs become behaviorally and morphologically female, so that they provide maternal care for the external reproductive body of the parasite, as do infested female crabs, rather than attempting to remove the parasite from their body. While the parasite has diverted all of the reproductive resources and capabilities of the crab to its own use, the crab otherwise carries out its life as a normal member of the intertidal community.

The Rhizocephala are highly modified barnacles that parasitize crustaceans, primarily Decapoda. They have degenerated to such an extent that they are recognizable as cirriped crustaceans only by their larval forms, the nauplius and the cyprid. Through retrogressive evolution female rhizocephalans have evolved a greatly simplified body plan, an internal absorptive system (interna) for food uptake and an external reproductive system (externa). The externa of rhizocephalans infesting crablike Decapoda resides beneath the host’s abdomen and, in effect, mimics the egg-mass of the host.

Historically, there has been considerable interest in the evolution of the complex life history of rhizocephalans. What selection pressures might have been responsible for the intercalation of the kentrogon larva into the barnacle’s life cycle? Why should there be indirect establishment of the parasite in the brood chamber formed by the reflexed abdomen of the host; why not simply direct establishment? To answer these questions it is necessary to understand the behavior and morphology of the host.

The life history of the rhizocephalan *Lernaeodiscus porcellanae* Müller, 1852, and its relationship with the porcelain crab *Petrolisthes cabrilloi* Glasell, 1945, was investigated from 1971 to 1976 at the Scripps Institution of Oceanography. It was possible to culture the female parasite through its entire life cycle: nauplius, cyprid, kentrogon, internal phase, virgin external phase, and sexually mature phase including entrance and fertilization by male cyprids (Fig. 1). Although kentrogons of a few rhizocephalan species have been obtained (Delage, 1884; Smith, 1906; Veillet, 1964; Yanagimachi, 1961c), the rearing of the larvae has caused much difficulty (Veillet, 1951). This is part of the reason that it has never before been possible in the laboratory successfully to introduce a female cyprid into a host animal and subsequently to observe the emergence of the same indi-
vidual as an externa. The ease with which kentrogons of *L. porcellanae* could be obtained opened the way for a variety of experiments and observations.

**MATERIALS AND METHODS**

Sampling of *P. cabrilloi* was carried out throughout the period of investigation at four stations near La Jolla. Crabs infested with *L. porcellanae* were isolated in beakers with sea water, which was changed regularly. Following spawning of the parasite, an infested crab was removed from the beaker to prevent it from feeding on the parasite's larvae. Once this procedure was established, rearing of *L. porcellanae* larvae was relatively easy because the larvae of rhizocephalans are nonfeeding. The newly released nauplii, transferred to new vessels with a change of sea water (filtered in the summer), required no further treatment. When the cyprid stage was reached after 3 to 5 days depending on temperature, cetyl alcohol (C16H34O) was added to reduce surface tension and prevent adhesion of larvae to the air-water interface (Yanagimachi, 1961b). The length of the carapace of 25–30 cyprids from each brood was measured with an ocular micrometer and the sex determined. The cyprids could be easily sexed on the basis of size, in agreement with the observations of Veillet (1943, 1945) and Yanagimachi (1961a).

For experiments of host infestation, about 100 female cyprids were introduced for every crab tested. Exposure was 6 hours although infestations may be obtained with exposures as short as 5 minutes.

The search for the site of kentrogon formation and its penetration began with a general survey of the crab using a dissection microscope. It was followed by a more thorough examination, with the aid of a compound microscope, of body parts mounted in Turtox “CMC” with acid fuchsin. Eventually it was discovered that the gills were the sole site of invasion. This was very convenient since the gills are easily removed and mounted for microscopic examination.

**RESULTS AND DISCUSSION**

The Life Cycle of the Parasite

The sexes of *L. porcellanae* are completely separate, and the life cycle, summarized in Fig. 1, conforms to the general scheme determined by Ichikawa and Yanagimachi (1960) for *Peltogaster paguri* and *Sacculina senta* and by Yanagimachi (1961c) for *Peltogasterella gracilis* (syn. *socialis*), except that females of *L. porcellanae* do not always produce broods of one sex but may shift after producing broods of either sex for a period.

Reproduction by the mature female parasite is continuous, with a succession of broods every 10–14 days depending on the time of year. The release of a batch of larvae follows within a day of the hatching of the first stage nauplii within the mantle cavity. Following release, a new brood of eggs varying in number from a few hundred up to 20,000 depending on size and age of the externa, is laid in the mantle cavity.

There are four naupliar stages before metamorphosis to cyprids. Male larvae are significantly larger than female larvae; the size difference is most pronounced in the cyprid stage (Fig. 2). While a single externa usually produces either male or female broods, as in *Peltogasterella* (Yanagimachi, 1961a), some parasites make abrupt shifts to production of larvae of the opposite sex. During the transition, an externa may produce one or a few mixed broods (Fig. 3B). Female batches were predominant in the summer, and males during the winter (Fig. 2). The winter maximum for male larvae is coincident with the high frequency of newly emerged, virgin female externae during this season.

Female cyprids enter the branchial chambers of the crab and attach to the gill lamellae, well-removed from the abdominal brood chamber of the prospective host (Fig. 4). This takes place no sooner than three to five days after the nauplius-cyprid molt. If infestation experiments were performed before this time no cyprids settled on the gills. Metamorphosis into the kentrogon starts immediately after
Fig. 1. Life cycle of *Lernaeodiscus porcellanae*, the rhizocephalan parasite of the porcelain crab *Petrolisthes cabrilloi* in southern California. First stage nauplii hatch within the mantle cavity of the parasite (A) and are subsequently released into the plankton as first and second stage nauplii (B). Fourth stage nauplii metamorphose into cyprids (C). Female cyprids, significantly smaller than males, enter the gill chambers of the host (D) and attach to gill lamellae (E) where, if not removed by host grooming, they metamorphose into kentrogons (F). The kentrogon injects the primordial parasite (G) into the host where it ramifies throughout the body before the virgin externa is produced and erupts on the ventral side of the host’s abdomen (H). When male cyprids locate a virgin externa they attach in the aperture and extrude into the mantle cavity male cells that migrate to the male-cell receptacles where they differentiate into spermatozoa. Subsequently the externa matures and produces eggs (I) which are periodically laid and fertilized in the mantle cavity (J).

settling and is extremely rapid; the cyprid shell may be discarded and metamorphosis completed 10–15 minutes after the cyprid first settles on a gill.

The kentrogon develops a hollow stylet on its ventral side in the position where the mouthparts would have been, 20–40 hours after attachment on the host crab. But, contrary to the situation in *Sacculina*, the stylet, “le dard” of Delage (1884), does not penetrate through the larval antenna. It punctures the host gill beneath the attached larva (Fig. 4C, D) and after 70–90 hours a small mass of cells is injected directly into the host. The time of injection is determined indirectly by the detection of empty kentrogons on the gills.

The injected cells, which constitute the female parasite in a primordial state, probably migrate through the hemocoel to the abdomen (Smith, 1906) and there develops the interna, or root system. The duration of the internal phase was
determined by the length of time required for the emergence of an externa after penetration of the kentrogon. For these experiments the crabs used had been isolated for one month prior to invasion in order to keep the number of crabs that might already have been invaded to a minimum. In one experiment 300 crabs had their cleaning limbs removed (see later) and were exposed to female cyprids for six hours. They were kept alive and inspected for emergence of externae after 87 and 114 days respectively. After 87 days 237 crabs (79.0%) were still alive and of these 14 had developed an externa (5.9% parasitism). Twelve of these 14 externae (85.7%) were virgin, indicating that they had only recently erupted. After 114 days 223 crabs survived (74.3%) and of these 73 had an externa (32.7% parasitism). Of these 73 externae 51 were in the virginal state. Consequently 59 externae (80.8% of the total evagination) had erupted between 87 and 114 days after invasion. In another experiment 326 crabs with their cleaning limbs removed were exposed to female cyprids and inspected after 135 days and 225 days. Fifty crabs used as controls were treated in a like manner except that they were not exposed to cyprids. Of the experimental crabs 210 (64.4%) survived the experiment, and of these 51 had developed an externa after 135 days (24.3% parasitism). Forty-seven control crabs (94.0%) survived and only three had developed exter-
nae after 135 days (6.4% parasitism). Neither experimental nor control crabs developed any additional externae during the three additional months of observation.

The externa, in which the female reproductive organs will develop, extrudes between the first and second abdominal sternites where it receives protection and, as it develops, conforms to the shape of the abdominal brood chamber of the host (Fig. 1H).

These observations verify the contention of Delage (1884) and Smith (1906) that rhizocephalan externae erupt some distance away from the region where the invasion took place.
The newly emerged externa does not reach sexual maturity unless it has been invaded by male cyprids, as demonstrated by Yanagimachi (1961c) in Peltogasterella. Upon extrusion, the externa has no opening to the mantle cavity. After about a week the virgin externa undergoes a molt into a stage with an open mantle aperture, at which time it becomes strongly attractive to male cyprids. They settle around and in the aperture, usually in numbers of 3–5, but up to as many as 10. In the laboratory, male cyprids will settle on the virgin externa in less than a minute after being introduced into a dish with a crab having one. The male cyprid does not form a kentrogon but extrudes a small mass of cells, which eventually comes to reside within the male cell receptacles of the female. These male cells then begin spermatogenesis. Soon afterwards egg production begins.

If ripe virgin externae on crabs are kept in isolation, they neither molt nor begin egg production. However, such externae can remain almost indefinitely and still reach sexual maturity upon exposure to male cyprids. Virgin externae of Sacculina carcini also need male cyprids in order to reach sexual maturity and likewise do not increase in size in their absence. But contrary to L. porcellanae they die if they are not hyperparasitized within a short period of time after they have become external (personal communication, J. Lützen, Institute of Comparative Anatomy, Copenhagen).

Crabs once infested are presumably parasitized for life. Infested crabs were kept in the laboratory for more than two years without the parasite showing ill effects. Regeneration of externae is quite common. They are apparently lost only when damaged. Crabs sometimes bear scars of lost externae. These scarred crabs
often have an apparently regenerated externa. Regeneration of externae was noted by Day (1935) in *Sacculina carcini*. Regeneration in this species was also studied by Lützen (1981) and found not to play a significant part in its life cycle. Hartnoll (1967) removed the externae of *S. bicuspidata* from four host crabs and observed that two of them regenerated a new one.

**Egg Mimicry**

*L. porcellanae*, like all other kentrogonid rhizocephalans, castrates its host, and infested male crabs develop behavioral and morphological female characters. In addition, the externa mimics the host's egg mass in form and position, and the host, males as well as females, treats the externa as its own brood. Infested *P. cabrilloi* were repeatedly observed caring for the parasite's externa; ventilating it by waving the abdomen and by frequently grooming it with the cleaning limbs. In common porcelain crabs, as in anomurans in general, the last pair of thoracopods are modified for grooming the gills and general body surfaces in both sexes, and the eggs in females. Parasitized male as well as female crabs display egg grooming and ventilating behavior. If the cleaning limbs are removed from a parasitized crab, the externa soon becomes fouled and necrotic. In particular, it seems to suffer from lack of assistance during molting, which occurs after each release of a brood, and unshed portions of the exoskeleton can be observed trailing from the mantle aperture.

When it is time for the parasite to release its larvae, the host assists by performing customary spawning behavior. Normally cryptic, the porcellanid climbs out from under a rock, elevates the body on tiptoes, and then lowers and raises the abdomen in a waving action. Simultaneously, the parasite expels its nauplii into the current generated by the host.

In studying more than 2,000 live crabs, it was clear that “parental” behavior and care for the parasite continued for life. Interestingly, an effect on the migratory behavior of the crab *Carcinus maenas* (L.), apparently caused by its parasite *S. carcini*, was noted by Rasmussen (1959).

**Behavioral Response of the Host to Female Cyprids**

Although female cyprids were successfully reared in large numbers in the laboratory, early attempts to induce infestation of *Petrolisthes cabrilloi* generally failed. Following exposure to female cyprids of different ages for varying intervals of time, crabs were sacrificed and examined for cyprids and/or kentrogons. However, larvae were rarely found crawling on the crabs.

Whenever cyprids were introduced the crabs would initiate cleaning behavior, usually within 30 seconds of first contact and particularly in the branchial chambers (Fig. 5). This is not surprising because grooming has adaptive value in decapod crustaceans in that it keeps the body clear of fouling organisms and general debris (Bauer, 1979). When a crab was exposed to several hundred cyprids, the fervent cleaning that followed became disorganized, and within half an hour or so the crab collapsed and eventually died.

These observations suggested that healthy *P. cabrilloi* averted infestation by grooming activity. To test this hypothesis crabs were prevented from grooming by ablation of the cleaning limbs and then exposed to female cyprids. Untreated crabs were used as controls. At various intervals after exposure, experimental and control crabs were sacrificed and examined for kentrogen metamorphosis and invasion. As expected, crabs without cleaning limbs were found with ken-
trogons on their gills. Depending on time of sacrifice after exposure, kentrogons were in varying stages of either stylet formation, penetration, or invasion.

Following this discovery, experiments were undertaken to explore the effectiveness of *Petrolisthes cabrilloi* cleaning behavior in preventing parasitism. Forty-two experiments were performed involving numerous permutations on the original design. In all, 1,479 treated and 1,358 untreated crabs were employed. The results from the sacrificed individuals are summarized in Fig. 6A, which illustrates the effectiveness of *P. cabrilloi* grooming behavior to remove kentrogons before invasion. Limb ablated crabs cannot remove kentrogons by grooming and the decrease in the mean number of kentrogons found on experimental crabs probably reflects the fact that kentrogons tend to fall off accidentally.

The only unambiguous way to determine whether the presence of empty kentrogons on the gills indicates that successful parasitization has taken place is to keep the suspected infested crabs alive for a prolonged period and to observe the number of erupting externae, as was done in the experiments designed to determine the length of the internal phase. When these experiments were repeated using as controls crabs with intact cleaning limbs, the resulting level of parasitism in four similar experiments was between 4.8% and 15.8% for the controls. The experimental crabs had levels of parasitism between 63.3% and 86.7% in these same four experiments.

Cleaning efficiency can be defined as the ability of a crab to remove all kentrogons before the invasion period. In those experiments where control crabs...
Fig. 6. Cleaning efficiency of *Petrolisthes* species after exposure to female cyprid larvae of *Lernaeodiscus porcellanae*. Abscissa: number of hours after exposure to female cyprids. Ordinate: mean number of kentrogons per host. (A) *Petrolisthes cabrilloi*, the normal host of *Lernaeodiscus porcellanae* in southern California. Experimental animals (triangles, N = 17), prevented from cleaning by ablation of the last pair of thoracic limbs, failed to remove all kentrogons after 140 hours, while
were not carefully selected for optimum condition, approximately 10% were unable to prevent invasion. Subsequent experiments indicated that crabs with slightly damaged cleaning limbs (e.g., intentionally injured at the tip by pinching with a pair of forceps), as well as crabs that were injured in some other way or were sick, were likely to become infested. Results from other experiments indicated that otherwise normal crabs nearing ecdysis were also more susceptible to invasion. Furthermore, *P. cabrilloi* with a visible externa, once their cleaning limbs were removed, became as readily invaded as uninfested crabs as evidenced by empty kentrogons on their gills. Only in very few instances did this result in subsequent appearance (four months later) of an additional externa.

The evidence from these experiments indicates that one of the functions of grooming is a defense against parasitism, and that impaired grooming dramatically increases the probability of infestation. Successful invasion of the parasite under natural conditions is probably due to illness, injury, or mechanical inadequacies imposed by softening of cleaning appendages prior to molting, or from any combination of these factors. The importance of impairment in determining parasite success in the field was demonstrated by the fact that crab populations living among loose cobbles on rocky shores have a greater incidence of parasitism (*x̄* = 35%; seasonal oscillations from 10% to 60%) compared to crabs living sheltered among mussels in equally high-energy environments (*x̄* = 10%; seasonal range from 2% to 18%). Injury resulting from shifting cobbles apparently renders these crabs more susceptible to infestation.

**Specificity of *Petrolisthes cabrilloi* Grooming Behavior**

Grooming behavior in one form or another is exhibited by all decapod crustaceans (Bauer, 1979). All porcelain crabs possess the same cleaning repertoire. With this in mind, the specificity of *P. cabrilloi* grooming defense against *L. porcellanae* was studied.

Three closely related species of *Petrolisthes* [*P. armatus* (Gibbes), *P. gracilis* Stimpson, *P. hirtipes* Lockington] were collected from the nearby Gulf of California. All are endemic to that region, none is sympatric with *P. cabrilloi*, and none is known to host a rhizocephalan. Kentrogon invasion experiments were performed on these species using *P. cabrilloi* as a control (Fig. 6B). In contrast to *P. cabrilloi*, these species did not immediately respond to the presence of female cyprids. However, they did initiate cleaning behavior after 5–10 minutes of exposure. Although the experimental crabs groomed their gill chambers, their activity was not nearly as vigorous as that observed for *P. cabrilloi*. Moreover, female cyprids of *L. porcellanae* accepted the branchiae of all experimental hosts as suitable substrates for attachment. Even more significant was the discovery that the grooming activity of all three experimental species failed to remove the kentrogons and thus prevent parasite invasion.

No experiments were purposely designed to see if *L. porcellanae* would be controls with intact cleaning limbs (circles, *N* = 23) were able to do so in less than 80 hours. (B) *Petrolisthes gracilis* (squares, *N* = 94), *P. hirtipes* (circles, *N* = 40), and *P. armatus* (triangles, *N* = 45), all from the Gulf of California, and not normally infested by a rhizocephalan parasite. With cleaning limbs intact, they failed to remove a significant number of attached kentrogons by 120 hours after exposure.

Vertical bars through mean values represent the 90% confidence limits. The "invasion zone," about 80 hours after exposure, is the time interval beyond which only empty kentrogons are found on the gills, indicating that the female cells of the parasite have been injected into the host.
able to continue developing internally and succeed in producing the externa stage on the three non-host species. However, in two instances, on *P. cinctipes* (Randall) and *P. hirtipes*, an *L. porcellanae* externa was produced. Yet, as already mentioned, none of these porcelain crabs are known to play host to a rhizocephalan. Either they have some other form of defense, or some non-crab related factor excludes an appropriate parasite from the region. In any event, their inability to prevent infestation when exposed to the parasite of *Petrolisthes cabrilloi* is instructive here in highlighting the specificity of the latter’s cleaning behavior.

The Co-evolution of Rhizocephalans and Their Hosts

During co-evolution of a parasite-host relationship, where fitness is impaired and especially where parasitic castration is involved, any or all mechanisms, structural, behavioral, and chemical, would be selected as defenses against the parasite. This principle has been amply demonstrated in the area of predator-prey relationships (Edmunds, 1974).

In the kentrogonid Rhizocephala host-parasite relationship, parasitism results in the permanent castration of the host, making it a nonbreeding competitor with its own species. This would appear to be the maximum price a parasite could extract from its host’s fitness. Thus, parasite success must supply a tremendous selection pressure for the acquisition of a host defense system that would minimize if not eliminate parasitism.

Grooming organs and behavior probably first evolved as a general defense against a broad range of animate and inanimate fouling targets. Once a cleaning mechanism has been initiated it can become progressively better adapted in discriminating between fouling objects according to the value placed upon their removal. In *P. cabrilloi*, for example, the organs and the behavior associated with cleaning became a precise mechanism for the recognition, location, and rapid removal of specific targets, such as the *L. porcellanae* cyprid and kentrogon. In contrast, the inability of the three non-host species, all with the appropriate grooming organs, to prevent parasite invasion, indicates a nonspecific grooming behavior. This lack of appropriate response is probably due to the absence of appropriate selective pressures on generalized behavioral patterns since these crabs apparently are not sympatric with this rhizocephalan parasite.

A Hypothetical Scheme for the Evolutionary Adaptation of Rhizocephalans to their Hosts

Baer (1951, 1971) noted the uniqueness of the rhizocephalan kentrogon. He stated that it is “one of the most astonishing adaptations to parasitism known” and so “teleological” in function that it is nearly impossible to trace its evolution. Yet, in all probability, the kentrogon phase was introduced into the life cycle of rhizocephalans as the end product of a counter-defensive trend; it evolved to circumvent cleaning defenses. The evolution of this counter-defense may be divided into three stages:

1) It is probable that the Rhizocephala first evolved as a purely ectoparasitic group. The establishment of the parasites of this evolutionary stage would have been direct, i.e., the adult parasite developed at the attachment site of the cyprid larva.

2) When the host’s grooming defense became effective in removing or damaging the ectoparasite, an internal (endoparasitic) phase could be a counter-defensive measure. Therefore, it is plausible that the internal phase of the life cycle evolved as a defense against grooming. This hypothetical stage would still be vulnerable
to grooming during the attachment and invasion phase of the larva. Increasing effectiveness of the host’s cleaning defense would have produced counter-defensive changes of the invading larva. The kentrogon is smaller, more firmly attached, and has a lower and smoother profile (without setae) than the cyprid (Fig. 5 B–D). This morphology impedes removal by grooming. In addition, perfection of the kentrogon must have included increasing the speed of development. Whereas the cyprid of *S. carcini* uses more than 24 hours to metamorphose into the kentrogon (Delage, 1884) the *L. porcellanae* cyprid completes metamorphosis into the kentrogon within 15 minutes. This is explained as a response to increasing effectiveness of the host’s grooming defense. That grooming differs among closely related crustacean families has been noted by Bauer (1979). The kentrogon evolved with one specific function as a vehicle of rapid penetration it assures successful establishment of the internal phase.

3) However, the parasite returns to the surface as the externa. What keeps the host from recognizing it as foreign or “parasite” and destroying it, since the cleaning behavior is still available? When an externa appears on the surface of the host, it must either be in a position or of a form that cannot be removed by the host, or it must be perceived as “self” and not harmed in any way. On ancestral crustacean hosts, it must have been one or the other of the first cases, but ultimately it was perceived as “self” and in crablike forms, evolution led to egg-brood mimicry and the benefits of maternal care and protection, even by males of the host species.

The evolution of host control, probably through some form of hormonal action (Veillet, 1955; Reinhard, 1956; Hartnoll, 1967), represents the ultimate counter-defensive adaptation of the Rhizocephala, for it nullifies the host’s defense system. Some such system is essential for survival on host groups that acquired sophisticated cleaning repertoires. Once host control is achieved, the host is in the absolute service of the parasite; for example, *P. cabrilloi* has no defense against an established infestation of *L. porcellanae*. Moreover, the host will work to prevent subsequent invasion by additional parasites, presumably to the advantage of the established parasite.

The strongest evidence for the proposed counter-defensive evolution of the kentrogonid Rhizocephala is found within the extant groups. The probably primitive Akentrogonida (cf. Newman *et al.*, 1969) are parasitic exclusively on non-cleaning host groups. The most primitive forms are ectoparasitic, e.g., *Chthamalophilus* Bocquet-Védrine (1961) and *Boschmaella* Bocquet-Védrine (1968) on barnacles, and *Duplorbis* Smith (1906) on an isopod. These forms lack the kentrogon stage and the reproductive body develops *in situ* at the site of attachment of the cyprid larva. The Kentrogonida have intercalated the endoparasitic phase into the life history; they are found only on grooming Decapoda. It is proposed that this advance is the counter-defensive evolution of the Rhizocephala to the cleaning defense of the host; that is, the evolution of the kentrogonid Rhizocephala was apparently driven by the development of cleaning defenses in their crustacean hosts.

A pivotal point in the life history of any parasite is the initiation of the parasitic phase. It follows that the development of remarkable specializations would be directed towards insuring this event. The evolution of the kentrogonid Rhizocephala is an extreme instance of a parasitic crustacean’s adaptations to maintain a bond with its host. What is really remarkable is the takeover of reproductive resources and capabilities of the host to the extent that for practical purposes the host carries out many of the reproductive needs of the parasite at the complete sacrifice of its own. This situation between two metazoans is in some way anal-
ogous to that between viruses and cells; particularly bacteriophage, which injects its contents into a bacterium which can then only make more phage.

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I (JTH) wish to express my deep admiration for the scientific work done by the late Larry Ritchie. His description of the life cycle of *Lernaeodiscus porcellanae* and culture techniques have been indispensable to the ultrastructural study of the larval stages of the Rhizocephala presently being carried out in Copenhagen. I wish also to thank Dr. William Newman for having made Larry Ritchie’s work available to me, while I was at the Scripps Institution of Oceanography studying the kentrogon of this rhizocephalan. This work was supported in part by a grant (DEB 78-15052) from the National Science Foundation.

Larry Ritchie, a doctoral student at the Scripps Institution of Oceanography, died in a camping accident on 22 May 1977 at the age of 30. A short manuscript, forming the basis of the present paper, was found among his files. Jens Høeg, who was aware of Larry’s work, agreed to help get it into publishable form.

Larry had a long-standing interest in parasitic relationships and early in his graduate school years published on a copepod parasite of certain deep-sea isopods (1975, Zoological Journal of the Linnean Society 57: 155–178) and reported on the relationship between cleaning and autogrooming and parasitic infection in certain crabs (Best Paper Award, Annual Meeting of the Western Society of Naturalists, 1975).

For four years he worked on a local rhizocephalan and its host. Part of his results, based on the many remarkable and original experiments that formed the substance of his doctoral work, are included in the present paper.

William A. Newman
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LITERATURE CITED

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