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BOCQUETIA ROSEA, NEW GENUS, NEW SPECIES, AN UNUSUAL RHIZOCEPHALAN PARASITE OF A SPONGE-INHABITING BARNACLE, *MEMBRANOBALANUS ORCUTTI* (PILSBRY), FROM CALIFORNIA

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ABSTRACT

Bocquetia rosea, new genus, new species, a rhizocephalan parasite of the sponge-inhabiting barnacle *Membranobalanus orcutti* is described from the coast of southern California. It constitutes the first "akentrogonid" rhizocephalan known from the Indo-Pacific and the first rhizocephalan known from an obligate commensal. It is most closely related to *Chthamalophilus delagei* and *Boschmaella balani* from the Atlantic coast of France, both of which are also barnacle parasites. *Bocquetia* is distinguished primarily from the other two genera by the greater extent to which the alimentary root system invades the host. The cyprid larvae lack natatory thoracic appendages and thereby appear to have limited dispersal capabilities. Except for a single individual, all specimens of *Bocquetia rosea* were found on the host barnacle *Membranobalanus orcutti* inhabiting the sponge *Spheciospongia confoederata* at only one of six locations.

The Rhizocephala comprises an order of highly specialized parasites which principally use decapod crustaceans as hosts (Lawler and Shepard, 1978). The cyprid larvae of most rhizocephalans attach to a suitable host, metamorphose into a kentrogon, and inject generative cells into the host, which grow, differentiate, and send out roots within the host's body. Upon maturation, an external reproductive sac emerges on the host surface, allowing for fertilization and development of eggs and subsequent release of larvae.

In 1957, Bocquet-Védrine described *Chthamalophilus delagei*, a rhizocephalan ectoparasitic on *Chthamalus stellatus* from Roscoff, France. Not only was this the first report of a rhizocephalan parasite of a barnacle, but the trophic mass of this unusual rhizocephalan was found to be relatively undeveloped, simply a bulb without digitations, and separated from the host by the host epithelium throughout development (Bocquet-Védrine, 1958, 1961). As such, it was assigned to the suborder Akentrogonida (Bocquet-Védrine, 1961; Newman *et al.*, 1969). A second parasite, *Boschmaella* (=*Microgaster*) *balani* was subsequently described from Arcachon, France, infesting the estuarine barnacle *Balanus improvisus* (Bocquet-Védrine, 1967). Unlike *Chthamalophilus delagei, Boschmaella balani* exhibited a trophic mass bearing short, bulbous, alimentary roots in intimate contact with the host tissues. A new, closely related rhizocephalan, *Bocquetia rosea*, parasite of the sponge-inhabiting barnacle *Membranobalanus orcutti* from San Diego, California, is reported in this paper.

Bocquetia, new genus

Diagnosis.—Alimentary root system extensive, dendritic; bearing only one external sac. Low incidence of multiple parasites on a single host. Males, if present, unknown.

Type-species.—*Bocquetia rosea*, new species.

Etymology.—After Jacqueline Bocquet-Védrine.

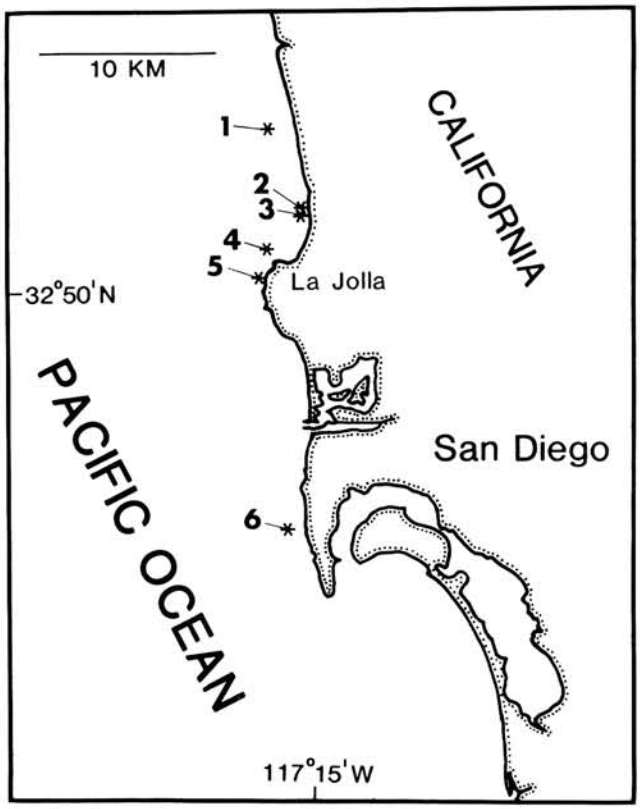

Fig. 1. Sponge collection sites. 1, Department of Fish and Game Artificial Reef number 19 (depth 25 m); 2, North Branch, Scripps Canyon (30 m); 3, Sumner Branch, Scripps Canyon (25 m); 4, Quast Rock (25 m); 5, Casa Cove (6 m); 6, Virgin Reef/Jeff's Reef, Point Loma (15 m).

Bocquetia rosea, new species
Figs. 2–4

Material.—Sixty-three individuals were found on the barnacle *Membranobalanus orcutti* (Pilsbry), a commensal of the sponge *Spheciospongia confoederata* deLaubenfels, collected in September 1984 and June 1985 at Virgin Reef and Jeff's Reef, off Point Loma, San Diego, California (Fig. 1). A single individual on the same host barnacle dwelling in the sponge *Cliona celata californiana* deLaubenfels was collected in September 1984 from the Sumner Branch of Scripps Canyon (Fig. 1). Holotype (USNM cat. no. 227051); paratypes (BMNH Reg. no. 1985.347; MNHNP (Paris) no. Ci989).

Description.—Relatively large, oblong external reproductive sac, mean length = 2.3 mm (N = 11, SD = 1.1 mm, range = 0.8–4.5 mm) (Fig. 2a, b, d). Sac pink to colorless, containing ovary attached to sac wall opposite pedicel. Remainder of mantle cavity comprising brood cavity, connecting to exterior by mesenteric canal running opposite pedicel between sac wall and ovary (Fig. 3a, b). Mesenteric canal opening to exterior obliquely opposite pedicel.

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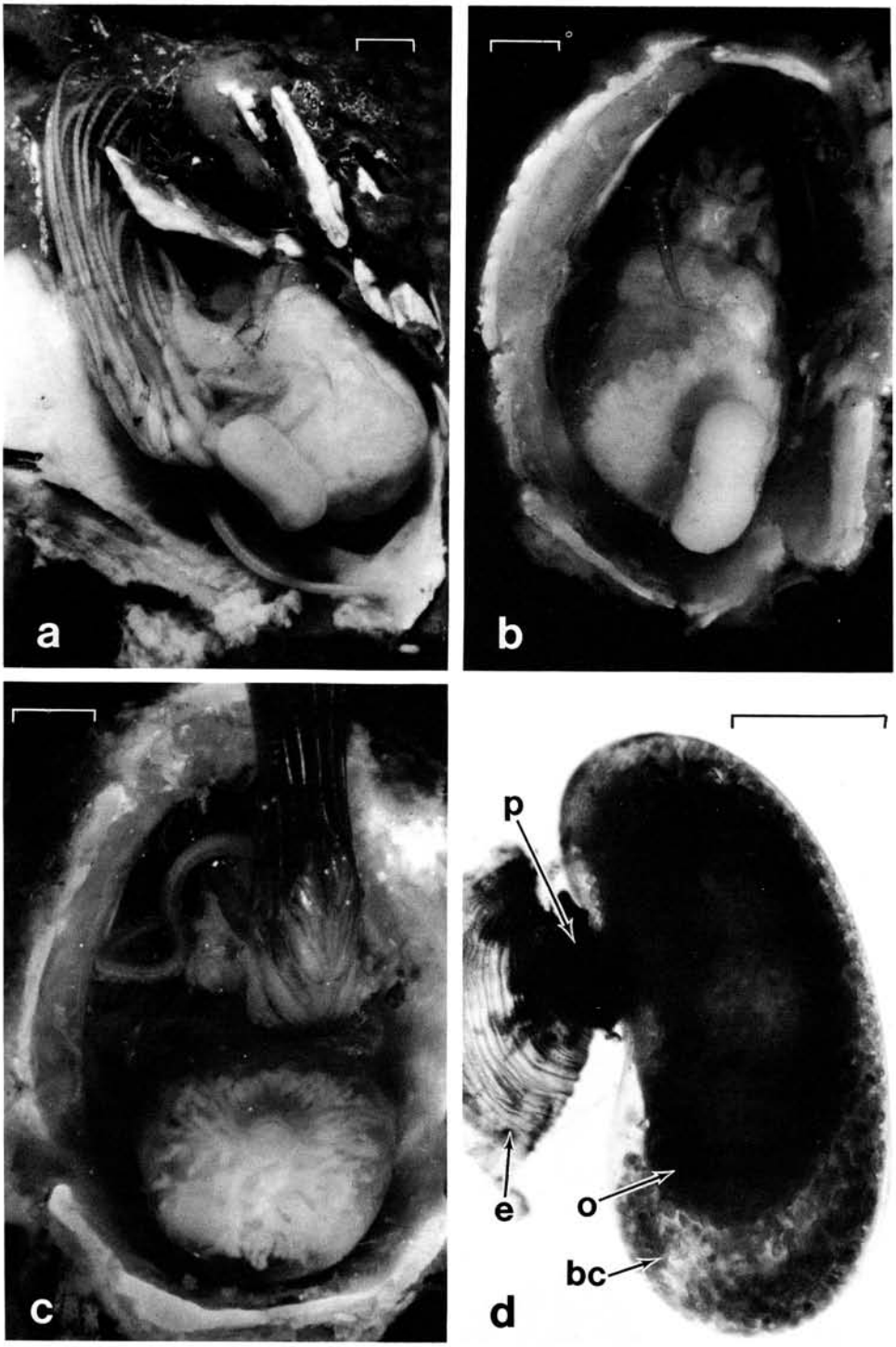
Fig. 2a–d. *Bocquetia rosea*, new genus, new species. a, mature specimen on *Membranobalanus orcutti*, attached to visceral mass behind base of cirri; b, attached to visceral mass showing extent of alimentary root system; c, external reproductive sac absent, showing dendritic root system; d, external reproductive



sac removed from host, showing unhatched cyprids in brood cavity. bc = brood cavity, e = annular cuticular rings, o = ovary, p = pedicel. Scale = 1.0 mm.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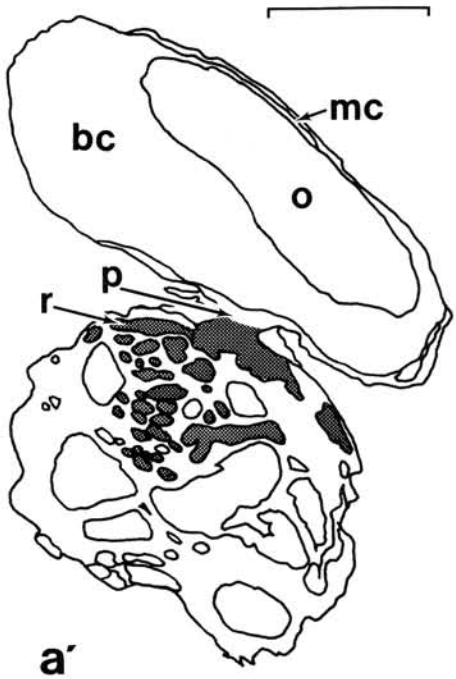
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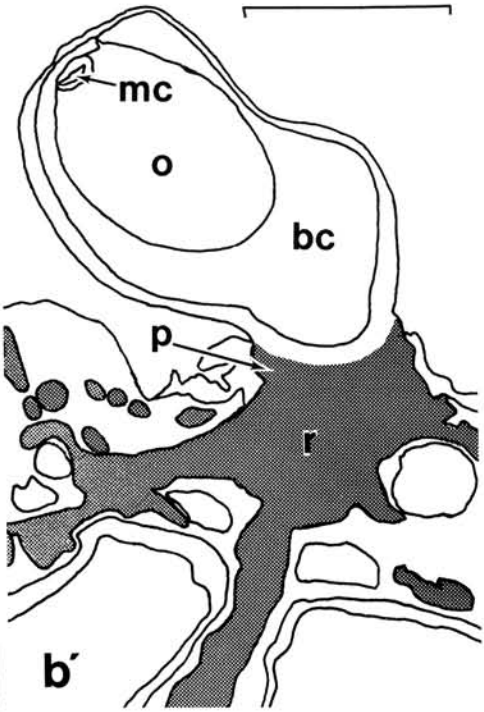
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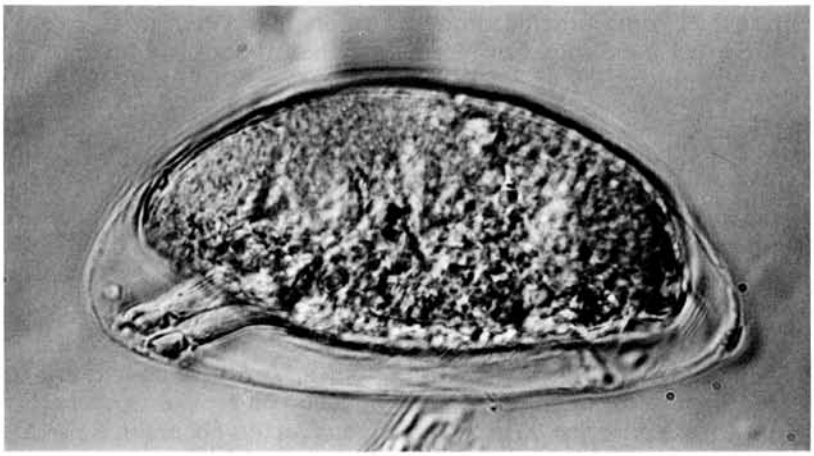

Fig. 4. *Bocquetia rosea,* new genus, new species. Cyprid larva, encased in egg membrane, removed from brood chamber. Length = 90 μm.

External sac attached to host body, usually visceral mass of host, by short pedicel. Base of pedicel surrounded by circular, amber-colored, cuticular shield bearing concentric annulations (Fig. 2d).

Alimentary root system observable through host cuticle as orange to bright red, circular plaque, 3–5 mm in diameter (Fig. 2c), extending within host from pedicel outward in dendritic fashion. Invasive root tissue consisting of highly vacuolated cells with darkly staining nuclei, as seen in 10-μm thick wax sections stained with cresyl violet (Fig. 3a, b).

Unhatched cyprid larvae, all at same developmental stage, frequently found in abundance in brood cavity. Cyprids possessing pair of antennules, but no other cephalic or thoracic appendages (Fig. 4). Mean cyprid length = 88.9 μm ($N = 20$ from 3 individual parasites, SD = 1.89 μm).

Etymology.—The specific epithet refers to the color and shape of the alimentary root system, *rosea,* like a rose.

Distribution and Natural History.—*Bocquetia rosea* was found on *Membranobalanus orcutti* commensal in the loggerhead sponge *Spheciospongia confoederata* from one site only—two adjacent reefs, Virgin Reef and Jeff's Reef, off Point Loma (Fig. 1). Over a two-year period, many hundreds of *M. orcutti* inhabiting *S. confoederata* collected for other research purposes from nearby sites, including Casa Cove, Quast Rock, and Department of Fish and Game Artificial Reef no. 19 (Fig. 1), were never found to be parasitized by *B. rosea.* One specimen of *B. rosea* was discovered on a single *M. orcutti* inhabiting the yellow boring sponge *Cliona celata californiana* from the Sumner Branch of Scripps Canyon (Fig. 1).

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Fig. 3a, b. *Bocquetia rosea,* new genus, new species, attached to visceral mass of *Membranobalanus orcutti.* Light micrographs of glutaraldehyde fixed, 10-μm thick, wax sections stained with cresyl violet. a, a′, sagittal section, scale = 1.0 mm; b, b′, transverse section, scale = 0.5 mm. Alimentary roots invading host barnacle tissues shaded in corresponding drawings. bc = brood cavity, mc = mesenteric canal, o = ovary, p = pedicel, r = roots.

No additional *B. rosea* were encountered among *M. orcutti* in *C. celata californiana* from either the Sumner or North Branches of Scripps Canyon.

In a demographic study of *Membranobalanus orcutti,* Jones (1978) made extensive collections over a two-year period of *M. orcutti* on both sponge species at Scripps Canyon, Casa Cove, and a site off Point Loma. She found that *Fecampia balanicola,* a parasitic flatworm, infested 25% of the *M. orcutti* inhabiting *S. confoederata,* and 3% of the barnacles inhabiting *C. celata californiana* (observed at approximately the same levels of infestation in the present study), but made no mention of encountering other parasites.

The limited distribution of *Bocquetia rosea* is probably the result of the poor dispersal capabilities of the cyprid larvae, which lack natatory thoracic appendages. Bocquet-Védrine (1972) attributed host specificity and the restricted range of both *Chthamalophilus delagei* and *Boschmaella balani* to constraints on larval motility. Nonswimming cyprids apparently depend on prevailing currents to carry them to new host barnacles. *Membranobalanus orcutti* occurs in *Spheciospongia confoederata* at densities of 0.7–5.5 barnacles per cm^2 of sponge area ($N = 10$, $\bar{x} = 2.0 \pm 1.4$ barnacles/cm^2; Jones, 1978), but the distribution of sponges with barnacles is limited to rocky, subtidal reefs which may be many kilometers apart (Fig. 1). Among *Membranobalanus orcutti* collected from the Point Loma site, rhizocephalan infestation rates were relatively high: for the 9 September 1984 collection, 12.6% of 199 *M. orcutti* were parasitized by *Bocquetia rosea,* for the 3 June 1985 collection, 10.5% of 200 barnacles were parasitized. Hence, while parasitic invasion of barnacles in the same sponge or between sponges on the same reef may occur readily, it appears that the nonswimming larval stage severely limits wider dispersal in this species. Comparable patchiness was observed for *Cryptophialus melampygos,* an acrothoracic cirriped symbiotic on molluscs, which has nonswimming larvae (Batham and Tomlinson, 1965).

Among parasitized barnacles, multiple parasites were less common than single parasites: of 45 infested barnacles, 34 (85.5%) bore single parasites (with or without external reproductive sacs), 6 (13.3%) carried 2 parasites, 4 (8.9%) bore 3 parasites, and one individual (2.2%) was infested with 4 parasites. This frequency distribution was not significantly different from a random, truncated Poisson distribution ($\chi^2 = 4.2$, $d.f. = 3$, $P > 0.05$; Cohen, 1960), indicating that infestation events occurred independently of one another. Individual alimentary root systems gave rise to only one external reproductive sac in each case; root systems were distinctly separate in cases of multiple parasites infesting a single host.

The majority of parasites were embedded in the visceral mass (prosoma) of the host barnacle, only 6 (9.7%) of 62 *Bocquetia rosea* were found embedded in the mantle of *Membranobalanus orcutti,* and these individuals displayed both smaller alimentary root systems and external sacs. External reproductive sacs were present in the majority of cases: of 62 parasites, only 11 (17.7%) lacked external sacs either due to immaturity or secondary loss.

The impact of parasitism by *Bocquetia rosea* on the host barnacle is not yet clear. None of the *Membranobalanus orcutti* collected that were parasitized by *B. rosea* had brooding larvae in their mantle cavities and most had undeveloped or degenerated ovaries. Host barnacles appeared to continue to molt, since torn pieces of cuticle frequently fouled the pedicel of the external sac of the parasite. Bocquet-Védrine (1961) similarly found that *Chthamalophilus delagei* did not inhibit molting of its host barnacle, *Chthamalus stellatus.*

An understanding of reproduction and sexuality in *Bocquetia rosea* will require further study. Nothing resembling "testes" was found in 10-μm serial sections of 11 parasites, 8 of which had external reproductive sacs. Bocquet-Védrine (1967,

Table 1. Comparison of the three species comprising the Chthamalophilidae.

	Chthamalophilus delagei	*Boschmaella balani*	*Bocquetia rosea*
Host barnacle	*Chthamalus stellatus*	*Balanus improvisus*	*Membranobalanus orcutti*
Collection locality	off Roscoff, France	Arcachon Bay, France	off Point Loma, San Diego, California
Typical placement in host	lateral to insertion of cirri	mantle	visceral mass
Condition of root system	separted from host by host epithelium; bulb without digitations	intimate with host; short, lobate digitations	intimate with host; extensive, dendritic digitations
Relative frequency of multiple parasites per host	low	high	low
Mean cyprid length	66 μm	100 μm	89 μm
External sac:			
Shape	spherical	oblong	oblong
Mean length	1.2 mm	1.6 mm	2.3 mm
Maximum length	1.5 mm	–	4.5 mm

1968) identified testes in sections of *Boschmaella balani,* but did not observe spermatogenesis, and suggested that there was a seasonal reproductive cycle in that species. Both testes and spermatogenesis were found and studied in *Chthamalophilus delagei,* which Bocquet-Védrine (1961, 1965) believed to be hermaphroditic.

Relationships.—*Bocquetia rosea* displays obvious affinities with *Chthamalophilus delagei* and *Boschmaella balani.* All three brood and release cyprid larvae that lack thoracic appendages (Bocquet-Védrine, 1961, 1969), all three have reproductive sacs with a similar internal arrangement, and all three parasitize barnacles. *Boschmaella* and *Chthamalophilus* were recently distinguished from other rhizocephalans which bear a mesenteric canal, primarily on the organization of the reproductive sac (Bocquet-Védrine and Bourdon, 1984). The characteristics described above warrant placement of *Bocquetia,* along with *Chthamalophilus* and *Boschmaella,* in the family Chthamalophilidae (Bocquet-Védrine, 1961).

A comparison of some of the characteristics of the three species comprising the Chthamalophilidae is presented in Table 1. Unlike *Chthamalophilus,* both *Boschmaella* and *Bocquetia* have root systems in intimate contact with host tissues, i.e., not separated from the host by the host epithelium. The alimentary roots of *Boschmaella* extend only superficially into the conjunctive tissues of its host (Bocquet-Védrine, 1968; Bocquet-Védrine and Parent, 1972a), while *Bocquetia* produces an extensive, dendritic alimentary root system. In *Boschmaella,* infested hosts most commonly bear a multitude of parasites (as many as 40 at various stages of development; Bocquet-Védrine and Parent, 1972b), which were believed to arise by asexual division of the immature parasite. Incidence of multiple parasitism in both *Chthamalophilus* and *Bocquetia* were comparatively low, and then never with more than 4 or 5 parasites per host.

Chthamalophilus delagei was placed in the suborder Akentrogonida (Bocquet-Védrine, 1961; Newman *et al.,* 1969) on account of the apparent lack of a kentrogon stage, the lack of parasite migration after host invasion and the poorly developed, ectoparasitic nature of the alimentary root system (Bocquet-Védrine, 1961). However, the roots of both *Boschmaella* and *Bocquetia* are not separated

from the host tissues by host epithelium, and therefore an internal phase cannot be excluded. Although *Bocquetia rosea* does not appear to migrate during development, most of its life history, including its sexuality, is still unknown. "Kentrogonid" status has generally been assigned on the basis of adult morphology; actual observations of the mode of rhizocephalan invasion have been rare (Delage, 1884; Høeg, 1985). Further study of *Bocquetia rosea* may reveal whether the Chthamalophilidae are, as a whole, exclusively "akentrogonid."

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NOTE ADDED IN PROOF

A March 1986 collection of 100–200 *Membranobalanus orcutti* inhabiting *Spheciospongia confoederata* from Jeff's Reef, Point Loma (Fig. 1), yielded only a single specimen of *Bocquetia rosea* (J. T. Høeg, personal communication). This drop in parasite abundance may have resulted from the removal of a large proportion of the infested *M. orcutti* at the site of previous collections. Inasmuch as only the surface of the sponge was removed in collecting the barnacles, uninfested *M. orcutti* would recolonize the regenerated sponge surface. Parasitic invasion of new recruits would then depend on several unknown factors, including the number of infested barnacles remaining at the site, and the frequency of reproduction and length of time to reproductive maturity for the parasite. An October 1986 collection of approximately 200 *M. orcutti* in *S. confoederata* from Casa Cove (Fig. 1) yielded four individual *B. rosea,* which had previously not been found at that site.