

Abstract.— A symbiotic nemertean worm found on spiny lobsters is described and compared with other members of the genus *Carcinonemertes*. The new species of *Carcinonemertes* has a relatively large basis, stylet, anterior and posterior proboscis chambers, and a voluminous seminal vesicle. In addition, lateral intestinal diverticula project anterior to the level of the middle proboscis chamber. These characters distinguish this species from others in the genus.

The life-history patterns of six species of *Carcinonemertes* appear related to the developmental timing of host embryogenesis. Portunid crabs with a short duration of embryogenesis are infested by the species *C. carcinophila* and *C. mitsukurii*. The worms settle only on mature female hosts; after eclosion the worms migrate to the branchial lamellae of the host where they lie dormant until the host oviposits a new clutch. Cancrid and grapsid crabs with an intermediate duration of embryogenesis are infested by the species *C. epialti* and *C. errans*. The worms settle on both sexes of crabs and are sexually transmitted to female hosts. At eclosion, the worms die or regress and migrate to the limb axillae. Lithodid crabs and panulirid lobsters with a long duration of embryogenesis are infested by *C. regicides* and *C. wickhami*. The nemerteans settle on ovigerous hosts and die or leave the host after eclosion.

***Carcinonemertes wickhami* n. sp. (Nemertea), a Symbiotic Egg Predator from the Spiny Lobster *Panulirus interruptus* in Southern California, with Remarks on Symbiont-Host Adaptations**

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Nemerteans of the genus *Carcinonemertes* (Kölliker, 1845) are specialized symbionts of decapod crustaceans. Several species of *Carcinonemertes* eat the eggs of their hosts (Humes 1942, Kuris 1978, Wickham 1980, Roe 1984); and this trophic habit may be diagnostic for the genus (Wickham 1986, Wickham and Kuris 1988). Three species have been described from the west coast of North America: *C. epialti* Coe, 1902; *C. errans* Wickham, 1978; and *C. regicides* Shields, Wickham, et Kuris, 1989. Nemerteans from the spiny lobster were distinct from these species in both morphology and life history. The nemertean from the spiny lobster represents the undescribed species listed by Wickham and Kuris (1985) for that host.

Here we describe the egg predator *Carcinonemertes wickhami* n. sp., from the broods of the spiny lobster *Panulirus interruptus* (Randall), from southern California. The distinctive morphological characters of the new species are discussed, and aspects of the life history of the new species are presented with those of other members of the genus.

Materials and methods

Spiny lobsters *Panulirus interruptus* were collected by University of California divers using SCUBA. Lobsters were caught by hand. Pleopods of infested female lobsters were examined macroscopically; those containing worms were excised and immediately placed in seawater. Nine ovigerous lobsters were examined in 1982, and 10 in 1988. Three of the lobsters collected in 1988 were held for 4–7 days after eclosion (post-ovigerous); they were then dissected and examined for worms. Particular attention was paid to the limb axillae, branchiae, and branchial chambers. Nemerteans found in the broods of lobsters were gently manipulated onto slides for measuring and photomicrography. Worms were measured with an ocular micrometer in a dissecting microscope. They were then covered with a coverslip, and various measurements of internal features were taken with an ocular micrometer in a compound microscope. Hatched nemertean larvae were examined alive. Measurements are in

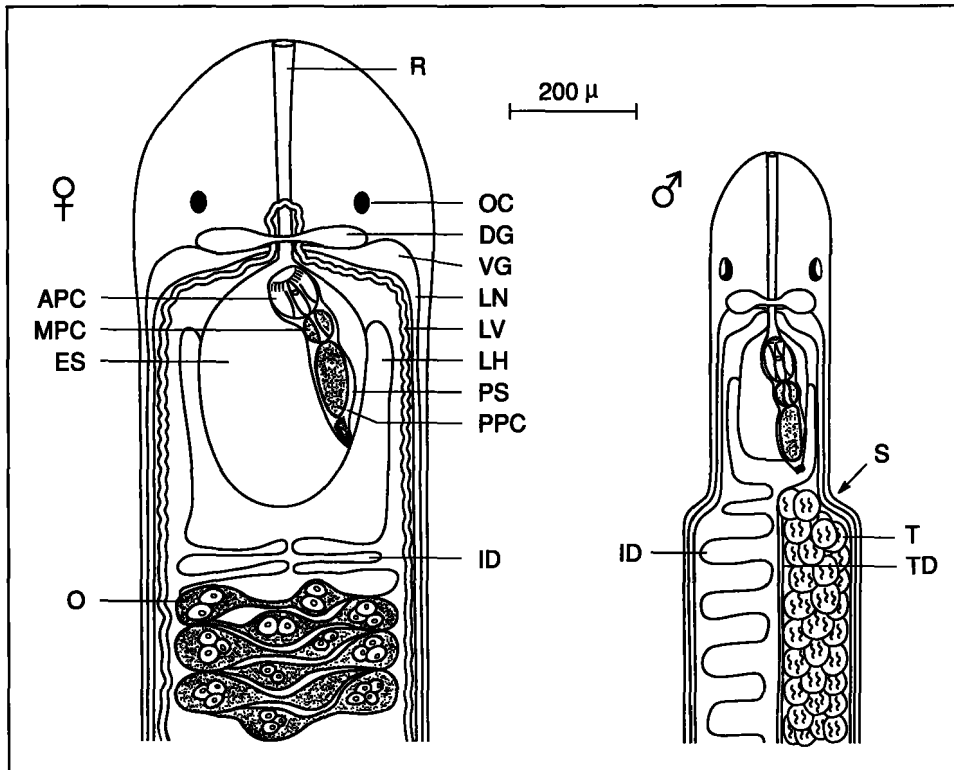


Figure 1

Composite drawing of female (left) and male (right) *Carcinonemertes wickhami* from *Panulirus interruptus*. Note the reproductive system of the male is represented on the right side of the body, while the digestive system is figured on the left side, and the circulatory system has been omitted for clarity. Key to labels: APC = anterior proboscis chamber; ES = foregut; DG = dorsal ganglia; ID = intestinal diverticula; LH = lateral horn of intestine; LN = lateral nerve cord; LV = lateral blood vessel; MPC = middle proboscis chamber; OC = ocellus; O = ovary; PPC = posterior proboscis chamber; PS = proboscis sheath; R = rhynchodaeum; S = shoulder; T = testis; TD = Taka-kura's duct system (vasa eferens, vas deferens, seminal vesicle, gonoduct); VG = ventral ganglion. Bar = 200 μ m.

micrometers unless otherwise stated. Means are given with ranges in parentheses.

Worms were fixed in hot AFA (acetic acid, formaldehyde, alcohol) or 5% formalin-seawater. Representative specimens were sectioned at 10 μ m and stained with hematoxylin and eosin.

Description

Carcinonemertes wickhami new species (Figs. 1-13)

Female (3 living specimens; 7 specimens, sectioned) Body slender, ciliated; orange color. Shape filiform with rounded anterior end, blunt posterior end; found in tough, glistening parchment-like sheaths, but often free. Sheaths with minute refractile lapilli, grainy in texture, slightly longer than accompanying worm. Worm length 10-30 mm, up to 50 mm when fully extended, average width 400 (345-456). Two ocelli anterior to prominent dorsal and ventral cerebral ganglia. Ocelli cup-shaped, conspicuous, 36 (34-39) long by 28 wide; located 145 (126-168) from anterior end. Distance between ocelli 257 (172-368). Rhynchodaeum and esophagus passing between commissures of the dorsal and ventral ganglia. Anterior portions of lateral blood vessels fuse between commissures of cephalic

commissures in a single anterior loop. Posterior portion of lateral blood vessel ventral to lateral nerve cord near anus. Proboscis with three chambers, dorsomedial or lateral to posterior part of foregut. Anterior proboscis chamber 98 (84-112) long by 80 (70-87) in diameter, with basis and stylet. Basis large, 40 (36-42) long by 14 in posterior diameter. Single large stylet, 20 (19-20) long, with posterior knob-like proximal piece. Middle proboscis chamber granular in appearance, 47 (39-59) in diameter. Posterior proboscis chamber long, slender, 125 (112-140) long by 42 (28-56) in diameter; glandular, with lumen. Foregut joins rhynchodaeum at or just posterior to cephalic commissure. Posterior part of foregut robust, 380 (280-517) long, by 244 (182-345) in diameter; muscular, ciliated. Musculature of foregut attached laterally to longitudinal musculature of body wall. Posterior part of foregut leading directly into intestine; pyloric stomach absent. Intestine with a pair of lateral diverticula extending anterior to level of middle proboscis chamber. Intestine posterior to foregut with numerous paired, unbranched diverticula. Anus terminal. Ovaries elongate, with medial and lateral lobes; numerous, regularly distributed between intestinal diverticula. Ovaries with indistinct ovarian pores. Ovarian field begins immediately posterior to posterior part of foregut, extends to near anus. In section, ovaries with appearance of four rows in immature and mature females (compare Figure 4 with Figure 1); but ovaries really in two distinct rows (Fig. 1). Ovaries

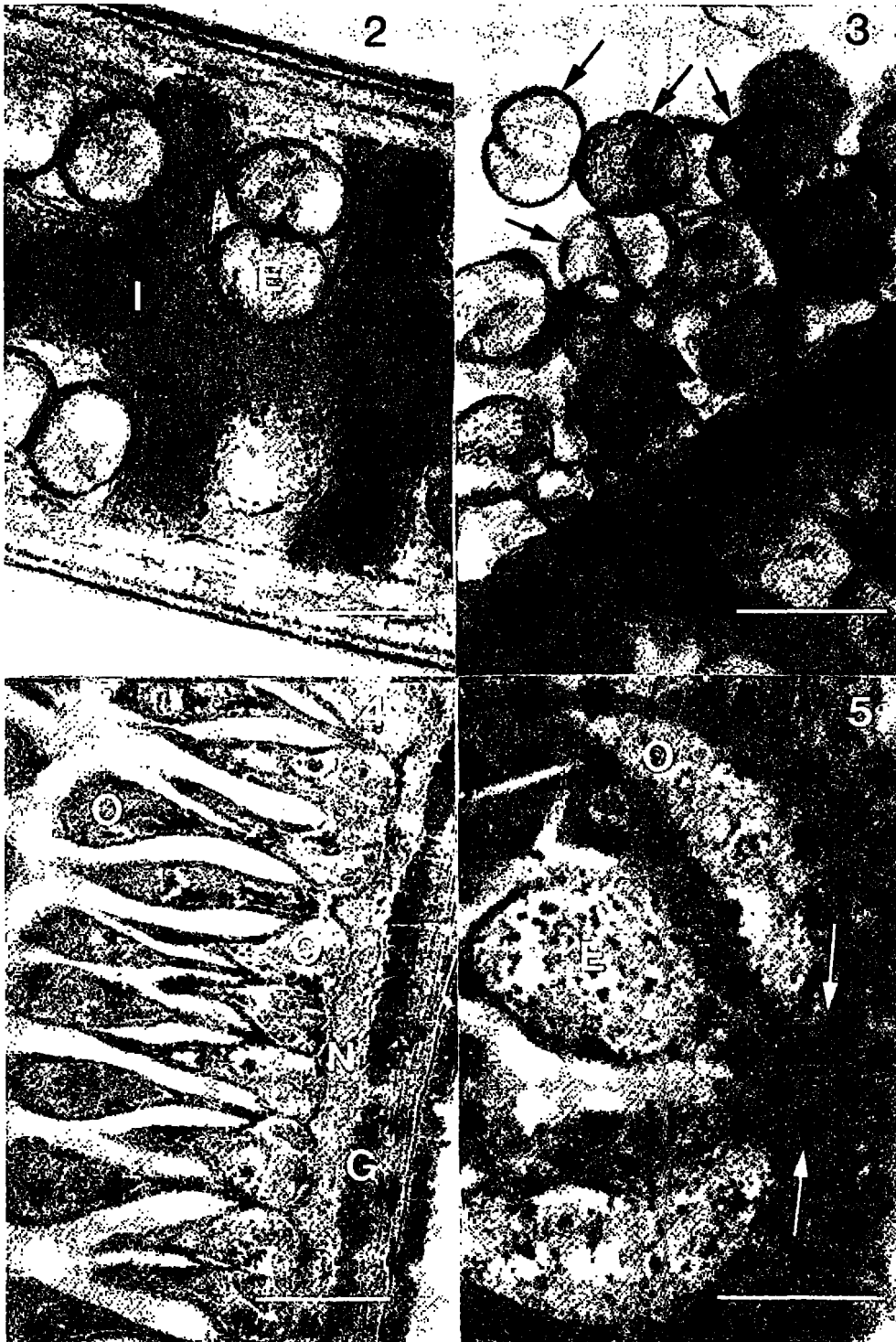


Figure 2

Fertilized embryos (E) within the ovary of a female *Carcinonemertes wickhami*; intestine (I) and lateral nerve (N). Bar = 100 μ m.

Figure 3

Artificially released embryos of *Carcinonemertes wickhami*; fertilized embryos (arrows). Bar = 100 μ m.

Figure 4

Sagittal section through the ovarian region of a female *Carcinonemertes wickhami*. The ovaries (O) appear in four rows but they are actually in two (only one side of worm in figure; compare with Figure 1); lateral nerve (N); submuscular glands (G). Bar = 100 μ m.

Figure 5

Indistinct ovarian pore (arrows) on the lateral, submarginal surface of a female *Carcinonemertes wickhami*; egg (E); ovary (O); Bar = 50 μ m.

variable in size in relation to developing ova, 196–294 long by 92–168 in diameter. Eggs faint pink, deposited in a flimsy, mucous matrix (cf. sac) secreted by female.

Male (3 living specimens, incomplete observations on 2 additional specimens) Similar in gross morphology

to female; differences include: diameter of worm expands at the beginning of the testicular field, setting off the anterior portion of the worm as a relatively slender head (cf. shoulder). Color pinkish white. Ensheathed with female or free in egg mass. Length 5–18 mm, up to 20 mm when fully extended. Ocelli located

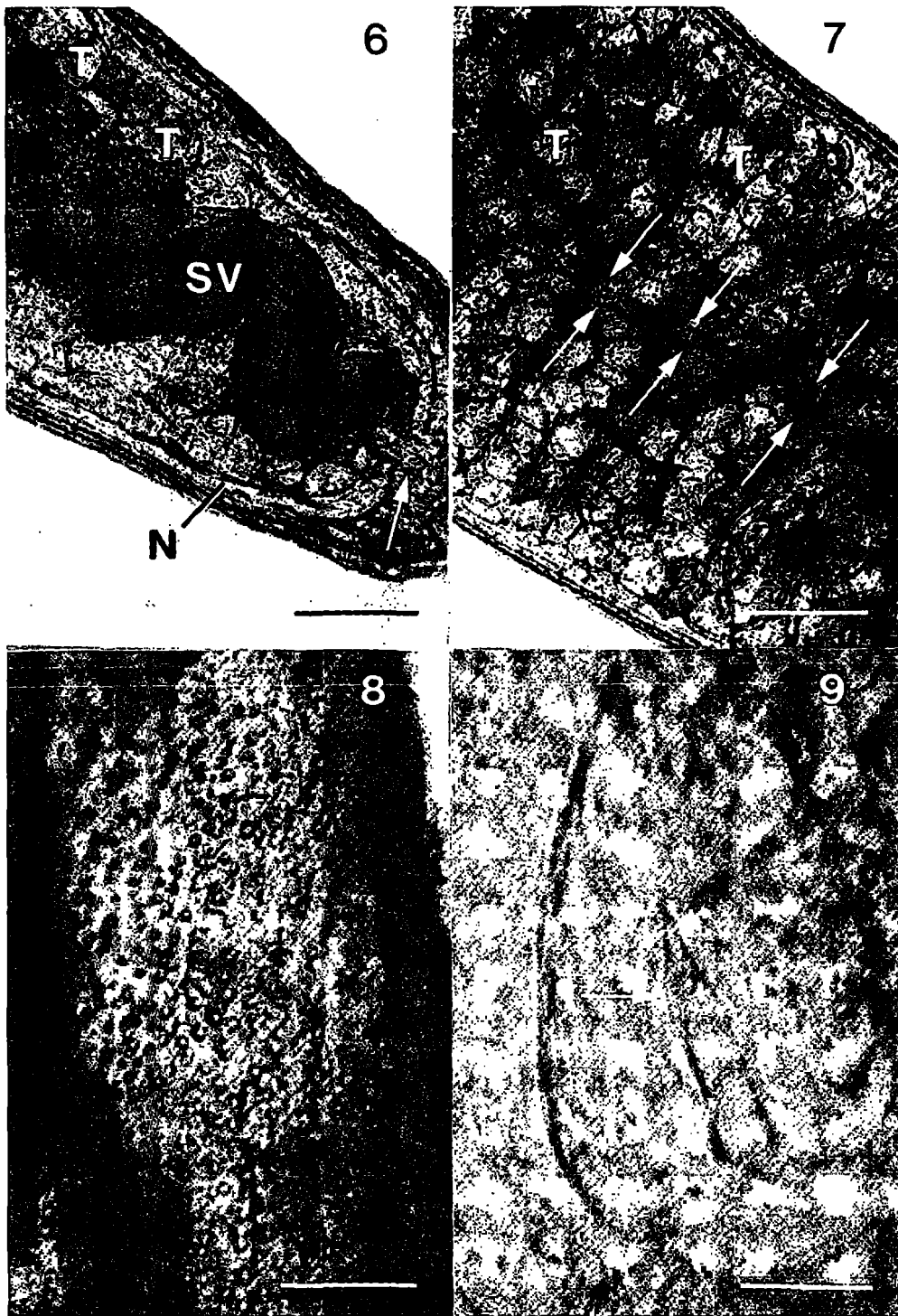


Figure 6

Posterior portion of Takakura's duct system from a live, mature male *Carcinonemertes wickhami* showing the enormous seminal vesicle (SV) and gonoduct (arrow); testis (T); lateral nerve cord (N). Note the lack of testes in the region surrounding the seminal vesicle. Bar = 100 μ .

Figure 7

Anterior portion of Takakura's duct system from a live mature male *Carcinonemertes wickhami*. The vas deferens (arrows) is distinctly visible; testis (T). Bar = 100 μ m.

Figure 8

Granular, lapillated sheath of a female *Carcinonemertes wickhami*. Bar = 50 μ m.

Figure 9

Stilet (arrow) and basis of *Carcinonemertes wickhami* lying in the anterior proboscis chamber. Bar = 25 μ .

163 (126-196) from anterior end; distance between ocelli 162 (151-182). Anterior proboscis chamber 79 (70-84) long by 57 (56-59) in diameter. Posterior proboscis chamber 149 (112-196) long by 47 (42-56) in diameter. Posterior part of foregut 196 (168-252) long by 151 (112-196) in diameter. Testicular field begins

immediately posterior to posterior portion of foregut, extends posteriorly to terminate 659 (632-690) from cloaca. Testes located between intestinal diverticula; not found adjacent to proximal portion of the seminal vesicle. Mature testes with striated appearance, ovoid, 60 (56-70) long by 52 (42-62) in diameter. Takakura's

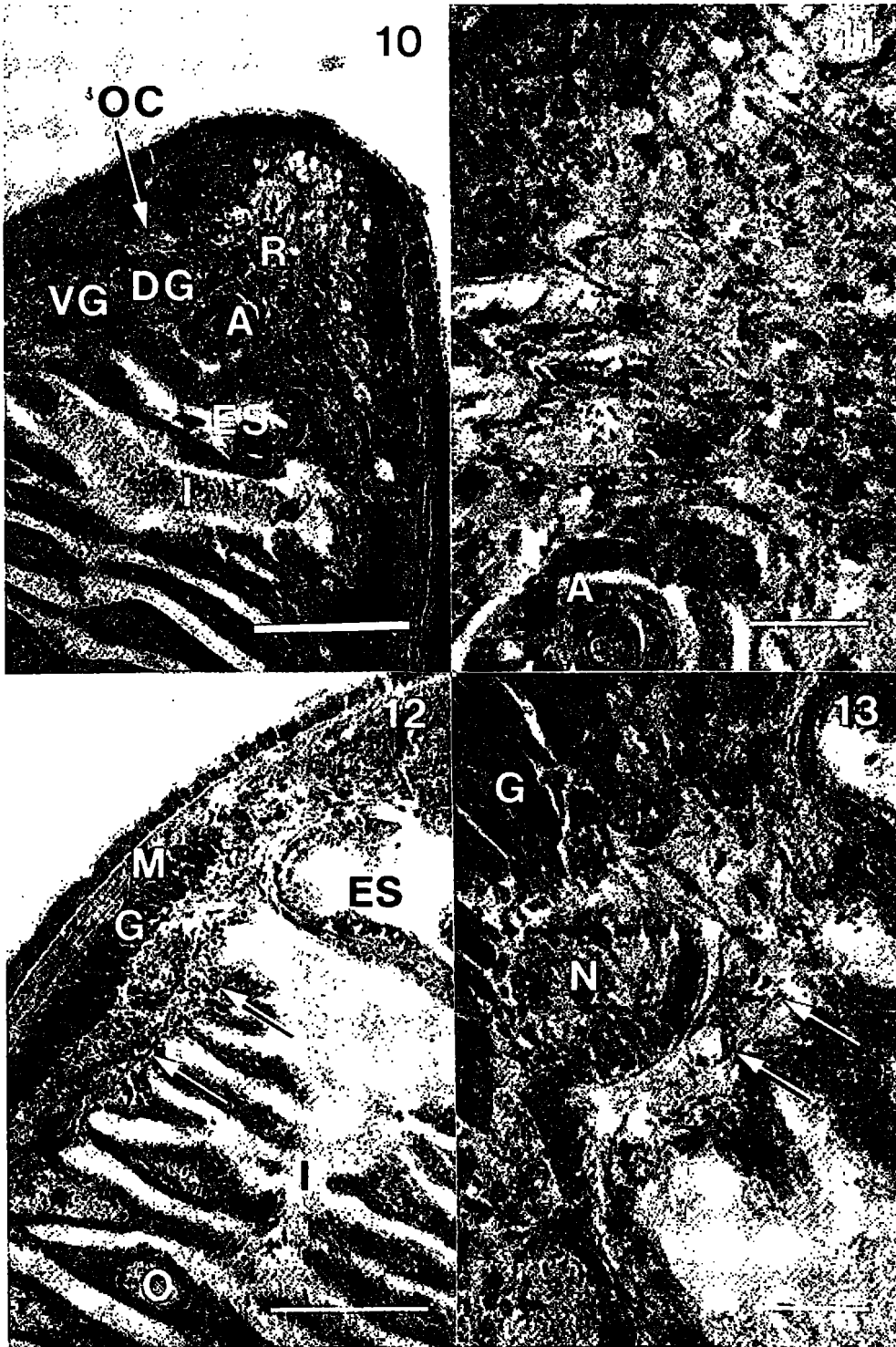


Figure 10

Sagittal section of the anterior end of a female *Carcinonemertes wickhami*; anterior proboscis chamber (A); ventral portion of the dorsal ganglion (DG); foregut (ES); intestine (I); ocellus (OC); rhynchodaeum (R); and ventral ganglion (VG). Bar = 100 μ m.

Figure 11

Detail of the cephalic region of *Carcinonemertes wickhami* in sagittal section. Note the criss-crossing of the cephalic musculature; anterior proboscis chamber (A). Bar = 25 μ m.

Figure 12

Sagittal section through the anterolateral portion of a female *Carcinonemertes wickhami*. Lateral blood vessels (arrows; see also Figure 13); foregut (ES); prominent submuscular glands (G); intestine (I) with intestinal diverticula; muscle layer (M) with longitudinal and circular muscles; and ovary (O). Bar = 100 μ m.

Figure 13

Detail of the lateral blood vessels (from Figure 12) in the weakly developed parenchyma anastomosing between the intestinal diverticula (right) and the lateral nerve (N); submuscular gland (G). Bar = 25 μ m.

duct system distinct, extending from antermost testes to gonopore. Seminal vesicle single, voluminous, near posterior end, 421 (402-460) long by 96 (58-115) in diameter, "S" or "double-S" shape in appearance, surrounded by thick muscular region (= ejaculatory mus-

cles?). Anus and gonoduct empty into common, ciliated cloaca with muscular sphincter.

Larvae (based on 5 living specimens) Typical hoplonemertean. Body completely ciliated, color white with

pink anterior. Larva spherical or ovoid, length approximately 84 (74–92). Anterior and posterior cirri or tufts, approximately 56 long. Two ocelli.

Taxonomic summary

Parasite *Carcinonemertes wickhami* (NEMERTEA: Carcinonemertidae).

Host California spiny lobster *Panulirus interruptus* (Randall). Found on 6 of 9 lobsters in July 1982, and 2 of 10 lobsters in August 1988.

Site of Infestation Egg-bearing pleopods of female lobsters. Sometimes attached to bases of uropods or pleopods adjacent to the egg mass. Not found in/on branchiae, branchial chamber, arthroal membranes, or limb apodemes of nonovigerous females. Not found on male lobsters.

Type locality CALIFORNIA: Santa Barbara, near More Mesa, depth of 5 meters.

Holotype USNM Helm. Coll. #80501: 1 slide—small female holotype in serial section (frontal); and larger female paratype in serial section. Date host collected: 7 July 1982.

Paratype USNM Helm. Coll. #80502: 1 vial—4 male worms; 1 vial—5 female worms; 1 vial—several egg strings attached to setae and eggs of host. Paratypes from two hosts. Hosts collected: More Mesa, 8 August 1988. Additional material in authors' collections.

Etymology The species is named in honor of Dr. Daniel E. Wickham for his contributions to the biology of the genus.

Definition Hoplonemertea, Monostilifera, Carcinonemertidae. Long, filiform nemerteans, up to 50 mm long by 400 μ m wide. Anterior proboscis chamber large, 98 (84–112) long by 80 (70–87) in diameter in females; 79 (70–84) long by 57 (56–59) in diameter in males. Basis robust, 40 (36–42) long by 14 basal diameter. Stylet large, with posterior hub, 20 (19–20) long. Posterior proboscis chamber long, slender, 125 (112–140) long by 42 (28–56) in diameter in females; 149 (112–196) long by 47 (42–56) in diameter in males. Posterior portion of foregut large, robust, up to 517 long by 345 in diameter. Lateral intestinal diverticula extending to level of middle proboscis chamber. Worms often found in tough, lapillated, parchment-like sheath. Female with indistinct ovarian pores. Diameter of male expands as a "shoulder" at the beginning of the testicular field. Males with voluminous seminal vesicle, up to

460 long by 115 in diameter. Hoplonemertean larva, 84 (78–92) long.

Diagnosis *Carcinonemertes wickhami* most closely resembles *C. mitsukurii* Takakura, 1910, *C. carcinophila carcinophila* (Kölliker, 1845), and *C. c. imminuta* Humes, 1942 (Table 1). These four nemerteans have relatively large adult forms. *Carcinonemertes wickhami* can be distinguished from these large species by its relatively larger basis and stylet, anterior and posterior proboscis chambers, larger foregut, and the voluminous seminal vesicle in males (Table 1). *Carcinonemertes wickhami* can be distinguished from the smaller species (*C. australiensis* Campbell, Gibson et Evan, 1989; *C. coei* Humes 1942; *C. epialti* Coe, 1902; *C. errans* Wickham, 1978; and *C. regicides* Shields, Wickham, et Kuris, 1989) by its larger size, relatively larger anterior and posterior proboscis chambers, the voluminous seminal vesicle in males, and by the presence of 2 rows of ovaries rather than 4 rows as in *C. coei* (Table 1).

Remarks and discussion

Humes (1942) and Wickham and Kuris (1988) have reviewed the genus *Carcinonemertes*, and Shields et al. (1989) and Campbell et al. (1989) have recently amended the family. Seven species are presently recognized, one of which contains two subspecies, *C. carcinophila carcinophila* and *C. c. imminuta* (Table 1). *Carcinonemertes wickhami* is the eighth species to be described, the second species described from a palinuran, and the first species described from southern California. It represents the undescribed species from the spiny lobster listed by Wickham and Kuris (1985).

Adult *C. wickhami* are often aligned along the tangled egg-bearing setae of the pleopods. The location of the worm along with its photonegative behavior make it difficult to observe this relatively large species in the egg mass of the lobster. Other species of *Carcinonemertes* also exhibit photonegative behavior (*C. epialti* and *C. regicides*; Shields et al. 1989).

The larger species of *Carcinonemertes* are well-muscled in comparison with the smaller species which exhibit a predominantly muco-ciliary movement (Shields et al. 1989). Active thrashing and peristaltic movements were noted in *C. wickhami*. Males were observed to form figure-8 loops by active muscular contraction. *Carcinonemertes wickhami* is also strongly adhesive, a property shared by *C. errans* and *C. regicides* but not by *C. epialti* and *C. mitsukurii* (Shields, pers. observ.).

Carcinonemertes wickhami, *C. australiensis*, and *C. regicides* have large anterior proboscis chambers,

Table 1

Morphological characteristics of the eight species of *Carcinonemertes*. APC = anterior proboscis chamber; PPC = posterior proboscis chamber. Measurements are in microns (except length which is mm) and represent means. NS = not seen.

Species	Sex	Length	Basis	Stylet	APC	PPC
<i>C. australiensis</i> Campbell, Gibson, et Evan, 1989	F&M	7.0	40.0	15-18	75	90 × 45
<i>C. c. carcinophila</i> (Kölliker, 1845)	F	70.0	25.0	9.0	NS	63 × 48
	M	20.0				
<i>C. c. imminuta</i> Humes, 1942	F	16.5	21.0	7.3	40-50	139 × 47
	M	8.7				
<i>C. coei</i> Humes, 1942	F	6.6	22.7	8.7	>32	78 × 47
	M	4.2				
<i>C. epialti</i> Coe, 1902	F&M	4.0-6.0	30.0	13.5	61-68	
<i>C. epialti</i> * (Shields, pers. observ.)	F	4.3	31.2	14.5	75	63 × 41
	M	2.2				
<i>C. errans</i> Wickham, 1978	F&M	4.0-6.0	35.2	11.0	>46	100 × 50
<i>C. mitsukurii</i> Takakura, 1910	F	30.0	27.0	8.0	48**	86 × 28**
	M	10.0				
<i>C. regicides</i> Shields et al., 1989	F	2.1	40.0	17.0	76	82 × 62
	M	1.6				
<i>C. wickhami</i> n. sp.	F	30.0	40.0	20.0	98	125 × 42
	M	10.0				

* ex. *Cancer antennarius*

** Shields, pers. observ.

bases, and stylet apparatus. These species prey on large host eggs. In addition, the morphology of the stylet of *C. wickhami* is similar to that of *C. regicides* (i.e., in the form of a broad, flat dagger). The above adaptations may allow penetration of the thick outer coat of these large eggs (Wickham and Kuris 1988).

The presence of ovarian pores may be of taxonomic value to the genus. Distinct ovarian pores were not observed on female *C. wickhami*. Similarly, Stricker (1986) did not find distinct ovarian pores on *C. epialti*. Takakura (1910) and Shields et al. (1989) reported distinct ovarian pores from *C. mitsukurii* and *C. regicides*, respectively. The ovarian pores of *C. regicides* are typically found prior to ovulation, but are not apparent prior to oviposition (Shields et al. 1989); *C. mitsukurii* appears to follow a similar pattern (Shields, pers. observ.).

The larvae of *C. wickhami* resemble the typical hoplonemertean larval form (Gibson 1972, p. 150), and are similar to the larvae of *C. epialti* in gross morphology (Stricker and Reed 1981). Larvae most likely undergo direct development into the juvenile stage upon settling onto their host (Stricker and Reed 1981). The larva of *C. wickhami* is similar to that of *C. carcinophila*, *C. epialti*, and *C. regicides*; the larvae do, however, differ in size. *Carcinonemertes wickhami* has the smallest larva yet described for the genus.

Mature *C. wickhami* were found only in the broods of ovigerous lobsters. Further, these nemertean have been collected only from lobsters with eggs in relatively advanced stages of development (development of eye placodes initiated—8 of 19 lobsters examined). No nemertean were recovered from 6 lobsters with relatively early broods nor from 3 lobsters held for dissection after eclosion. *Carcinonemertes wickhami* does not appear to migrate to the branchial chamber and into the branchiae after host eclosion, nor does it move to the limb apodemes and axillae (see below).

Three distinct life-history patterns have emerged for six of the eight species of *Carcinonemertes*. These patterns appear related to the developmental timing of host embryogenesis (oviposition to eclosion): embryogenesis in various reptantian decapods can be of short (e.g., 13-16 days), moderate (e.g., 40-120 days), or long duration (e.g., 120-300+ days). In addition, life-history patterns may be useful taxonomic characters as few differences in morphology aid in distinguishing between species.

1 Portunid crabs have a short duration of embryogenesis (Churchill 1919, Sandoz and Rogers 1944). Carcinonemertid larvae settle primarily on ovigerous female crabs where they quickly metamorphose and mature. After eclosion, adult worms migrate to the

branchial chamber, encyst between the branchial lamellae, and lie dormant until the female crab oviposits (Humes 1942). Adult worms then migrate back to the clutch (Humes 1942, Hopkins 1947). Two species of *Carcinonemertes* follow this pattern: *C. carcinophila* and *C. mitsukurii*.

2 Embryogenesis of cancrid and grapsid hosts is of moderate duration (Kuris 1971, Roe 1979, Wickham 1980, Shields et al. In press). Carcinonemertid larvae settle on male and female crabs, metamorphose into juveniles, and migrate to the limb apodemes, axillae, and abdomens of their hosts. Juveniles transfer from male to female crabs during host copulation (Wickham et al. 1985). The juveniles then lie dormant, absorbing amino acids and other nutrients (Roe et al. 1982), until the host oviposits her clutch. Juvenile worms then migrate into the egg clutch and mature after eating crab eggs. Two nemerteans follow this pattern: *C. errans* and *C. epialti*.

3 Spiny lobsters and king crabs brood their eggs for long periods (Marukawa 1933; Shields, pers. observ.). Nemertean larvae settle, metamorphose, and mature only on ovigerous female crabs. Adult worms die or leave the host at eclosion. Circumstantial evidence suggests that planktonic larvae may, in at least one species (*C. regicides*), reinfect hosts immediately upon hatching (Kuris et al. In prep.). Two species follow this pattern: *C. regicides* and *C. wickhami*.

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