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Number 6

1 July 1991

Redescription, Ontogeny, and Demography of *Parascothorax synagogoides* (Crustacea: Ascothoracida), Parasitic on *Ophiophthalmus normani* (Ophiuroidea) in the Bathyal Basins off Southern California

Mark J. Grygier

Sesoko Marine Science Center, University of the Ryukyus, Sesoko, Motobu-cho, Okinawa 905-02, Japan
Current address: 14804 Notley Road, Silver Spring, Maryland 20905, U.S.A.

ABSTRACT.—A lectotype is designated for the ascothoracidan *Parascothorax synagogoides* Wagin, and this species' host ophiuroid in the Sea of Okhotsk is reidentified as *Ophiophthalmus normani* (Lyman). Both sexes of *P. synagogoides* infesting *O. normani* in the bathyal basins of the Southern California Continental Borderland are described, and a distinct post-larval stage is recognized. *Parascothorax* is distinguished from *Ascothorax* mostly by plesiomorphies, and ontogenetic variability in male *Parascothorax* makes the previous use of male features in diagnosing species of *Ascothorax* unreliable. Three brooded naupliar stages corresponding to at least five instars are described, as well as the first- and last-instar ascothoracid larvae. The parasite's cyst, which partly blocks one of the host's bursal openings, develops principally as a proliferation of the host's genital bar; as the cyst grows, it becomes perforated and finally breaks open, leaving a permanent scar. The overall infestation rate in over 15,000 *O. normani* collected off southern California was 5.0% (an underestimate due to missed small cysts) and ranged from 0.5% in the Tanner Basin to 9.0% in the San Diego Trough. Multiple infestations were more common than expected by chance; in double but not triple infestations, bursal openings flanking the same arm were preferred. Most cysts housed one female, never more, and zero to five males and/or last-instar ascothoracid larvae, the latter often being ready to molt into post-larval males. Most males apparently join females when the latter are small and the cyst is not yet closed. Brood sizes ranged from 3 to 183 depending on the female's size; individual broods were synchronous, and evidence suggests that females have more than one brood. A hyperparasitic cryptoniscid isopod infested *P. synagogoides* with a prevalence of 1.5 to 15.4%; female isopods prevented brood deposition. These demographic findings are compared to published data on two species of *Ascothorax* and a chordeumiid copepod that are bursal parasites of other ophiuroids.

INTRODUCTION

Superorder Ascothoracida.—The ascothoracidan crustaceans are parasites of echinoderms and anthozoans. About 90 species in five families have been described worldwide (Grygier, 1987d). They are characterized primitively by a bivalved carapace enclosing the body, a pair of large, grasping antennules, piercing mouthparts enclosed in an oral cone, six thoracomeres and six pairs of biramous thoracopods, and a five-segmented abdomen with a penis on the first segment and large furcal rami on the last. There are trends within the higher Ascothoracida for the females to undergo reduction of the thorax and abdomen, including simplification or loss of limbs, with a concomitant increase in the relative size, morphological complexity, and presumably physiological importance of the carapace, within which the eggs and larvae are brooded. There is also a more or less pronounced sexual dimorphism, often manifested in the dwarfism of males, except in the one hermaphroditic family. No complete life histories are known, and information about settlement and metamorphosis is especially lacking. In most genera brooded and sometimes planktonic nauplii are known (Grygier, 1987b), followed by less extensively documented bivalved ascothoracid larvae. There have been few biological studies of

ascothoracidans, and the only large-scale autecological survey has been that of Brattström (1947) on *Ulophysema oeresundense* Brattström, which infests Scandinavian heart urchins.

I have had the opportunity to examine a large collection of an ascothoracidan found off southern California that belongs to the genus *Parascothorax*, and to collect it alive. This has provided not only material for a taxonomic description, but also for rearing the larvae, observing the parasite's behavior and its effects on its host, and documenting its population structure and demographics. All these subjects are treated in the present paper, which I hope will serve alongside Brattström's as a benchmark for biological studies on ascothoracidans.

Parascothorax.—This is a monotypic genus in the ophiuroid-infesting family Ascothoracidae, part of the order Dendrogastrida, which includes most of the ascothoracidans with echinoderm hosts. *Parascothorax synagogoides* Wagin was first reported to infest *Ophiura quadrispina* Clark at a depth of 1197 m in the Sea of Okhotsk, where 57 of 270 examined ophiuroids were infested (Wagin, 1964). Unfortunately, the original host was misidentified; following my inquiry Dr. I. S. Smirnov has reidentified 12 infested ophiuroids from the parasite's type lot in the Zoological Institute in Leningrad as *Ophiophthalmus* (= *Ophiacantha*) *normani* (Lyman).

Wagin described females and dwarf males living within perforated cysts that occlude the host's bursal openings. He considered *Parascothorax* morphologically intermediate between generalized ectoparasitic species now divided between *Synagoga* and *Waginella* in the family Synagogidae and the more advanced genus *Ascothorax*, which also infests ophiuroids. In this context Wagin (1964, 1970) also discussed the historical biogeographical significance of *Parascothorax*.

Rokop (1975) noted a low prevalence of an ascothoracidan parasitizing *O. normani* in the San Diego Trough, a bathyal basin off southern California. This species of ophiuroid occurs in the North Pacific from the Gulf of California to Japan at depths of roughly 70–3000 m (Clark, 1911; D'yakonov, 1967). In the Southern California Continental Borderland, a topographically complex regime of islands, ridges, and bathyal basins (Fig. 1), *O. normani* is by far the dominant epibenthic organism in at least the Catalina Basin (Smith and Hamilton, 1983), as well as an important animal in the San Diego Trough. Rokop's parasite proved to belong to *Parascothorax*, and I have already remarked on its sexuality, described the larval ontogeny of its antennules, and briefly summarized its occurrence and host relations (Grygier, 1987a, 1987b, 1988). A comparison with type specimens from the Soviet Union shows that the Californian form is also *P. synagogoides*.

METHODS AND MATERIALS

Soviet specimens.—I found twelve specimens of *Ophiophthalmus normani* bearing multiple cysts and labelled in Russian in V. L. Wagin's handwriting as "*Parascothorax synagogoides*, Sea of Okhotsk, 1949, Ushakov" in the Zoological Institute in Leningrad in 1989. These I assume to be syntypes. I borrowed one of these ophiuroids, with two cysts and the enclosed parasites in good condition, for detailed study. Another infested *O. normani* with five cysts (misidentified as *Ophiura quadrispina*; one cyst opened and a female parasite displayed separately) is housed in the teaching collection of the Department of Invertebrate Zoology at Leningrad State University (shelf A8). Wagin had deposited this lot in the Department many years before he published his description of *P. synagogoides*, and it bears a manuscript name, "*Ascothorax witjasi* n. sp." I consider this another lot of syntypes of *P. synagogoides*.

Californian specimens.—The Scripps Institution of Oceanography (SIO) Benthic Invertebrate Collection houses many sorted lots of *Ophiophthalmus normani* [see Luke (1982:34–35) for catalogue numbers and detailed collection data] as well as unsorted trawl samples containing large numbers of this species (Table 1). They were collected between northern Mexico and Big Sur (32°25'–35°37' N), mostly in the various bathyal basins of the Southern California Continental Borderland (Fig. 1), and from the southern half of the Gulf of California (25°17'–27°43' N), at depths of approximately 900–1900 m by various investigators between 1951 and 1981. A few additional samples collected in the Catalina Basin by K. L. Smith and colleagues were made available. All these samples, comprising 15,373 individuals of *O. normani*, were surveyed for infestations of *P. synagogoides*; in large samples, aliquots of 200–800 individuals were examined. All the ophiuroids with evident *Parascothorax* cysts were isolated, and the number of cysts, including broken, healed ones, was noted. In the earliest stage of the study, small numbers of other species of ophiuroids may inadvertently have been counted as uninfested *O. normani*.

Wet and dry collections of *Ophiophthalmus normani* (labeled *Ophiacantha* or *Ophialcaea normani*), taken by the U.S. Fisheries Steamer *Albatross* between southern California and Japan and housed in the National Museum of Natural History, Smithsonian Institution, were examined for additional distribution records of *Parascothorax*.

Living specimens.—I obtained living specimens of *Parascothorax synagogoides* for laboratory rearing of larvae and observations of behavior from an otter-trawl sample consisting mostly of *O. normani* taken on 19 May 1982 in the San Diego Trough, 33°35.5' N, 117°30.0' W, at a depth of about 1200 m. Twenty-six ophiuroids bearing large cysts were placed in seawater slush for transport to the laboratory (about 10 hr), where they were transferred to Whatman #2-filtered seawater at 8°C. When I removed the parasites from their cysts four days later, I found living individuals in 21 ophiuroids, dead ones in three, and only healed cysts in two. The living females and males of *Parascothorax* were kept in a refrigerator in a large bowl of filtered seawater, occasionally changed. Many died during the first three weeks after capture, but about one-third of the males and one-quarter of the females were still alive on 18 July 1982, two months after capture, when they were preserved. Escaped eggs and larvae from females' brood chambers were transferred at intervals to a separate bowl; subcultures of offspring were maintained in petri dishes of filtered seawater. Nauplii did not molt in culture except for some late metanauplii that molted to the first-instar ascothoracid larva; some of the latter isolated into a subculture were still alive on 26 July 1982 (9.5 weeks), when they were preserved.

Demography.—A detailed survey was conducted on the largest available SIO samples (E1439, E1668, E1782, R7139, R7145) and one small one (R7128). E1439 was from the Catalina Basin, and the others were from the San Diego Trough. With an ocular micrometer I measured the radii of the ophiuroid discs (mean distance from center to interambulacral margins), the diameters of the cysts in the direction parallel to the bursal slit, the carapace widths of the female parasites (no allowance made for distortions; newer stage measured in molting specimens), and the carapace lengths of males and/or last-instar ascothoracid larvae that accompanied the females (newer stage measured in molting specimens; both stages measured in ascothoracid larvae molting to post-larval males). The reproductive state of the females (immature, gonads visible in carapace, or brooding), the number and type of progeny present in the brood chamber (eggs, embryos, or nauplii of three distinguishable stages), and the incidence of hyperparasitic cryptoniscid isopods were also noted. Nauplii were easy to count, but undeveloped eggs were very fragile and could not be separated for counting without damage; therefore, numbers of eggs were often estimated. For each multiple infestation, the spatial relationship of the affected bursal slits was noted. This detailed study revealed previously unnoticed sites of infestation, usually involving very small cysts, on ophiuroids already known to be infested. Therefore, one lightly (E2125) and two heavily (E1668, R7139) infested whole samples were reexamined for additional infested hosts, and any additional data were logged as described above.

DESCRIPTION

Parascothorax Wagin, 1964

Diagnosis.—Carapace of female a rounded pentagon in dorsal view, with T-shaped array of longitudinal and transverse grooves; pair of lappets flanking antennules. Four setae and two teeth on antennular chin; antennular claw movable; claw guard with two setae and up to two small spines. First three thoracomeres in females with transverse ridges, fourth and fifth with smaller medial humps. Filamentary appendages short, conical. Round lateral swellings at bases of several thoracopodal coxae; coxa of sixth thoracopod produced into large, rounded plate. Epaulets knob-shaped. Older males with more than four terminal furcal setae. Parasites in cysts formed from genital bar and bursal wall of ophiuroids.

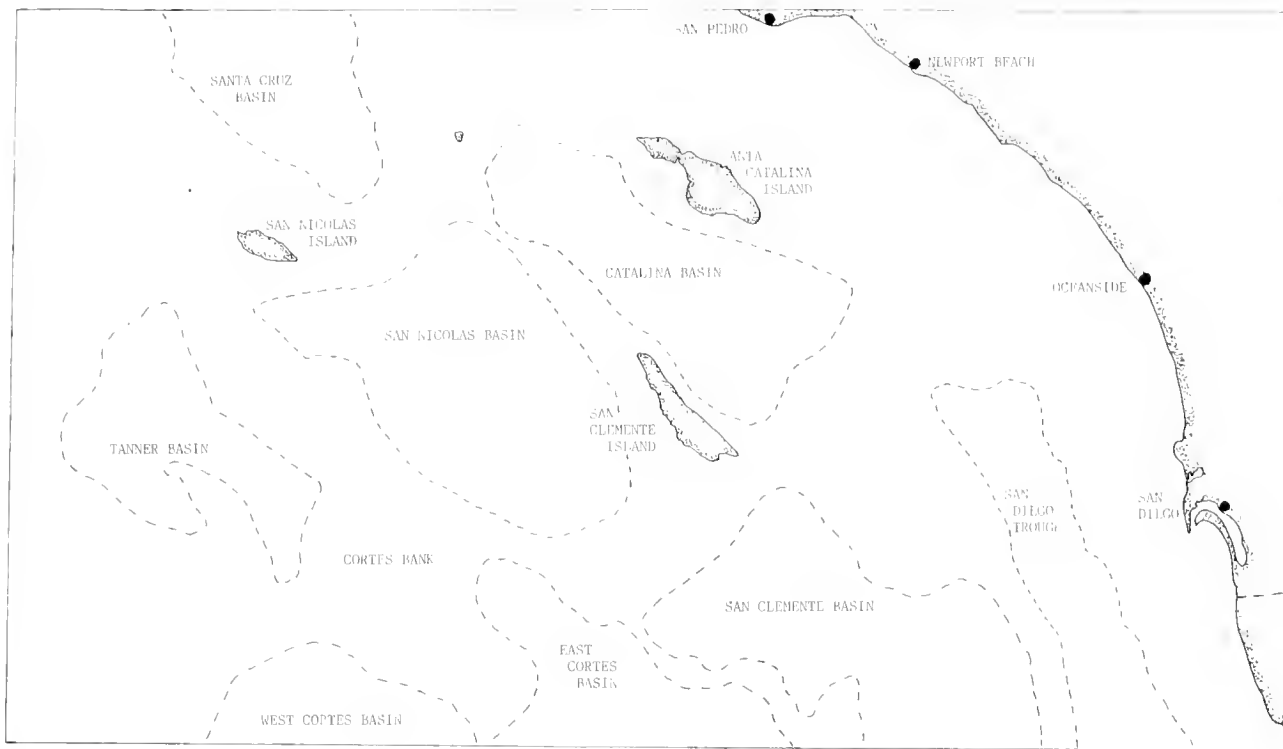


Figure 1. Part of the Southern California Continental Borderland. Outlines of bathyal basins roughly follow the 500-fathom isobath.

Type species.—*Parascothorax synagogoides* Wagin, 1964, by monotypy.

Remarks.—Species of the other genus in the family Ascothoracidae, *Ascothorax*, live entirely within their hosts' bursal cavities. Grygier (1983) remarked on the difficulty of telling *Parascothorax* from *Ascothorax* without knowing whether a cyst was formed. Wagin (1964) proposed discriminative features that are inadequate (Grygier, 1983), and though the diagnosis above includes a few more features, doubts about the distinctness of *Parascothorax* remain. *Ascothorax pilocaudatus* Grygier has a pair of vanes on each of the first three thoracomeres, and its males have more furcal setae than is usual in the genus, both features reminiscent of *Parascothorax*. *Ascothorax brattstroemi* Grygier has little thoracic expansion and no elaborations; its sixth thoracopods have enlarged coxae, as in females of *Parascothorax*. Most species of *Ascothorax* lack seminal receptacles in the second thoracopods (Grygier, 1983). Mortensen (1936) reported "a heavily plated cyst, opening through a pore in the ventral interradius" of *Amphiura belgicae* Koehler that enclosed *Ascothorax bulbosus* Heegaard, but Heegaard (1951) did not mention such a cyst when he described the species, just that the parasites were in a bursa. The dorsal groove gives *P. synagogoides* an incipiently lobed carapace. A better developed, bilobed brood chamber occurs in *Ascothorax ophiocentis* Djakonov and the undescribed *Ascothorax* sp. B of Grygier (1983).

Wagin (1964) considered *Parascothorax* a grade of organization intermediate between *Synagoga* and *Ascothorax*. In fact, it is organized in much the same way as is *Ascothorax* but has antennules slightly more generalized and better armed and a thorax less hypertrophied than in most species of *Ascothorax*. No small spines are recorded from the antennular claw guard of any species of *Ascothorax*, and though one of the teeth on the fourth antennular segment's chin in *A. gigas* Wagin and *A. sosci* Grygier is bifid (the medial and the lateral one, respectively), no vestigial seta on the

medial side of the chin, like that of *Parascothorax*, is recorded in any species of that genus (Grygier, 1983; Grygier and Fratt, 1984). Since these morphological differences are plesiomorphies, it is primarily the effect on the host and secondarily the carapace morphology that lead me to retain *Parascothorax* as a separate genus.

Parascothorax synagogoides Wagin, 1964

Diagnosis.—As for genus.

Type material.—Lectotype female 3.3 mm wide, allolectotype male 0.7 mm long, here designated (ZIN 1/66582), from the same cyst in one of 12 specimens of multiply infested *Ophiophthalmus normani* in the Zoological Institute, USSR Academy of Sciences, Leningrad, collected by A. I. Savilov and P. V. Ushakov, "Vityaz'" sta. 114, Sea of Okhotsk, 52°02' N, 147°58' E, depth 1197 m, 1947. I designate as paralectotypes the remaining specimens of *P. synagogoides* from these 12 ophiuroids and those housed in the Department of Invertebrate Zoology of Leningrad State University (display shelf A8, labeled "*Ascothorax witjasi* n. sp.>").

Other material.—Hundreds of female and male specimens, some of the females brooding offspring, obtained from southern Californian *Ophiophthalmus normani* (Table 1). Specimens from the six samples studied in detail are in my possession; the other infested but undissected ophiuroids are in the SIO Benthic Invertebrate Collection.

Californian Females

Carapace.—The carapace is more or less globular, 0.41–3.85 mm wide, and at maturity is shaped like a rounded pentagon in dorsal view (Fig. 2a); it is also rounded in most juvenile specimens. The carapace's aperture occupies about 40% of the sagittal circumference; its margins are considerably thicker than the rest of the carapace, and the anterior end of the aperture is flanked by a pair of

TABLE 1. Infestation of *Ophiophthalmus normani* by *Parascythorax synagogoides* in four bathyal basins off southern California, based on samples in the Scripps Institution of Oceanography Benthic Invertebrate Collection.

Sample ^a	Number of Cysts			Percent Infested	Sample	Number of Cysts			Percent Infested		
	n	1	2 >2			n	1	2 >2			
Tanner Basin											
E2134	405	2	—	0.5	E2125	403	1	—	0.2		
E2130	250	1	—	0.4	E2155	356	1	—	0.3		
E2121	617	3	—	0.5	E1656	472	1	—	0.2		
E2180	366	5	—	1.4							
San Clemente Basin											
E1641	1	—	—	0	E1747	65	4	—	6.2		
E1750	9	—	—	0	E1649	736	20	1	2.9		
B17427	337	1	—	0.3	E1758	2	—	—	0		
B17427: 4Apr 1974, 33°05'N, 118°17'W, 1114 m.											
Catalina Basin											
E1755	2	—	—	0	E352	158	3	—	1.9		
E1789	227	3	—	1.3	E356	81	2	—	2.5		
E1651	710	2	—	0.3	E683	350	1	—	0.3		
E1439 ^b	800 ^c	59	17	4	10.0	SV	596	—	—	0	
E1632	395	33	4	—	9.4	E1629	121	2	—	1.7	
SX	427	2	—	0.5	MII	635	59	18	—	12.1	
SV: SABRAT V, 33°12'N, 118°08'W, 1050 m.											
SX: SABRAT X, 23 Apr 1981, 33°35'N, 118°22'W, 1098–1116 m.											
MII: MET II Sta. 103, 13 Jun 1981, 1350 m.											
San Diego Trough											
E1856	112	2	—	1.8	E1853	59	2	1	—	5.1	
E1812	20	—	—	0	E947	3	—	—	—	0	
E1866	20	3	3	—	30.0	E1663	778	27	2	—	3.7
E1782 ^b	800 ^c	62	12	6	10.0	R7120	200 ^c	7	—	—	3.5
R7128 ^b	191	4	6	1	6.3	R7137	260	32	1	2	13.5
R7138	549	19	2	—	3.8	E1668 ^b	632	108	23	6	21.7
R7139 ^b	396	50	10	—	15.2	R7145 ^b	748 ^c	49	12	2	8.4
E1806	17	—	—	0	E1777	4	—	—	—	0	
E1679	4	—	—	0	E2715	32	1	—	—	3.0	
E638	56	2	—	3.6	E1446	35	3	—	—	8.6	
SIV	108	3	—	2.8							
R7120: 18/19 Jan 1971, 32°27'N, 117°29'W, 1204–1226 m.											
R7128: 21 Jan 1971, 32°35'N, 117°34'W, 1184–1217 m.											
R7137: 21 Apr 1971, 32°26'N, 117°30'W, 1098–1195 m.											
R7138: 21 Apr 1971, 32°34'N, 117°30'W, 1208 m.											
R7139: 12 Jul 1971, 32°37'N, 117°33'W, 1162–1199 m.											
R7145: 14 Jul 1971, 32°25'N, 117°27'W, 1208–1244 m.											
SIV: SABRAT IV, 12 Aug 1980, 32°25'N, 117°41'W, 1100 m.											

^aCollection data for most samples were given by Luke (1982); data for those that were not are given here. Additional samples from other localities were also examined: E1681, E1745, E1715, E612, E626, E1814, E1760, E766, E1808, E1710, E1948, E2056, E1937, E2165.

^bSample used in demographic analysis.

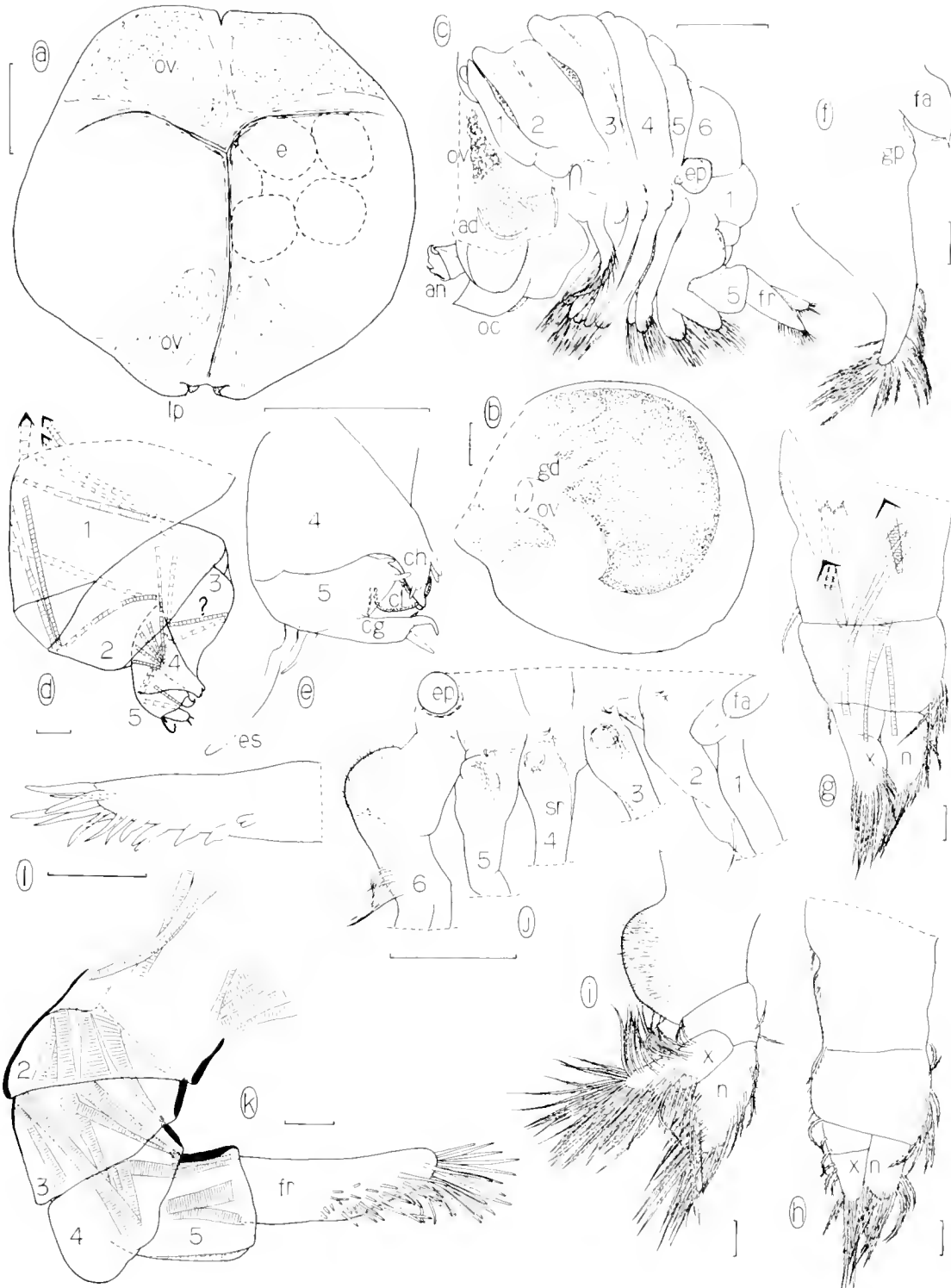
^cAliquot.

lappets that partly cover the antennules. The thin-walled dorsal brood chamber is split by a longitudinal groove beginning above the anterior end of the aperture and is bounded behind by a pair of transverse grooves. A shorter anterior pair of grooves is sometimes visible and is very clear in the lectotype. The ovary diverticula of older females loop within the carapace from the side of the head to the anterior part of the aperture, then split into a short anterior and long posterior branch parallel to the aperture (Fig. 2b). The gut diverticula follow the ovary diverticula, with proximal branching into the thin wall of the brood chamber.

Antennules.—The five-segmented antennules (Fig. 2d) reach as far ventrally as the oral cone. The first segment forms a flat cup applied to the side of the head. The second segment is as broad as the first but shorter and is partly retracted into it. The distal three segments are much narrower than the basal two. The third segment

is trapezoidal, longer than wide. The fourth is sector-shaped (Fig. 2e); its anterior chin has two strong apical teeth, a subapical pair of short, vestigial setae on the proximal side, another such seta next to the medial tooth (not always visible in mounted preparations), and a fourth vestigial seta laterally on the distal side. The fifth segment (Fig. 2e) is small, roughly square in side view, narrower than the fourth, and is armed along its anterior edge with a stalked aesthetasc, a seta, a short, stubby claw guard with two setae and up to two small distal spines (latter sometimes difficult to see), and a movable claw with three vestigial setae at the base.

The antennular musculature, shown schematically in Figure 2d (also valid for males), was previously illustrated by Wagin (1964: fig. 7A). Most of the individual muscles correspond to ones illustrated by Grygier (1987c: fig. 7A) in the six-segmented antennules of a relatively generalized synagogiid ascithoracid.



Gorgonolaureus muzikae Grygier, but there are several differences. In *P. synagogoides* but not *G. muzikae* the lateral extensor of segment 2 is divided, the extra part originating on the edge of segment 1. The lateral and medial flexors of segment 4, originating in segment 2, are parallel, so differing from *G. muzikae*. The more proximal of the two muscles extending between the anterior edge of segment 3 and the opposite proximal edge of segment 4 is not readily identifiable with any muscle in segments 3 and 4 in *G. muzikae*. The medial extensors of the last segment originate only on the side of segment 4, none more proximally. The two claw retractors both originate from the sides of the last segment, not from the medial side and proximal corner.

Mouthparts.—The oral cone is very small relative to the body (Fig. 2c), and the mouthparts are like those of the males (cf. Fig. 4e). The labrum is open behind, the mandibles are long and slender with setulate tips, the maxillules are short and blunt, and the maxillae are basally united, with harpoon-like bifid tips. A pair of maxillary-gland papillae protrudes from the base of the maxillae.

Thorax and thoracopods.—The thorax is moderately expanded (Fig. 2c). The first thoracomere is distinct from the head. The first three segments are usually broader than the rest, and each has an anterior transverse ridge or flap that is sometimes interrupted at the midline or ornamented with low lateral and medial processes. The fourth segment often has a medial hump, and the fifth has a smaller one. The sixth segment is unmodified except for a pair of knob-shaped lateral epaulets.

There are six pairs of thoracopods. The first pair is uniramous (no endopod) and bears short plumose distal setae (Fig. 2f). At its base is a genital papilla and, usually sitting reflexed over the base of the limb, a small filamentary appendage ending in one or two short spines (Fig. 2f, j). Thoracopods 2–5 are leaf-like with the posterior ones narrower (Fig. 2g, h); a tiny seta arises from the body wall just above each limb insertion (Fig. 2j). The coxa is relatively shorter in thoracopod 2 than in the other pairs, and the basis is shorter than wide in all pairs. The basolateral part of the coxa has a round proximal process on which the seminal receptacles open in thoracopods 3–5 (Fig. 2j); there are fewer than 10 narrow elongate receptacles per thoracopod, and they are usually or always absent in thoracopod 2. The tapered, usually unsegmented rami are no longer than the basis, with the endopod wider and slightly longer than the exopod; occasionally two segments are evident, most often on an exopod (Fig. 2g, h). Short plumose setae line the rami and the distal parts of both edges of the protopod, more found medially than laterally. The sixth thoracopods are flattened against the sides of the abdomen; the coxa has a large, rounded, posterior plate covered with short hairs (Fig. 2i), and the coxa–basis articulation is usually indistinct; the rami are unsegmented and more densely setose than those of the other thoracopods.

The musculature of thoracopods 2–5 (Fig. 2g) is simpler than that illustrated by Grygier (1987c: fig. 7C) for the generalized thoracopods of *Gorgonolaureus muzikae*. No lateral diagonal coxal muscle was positively identified, and only one muscle was seen reaching to the midlength of each ramus (*G. muzikae* has two).

Abdomen.—The abdomen has five unequal segments, the first with a ventral penis lobe and the fourth with a moderate ventral protrusion. The musculature is shown in Figure 2k. The straight, tapered furcal rami are about three times as long as their basal height and have 10–20 short, simple terminal setae and several shorter, slightly lateral setae along the distal half or so of the ventral edge (Fig. 2k-l); an occasional seta is bifid or trifid.

Post-larvae (Fig. 3).—The smallest settled females are considered post-larvae. While their carapaces are rounded, unlike the laterally flattened ones of males, their bodies are almost exactly like those of post-larval males (males described and illustrated below). At that stage there are no differences between the sexes in the antennules and oral cone. Both sexes have thoracopods with few or

no setae and no filamentary appendages, and the furcal rami are only as long as the telson, with three or four terminal setae. I observed a nub-like frontal filament in one female post-larva in contrast to the longer filaments of males; older females seem to have no frontal filaments.

Californian Males

General features.—The carapace is bivalved, oval, and laterally compressed (Fig. 4a), 0.47–1.34 mm long, and 0.75–0.90 times as high as long. The valves are soft and flabby with clusters of internal guard hairs along the free margins except anteriorly. The body tagmosis is 5-6-5 if only limb-bearing segments are considered as thoracic; the thorax is lightly arched, and the abdomen is U-shaped (Fig. 4b, l). The smallest males (post-larvae, see below) lack testes, but larger ones have testes and short-headed sperm in the carapace.

Cephalic appendages.—The antennules consists of five segments, and segments 3 and 4 are immovably joined (Fig. 4c). Segments 4 and 5 form a subchela (Fig. 4d) and agree structurally with those of females in most respects. The chin is more pronounced in the males, and the subapical pair of vestigial setae on its proximal side is larger. The fifth segment's aesthetasc is somewhat longer than the segment and appears to have a pore at its tip (pore also seen in lectotype female; not a true aesthetasc?).

Antennae and eyes are absent, but a pair of frontal filaments arises from the inner surfaces of the carapace valves next to the antennules (Fig. 4c). The oral cone is like that of the females (Fig. 4e) but much larger relative to the body (Fig. 4b).

Thorax and thoracopods.—The thoracic segments are unmodified dorsally, but the posterior ones are slightly longer, with a pair of knob-like epaulets on the sixth segment (Fig. 4b). There are six pairs of thoracopods. The first pair is shorter than the others and is uniramous with one or two setae. The other five pairs are



Figure 3. *Parascythorax synagogoides*, Californian female post-larvae. a, body removed from carapace, some thoracopods obscured, frontal filament added from another specimen; b, left thoracopods of another specimen. ad, adductor muscle; an, antennule; d, mandible; ep, epaulet; ff, frontal filament; fr, furcal ramus; la, labrum; ml, maxillule; mx, maxillae. Scale bars 0.1 mm.

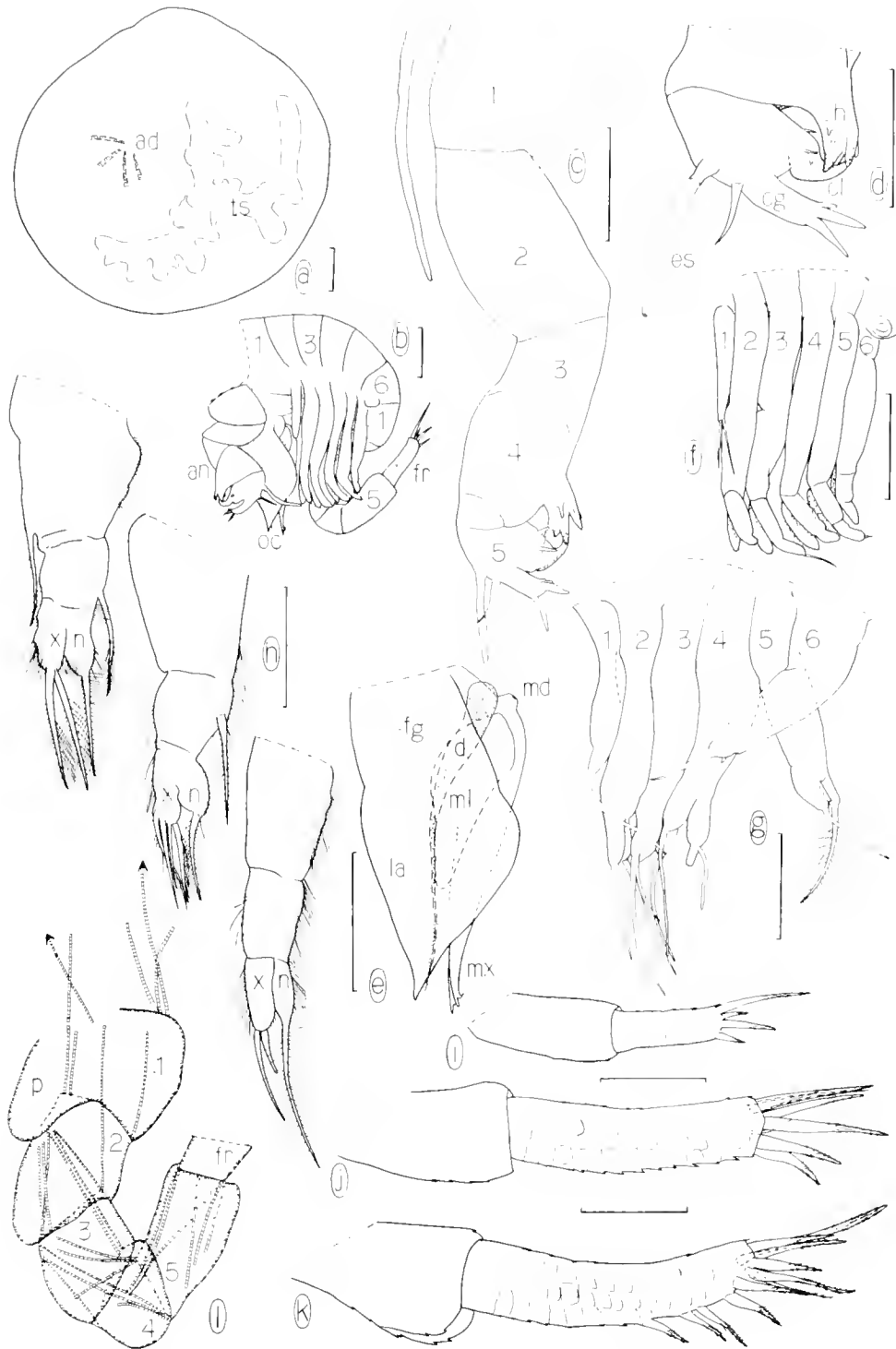


Figure 4. *Parascothorax synagogoides*, Californian males. a, carapace, lateral view, front end left; b, body of post-larva; c, antennule of mature male and frontal filament; d, distal antennular segments, lateral view; e, oral cone; f, thoracopods of post-larva; g, thoracopods of medium-sized male, fine hairs omitted except on one seta; h, thoracopods of large male, progressively more posterior from left to right; i, furcal ramus of post-larva; j-k, furcal rami of mature males; l, schematic diagram of abdominal musculature of young male, all illustrated muscles actually paired, proximal ones without arrows originating in sixth thoracomere, left one with arrow the ventral longitudinal muscle. ad, adductor muscle; an, antennule; cg, claw guard; ch, chin; cl, claw; d, mandible; es, aesthetasc; fg, foregut; fr, furcal ramus; la, labrum; md, maxillary gland duct; ml, maxillule; mx, maxillae; n, endopod; oc, oral cone; ts, testes; x, exopod. Scale bars 0.1 mm.

biramous; the endopod is sometimes small in the sixth pair, but otherwise the endopods are approximately equal to or slightly shorter than the exopods. The rami are obscurely segmented, but often two segments are visible. The setal armament varies with the male's size (Fig. 4f–h). In the smallest males, there are just fine hairs on the endopods and one simple seta on some exopods. In medium-sized males, the edges of the thoracopods are hirsute and each ramus has one or two plumose setae. Larger males additionally have a lateral coxal and medial basal seta on the second and sometimes third thoracopods. The largest males have up to four plumose setae on the exopods of thoracopods 2–4.

Abdomen.—The abdomen is five-segmented with a furca (Fig. 4l). The first segment has a simple midventral penis lobe. The fourth segment is short, the others subequal, and the fifth is broadened posteriorly, with ctenate ventral scales. The furcal rami are rectangular and elongate, shorter than the telson in the smallest males, but otherwise at least 1.5 times as long as the telson (Fig. 4i–k). The lateral and medial faces of the rami have ctenate scales. The smallest males have three or four terminal setae, and the largest ones have ventral setae as well (1 observed at most 13). The distal halves of the furcal setae are pilose.

The abdominal musculature is shown diagrammatically in Figure 4l. All the described muscles are actually paired. Muscles insert at the bases of the furcal rami dorsolaterally, ventrolaterally and ventromedially, and at midheight medially; in younger but apparently not in older males, a ventromedially inserting furcal muscle arises in the fourth segment. Abdominal segments 1–4 each have one to three dorsal flexor muscles and one to three ventral extensors. The ventral longitudinal muscles of the thorax insert ventrolaterally in the first abdominal segment.

Post-larvae.—I propose that a distinct post-larval stage be recognized for the smallest males, which as yet have no testes developed, almost no thoracopodal setation, and furcal rami remarkably small compared to those of larger males (Fig. 4b, f, i). As mentioned above, aside from the shape of the carapace and the length of the frontal filaments, male post-larvae are morphologically indistinguishable from the smallest females, which I also term post-larvae.

Adult Behavior

Living females exhibited little behavior. They could open the carapace but not close it completely, so eggs and larvae readily escaped from females removed from their cysts. They could abduct and adduct their furcal rami and point the oral cone in different directions. They usually beat the rear pairs of thoracopods, sometimes in a slow metachrony, but more usually in a less organized manner with a simultaneous recovery stroke. Their most consistent behavior was to extend the antennules ahead one at a time from below, opening the subchela when doing so, and then to retract them, all in one continuous motion.

Males were immotile. However, the oral cone was in constant motion, protruding and retracting and bending somewhat in all directions. Males extended their antennules alternately straight ahead, as did the females, with an open subchela that was closed before being withdrawn. The abdomen, usually curled under the thorax, sometimes beat as an unstraightened unit with some motion of the splayed furcal rami, but the furca and thoracopods did not beat for locomotion.

Comparison to Types

Wagin's (1964) females of *Parascothorax synagogoides* averaged 4 mm in diameter, and reached 6 mm (those I examined were not so large), while the Californian specimens are smaller than 4 mm. Wagin's males were 0.7–1.2 mm long, as are the Californian

ones. Examination of the antennules of the lectotype (Fig. 5a, b) and allolectotype (Fig. 5e, f) shows the same armament of the chin and basically the same armament of the fifth segment, except that both the male and the female probably have only one small spine on the claw guard (variable in the Californian material). Wagin (1964: fig. 8E) confused the mandibles and maxillules and drew the former as halves of a sucking tube lacking setules at the tips; he did not draw the tips of the maxillules as bifid. In the type specimens the maxillae are minutely bifid (Fig. 5c), but the tips of the mandibles are hidden from view within the oral cone. The furcal rami of the males have, according to Wagin, five to seven setae and a hairy surface. The vertical grooves he drew on the lateral surfaces of the rami are exaggerated (compare Fig. 5f and Wagin, 1964: fig. 9), and the true sculpturing is a slightly weaker version of that of the Californian males (Fig. 4i–k); in the allolectotype not all of the furcal setae are pilose. In all significant respects, therefore, specimens of *Parascothorax* from California agree with the original specimens from the Sea of Okhotsk, and I consider them to represent the same species.

Post-larvae.—Grygier and Fratt (1984) proposed that the molt at which natatory setae are lost be considered the end of larval development. Now I have proposed that the early post-settlement stage of males and females in *Parascothorax* be considered a post-larval stage. The male post-larvae are smaller than the settled last-instar ascothoracid larvae (Fig. 6) but the same size as the males that were about to molt from those ascothoracid larvae. The number of instars in either sex after the metamorphosis to the post-larva is unclear. Most of the preserved females examined, no matter what their size, had loose cuticles, so females seem to have no terminal molt.

Taxonomic remarks.—In males the marked changes from post-larva to maturity in features such as size, thoracopodal setation, and relative length of the furcal rami (Fig. 4f–h, i–k) suggest that these features are probably variable and size-dependent in the closely related genus *Ascothorax*. It is likely that most of the male characters employed by Grygier (1983) in diagnoses of species of *Ascothorax* are unreliable.

LARVAL DEVELOPMENT

General remarks.—Wagin (1964) gave very little information about the larvae of *Parascothorax synagogoides*. However, an ontogenetic sequence based in part on laboratory-reared larvae is available for the Californian population. Grygier (1987a) discussed some aberrant, possibly female nauplii in connection with sex determination; here only ordinary nauplii (possibly all males) are discussed. The ontogenetic sequence includes brooded eggs, three brooded naupliar stages not conclusively linked to instars and referred to here as nauplii, early metanauplii, and late metanauplii, and at least two non-brooded cypris-like larvae, referred to as first-instar and last-instar ascothoracid larvae.

I estimated the number of naupliar instars by counting the unshed exuvia of older larvae, of both cultured ones and ones preserved upon capture, as I did for another ascothoracidan, *Gorgonolaureus muzikae* (see Grygier, 1987b). I have often found brooded larvae with several nested, unshed cuticles in preserved ascothoracidans, and I assume this to be normal for this group. The maximum replicable observation in *P. synagogoides* was five old cuticles investing the ascothoracid larva ready to molt, so there must be at least five naupliar instars.

All of the available first-instar ascothoracid larvae were derived from late metanauplii that molted in culture, usually one or two days after release from a brooding female; none of these molted again in culture. Since I never observed this stage being brooded, it must appear in nature only after the metanauplii are released and



Figure 5. *Paraschothorax synagogoides*, type specimens from Sea of Okhotsk. a–d, lectotype female; a, whole animal with right carapace valve removed; b, distal antennular segments; c, tip of oral cone; d, distal half of left furcal ramus (setae do not go so far proximally on right one); e–f, allolectotype male; e, whole animal; f, body removed from carapace. ad, adductor muscle; an, antennule; cg, claw guard; ch, chin; cl, claw; e, eggs; ep, epaulet; es, aesthetasc; ff, frontal filament; fr, furcal ramus; gd, gut diverticula; md, maxillary gland duct; mx, maxillae; oc, oral cone; ov, ovary; p, penis rudiment. Scale bars 1 mm in a and b, otherwise 0.1 mm.

undergo a final molt. I found last-instar ascothoracid larvae, all apparently male, together with females as independent individuals, never brooded, and they were often ready to molt to the post-larval male. None bore an unshed cuticle of any earlier larva, and it is unclear, though unlikely, whether any additional free-living instars exist between the two known ascothoracid larvae.

Eggs.—Brooded eggs are spherical, dark red, and 440 μm in diameter.

Nauplius (Fig. 7a–e).—The earliest larvae are rotund, almost 0.7 mm long, filled with yolk, and provided with a small protruding labrum, two furcal and one terminal papillae, and no frontal filaments or eyes (Fig. 7a, b). The antennules are unsegmented with the setation 1m-1m-2m.11-2t (Fig. 7c). The antennae have a small enditic spine on the coxa and a short medial protuberance on the basis; the endopod is unsegmented with two terminal and often one subterminal setae; the exopod is unsegmented with four or five setae (Fig. 7d). The mandibles resemble the antennae, but the protopod has only a small medial coxal flange, the endopod has no subterminal setae, and the exopod has three to five setae in different specimens (Fig. 7e).

Early metanauplius (Fig. 7f, g).—This larva has a kite-shaped dorsal shield flatter than that of the nauplius. It is unclear whether papilliform frontal filaments are present. The limbs are unchanged from the nauplius except that the protopods are unarmed. Rudiments of maxillules, maxillae, and the first two pairs of thoracopods are apparent under the cuticle. The yolk mass is arrowhead-shaped, pointing backward.

Late metanauplius (Fig. 7h–n).—The bowl-shaped dorsal shield is 0.67–0.80 mm long and 0.55–0.66 mm wide and is slightly indented at the midline at both ends (Fig. 7h–j); it contains the bivalved

carapace of the developing ascothoracid larva. Frontal filaments are present, and the labrum is short and pointed. The unsegmented antennules have new medial setae, and the apical setae are disposed differently, so the setation is 1m-1m-1m-2m.2l-1t (Fig. 7k). The antennal and mandibular protopods are unarmed, the endopods have a terminal and subterminal seta, and the exopods are annulate with six setae, the distal seta being short (Fig. 7l, m). The maxillules and maxillae are represented externally by a pair of knobs bearing two bumps or spines each, and the thoracopods are represented by several pairs of spinules (Fig. 7n). The furcal region is developed into a pair of lobes protruding beyond the end of the dorsal shield, with cuticular ctenae and four spines on each lobe; there is a tiny terminal spine. Rudiments of all postcephalic appendages including the furca are present beneath the cuticle (Fig. 7j), the medially unfused maxillae being the largest and all but the first pair of thoracopods being biramous. The yolk is confined to a small central mass with lateral lobes corresponding to the future gut diverticula.

First-Instar Ascothoracid Larva

General features.—The carapace is bivalved, but the valves are inflated with rounded edges and are held partly splayed, not fully enclosing the main body (Fig. 8a). The valves are 0.67 mm long and 0.39 mm high, with more or less straight dorsal and ventral margins, the anterior end higher than the posterior, and the dorsal hinge line extending for over two-thirds of the total length (Fig. 8a, b). The body is divided into a head, thorax, and abdomen (Fig. 8c).

Antennules.—The antennules are almost straight and indistinctly segmented (Fig. 8d). The first, fourth, and fifth segments are about as long as wide, and the second and third ones are shorter. The

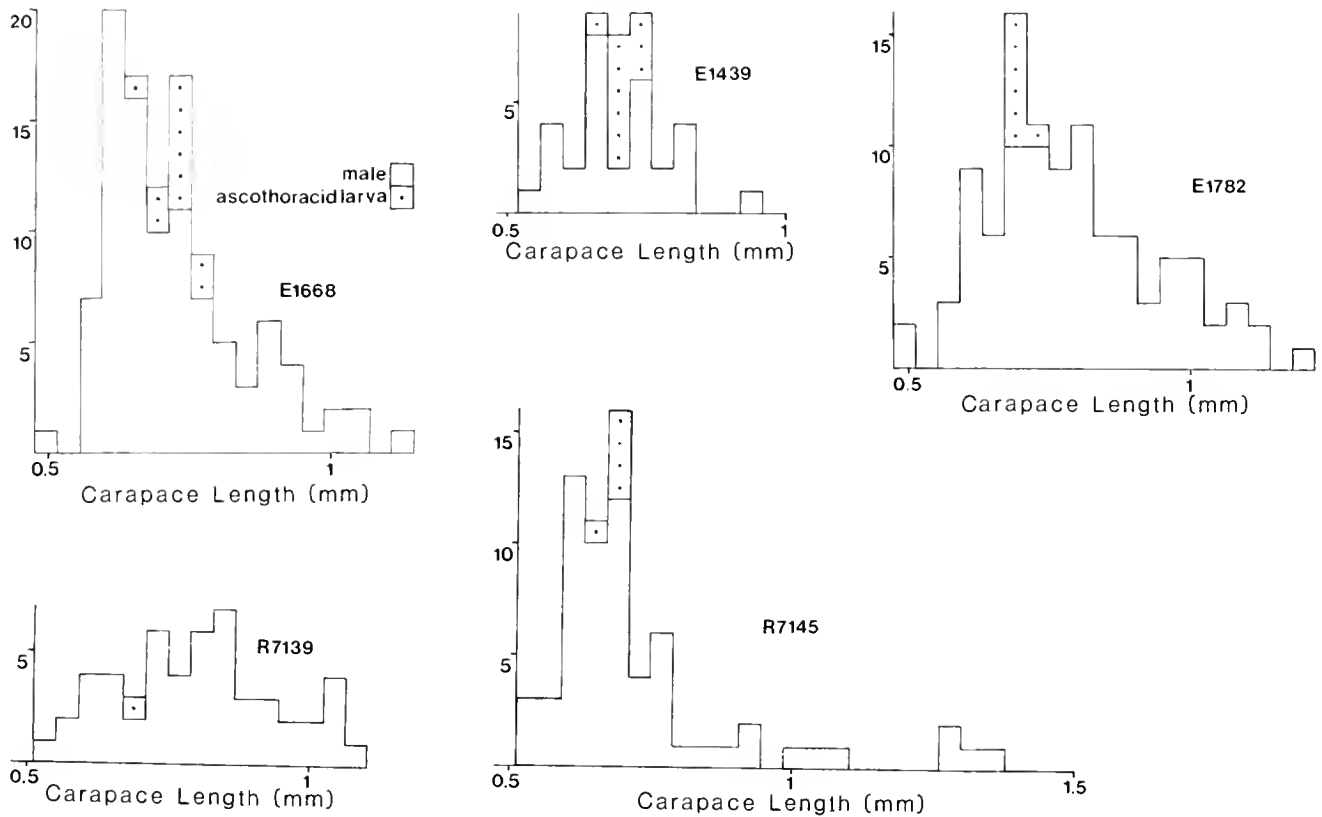


Figure 6. Size-frequency histograms of males and last-instar ascothoracid larvae from five samples of *Parascythorax synagogoides*. The smallest males are post-larvae.

anterior side of the fourth segment has a chin-like protrusion at midlength with two basal setae, two apical spines, and a subapical seta on the distal side. The claw on the distal corner of the fifth segment has three setae around its base, and there are three setae on the posterior side of this segment, the proximal one longest and the third one shortest and sometimes absent. The claw guard is twice as long as the claw, with a small cylindrical tube proximally in most specimens and two to four (usually three) short distal setae, one longer than the rest. A frontal filament complex, consisting of a knob and an aesthetasc, arises from the inner wall of each valve just posterolateral to the antennules (Fig. 8e).

Mouthparts.—The labrum is a slightly curved triangular plate in front of the other mouthparts (Fig. 8e). The antennae and mandibles are reduced versions of the naupliar limbs, twice as large in freshly molted specimens as in ones kept in culture for several weeks (Fig. 8c, e–g). The antennae are lateral to the labrum and the mandibles arise behind them; both are biramous with vestigial setae on the exopods and usually inconspicuous endopods. The mandibles have a stout protopodal endite formed *de novo* and bearing an apical spine. The maxillules are a pair of sharp cones medial to the mandibles behind the labrum (Fig. 8c, e), and the unfused maxillae are behind them and about twice as long, with bifid or trifid tips (Fig. 8c, e, h).

Thorax and thoracopods.—The six thoracomeres become longer and slightly lower posteriorly, and the first is not separated from the head by a suture. There are no elaborations or setae on any segment, but the sixth has a pair of small epaulets (Fig. 8c). Each segment has a pair of thoracopods with short setae, all except the first pair being biramous (Fig. 8c). The first thoracopod is shorter and much narrower than the others, with two distal setae and occasionally a medial one. The next four thoracopods are much alike but become somewhat shorter posteriorly: the elongate coxa

has a basolateral bump, the basis is square, the exopod is two-segmented, and the endopod is three-segmented (segmentation better defined in older larvae), with four terminal setae on the former ramus and three on the latter, the segments of the exopod being nearly equal but the distal one on the endopod being longer than the other two. The sixth thoracopod is the shortest, with a proximal constriction in the posterior part of the coxa setting off a "precoxa"; the two-segmented rami each have a longer second segment, that of the exopod bearing three terminal setae, that of the endopod bearing two.

Abdomen.—The abdomen is four-segmented and bent into a U, with a pair of furcal rami not clearly separated from the last segment (Fig. 8c). The first and third segments are as long as wide, while the second and fourth are much longer, and the first segment bears a rudimentary penis. The furcal rami are rectangular, 2.5 times longer than high and possessing some dorsal and ventral spinules, usually a dorsodistal spine, and seven setae set into deep pockets (probably three terminal and four medial); all the setae are about as long as the furcal rami.

Last-Instar Ascothoracid Larva

General features.—The carapace is bivalved with a distinct hinge and sharp valve margins, about 0.67 mm long, 0.47 mm high, 0.29 mm wide (almost no variation; Fig. 6), and lenticular in shape except for the rear being slightly more produced than the front (Fig. 9a). The outer cuticle has a weak polygonal pattern of ridges and scattered conical pores; each valve also has two cardiac organs (Itô and Grygier, 1990), elongate pits with thickened rims, near the front of the hinge and two more close together at the rear of the hinge. The anterodorsal part of the valve margin is irregularly pitted (Fig.

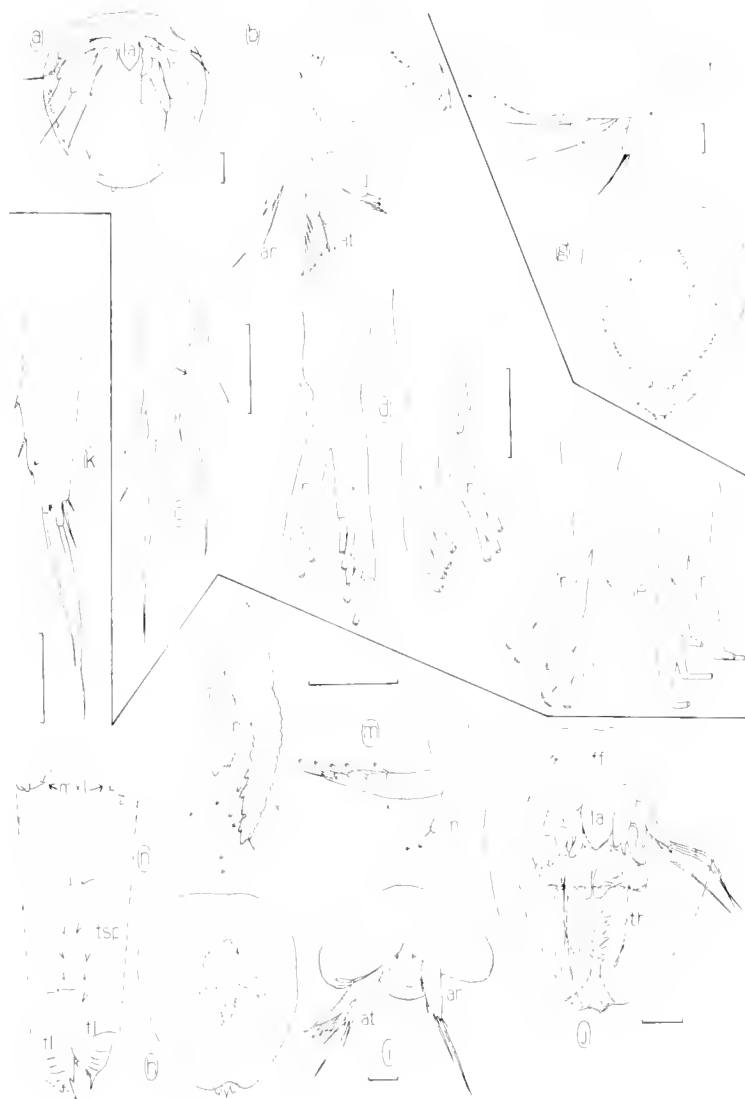


Figure 7. Normal naupliar development of Californian *Parascothorax synagogoides*, based in part on reared larvae. a-e, "nauplii"; a, ventral view; b, lateral view; c, antennule; d, two antennae; e, two mandibles (setae cut short in d and e); f-g, "early metanauplii," lateral and dorsal views; h-n, "late metanauplii"; h, dorsal view; i, anterior view with selected limbs shown (redrawn from Grygier, 1987a); j, ventral view showing developing appendages of ascothoracid larva; k, antennule; l, antenna; m, mandible (setae cut short in l and m); n, ventral and caudal armament. Arrows in c and k mark site of newly formed seta; many setae omitted in a, b, f, and j. ad, adductor muscle; an, antennule; at, antenna; d, mandible; ff, frontal filament; fl, furcal lobe; la, labrum; mxl, maxillary rudiments; n, endopod; th, developing thoracopods; isp, thoracic spines; x, exopod; y, yolk. Scale bars 0.1 mm.

9b). Cuticular ctenae line the posterior end internally. No gonads are present within the carapace. The retracted body occupies no more than two-thirds of the space between the valves (Fig. 9a). It has a head, a six-segmented thorax with natatory thoracopods, and a five-segmented abdomen with a furca.

Cephalic appendages.—The antennules are five-segmented, all the segments being roughly equal (Fig. 9c). The third segment has tufts of fine hairs anteriorly. The fourth segment has a chin relatively longer than the adult's, with two distal teeth (lateral one larger), two unequal soft and vestigial setae on the proximal side, and one (two?) seta on the distal side. The fifth segment forms a subchela with the fourth, and it bears a claw with three basal setae, a claw guard with two short and one minute distal setae, a long seta behind the claw guard, and a posterobasal strap-like aesthetasc about as long as the antennule. There is a pair of frontal filament complexes as in the first

ascothoracid larva (Fig. 9d) but no antennae. The conical labrum surrounds a pair of distally attenuated mandibles and the long, harpoon-like maxillae. The mandibles are probably unarmed distally, and the maxillules were not visible in whole mounts.

Thorax and thoracopods.—The thorax is somewhat arched, and its segments become a little longer and lower posteriorly. The sixth segment has small lateral epaulets and a dorsal band of fine setae. The first thoracopods are small and uniramous, with one or two distal setae (Fig. 9e). Thoracopods 2-5 each have a distinct and oblong coxa and basis, a laterodistal coxal seta and mediodistal basal setae on thoracopods 2-4 only, a two-segmented exopod with four distal setae on the rather narrow second segment, and a three-segmented endopod with one seta on the second segment and three on the very narrow distal segment (Fig. 9f). The sixth thoracopod is much the same except for a "precoxa" and a two-segmented

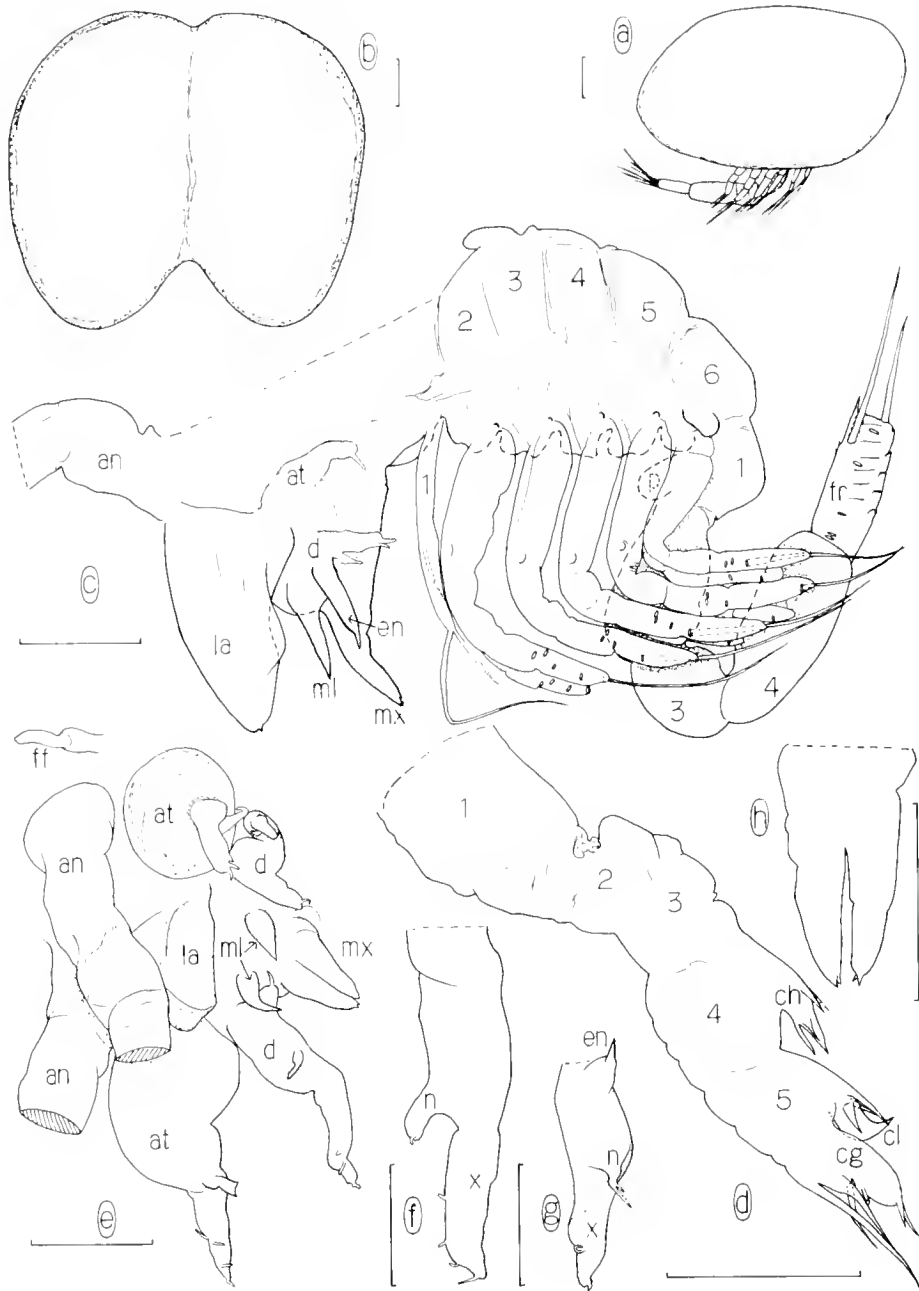


Figure 8. First-instar ascothoracid larva of Californian *Parascythorax synagogoides*, based on reared larvae. a, whole larva, side view, from life; b, carapace, flattened ventral view; c, body of several-week-old larva, only invaginated bases of most thoracopodal and furcal setae shown; d, antennule (redrawn from Grygier, 1987b); e, ventral view of mouth field and cephalic appendages on newly molted larva; f, antenna; g, mandible; h, maxillae. an, antennule; at, antenna; cg, claw guard; ch, chint; cl, claw; d, mandible; en, mandibular endite; ff, frontal filament; fr, furcal ramus; la, labrum; ml, maxillule; mx, maxillae; n, endopod; p, penis rudiment; x, exopod. Scale bars 0.1 mm.

endopod (Fig. 9g); its exopod has three terminal setae and the endopod has two. The setae on the thoracopodal rami are long with long, widely spaced setules; the protopodal setae are plumose when present.

Abdomen.—The second and fifth abdominal segments are twice as long as thick, the first and third are shorter and equal to each other, and the fourth segment is the shortest (Fig. 9a, b). The first segment has a very poorly developed flap-like ventral penis rudiment, and the fifth segment is scaly ventrally. The furcal rami are rectangular, about twice as long as high, and have four distal setae

(three long ones and a much shorter ventral one), a dorsodistal spine, and 5 medial setae as long as the terminal ones, four of these arising more or less basally, the other mediadorsally.

Larval behavior.—The eggs and naupliar stages were neutrally or slightly positively buoyant in life. The nauplii did not actively swim. The first ascothoracid larvae were also buoyant at first, but in culture they eventually sank. When floating, the first-instar ascothoracid larvae had the abdomen tucked forward and the carapace valves closed as tightly as possible. They swam on their backs, with interspersed periods of non-locomotory abdominal



Figure 9. Last-instar ascothoracid larva of Californian *Parascothorax synagogoides* (male larvae). a, whole larva with right carapace valve removed; b, pits along anterodorsal edge of valve, dorsal end above; c, antennule, lateral view; d, frontal filament complex (redrawn from Grygier, 1987c); e, thoracopod 1; f, thoracopod 4; g, thoracopod 6 (setae cut short in f and g); h, most of abdomen. ad, adductor muscle; an, antennule; cg, claw guard; ch, chin; cl, claw; co, cardiac organs; es, aesthetasc; fr, furcal ramus; n, endopod; oc, oral cone; x, exopod. Scale bars 0.1 mm.

contractures, during which they sometimes directed the abdomen forward beneath the body. In swimming they employed tail flicks (furcal strokes), spreading the rami at the top of the stroke as each downbeat began. The power stroke of the thoracopods was metachronal from rear to front and involved all but the reduced first pair of legs. To the eye the furcal downstroke seemed to be simultaneous with the thoracopods' unified recovery stroke, but efforts to confirm this cinematographically were unsuccessful. The stroke rate was over 2 per second, and over 3 per second in one individual, but their swimming efforts were rather ineffectual because of the

shortness of the thoracopodal setae.

Remarks.—Grygier (1987b) divided ascothoracid nauplii into those with complex protopodal armament of the antennae and mandibles and well-developed natatory rami, those with simple protopods and well-developed rami, and those with vestigial limbs. The nauplii of *P. synagogoides* belong to the second group, and those of the various species of *Ascothorax* belong to the second and third groups (Grygier, 1983), so the type of nauplius is not useful in discriminating the two genera. Possession of at least five naupliar instars is a plesiomorphy, at least relative to the two naupliar instars

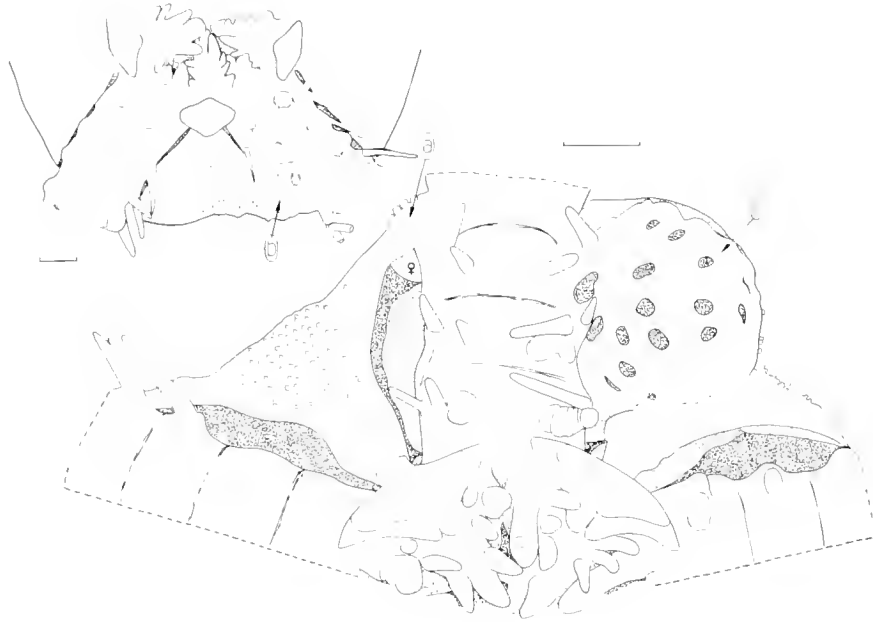


Figure 10. Cysts formed by Californian *Parascothorax synagogoides* on *Ophiophthalmus normani*, genital bars of host out of view alongside basal arm ossicles just within bursal slits. a, incipient cyst forming around newly settled female parasite; b, completed cyst; c, older, perforated cyst. Scale bars 1 mm.

of another ascothoracidan in the same order, *Ulophysema oeresundense* (see Brattström, 1948); the greatest number accurately known in the Ascothoracida is six, the basic maxillopodan number, for a species of *Baccalaureus* (Itô and Grygier, 1990) in the other order, Laurida.

Two instars of ascothoracid larvae, the first being incompletely formed, occur in other members of the order Dendrogastrida, the best documented examples being *Ulophysema oeresundense* and *Ascothorax gigas* (Brattström, 1948; Grygier and Fratt, 1984). I have taken this as evidence of a more anamorphic and thus more primitive ontogeny in the Ascothoracida than in the Cirripedia, where there is a single cyprid larval instar (Grygier, 1987c). However, laboratory rearing did not reveal more than one instar of the ascothoracid larva in the aforementioned species of *Baccalaureus* (Itô and Grygier, 1990), so the more gradual development may actually be restricted to the Dendrogastrida, or to part of it.

I have previously (Grygier, 1987b) addressed the significance of the naupliar and ascothoracid larval antennules in the compara-

tive morphology and systematics of the Ascothoracida. *Parascothorax synagogoides* rather clearly shows how the claw arises subterminally in ontogeny and that the more distal part of the naupliar antennule moves to the posterior side of the appendage and gives rise to the various sensory elements there (claw guard, proximal sensory complex). The small tube on the antennular claw guard in the first-instar ascothoracid larva may be homologous to a similar tube-like structure seen apically on the aforementioned ascothoracid larva of *Baccalaureus* (Itô and Grygier, 1990), where it is surrounded by an "apical hood."

There is a progressive reduction in the first-instar ascothoracid larva of the vestigial rami of the naupliar antennae and mandibles, and an appearance *de novo* of a large protopodal spine on the mandible. This shows that the basal part of the mandible in adult *Parascothorax* and other ascothoracidans represents part of the protopod and that the usually elongate, more or less complexly armed distal part of the mandible is an endite or gnathobase.

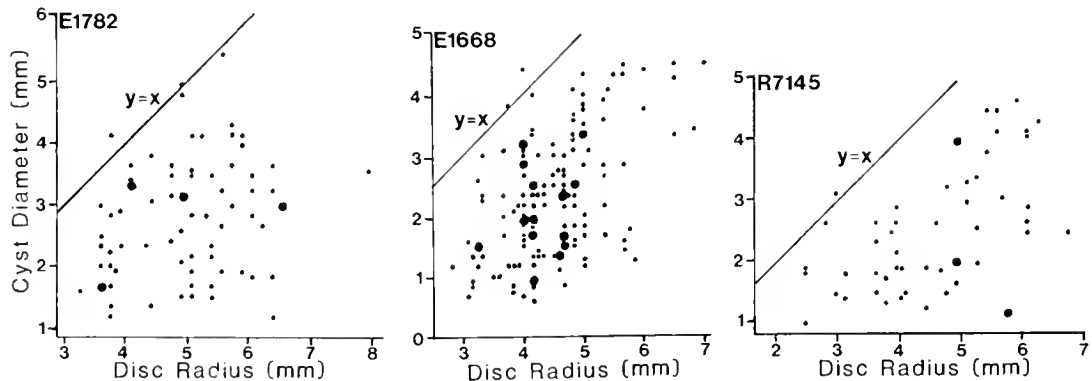


Figure 11. Relationship in three samples between host disc radius and cyst diameter in *Ophiophthalmus normani* infested with *Parascothorax synagogoides* off California. Cysts grow to a diameter just under the host disc radius. Large dots represent superimposed records.

CYSTS

Cyst cycle.—Wagin (1964, 1976) described a cycle of cyst formation and rupture in brittle stars infested with *P. synagogoides*. On the basis of the Californian specimens I review the cycle here in more detail (Fig. 10; also see Grygier, 1988:778).

A settling female establishes itself within the outer end of a bursal slit. One female post-larva was found thus *in situ* with cyst formation not yet begun, and another was found on the outer surface of an ophiuroid near a slit. The distal part of the genital bar, a long ossicle bordering the ambulacral side of the bursal slit (not visible in Fig. 10), proliferates to cover the end of the slit and also to thicken the aboral surface above the parasite. The female, most often still a post-larva, is not yet walled in on the side facing the interior of the bursa (Fig. 10a).

Later the cyst closes when the proliferating genital bar fuses with the opposite wall of the bursa. The incorporated bursal wall does not become as thick as the rest of the cyst and remains composed of very thin skeletal plates. The exposed part of the cyst has a very thin skin without the small granules that are otherwise common externally on the host's disc. At this point about half of the bursal slit is closed and the cyst barely protrudes beyond the edge of the disc (Fig. 10b).

As the parasite grows, the diameter of the cyst increases to just less than the host's disc radius (Fig. 11). The cyst protrudes noticeably below and beyond the margins of the host's disc and gives the impression of a sphere partly embedded in the ophiuroid (Fig. 10c; also see Grygier, 1988: fig. 7). The aboral part connects with the nearest radial shield. Interstices develop between the small ossicles of the exposed portion, and these eventually perforate the half of the oral face nearest the arm and the exposed outer and aboral faces; i.e., small holes develop through all the thickened regions but not through the bursal wall into the body cavity. The cyst is now held to the genital bar by numerous trabeculae, is anchored to a radial shield aborally, and has host skin attached in a arc along the interambulacral side. Most of the bursal slit becomes blocked, but the innermost end always remains open because the genital bar does not reach that far.

Such a cyst is fragile and easily broken, whereupon the parasites and the outer, oral side of the cyst is lost. The remainder heals, leaving a gaping scar that permanently disfigures the host.

Wagin (1964) believed that *Parascothorax* was exploiting a defense reaction of its host. The ophiuroid supposedly encapsulates the settled parasite as an irritant and eventually expels it. Encapsulation certainly does occur, but there is no obvious translocation of the cyst; it simply grows and remains attached to the genital bar without any activity on the host's part to expel it.

Host relations.—*Ophiophthalmus normani* has a disc diameter of 3.5 to 22 mm (Clark, 1911). Californian specimens infested with *Parascothorax synagogoides* covered much of this range (2.5–8.0 mm radius). Female parasites were generally loose within a cyst, but males commonly grasped the thin tissue lining the inside of the cyst with their antennules. The females fit so snugly that males left indentations in their carapaces. Males were most often found against or near the host's genital bar but could also be found elsewhere. Specimens of *O. normani* infested with *Parascothorax* often have well-developed gonads.

DEMOGRAPHY

Distribution and prevalence.—Of the 15,373 *Ophiophthalmus normani* examined at Scripps Institution of Oceanography, 769 were recorded as being infested with *Parascothorax* at the time of capture or having healed scars of old infestations (5.0% aggregate infestation). This was an underestimate for reasons explained be-

low. Few samples were entirely free of parasites, and most such samples were small. The southern Gulf of California (88 ophiuroids), the East Cortez Basin (145), the West Cortez Basin (4), a rather shallow site off La Jolla (896 m; 34 ophiuroids), and an area off Piedras Blancas Point near Big Sur (252) yielded no *Parascothorax*. There was too little comparative material, one or two samples each, to make much of the incidence in the San Nicolas Basin (33 of 801 ophiuroids infested), Santa Cruz Basin (1 of 73), an area east of San Clemente Island (14 of 266), and Bahia Descanso, Baja California (1 of 16), except to say that *Parascothorax* does occur there.

I examined a good number of mostly large samples from four offshore basins, the San Diego Trough (21 samples), the Catalina Basin (13 samples), the Tanner Basin (7 samples), and the San Clemente Basin (6 samples) (Fig. 1, Table 1). The Tanner Basin had the most consistent infestation rate, 0.2–1.4% (aggregate 0.5%). The San Clemente Basin and the Catalina Basin had a much wider range among samples (0.0–6.2%, aggregate 2.3%, and 0.0–12.1%, aggregate 4.5%, respectively), but in the Catalina Basin three of the samples were much more highly infested (9.4–12.1%) than the other ten, which together had an aggregate infestation rate of only 0.6%, similar to that in the Tanner Basin. In the San Diego Trough the prevalence of *Parascothorax* varied the most, from 0 to 30%, and the aggregate incidence was 9.0%, considerably higher than at any other censused locality and greater than the 1% reported by Rokop (1975) from the same area (Rokop's samples were included in my study).

Additional positive records based on Smithsonian ophiuroids include USNM 39242 (crustaceans: USNM 242371), *Albatross* sta. 2919, off southern California, south of Cortez Bank, 1799 m, 3 of 18 *O. normani* infested; USNM 8744, *Albatross* sta. 4381, off Los Coronados Islands near San Diego, 1131–1221 m, 1 of 75 infested; and USNM 26107, *Albatross* sta. 4767, Bowers Bank, Bering Sea, 1411 m, 1 of 2 infested. The last is significant because it serves partly to link the discontinuous known range of *P. synagogoides* in the Sea of Okhotsk and off California. Finally, a sample of *O. normani* from the Catalina Basin that I examined at the Allan Hancock Foundation (AHF 8714.63) included some infested individuals.

Undercounts.—The infestation rates mentioned above are often underestimates because some small cysts were overlooked in the initial sorting. In detailed resurveys of six samples of sorted, infested ophiuroids, 1.8–13.9% of the cysts actually present had not been seen and counted the first time. Numerous previously unsuspected infestations were found among the supposedly uninfested *O. normani* of two samples: for E1668 the initially estimated rate was 14.6% and the revised one was 21.7%, and for R7139 the respective values were 12.4% and 15.2%. The other heavily infested samples in Table 1 were probably undercounted by similar margins. On the other hand, the large sample E2125, in which only one infested ophiuroid was found originally, revealed no new finds after half the sample was reexamined. Therefore, the reported low incidences in Table 1 are probably trustworthy. The overlooked parasites were almost all very small, sometimes inhabiting incompletely formed, unperforated, non-protruding cysts, and a few had not yet begun to form a cyst. Their omission does not affect the data on the distribution of males and brooded offspring, both of which are restricted to larger females, but the missed specimens could have biased the data on multiple infestations.

Depth distribution.—*Parascothorax synagogoides* occurred over almost the whole depth range of its host off southern California (1006–1910 m). The well-sampled basins, listed from deepest to shallowest, are the San Clemente (sampled to 1929 m), Tanner (to 1397 m), and Catalina basins (to 1350 m) and the San Diego Trough (to 1250 m). The aggregate parasite prevalences in the last three are

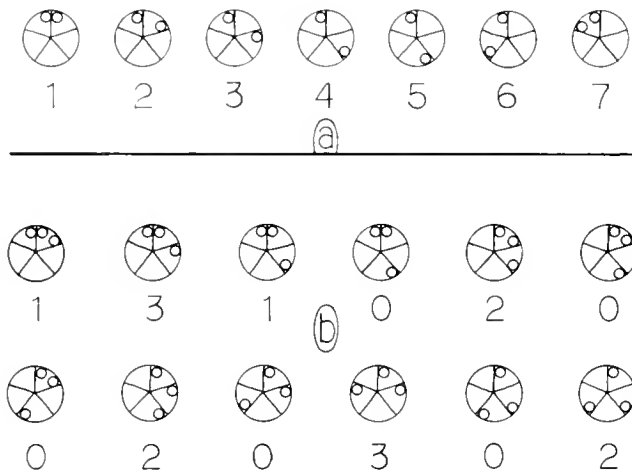


Figure 12. Geometry of multiple infestations of *Ophiophthalmus normani* by *Parascothorax synagogoides*. a, possible spatial arrangements of non-superimposed double infestations, cases 2 and 4 being twice as likely to appear by chance as the others; b, possible spatial arrangements of non-superimposed triple infestations, all cases equally likely to appear by chance, with number of observations of each pattern given for pooled samples E1668, E1439, E1782, and R7145.

progressively higher, but that of the San Clemente Basin is higher than that of the Tanner Basin, so there is no simple decline in infestation with depth. In fact, the reverse, an increase with depth, is evident in the three large samples from the San Clemente Basin (0.3% at 1114 m, 2.9% at 1535 m, 6.2% at 1830 m), and the three most heavily infested samples from the Catalina Basin were the deepest ones, 1275–1350 m versus 875–1250 m for the other samples). Infestation rates in the San Diego Trough showed no particular pattern related to depth.

Multiple Infestation

Clumping.—Most often a single bursal opening was afflicted with *Parascothorax*, but double or triple infestations were not uncommon. As many as six bursal slits could be involved in rare

cases. This is essentially the same pattern that Wagin (1964) found in the Okhotsk population. I checked the distribution of the number of cysts per host against a random (Poisson) distribution by a chi-square goodness-of-fit test of the data from Table 1 for samples E1668 and R7139, which were not undercounted, and samples E1439 and E1762, in which only the initially sorted specimens were counted. The categories were uninfested, singly infested, and multiply infested ophiuroids. All these samples differed significantly or very significantly from the expected Poisson distribution. There were too few single infestations and too many uninfested and multiply infested ophiuroids. I obtained the same results when the test was repeated without including the empty, broken, and healed cysts. Therefore, I conclude that *Parascothorax* has a clumped distribution among its hosts.

The most obvious explanation for this clumping is that once infested, an ophiuroid is less resistant to attack by later arrivals. Because *Ophiophthalmus normani* is an extremely abundant animal (Smith and Hamilton, 1983), there is no great need to invoke chemical attraction of female larvae by settled females, as there might be if the host were rare.

Double infestations.—In samples E1668, E1439, E1782, R7139, and R7145 I noted 73 double infestations. Cyst positions were inadvertently not recorded for three of these, but I compared the other 70 by a chi-square goodness-of-fit test to the expected random distribution of spatial relationships. If the host is considered to be purely pentaradial, there are seven distinct ways to place two cysts so each occupies a distinct bursal slit, and two arrangements are twice as likely as the others (Fig. 12a). I observed reoccupation of a previously occupied bursal slit twice, but since the conditions under which this may occur are different from infestation of a "virgin" slit, superposition is not included in this analysis. The observed spatial distribution of double infestations was decidedly non-random ($p < 0.005$), and it was clear from inspection that this is due to a tendency for two cysts to occupy a pair of bursal slits that lie on opposite sides of the same arm (case 1 in Fig. 12a; 26 occurrences observed versus 7.8 expected). Conversely, finding both slits of the same interradius occupied (case 7), or slits on the far sides of adjacent interradii (case 6), was exceedingly uncommon (2 and 1 occurrences observed, respectively, versus 7.8 expected for each). The other possible arrangements differed little in actual occurrence from expectations.

Triple infestations.—There are 12 equally likely distinct arrangements of three cysts without superposition. The samples listed

TABLE 2. Infestation and population statistics of *Parascothorax synagogoides* in some samples of *Ophiophthalmus normani*^a

Statistic	Sample					
	R7139	E1668	R7128	E1782	R7145	E1439
Number of cysts	70	174	19	107	79	108
Inhabited	55 (79)	153 (88)	15 (79)	89 (83)	73 (92)	66 (61)
With females	54–55	152–153	15	85–87	72–73	65
With lone males	0–1	0–1	0	2–4	0–1	1
Empty or healed	15 (21)	21 (12)	4 (21)	18 (17)	6 (8)	42 (39)
Number of brooding females	32 (59)	22 (14)	7 (47)	28 (33)	20 (28)	26 (40)
Without mates	1 (3)	1 (5)	0 (0)	1 (4)	1 (5)	10 (38)
Brood size	4–160	13–129	13–183	3–114	17–98 ^b	3–48
Mean	73.1	52.5	77.7	53.6	54.5	21.1
Standard error	14.7	13.4	38.1	12.2	14.0	4.8
Number of females with last-instar ascothoracid larvae	1 (2)	8 (5)	0 (0)	5 (6)	5 (7)	9 (14)
Number of females with isopods	3 (6)	6 (4)	1 (7)	5 (6)	3 (4)	1 (2)

^aPercentages in parentheses.

^bOne isopod-infested female had one egg.

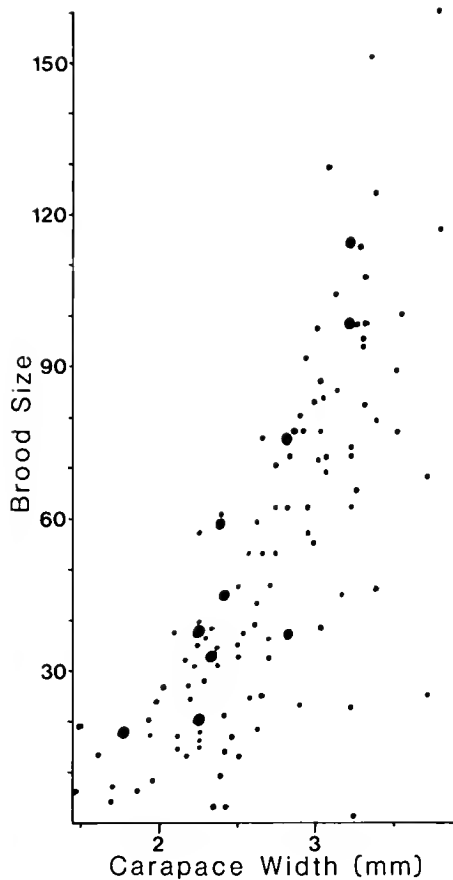


Figure 13. Relation of brood size to female carapace width for five pooled samples of Californian *Parascothorax synagogoides* (R7139, E1668, R7145, E1782, E1439). Large dots represent duplicate records.

above, together with R7128, contained 14 triple infestations. Five possible distributions did not occur, two appeared three times each, and three appeared twice (Fig. 12b). There are no obvious characteristics distinguishing the preferred from the unutilized configurations. Curiously, there is no excess of cases with two of the three cysts opposite the same arm, as would be expected from the pattern in double infestations. By chance, one-third of the ophiuroids should show this configuration, and in fact just five of 14 do. Also, the two configurations that are rare in double infestations occur often in triple infestations.

There are too few instances of quadruple or higher infestations to permit a similar analysis.

Population structure.—In various samples, from 8 to 39% of the cysts examined were old, broken, partly healed, or empty of parasites (Table 2). The vast majority of inhabited cysts had a single female, never more, and zero to five males and/or last-instar ascothoracid larvae (not more than three of the latter). Depending on the sample, 14–59% of the females were brooding eggs or nauplii within their carapaces (Table 2; the probable undercount of small females in some samples could lower these percentages). The number of offspring varied enormously, from 3 to 183, largely depending on the size of the female (Fig. 13). The mean brood size for those with eggs or larvae was 52–55 in three samples, 73–78 in two others, and 21 in a sixth, all with large ranges (Table 2). Broods were always synchronous in development except for a small number of aborted, perhaps unfertilized eggs in many broods of nauplii.

Not more than six to eight of the 461 inhabited cysts contained just a male *Parascothorax* (Table 2). Such occurrences may have

been due to cysts being broken before examination so the female could have fallen out, or to severely damaged young females being mistaken for males. It was unusual for a brooding female to lack an accompanying male (Table 2). Most such instances were rare enough to be attributable to observer error, and the carapace of one supposedly lone female was dented as though a male had been present but not found. However, I found fully 10 of the 26 brooding females in sample E1439 to be unaccompanied. Six of these were brooding undeveloped, presumably infertile eggs, but the other four had metanauplii, implying that a male had once been present. The seminal receptacles of these 10 females were not examined, since they were pooled with the other females after the brood had been counted.

Maturation and mating.—Figures 14 and 15 are size–frequency histograms for females of *Parascothorax* in five samples with respect to their cyst companions and reproductive state, respectively. With the exceptions of samples E1668 and R7139, where there was no undercount, the lower ranges of the histograms are probably incomplete. Most if not all of the overlooked females would have been immatures without mates (black squares). Despite this source of error, there does seem to be a much higher proportion of immature females in sample E1668 than in sample R7139, collected just 6 weeks later; both samples were from the San Diego Trough, though not from precisely the same spot. The difference could be due to patchy recruitment, differential mortality of newly invaded ophiuroids, or high mortality of newly recruited *Parascothorax*. The later sample did have a higher proportion of empty and healed cysts (21% versus 12%; Table 2), but I don't think these can usually be attributed to the loss of small parasites.

The threshold size for females of *Parascothorax* to begin acquiring mates is less than that for female maturity, and the size at which all females have mates is less than that at which all are brooding (Figs. 14, 15). Immature females, those without developing oocytes in the ovary diverticula, range roughly from 0.4 to 1.9 mm in carapace width. Except in sample E1439, which, as noted above, had an unusually high rate of unaccompanied brooding females, it was unusual for females larger than about 1.3 mm to be alone in their cysts. Some down to 1.0 mm or even smaller had males or last-instar ascothoracid larvae with them. Oocytes begin to appear between 1.5 and 1.9 mm, and broods begin to appear almost immediately thereafter. By 2.6 mm, almost all females are brooding except for a few spent ones or those infested by isopods.

Since males are immotile, they must join a female as a swimming ascothoracid larva. Such newly arrived larvae, usually in the process of molting to the male post-larva, are common in cysts. They usually occur alone with a female, but sometimes also with other ascothoracid larvae or males (Table 2). Two lines of evidence suggest that most of these larvae arrive before the cyst fully closes and temporarily cuts off access to the female. If females accrue additional mates throughout their lives and there is no significant male mortality, then larger females should have more mates. Table 3 shows the mean sizes of females with different numbers of mates in

TABLE 3. Mean carapace widths (mm) of mated female *Parascothorax* with different numbers of mates (males and last-instar ascothoracid larvae).

Sample	1 Mate		2 Mates		3 Mates		5 Mates	
	n	Mean Width	n	Mean Width	n	Mean Width	n	Mean Width
E1668	59	1.90	16	1.94	5	1.56	—	—
E1782	47	2.07	12	2.32	5	2.75	2	2.84
R7139	37	2.91	5	2.22	—	—	—	—
R7145	40	1.86	8	2.58	4	1.90	—	—

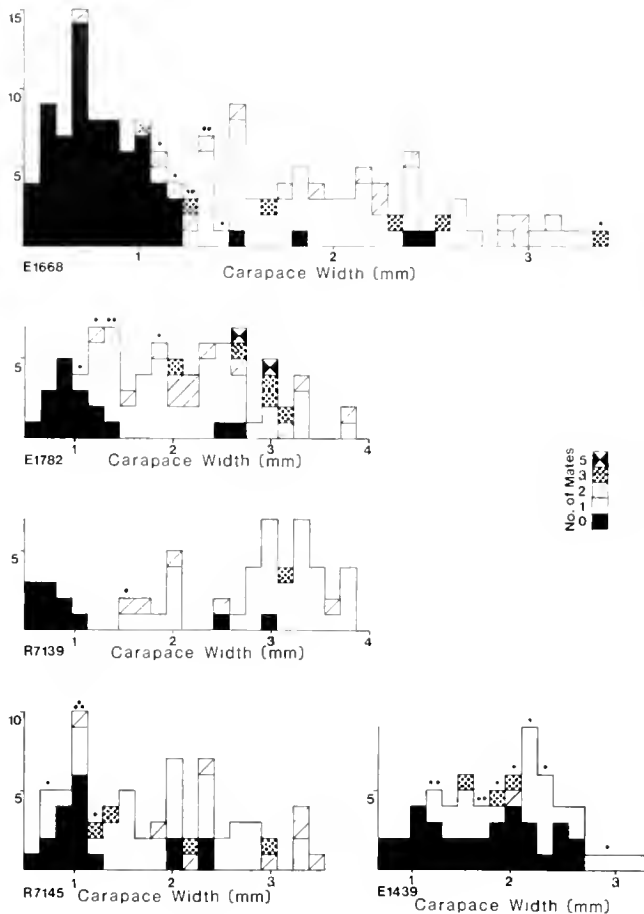


Figure 14. Size-frequency histograms of female carapace width in five samples of *Parascothorax synagoides*. E1439 is from the Catalina Basin; the others are from the San Diego Trough. Each female is represented by one square, and the pattern within the square signifies the number of mates (0–5 males and/or last-instar ascothoracid larvae) accompanying that female, according to the key on the right. Each dot above a size-class column represents a female in that column with one or more ascothoracid larvae as partners. There was no undercount in E1668 and R7139, collected 6 weeks apart, but some females at the small end of the size range were probably missed in the other samples.

five samples, and only one sample shows the expected pattern. Additional evidence comes from the distribution of ascothoracid larvae among females of different sizes (Fig. 14). Of 28 females accompanied by these larvae, most were quite small (24 under 2 mm carapace width, 19 under 1.5 mm), suggesting that most of the larvae join the females before the cysts close. The few found with large females probably entered the cysts later, through the secondary perforations in the cyst wall.

Number of broods.—Wagin (1964) thought that each female of *Parascothorax synagoides* produces a single synchronously developing brood that is released when the cyst breaks open. Eggs and larvae do escape readily from living females removed from their cysts, so in nature some broods may be lost from prematurely broken cysts. But this model poses some problems. The size and fecundity ranges of brooding females are very broad. For some females to have only four young and others over 180 in their only brood is difficult to rationalize. Also, ovaries with oocytes are still well developed in brooding individuals, and there is apparently no terminal molt in females; surely a brood must be released before a

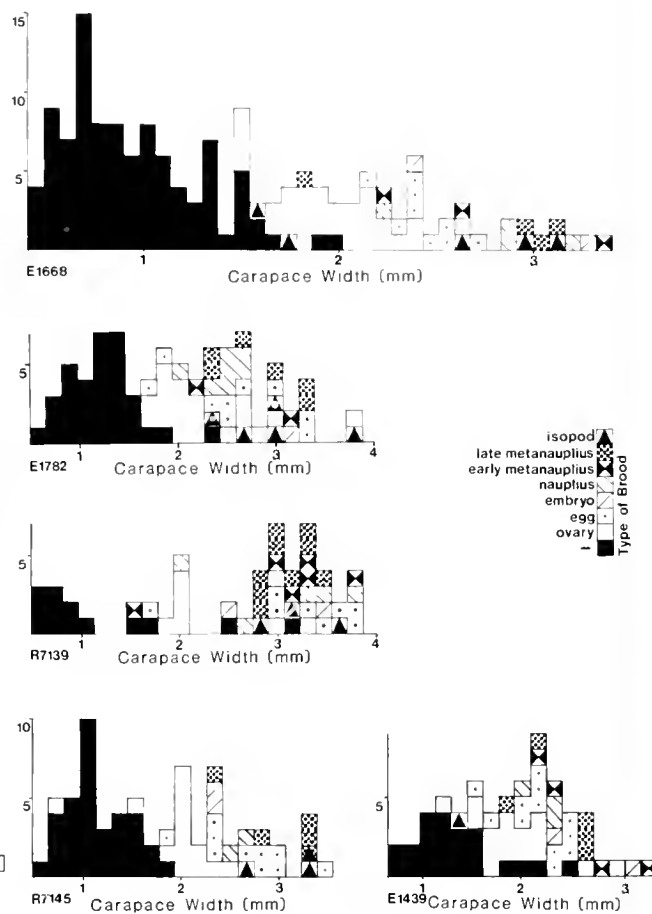


Figure 15. Size-frequency histograms of female carapace width for the same five samples of *Parascothorax synagoides* as in Fig. 14. Each female is represented by one square, and the pattern within the square signifies that female's state of sexual maturity, brood composition, and presence or absence of hyperparasitic cryptoniscid isopods, according to the key on the right. Explanation of key: -, no gonads; ovary, gonads evident but no brood; egg to late metanauplius, five successive stages of brooded young; isopod, either cryptoniscus stage or adult female isopod present, and this symbol is sometimes superimposed on the other patterns.

molt. I think it somewhat likely that *P. synagoides* has more than one successive brood. The length of time a brood takes to develop and reproductive seasonality cannot be ascertained with present information.

Hyperparasitism.—In the six samples studied in detail, the percent infestation of female *Parascothorax* by an undescribed cryptoniscid isopod was 1.5–15.4% (aggregate 4.3%; Table 2). In E1668 and R7139, where *Parascothorax* was not undercounted, the rates were about 6%. Eight of 19 cases involved only a cryptoniscus (larva or male); the others involved a cryptoniscus and a female (6 cases) or a lone female (5 cases). Cryptonisci could be found within the host's brood chamber or outside of it but still within the ophiuroid cyst. Female isopods usually lived within the carapace, filling the brood chamber, but one was found outside the host within the cyst. Male *Parascothorax* accompanied all but one of the infested females, but males never had attached isopods. In multiply infested ophiuroids, I never found isopods in more than one cyst. Figure 15 shows that isopods occurred mostly with larger female *Parascothorax* that would normally have ripe gonads or be brood-

ing. The presence of a cryptoniscus apparently does not greatly inhibit the host's reproductive capacity, although some eggs are probably lost to the parasite. Of the female isopods, only one very small one was sharing a brood chamber with host eggs; large female isopods completely prevent the host's brood deposition and are therefore parasitic castrators.

Comparison to Other Crustacean Parasites of Ophiuroid Bursae

The demography of two other ophiuroid-associated species of Ascothoracida and one endoparasitic copepod, *Ascothorax ophiocetis*, *A. gigas*, and *Parachordeumium* (= *Amphiuophilus*) *amphiuurae* (Héroutard), has been investigated in sufficient detail for comparison with that of *Parascothorax synagogoides*.

Ascothorax ophiocetis.—This is a bursal parasite of shallow-water Arctic and North Atlantic hosts, *Ophiocetis sericeum* (Forbes) and *O. gracilis* (G. O. Sars). Wagin (1947) examined about 60,000 *O. sericeum* from 32 to 178 m collected in August and September at 20 stations in the Kara Sea; because infestations were detected by swellings of the host disc and sorting was done hastily, he thought that many infested specimens, especially ones with juvenile parasites, must have been missed. At 16 stations from which over 100 ophiuroids each were examined, the observed infestation rate ranged from 0.02 to 2.05% with an aggregate rate of 0.22%, considerably less than the infestation rate of *Parascothorax* off California except in the Tanner Basin (0.5%). Ordinarily each infected bursa (double and triple infestations were observed but not enumerated) contained one adult female and one to four males; no detailed data on the distribution of the latter was given. Very rarely males were absent, although the condition of the female's brood under this circumstance was not stated, and in one case a single bursa had two adult females and a male, a situation never encountered in *Parascothorax*. In cases of multiple infestation, it was normal for parasites in different bursae to be of different ages, as with *Parascothorax* (Fig. 10). Unlike *P. synagogoides*, *A. ophiocetis* ordinarily causes complete castration of the host ophiuroid.

Ascothorax gigas.—Grygier and Fratt (1984) reported on the infestation of *Ophionotus victoriae* Bell by *A. gigas* at 49 to 272 m around the South Sandwich Islands and Antarctic Peninsula. The parasites inhabit bursae without developing a cyst, and the infestation is generally not detectable externally. At four stations in the South Sandwich Islands, 0–10.5% of 20 to 355 ophiuroids were infested; at six stations along the Antarctic Peninsula, 0–20.6% of 109 to 437 ophiuroids were infested. At two of the latter stations, the number of parasites per host ranged from 1 to 29 (mean of 7); multiple infestations were common, up to seven bursae with up to seven parasites each being infested. Unlike *P. synagogoides* and *A. ophiocetis*, *A. gigas* could fit up to three brooding females or a mixture of brooding and immature females in the same bursa; a few cases of brooding females without accompanying males were noted, as in *P. synagogoides*. The effect of even heavy infestation on the host was reduced gonad development, not castration.

Parachordeumium amphiuurae.—In a recent ecological study of this copepod living in the bursae of British intertidal *Amphiuura squamata* Delle Chiaje (Emson *et al.*, 1988; Whitfield and Emson, 1988), over 5000 ophiuroids were examined over 13 months. The copepod occurred with a seasonally varying prevalence of 10 to 30% (highest in summer), with up to five female copepods per host. The distribution of copepods over potential hosts was clumped, as in *Parascothorax*. The smallest ophiuroids were uninfested, and the prevalence and incidence of infestation increased with host size except for a reduction in the largest ophiuroids. The reproduction of infested hosts was delayed and reduced or in cases of multiple infestations prevented.

Conclusions.—It is clear that not all crustacean bursal parasites

of ophiuroids infest their hosts at the same rate and have the same physiological effect on them. In most, however, multiple infestations may be more commonplace than chance would predict. In part, different variables were measured in the different studies, limiting their comparability. In the future, standardized information about such host–parasite systems would be useful.

The present data on *Parascothorax* represent a rare example of a detailed ecological study of a parasite (and its hyperparasite) that afflicts a community-dominating deep-sea invertebrate. Such studies are so uncommon that no review of invertebrate parasitism in the deep sea has ever been published. My study was made possible by the availability of extensive collections from the region, so many specimens could be spared for parasitological examination. I hope that other large collections of deep-sea invertebrates, perhaps derived from environmental surveys, can be made available to parasitologists.

ACKNOWLEDGMENTS

Most of this work formed part of a Ph.D. Dissertation submitted to the University of California San Diego. I thank Dr. W. A. Newman and Mr. S. R. Luke, curator and collections manager, respectively, of the SIO Benthic Invertebrate Collection, for granting me access to specimens, Dr. K. L. Smith and Ms. N. Brown for providing additional samples of the host ophiuroid, Dr. Newman for laboratory facilities, and him and Drs. R. R. Hessler, N. D. Holland, W. H. Berger, and D. S. Woodruff for comments on my dissertation. I thank P. Unitt and two anonymous referees for helping me streamline the manuscript. Mss. M. Downey and C. Ahearn assisted me at the Smithsonian Institution. I thank Drs. Ya. I. Starobogatov, I. S. Smirnov, N. V. Vyshkvartseva, and Ye. L. Markhaseva (Zoological Institute, USSR Academy of Sciences) and Dr. T. A. Ginetinskaya (Leningrad State University) for their cooperation during my stay in Leningrad under the auspices of the National Academy of Sciences Soviet and East European Exchange Program. The published manuscript was prepared during a term as a Visiting Foreign Researcher at the Sesoko Marine Science Center, University of the Ryukyus, and is a Contribution of Scripps Institution of Oceanography, new series.

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