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GENERAL BIOLOGY

Feeding of the Symbiotic Polychaete Gastrolepidia clavigera (Polynoidae) and Its Interactions with Its Hosts

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Parasitism is less widespread in polychaetes than commensalism is. The latest review [1] describes 375 species of symbiotic polychaetes, with 294 of them being considered commensal and only 81, parasitic. This situation is even more distinct in the family Polynoidae (scale-worms), which includes more than 50 of symbiotic polychaetes. Only one out of 160 species of symbiotic scale-worms (*Thormora johnstoni*) is considered parasitic [2]. Thus, parasitism is generally considered to be an exceptionally rare phenomenon in scale-worms. On the one hand, this situation reflects evolutionary trends in the class Polychaeta and the family Polynoidae; on the other hand, it is explained by the fact that the biology of symbionts has not been studied sufficiently (see [1] for definitions of the terms). Most symbiotic polychaete species has been assigned to commensals without special studies, only due to the absence of manifest "parasitic" features in their organi-zation.

There are various approaches to studying the inter-actions between symbionts. In theory, it is necessary to analyze the effects of symbionts on the mortality and metabolism of their hosts to determine the type of their interactions. However, for many associations, this approach is too difficult because it requires much time and special equipment. Therefore, such studies are seldom performed on symbiotic associations of marine animals (see, e.g., [3]); there are no published studies of this type on any association containing polychaetes. At the same time, the type of the symbiont-host interactions may sometimes be determined by indirect methods, such as morphological and functional analysis of the food-procuring system and the digestive tract [4], direct observation of the feeding [5], and analysis of the intestinal contents [6].

The object of this study was the polychaete *Gastrol-epidia clavigera* Schmarda from family Polynoidae. This polychaete is widely spread in the Indian-West Pacific region and is a symbiont of holothurians of families Holothuridae and Stichopodidae. The polychaetes are located near the end of the host body (either anterior or posterior); in the case of any hazard, they crawl into the mouth or cloaca of the holothurian [7]. Their inter-actions with their hosts have not been specially studied; however, they have been regarded as commensalism thus far [7, 8].

The morphological and functional approach is hardly applicable to the given case, because the structures of the food-procuring and digestive organs are similar in all members of family Polynoidae. All of these polychaetes have a pair of chitin jaws, a strong muscular throat [9], and a straight intestine with paired metameric diverticula, which agrees with the characteristic of these polychaetes as polyphagous predators [10]. The purpose of this study was to analyze the food composition of *G. clavigera* and to estimate their inter-actions with holothurians as their hosts.

Holothurians with symbionts were collected in Nha Trang Bay in southern Vietnam in 1985 and 1990. The map of the stations and the method of sampling were published earlier [7]. For studying food composition, we collected 10, 10, and 45 *G. clavigera* specimens from the holothurians *Actinopyga echinites*, *Holothuria atra*, and *Stichopus chloronotus*, respectively. In the laboratory, the polychaetes were dissected, the intestine was isolated and prepared, and its contents were placed into a 1 : 1 mixture of 70 alcohol and glycerin on a mount. The preparations were examined under a Mik-med-2 microscope. The photographs were made by means of a Pixera Pro digital camera and a Leitz Diaplan microscope.

We found food fragments and nonfood particles in the intestines of 57 polychaetes (86.2 of their total number). The proportions of polychaetes with full intestines collected from different hosts were similar. Food remnants were found in the intestines of 39 out of 45 (86.7), 9 out of 10 (90), and 8 out of 10 (80) polychaetes collected from *S. chloronotus*, *H. attra*, and *A. echinites*, respectively. The polychaete intestines contained tissue fragments and spicules of holothurians, fragments of crustaceans, multicellular and unicellular algae, chaetae and jaws of polychaetes, grains of sand. detritus, foraminifera. and fragments of the shells

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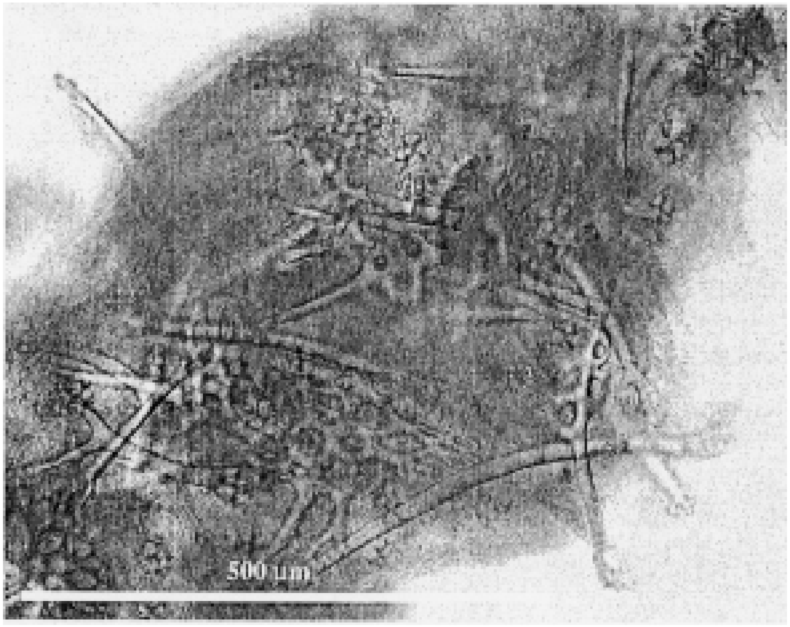

Fig. 1. Tissues and spicules of the holothurian S. chloronotus forming a cord in the intestine of the polychaete G. clavigera.

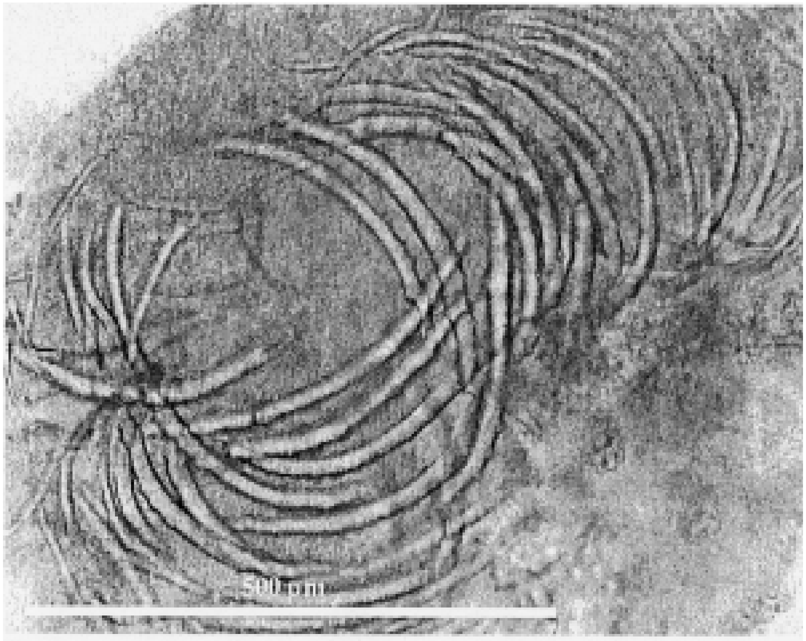

Fig. 2. Tissues and spicules of the holothurian S. chloronotus forming a lump in the intestine of the polychaete G. clavigera.

of bivalves (Table 1). Holothurian spicules surrounded with fragments of tissue were the most frequent (Figs. 1 and 2). If the intestine contained many large spicules, they aggregated to form distinctive cords (Fig. 1) or lumps (Fig. 2), which probably facilitated their passage through the intestine. The shape of the spicules is a diagnostic character that may serve for identification of holothurian species [11]. Different types of spicules that we found in the intestines of symbionts belonged to holothurians of the same species from which the polychaetes were collected, which indicated that the polychaetes fed on the tissues of their hosts. Spicules are not uniformly distributed over holothurian tissues, which sometimes allowed us to determine which parts of the holothurian body had been swallowed by the polychaete. In the intestine of the polychaetes that were

Food composition and the frequencies of different food objects and nonfood particles in the intestine of the polychaete G. clavigera associated with different hosts

Food spectrum	Host species			Total
	S. chloroiiotus, n = 39	H. atra, n == 9	A. echinites, n = 8	
Spicules ofholothurians	74.4 (29)	55.6 (5)	50.0 (4)	67.9 (38)
Fragments of crustaceans	38.5 (15)	22.2 (2)	25.0 (2)	33.9 (19)
Fragments of polychaetes	15.4 (6)	0 (0)	0 (0)	10.7 (6)
Algae	17.9 (7)	H.1(1)	0 (0)	14.3 (8)
Grains of sand	25.6 (10)	33.3 (3)	0 (0)	23.2 (13)
Detritus	15.4 (6)	33.3 (3)	37.5 (3)	21.4 (12)
Foraminifera	10.3 (4)	11.1(1)	0 (0)	8.9 (5)
Remnants of Bivalvia	2.6 (1)	0 (0)	0 (0)	1.8 (1)

Note: Numbers of findings are indicated in parentheses.

collected from A. echinites, we identified relatively large (about 200 u.m) spicules from the ambulacra and mouth tentacles of the host. In the intestine of the sym-bionts of//, atra, we found all spicules characteristic of this species except for rod-shaped one, which are located only on the tentacles. In the symbionts of S. chloronotus, we found the spicules that were charac-teristic of their tentacles, ambulacra, and dorsal papillae, i.e., all types of spicules described for this species [12].

Fragments of crustaceans were the second most fre-quent component of the contents of the polychaete intestine (table). Most of them were in a bad state of preservation. We could only identify remnants ofPera-carida (three findings) and symbiotic copepods (four findings), two of which were identified accurate to the genus (Scambicomus sp.) (Fig. 3). The digestive tracts of some crustaceans contained remnants of detritus. Fragments of polychaetes (chaetae, aciculae, and jaws) were found in the intestines of six G. clavigera (10.5). Three findings were single chaetae of the polychaetes G. clavigera. In two cases, we found chae-tae whose structure allowed us to classify the polycha-etes with either Adyte or Paradyte genus ofPolynoidae. One finding was chaetae and jaws that had probably belonged to a free-living polychaete of family Nereidae (Fig. 4).

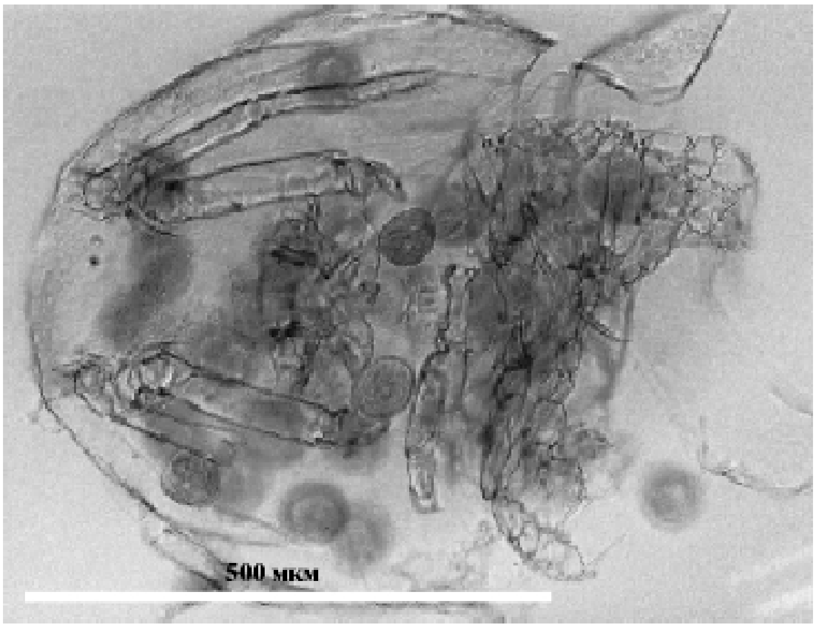

Fig. 3. The symbiotic copepod Scambicornus sp. from the intestine of G. clavigera associated with the holothurian S. chlomnotiis.

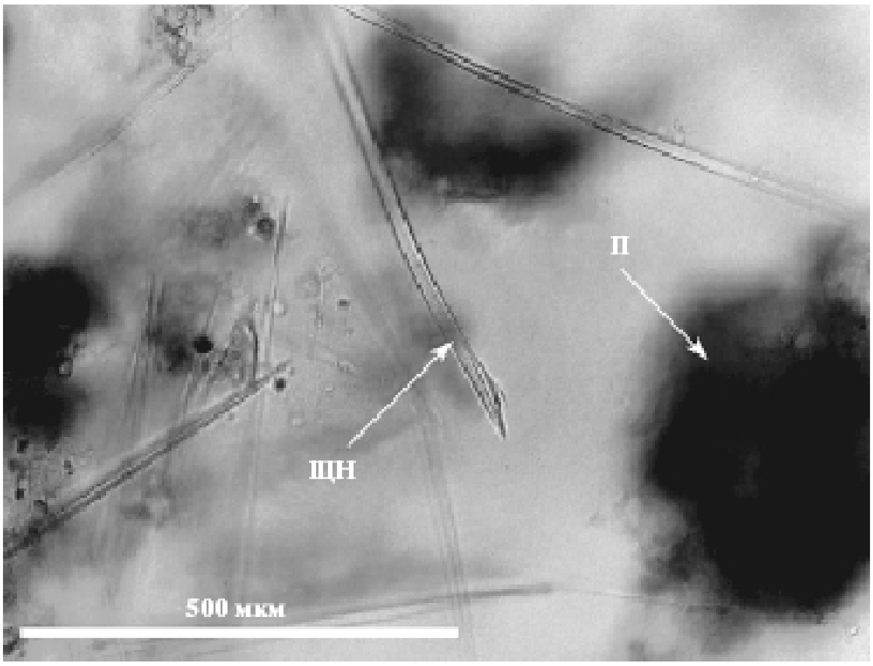

Fig. 4. Chaetae of a free-living nereis (CN) in the intestine of G. clavigera. Grains of sand (GS) can be seen.

The fact that the fragments of tissues and spicules of the holothurian hosts were common in the contents of the G. clavigera intestine demonstrated that the symbionts fed on the host's tissues. Analysis of the spectrum of spicules found in the intestines indicated that the food of the symbionts included all covering tissues of holothurian ambulacra, tentacles, papillae, and integument. The second source of food was cope-pods. Representatives of this order are parasites of marine animals [13]. Probably, the species of genus Scambicornus that we found parasitize on the same holothurians as G. clavigera does. The third source of food was small free-living crustaceans and poly-chaetes living in the benthos and bottom layers of water.

The shells of foraminifera and bivalves, sand grains, and detritus are apparently accidental com-ponents of food, swallowed by G. clavigera along with prey. This is evidenced by the large amount of sand grains that were found in the intestine together with remnants of free-living polychaetes (Fig. 4) and detritus found in the digestive tract of the swallowed crustaceans.

The rinding of algae in the intestine of G. clavigera is of special interest. Algae are often found in the intes-tines of typical "predatory" Polynoidae, such as Lepi-donotus squamatus and Harmothoe imbricata [10, 14], and their role in the feeding of these species is debated [10]. However, in the given case, the role of algae in the feeding of G. clavigera was insignificant, irrespective of how well the polychaetes assimilate them.

Thus, both parasitic feeding on the host's tissues and predatoriness are characteristic of C, clavigera. This makes up a complex system of interactions between G. clavigera and holothurians as their hosts. On the one hand, G. clavigera is distinctly a parasite, because it feeds on tissues of holothurians; on the other hand, it eats copepods, which are considered to be parasites of holothurians. Taking into account that the damage inflicted to holothurians by polychaetes is evidently much more serious than the damage inflicted by cope-pods, these interactions may be described as parasitism with elements of mutualism.

The feeding of G. clavigera on holothurian tissues indicates that the associations studied are highly spe-cialized. Note that holothurian tissues contain a highly toxic compound (holothurin). Moreover, some species, e.g., H. atra, may exert a distant effect on predators, because they release holothurin into water upon a slight irritation [15]. The resistance of G. clavigera to the effect of holothurin has apparently resulted from a pro-longed coevolution. These data agree with the specific-ity of G. clavigera and adaptive characteristics in the structural organization of this species, such as ventral attachment paddles, hook-shaped chaetae, and body appendages that mimic the papillae of the holothurian host [7]. The chaetae ofconspecific polychaetes found in the intestine of G. clavigera are of special interest. These findings confirm the suggestion on territorial conflicts in G. clavigera, which was made based on the analysis of their distribution among hosts and their traumatism [7].

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