

AN ABSTRACT OF THE THESIS OF

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Title THE SYMBIOTIC RELATIONSHIPS AND MORPHOLOGY OF PARAVORTEX SP.
NOV. (TURBELLARIA, RHABDOCOELIDA), A PARASITE OF MACOMA NASUTA
CONRAD, 1837

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Rhabdocoels of the genus Paravortex are parasites of marine molluscs. The bent-nosed clams, Macoma nasuta (Conrad, 1837) of Yaquina Bay, Lincoln County, Oregon are commonly infected with a new species of Paravortex. The morphology of the adult worm has been described and it has been compared to the other three species of this genus.

The percent infection increased as the size of the clams increased. Analysis of the size frequency distribution of the clam population suggests at least two age classes. Incidence of infection was substantially lower in the younger of these two classes. Clams less than 14 mm in length were not infected. Possible reasons for this distribution of the parasite population were discussed.

A peak in the percent of infection, in the incidence of multiple infection, and in the abundance of immature worms was found during April, May, and June, 1968. These data suggest a seasonal periodicity in the reproduction of Paravortex sp. nov.

A correlation between the sex of the bent-nosed clams and the incidence and degree of infection could not be established.

Paravortex sp. nov. was found only in the pericardial cavity of Macoma nasuta. It is postulated that the rhabdocoel enters this cavity from the suprabranchial space by passing through the kidney. Possible methods by which this endoparasitic rhabdocoel obtains food were discussed.

Physical damage to the host clam could not be shown to be the result of parasitic infections. Multiple infections of as many as 28 worms did not appear to physically impair the clam.

Observations of the morphology and behavior of living worms were made and conclusions were reached concerning the nature of the symbiotic relationship between Paravortex sp. nov. and its host.

Examination of collections of Macoma nasuta made in Coos Bay, Oregon, and Puget Sound, Washington, produced no rhabdocoels.

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MORPHOLOGY OF PARAVORTEX SP. NOV. (TURBELLARIA,
RHABDOCOELIDA), A PARASITE OF MACOMA NASUTA CONRAD, 1837

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INTRODUCTION

Rhabdocoels of the genus Paravortex Wahl (1906), are parasites of the viscera, body spaces or mantle cavity of marine molluscs. Two species have been described from Europe and a third species from the Northeastern United States. There is, however, no report in the literature of Paravortex from the West Coast of North America.

The endoparasitic rhabdocoel described in this paper was first observed while examining bent-nosed clams, Macoma nasuta Conrad (1837) from Yaquina Bay, Lincoln County, Oregon. Collections and ecological observations were made from June, 1967 to June, 1968.

Von Graff (1882), in his monograph on the Turbellaria, cites Ihering (1880) as the describer of the genus Graffilla. It is identified as being endoparasitic in marine molluscs. The characteristics of this genus include long, slender, paired ovaries, ramified yolk glands, paired, short-lobed testes and one seminal bursa. Von Graff recognized three species. This genus is very similar to Paravortex and some confusion exists in the early literature.

The genus Paravortex was established by Wahl (1906) for a species of turbellarian parasitic in the intestine of the clams, Scrobicularia tenuis and S. piperata. The worm was originally observed and inaccurately figured by Villot (1878). Von Graff (1882) called this animal Macrostomum scrobiculariae, but Wahl decided that it should be placed in a new genus. He also found von Graff's

Provortex tellinae to be identical to the worm he designated Paravortex scrobiculariae.

Wahl's brief description of the new genus is as follows:

"Dalyelliidae mit am Vorderende des Körpers gelegnem Pharynx, paarigem Keimstöcken, verzweigten Dotterstöcken, rundlichen Hoden und ventral vor der Körpermitte gelegener Geschlechtsöffnung."

Wahl's paper includes a description of the genus Graffilla as:

"Dalyelliidae mit am Vorderende des Körpers gelegnem Pharynx, paarigen Keimstöcken von der Form gewonderen Bänder und davon getrennten Dotterstöcken. Geschlechtsöffnung mittelständig, Hoden schlauchartig."

Ecological observations made by Wahl at two collecting areas included only the percentage of clams infected, the total number of worms collected, and the maximum number of worms found in a single clam. His collections from the two species of Scrobicularia clams were made in the area of Trieste. In addition, he observed the same worm in the gut of Tapes decussata collected near Naples.

Nicoll (1906), in describing a series of digenetic trematode intermediate stages found in the cockle, Cardium edule, erroneously included a rhabdocoel he found in the liver and intestine of the clam. Nicoll's description and drawings of the worm as a ciliated sporocyst, with eyespots, a pharynx, and containing six to eight cysts with daughter sporocysts inside is not correct. The worm was later described as a species of Paravortex.

Von Graff (1908) gave a key to the family Graffillidae.

Included are six genera and Paravortex is distinguished from the others on the basis of its having two ovaries, two long unbranched vitellaria, paired testes and a genital pore located on the ventral surface.

In 1908, Hallez described a parasite of the cockle, Cardium edule. This was the same worm Nicoll mistook for a trematode sporocyst. Hallez called this rhabdocoel Paravortex cardii and in 1909 published a detailed account of the biology, histology and embryology of the worm.

In order to classify Paravortex cardii, Hallez, in 1909, published the following key to the genera of the family Graffillidae:

1. A single ovary. Body more or less flattened. . 2
Ovaries and vitellaria paired 3
2. Ovary large, irregularly lobed. Genital pore posterior. Anaploidium
Ovary small. Genital pore at the beginning of the last quarter of the body. Didymorchis
3. Vitellaria unbranched Collastoma
Vitellaria branched or reticulated. 4
4. Genital pore posterior. 5
Genital pore ventral in first half of the body 6
5. Intestine lobed. A pharynx Syndesmis
Intestine straight. No pharynx in adult. Fecampia
6. A bursa seminalis Graffilla
No bursa seminalis. Paravortex

The collections of Hallez extended over a four month period and provided data on the percent infection, the incidence of multiple infection, and the changes in each of the above over the four months.

The largest part of his 1909 paper was devoted to the embryology and larval development of the worm.

In 1910, Linton reported the discovery of a rhabdocoel living in the ribbed mussel, Modiolus demissus. He referred it to the genus Graffilla with some hesitation, stating that it belongs to "this or a closely related genus but is quite different from any species noted by von Graff in his Monographie der Turbellarien". Linton was unaware of the genus Paravortex established four years earlier by Wahl or of the key to Graffillidae by Hallez.

The worm described by Linton was found while examining mussels for digenetic trematode sporocysts and rediae. His collections were made near Woods Hole, Massachusetts, and he reported substantial variation in rates of infection between mussel beds. His paper included a suggestion that the paired encapsulated embryos he observed in the adult parenchyma were derived from a single ovum by separation of the blastomeres after first cleavage. This idea was later shown to be erroneous.

Two years after Linton's paper appeared, Patterson (1912) published an account of his investigations of the embryology of the worm Linton had originally described. Patterson continued to use the specific name Graffilla gemellipara Linton (1910), although he, too, expressed some doubt as to the accuracy of this designation.

Linton originally described Graffilla gemellipara as inhabiting the mantle cavity of the ribbed mussel. Patterson, collecting these mussels from the same area as Linton, stated that he found them in the kidneys of the bivalves. Patterson also included data

concerning the changes in infection rates during the six month period in which his collections were made. The largest part of his publication is devoted to an examination of the early embryology of the rhabdocoel, and in particular, an explanation of the origin of the paired encapsulated embryos.

The work done by both Linton and Patterson left a number of questions unanswered. Ball (1916) undertook to reexamine the embryology and larval development of the worm as well as to define precisely its systematic position. The explanation of the origin of twin embryos in a single capsule as given by Patterson (1912) was revised by Ball. The development of the rhabdocoel was described carefully from gametogenesis to birth of the larval worm. Ball also described organogenesis in newly hatched worms maintained in aquaria.

In his 1916 paper, Ball discussed the relationship of Graffilla gemellipara to the rest of the members of the family Graffillidae. He compared it specifically to Paravortex cardii (Hallez) and to the criteria used by Wahl to establish the genus Paravortex. He concluded that the generic name used by Linton was not appropriate, and that the rhabdocoel was actually a species of Paravortex. Since it was a species obviously different from the two European forms, the specific name used by Linton was retained by Ball.

Ball, after examining previous descriptions and keys, summarized the distinction between the two genera in the following manner:

Graffilla

1. Two extremely long cylindrical ovaries
2. Genital pore ventral, not anterior to the middle of the body
3. A large distinct bursa seminalis (receptaculum seminis)
4. No vestibule between pharynx and mouth

Paravortex

1. Two club-shaped ovaries
2. Genital pore ventral, anterior to the middle of the body
3. Bursa seminalis lacking
4. Vestibule

Ball gave experimental evidence that Paravortex gemellipara inhabited only the mantle cavity of the mussel. He presented data on collections made during a two year period, and described his observations of the behavior of living worms.

Leigh-Sharpe (1933) in a note on the occurrence of a turbellarian in Cardium edule from Plymouth, England, appeared to have wrongly identified it as Graffilla gemellipara. The animal he figured had the appearance of being somewhat compressed. It had the same dimensions and host as Paravortex cardii, but no details of the internal structures were given. Seven specimens from a single cockle were observed.

Atkins (1934), in response to reports of serious mortality among Cardium edule in 1933, investigated the parasites of this bivalve. His collections, made in the area of Plymouth, England, yielded information about the distribution of infected clams, the rates of infection and the seasonal variability of the infection rate. He found that the organism was identical with Paravortex cardii Hallez (1908).

Luther (1948) established two subfamilies: Pseudograffillinae and Graffillinae of the family Graffillidae. Marcus (1954) retained these subfamilies and provided a key to the Graffillidae as follows (in part):

1. Seminal vesicle and granular vesicle united
(Graffillinae). 2
Seminal vesicle and granular vesicle separated
(Pseudograffillinae). 4
2. Ovaries paired, female genital canal present . . 3
Ovary unpaired; female genital canal absent. . .
. Bresslauilla Reisinger (1929)
in fresh and brackish water but not marine
3. With seminal bursa; ovaries very long,
cylindrical; genital pore posterior to middle
of body Graffilla Ihering (1880)
in marine gastropods and lamellibranchs
Without seminal bursa; ovaries club shaped;
genital pore anterior to middle of body
. Paravortex Wahl (1906) Ball (1916)
in marine gastropods
4. Ovary unpaired; vitellaria ramified, testes
lobed; male copulatory organ unarmed.
. . . Pseudograffilla Meixner (1938) Luther (1948)
in marine and brackish water
Ovaries paired; vitellaria compact; testes
entire; male copulatory organ with stylet . . .
. Nyngulcus gen. nov.
marine

Hart (1963) examined razor clams, Siliqua patula Dixon (1788) during a four year period from 1958 to 1962 in Humboldt County, California. In a master's thesis at Humboldt State College she described a species of Graffilla found in the pericardial cavity of that clam and provided data on the infection rates during those years. Her collections during the four years were made only during the months from March to July; no data are available during the other parts of

those years.

The present study includes a full year of collections and data in order to obtain the following information:

- 1) To collect, prepare and describe examples of a new rhabdocoel turbellarian found in the pericardial cavity of the bent-nosed clam, Macoma nasuta.
- 2) To ascertain the relationship of the worm to the clam and to determine any pathological effects of the turbellarian on the clam.
- 3) To follow the incidence of infection over a 12 month period.
- 4) To correlate the size of clam to the number of rhabdocoels present in an attempt to describe origin and longevity of the infections.
- 5) To provide information concerning the geographical range of the turbellarian infection.
- 6) To describe some aspects of the behavior of the worm when outside the host clam.

MATERIALS AND METHODS

Routine monthly samples of bent-nosed clams, Macoma nasuta were taken from the mud flat at Coquille Point in Yaquina Bay, Lincoln County, Oregon. The sampling period extended from June, 1967, to May, 1968. In addition, two more large collections were made during July and August of 1967 for the purpose of size frequency analysis. Single samples were taken from South Slough, Coos Bay County, Oregon, and from Puget Sound at Penrose Point, Mason County, Washington.

The clams were dug with a shovel and the sandy-mud was turned over at regular intervals along a transect extending from the upper to the lower limits of the clam bed. Each shovel full of sandy-mud was thoroughly broken apart by hand and all bent-nosed clams were placed in a plastic bucket, without water, for transport to the Oregon State University Marine Science Center, Newport, Oregon. At the Center, the clams were placed in fresh sea water either in four inch finger bowls which were put onto a water table or in plastic bags which were transported to cold rooms in Cordley Hall, Oregon State University, Corvallis, Oregon. At no time were more than ten clams kept in a single container, and all containers were aerated continually except during transport. Host clams were sexed by examining smears of gonad.

Each clam was measured to the nearest millimeter along the anterior-posterior axis and was assigned a number which was recorded on a posting sheet. The adductor muscles and mantle edge were separated from one valve, the hinge ligament was cut and the loose valve discarded. The clam was placed under a Wild M-5 dissecting

microscope where the pericardial cavity was carefully opened. Other areas examined included the gills and labial palps, mantle and mantle cavity, stomach and intestine, foot, gonads, digestive glands and kidney. Any rhabdocoels found were removed and placed in fresh, filtered sea water. Each worm was recorded on the posting sheet when it was found. All residual water in which the clams were held was examined for rhabdocoels. In no instance were the clams held longer than 36 hours before examination. Any clams which were broken or damaged during collection or transit were discarded.

Living worms were observed, using both the dissecting microscope and a Wild M-20 compound microscope with phase contrast optics. Sketches from life were made using a drawing attachment on the compound microscope.

The rhabdocoels were fixed with either AFA fixative, Bouin's solution, or 3% glutaraldehyde (pH 7.2 in aqueous solution). Flattened worms were prepared, using coverslip pressure during immersion in hot AFA.

Worms were stained with Semicon's aceto-carmin or with Grenacher's borax-carmin according to the method described by Weesner (1960). The specimens were dehydrated, cleared and stored in xylol in labeled vials. Whole mounts were prepared by placing the worms on slides using Harleco's Synthetic Resin.

Serial sections of worms were made after imbedding in paraffin. Sections were cut at ten microns and stained with Mayer's hematoxylin and counter-stained with eosin. Transverse, sagittal and frontal sections were made, orientation being achieved using the

methods outlined by Kosloff (1965) and by Gonor (personal communication).

Examination and drawings of serial sections were made with the aid of a Leitz Prado microprojector.

All morphological measurements were made in millimeters with a calibrated ocular micrometer.

Worms which were used in experiments were held in fresh, filtered sea water in cold rooms at 10° C. All worms were maintained singly in two-inch finger bowls and were never used more than 24 hours after removal from the clam.

Analysis of the population distribution of Macoma nasuta was done following the method of Cassie (1954). A two-month sample (July and August, 1967) was analyzed.

MORPHOLOGICAL OBSERVATIONS

Living worms, when swimming in dishes of sea water, are about three times as long as wide; the greatest width being one-fourth of the distance from the anterior end. The front quarter is bluntly rounded; the middle two quarters are almost cylindrical and the posterior quarter tapers to an acutely pointed tip. The largest specimens are nearly 1.5 mm long and 0.5 mm wide. Living worms are very elastic and will commonly assume a spherical shape. The worms can also increase their length by one-fourth with a corresponding decrease in diameter. Worms in close contact with the substrate flatten the ventral surface and as a result, the dorsal surface bulges upward.

In reflected light the body is a pale orange except where the vitellaria appear white through the body wall. In transmitted light the body is opaque except in the region of the anterior portion of the gut.

The body is covered by a squamous epithelium, the cells of which are polygonal. The cells average 0.012 mm across by 0.005 mm thick. The surface is uniformly ciliated; the cilia being 0.009 mm long.

Beneath the epithelium is a thick muscular sheet. An outer layer of circular muscles overlays a loose set of diagonal fibers, beneath which is a layer of longitudinal fibers. The diagonal muscles are much more sparse than the other two layers. The total thickness of muscle sheet averages 0.012 mm. In the parenchyma are scattered longitudinal and dorsoventral muscle fibers.

The principal elements of the nervous system consist of two ganglia located dorsolateral to the pharynx. The ganglia are connected by a commissure. A pair of nerve tracts extends from each; one to the eyes and the second running posterolaterally and soon separating into individual fibers. Eyes are located dorsolateral to the front edge of the pharynx. They are of the pigment-cup type made up of black pigmented cells. The concave side faces laterally and contains a refractive body which appears transparent in the living animal. The diameter of each eye is 0.035 mm.

Two groups of frontal gland cells are located at the anterior end of the animal, each group having about a dozen cells. Since individual cells discharge separately, no common ducts are formed. A group of pores is located on the anterior tip of the animal, lateral to the midline. The glands discharge at the pores and extend about 0.10 mm back toward the level of the eyes.

The small, subterminal mouth opens on the ventral surface about 0.15 mm from the anterior end. A small vestibule precedes a strongly muscular pharynx which is nearly spherical, about 0.010 mm in diameter. The pharynx opens directly into an intestine which extends to the posterior fifth of the worm. The gut is widest at the anterior end and tapers gradually to a point. The cells of the intestinal wall are columnar and contain numerous vacuoles of various sizes.

The vitellaria extend from the level of the pharynx to the posterior end of the worm. The glands are paired and lie dorsolateral to the gut. The vitellaria are antero-posteriorly oriented

anastomosing strands of varying length.

The paired ovaries lie ventrolateral to the gut in the anterior half of the worm. Each ovary is folded back upon itself a number of times so that the total length is two to three times the antero-posterior distance occupied in the parenchyma. The ovary is claviform, the diameter at the posterior being three times that of the anterior. The posterior end of each ovary extends medially and joins with the vitellaria to form a common duct leading from each side to the postero-dorsal quadrant of the genital antrum. The ovary is composed of a series of disc-like cells stacked one against the next. Each cell has a prominent nucleus and a large dark staining nucleolus.

The genital antrum is located above the midpoint of the ventral side of the animal. It consistently contains from one to as many as 12 encapsulated embryos in various stages of development. The antrum varies in diameter from 0.13 mm to 0.29 mm depending on the number of capsules within. As the embryos mature the capsules are released from the genital antrum into the maternal parenchyma. A maximum of 26 embryo capsules have been counted in the parenchyma. The enclosed worms are in various stages of development. Eyespots are often seen in the embryonic worms and well developed, ciliated young can occasionally be observed in motion inside the capsules. Larval worms escape by rupture of the maternal tissues.

A seminal vesicle, 0.07 mm in diameter, is located ahead of and slightly dorsal to the genital antrum. The wall of the receptacle is muscular and the structure is full of active sperm. A duct connects the seminal vesicle to the genital antrum. Each mature

sperm is 0.013 mm long with a 0.004 mm filamentous head differing little in diameter from the tail.

A genital pore leads from the midventral surface of the genital antrum to the outside of the animal. A dorsal outpocketing of the genital antrum serves as a seminal bursa and contains mature sperm. Dorsal to the genital antrum and surrounding the seminal bursa are about 40 gland cells. A duct from each cell leads independently to the genital antrum.

Testes were not observed in any of the stained worms. About 75 living animals were studied. In only two were testes observed, in the posterior one-fourth of worm. These structures were 0.180 mm in diameter and were paired. Each appeared to contain both active and immature sperm.

Figures 1 through 4 illustrate the morphology of the rhabdocoel as described above.

ECOLOGICAL OBSERVATIONS

During July and August, 1967, 438 bent-nosed clams were measured and examined for the rhabdocoel worms in their pericardial cavities. Examination of the length-frequency distribution of the clams using both Cassies' method (1954) and a simple length-frequency histogram indicated two distinct size classes (Figure 5). Of a total of 106 clams 28 mm or less in length, 12 were infected (11.3%). The larger class (29 mm to 65 mm) included 332 clams, 131 (39.4%) of which were infected with worms.

Table 1 contains monthly summaries of the data taken during the collecting period, July, 1967, to June, 1968. Clams examined ranged in size from less than 5 mm to 65 mm in length. Monthly samples included 20 to 30 clams of the 5 mm to 14 mm category, none of which was ever found to harbor rhabdocoels. For this reason these small clams were not included with the tabulated monthly totals.

Figure 6 summarizes the monthly variation in size distribution of the host clams. July, August, September and October samples have two peaks in the size frequency with the smaller size class tending to increase in mean length over this four month period. From November to June the two size classes were not separable. During the months of January and February clams of the 45 to 55 mm category were infrequently found. In March, April, May and June a single size class was observed, the average size of which tended to increase steadily over the four month period.

Figure 6 also summarizes the incidence of infection for each of the host size categories for the 12 month period. During the

months of low infection, the number of rhabdocoels per clam was low for all size categories. During the months of higher infectivity (>25%) the incidence of parasitism increases in the clams of the larger of the two size classes.

Multiple infections were common. Of the 368 infections encountered, 169 or 46% involved a single worm while 199 (54%) consisted of two or more worms. The number of worms found in the pericardial cavity of individual clams ranged from zero to 28. In March, 1968, and again in May, 1968, there were exceptionally high rates of multiple infections (82.5% and 81.8% respectively). Incidence of infections were related to size of the host animal. Figure 7 summarizes the relationship between percent infection and the size of the host animal.

Figure 8 summarizes the occurrence and monthly trends of the rhabdocoel populations from the bent-nosed clams. An increase in the percent infection during May, June and July is in contrast to the relatively steady infection rates recorded during the rest of the year. The monthly changes in mean number of worms in infected clams is characterized by a sharp increase in May followed by a decrease during June. The rest of the year these data show a much lesser variation.

All rhabdocoels were found in the pericardial cavity of the host clam. Careful dissection of about 20% (85 individuals) of the larger July and August, 1967, samples produced no rhabdocoels other than those found within the pericardial cavity.

Of 50 male clams examined in June of 1968, 29 were infected

with the rhabdocoels; 25 of 50 female clams examined during the same period were infected. There was no difference in the incidence of multiple infection in the two sexes of the host clams. Fifteen of 29 male clams had single worms; 12 of 25 females had one worm each.

Worms bearing embryos imbedded within the parental parenchyma were common in all of the monthly samples. Total numbers of worms bearing embryos were not recorded, but the numbers of immature worms found free in the pericardial cavity were taken. Worms were judged immature by their lesser size and absence of vitellaria. From August to April the number of immature worms averaged about one-third of the total. In April and May, this number almost doubled (61% and 64% respectively) and during June it was 46% of the worm population (Table 1).

No visible damage directly related to the presence of the worm was observed. As many as 28 worms in a single clam produced no obvious physical damage to the lining of the pericardial cavity, to the heart, or to the intestine which passes through the cavity. However, numerous abnormalities in the pericardial region were found in both uninfected and infected animals. The most common defect was a distinct discoloration and thickening of the lining of the cavity. The color of the wall was bright orange. Also, in some clams, there was a soft, white stringy substance lying loose in the pericardial cavity, which, when examined under the compound microscope, was amorphous.

Eighty-one bent-nosed clams from South Slough in Coos Bay, were examined for rhabdocoels in August of 1967. The sizes ranged

from 14 mm to 53 mm. In none of these clams was any rhabdocoel found. In May of 1968, 47 bent-nosed clams collected at Penrose Point in Puget Sound lacked rhabdocoels.

Rhabdocoels removed from clams were put in the coldroom at 10° C in individual dishes of filtered sea water. Water was changed every three days and total survival time was measured. Of 33 worms, the first died after two days, 50% were dead after 37 days and the last worm survived for 50 days.

Six worms were tested for their response to light. The worms were placed individually in two-inch Stender dishes one side of which had previously been painted black. The dish covers were also blackened on one side. The covered dishes were placed on a dissecting microscope stage and a strong light was directed upward from the mirror below. The half painted dishes provided the worms a choice between two areas of extremely different light intensity. During 20 minutes exposure for each, the maximum amount of time spent by any individual in the lighted area was seven minutes and 52 seconds. The minimum time was 14 seconds and the average time was four minutes, 24 seconds. Therefore more than 15 minutes were spent in the dark area of the dish, indicating a probable photonegativity.

DISCUSSION

The worm described in this paper is a rhabdocoel belonging to the suborder Lecithophora. Hyman (1951) divided this suborder into three sections. The section Dalyellioida includes the Lecithophora without a proboscis, with a pharynx of the doliiform type, mouth at the anterior tip or nearly so; gonopore single; without rhammite tracts. The worm under discussion here is properly included in this section. Hyman further separates the Dalyellioida into three families based on the position of the gonopore, the type of penis, the shape of the pharynx, and the type of yolk glands. The family Graffillidae, with anterior gonopore and unarmed penis, includes the worms of the type found in Macoma nasuta. This is the lowest subdivision used by Hyman. Marcus (1954) in his key to the Graffillidae included two subfamilies and five genera. This worm has joined ovaries and vitellaria, lacks a separate seminal bursa, has club shaped ovaries and a gonopore anterior to the middle of the body. By Marcus' definition, it is of the subfamily Graffillinae and the genus Paravortex. It also fits the description for this genus as originally set forth by Wahl in 1906 and as redefined by Ball (1916).

The genus Paravortex includes three previously described species. Paravortex scrobiculariae Wahl (1906) differs from the species under discussion in that it is smaller, has anterior paired testes and the ovaries are much smaller and with a different shape. In addition it occupies a different site in a lamellibranch of another species.

Paravortex cardii Hallez (1909) is only two-thirds the length of the species from Macoma nasuta. P. cardii has a long esophagus, vitellaria made up of strands, smaller oval-shaped ovaries, and it lives in the gut of Cardium edule. All of these characteristics are significantly different from the species under consideration in this thesis.

Paravortex gemellipara Linton (1910) has a short esophagus, a more anteriorly placed genital pore, small anterior testes, and smaller unconvoluted ovaries. It is found in the mantle cavity of Modiolus demissus. In all of the above features P. gemellipara also differs substantially from the species from Macoma nasuta.

The essential differences as well as the similarities between the rhabdocoel described in this paper and the other three known species of this genus are summarized in Table 2. It is to be concluded that the worm found in the pericardial cavity of Macoma nasuta is a new and unique species of Paravortex. A species description will be published shortly.

Dogiel (1966) suggested that the study of any parasitic organism should include a consideration of the host animal and the environment in which the host exists. Concerning the parasites, he stated that "the host, their immediate environment, constitutes their microenvironment, but they are also tied by many links to the host's external environment, which may be termed the macroenvironment." Noble and Noble (1961) wrote: "When a parasite is studied by itself, apart from its environment, only a part, and often a small part, of its total biology can be understood."

Paravortex sp. nov. inhabits a microenvironment consisting of the pericardial cavity of Macoma nasuta. The bent-nosed clam is an estuarine organism which feeds upon the surface detritus of intertidal sandy-mud flats. It is commonly found in or near eelgrass beds from a tidal level of 0.0 to 2.0 feet above mean lower low water. This bivalve lives from two to about 20 centimeters below the surface of the sand and extends separate incurrent and excurrent siphons upward into the water. The incurrent siphon is extended along the sand flat surface and detritus, settling out of the water, is taken up along with the sea water from just above the bottom. This clam has a maximum length of approximately seven centimeters.

An examination of 438 clams collected in July and August of 1967, indicates that the population can be divided into two, possibly three, size categories (Figure 5). A group of 106 clams averaged slightly over 20 mm in length while a second group of 338 clams averaged approximately 43 mm long. A portion of the latter group (clams of 55 to 65 mm length) may constitute a separate size class but the distinction between these and the next smaller group is not sufficient to justify making a positive statement to that effect.

If the size distribution of clams during a 12 month period is examined, some tentative conclusions concerning the age and growth of the animals can be reached (Figure 6). The July, August, September and October collections have a bimodal distribution with the average length of the small clams increasing steadily over this four month period. By November the two classes merge to form a relatively uniform distribution around a mean of about 39 mm. These data suggest

a population of younger, relatively more rapidly growing clams, which grows to a minimum adult size, comparable to the clams from previous years, by November.

In November, and especially in December and January, the larger clams are substantially reduced in number. The mean size of clams is markedly less and this suggests mortality of the clams of five to seven centimeters in Macoma nasuta. Large numbers of larger shells litter the sand flats at this time of year.

For the next five months the relatively uniform distribution continues and the mean population size increases steadily. By July a generation of very small clams can be found. In summation, it may be concluded that an over-wintering population of unknown age composition, but including at least one- and probably two-year old animals, spawns during the spring, probably April and May based upon gonad observations. These newly-spawned animals grow rapidly, reaching 25 to 30 mm after four to five months. During the winter months, the oldest of the clam population die in a relatively short time, leaving a population composed of animals from the previous spring spawn plus clams from an unknown number of spawning seasons prior to that. The average life span of Macoma nasuta is unknown.

Time of infection of clams by the worms is probably related to the size of the host animal. Hart (1963) suggested that Graffilla siliqua enters the pericardial cavity of the razor clam by passing through the kidney. In Macoma nasuta, as in other lamellibranchs, the kidney is a tubelike structure, opening into the suprabranchial space via an excretory pore. At the other end of the kidney an

opening, the reno-pericardial aperture connects to the pericardial space. It is quite likely that Paravortex sp. nov. also uses the kidney as a means of gaining access to the pericardial cavity. If this is correct, only clams with renal ducts large enough to accommodate rhabdocoels about 0.22 mm long (the average size of newly hatched worms) are capable of becoming infected. The examination of small clams indicates the minimum size is about 15 mm. One 14 mm clam was found to be infected with one immature rhabdocoel when examined in December, 1967. Approximately 300 clams ranging from five to 15 mm were examined during the 12 month study period.

The data further suggest that small clams ranging in size from 15 mm to about 28 mm are much less likely to be infected than are clams over 30 mm (Figure 7). The clams are infected at all sizes above 15 mm, but the older, larger clams consistently have infection rates of 30 to 40% compared to rates of under 25% for the smaller clams (<30 mm). Multiple infections are also more common in larger clams. Since there appears to be no age-induced immunity to infection, the higher incidences of worms found in larger clams is probably a result of their longer exposure to the infective stages of the worms. This could also account for the increase in multiple infection noted with increased size. However, multiple infections may result from reproduction of the worm inside the pericardial cavity.

The infection rate for the clam population varied substantially throughout the year (Figure 8). Immature worms are found at all months of the year, but the rapid increase in infections during

May and June appears to be the result of a period of increased reproduction within the rhabdocoel population. This is substantiated by a correlated increase in the occurrence of immature worms in the clams examined during these months and by a sharp increase in the mean number of worms per clam (Table 1 and Figure 8). In June, the number of immature worms, as well as the mean number of worms per infection, is reduced from the earlier highs. This, combined with the fact that the percent infection is highest during this month, suggests that the young worms leave the clam in which they were born and the establishment of new infections by the young worms reaches its peak in the early summer. Patterson (1912) found a reproductive periodicity in Graffilla gemellipara consisting of a period of rapid increase during June and a second period of increase in August. The months between were characterized by low incidences of infection. Patterson's collections continued through October when he thought he detected a possible third period of reproductive activity. Graffilla gemellipara populations appear to fluctuate much more than do those of Paravortex sp. nov. Collection records for an entire year were not made by Patterson. Paravortex sp. nov. rates of infection decline steadily through the fall and winter months reaching a minimum in March. The lowest incidences are coincident with the winter mortality in clams of larger size. The rates of infection remain low (<21%) until the spring increase in reproduction occurs in May and June. The increase in reproductive activity by the rhabdocoels parallels the possible increase in metabolic and reproductive activity that may be taking place at this time of reproduction in the bent-nosed clams.

Atkin's (1934) data indicated substantial variation in incidence of Paravortex cardii in Cardium edule collected at seven locations. Infection rates ranged from 23 to 92%. His data included only four months of collecting and seasonal trends could not be evaluated. Other papers dealing with Paravortex infections (Wahl, 1906; Hallez, 1908, 1909; Linton, 1910; Ball, 1916) did not include seasonal changes in the infection rates.

Paravortex sp. nov. has been found only in Macoma nasuta and only in the pericardial cavity of this clam. Bivalves of 12 other species : Ostrea lurida Carpenter, 1864; Mytilus edulis Linnaeus, 1758; Clinocardium nuttalli (Conrad, 1837); Protothaca staminea (Conrad, 1837); Tellina bodegensis Hinds, 1845; Macoma secta (Conrad, 1837); Siliqua patula Dixon, 1788; Tresus capax Gould, 1850; Mya arenaria Linnaeus, 1758; Macoma inquinata (Deshayes, 1854); Mytilus californicus Conrad, 1837; Botula falcata (Gould, 1851); were collected and examined in or near Yaquina Bay. A turbellarian, Graffilla siliqua, was found in the pericardial cavity of Siliqua patula, as described previously by Hart (1963).

Nine rhabdocoels were sectioned, stained with hematoxylin and eosin and studied for details of the anatomy. The digestive tracts of the worms were empty, giving no hint of their food. The individuals were fixed immediately upon removal from the pericardial cavity of the clam so that materials could not have been lost from the gastrovascular cavity before fixation. The means by which Paravortex sp. nov. obtains the necessary nutrients can only be conjectured. Hart (1963) suggested that Graffilla siliqua absorbs nutrients from

the clam's tissue fluids and possibly ingests amoebocytes. Martin and Harrison (1966) describe the pericardial cavity of lamellibranchs as being a site of fluid formation which then flows through the renopericardial canal and serves to flush out the secretions of the glandular parts of the kidney. The filtrate produced is rich in dissolved salts, glucose and other nutrient substances. Martin et al. (1965) have shown that resorption of the glucose from the urine occurs in the kidney of gastropods. Florkin and Duchateau (1948) reported a similar resorption site for specific ions in the freshwater bivalve, Anodonta. The pericardial fluid, then, is a nutritionally rich environment and it is likely that Paravortex sp. nov. meets its nutritional requirements by ingestion of this fluid. Since the lengths of neither the free living nor the parasitic periods are known, the possibility exists that this worm may build up sufficient food reserves during its free living time to last throughout its symbiotic existence. A definitive answer to the question of the nutrition of these worms requires the development of techniques for experimental introduction of rhabdocoels of known growth and nutritional state into parasite-free clams.

Paravortex sp. nov. infects clams of either sex with approximately equal frequency. Both the rate of infection and the incidence of multiple infections in samples of all male or all female clams is very similar to the data recorded for randomly chosen clams during the same period; therefore, the sex of the host is not related to the incidence of infection.

The data suggest, as mentioned before, that Paravortex sp.

nov. does have a seasonal trend in reproductive activity (Table 1, Figure 8). Adults bearing embryo capsules and immature worms were found in substantial numbers throughout the year. During the spring months (April, May and June), the infections were characterized by increased numbers of immature worms (Table 1).

Paravortex sp. nov. differs markedly from the other three species in this genus in the method of producing and holding encapsulated embryos. The genital antrum in this species acts as a uterus within which as many as 12 capsules are held. In the other three species, the capsules are formed in the antrum, but are rapidly moved into the parenchyma so that no more than one capsule is in the genital antrum at any given time. The total numbers of embryo capsules is less than in P. cardii and P. (=Graffilla) gemellipara (Hallez 1909, Linton 1910). Comparable data for P. scrobiculariae are not available.

The capsules are contained in the maternal parenchyma until actively moving ciliated embryos are formed. Adult worms with 20 or more of these capsules have embryos of a wide range of developmental stages. The space available for internal organs in such worms is reduced by at least one-half. In worms containing a large number of capsules, most are located in the posterior end of the animal. Hatching of the young worms has not been observed in Paravortex sp. nov. However, worms have been maintained in sea water until the event has taken place. When this happens the worm ruptures and dies, liberating the embryo capsules. Freed larval worms were always seen outside of the capsules and swimming freely in sea water. Embryo

capsules containing less than fully developed larvae normally rupture when exposed to sea water and the larvae perish. For these it appears that the hatching in sea water was premature. Hallez (1909) and Ball (1916) reported that P. cardii and P. gemellipara hatchings resulted in death by rupture of the parental worm, but that hatching did not occur until virtually all of the capsules contained well developed active embryos.

It appears that the presence of Paravortex sp. nov. produces no physical damage to the host clams. Of the 438 Macoma nasuta examined in July and August of 1967, 39 had easily observable abnormalities in the pericardial cavities; of these 16 were infected and 23 were uninfected. All of the clams having very large infections (15 or more worms) had no obvious physical defects in the pericardia, hearts or in the intestines. Hart (1963) could find no damage to the pericardial cavities or associated organs of Siliqua patula resulting from Graffilla siliqua infections.

Macoma nasuta acts as an intermediate host for metacercaria of a digenetic trematode of a type commonly found in birds. The coincident infections of Paravortex sp. nov. in no way affects the metacercarial infections since virtually every clam examined had metacercariae in some numbers. It is unlikely that the metacercariae have any direct effect on the Paravortex in the pericardial cavity. The trematodes are very small (0.25 mm in length) and limited in numbers (generally <15) in the clams. Their position between the mantle and valve also suggests that no interaction between the two species can occur.

Bent-nosed clams from five widely separated collecting locations in Yaquina Bay were found to contain rhabdocoels. Clams of the same species collected at Coos Bay and at Penrose Point in Puget Sound lacked the worms. Linton (1910) reported similar discontinuities in the distribution of Paravortex (=Graffilla) gemellipara. He even observed variations between adjacent mussel beds, giving the example of 36 mussels from one bed yielding no worms while 34 mussels from a bed 50 yards away harbored 75 of these parasites. Atkins (1934) in his examination of cockles for P. cardii from seven localities near Plymouth, England, found infections present at all sites. Since Paravortex sp. nov. lacks a pelagic stage and if the free-living period is short, the widely separated estuaries of the Oregon Coast could easily become barriers to distribution. The method of establishment of the infection in any single estuary is open to speculation and a more thorough examination of the estuaries of the Oregon Coast might yield new records which would suggest a pattern of distribution.

The survival times of worms removed from clams indicates that the relationship between Paravortex sp. nov. and its host is not as well developed as in certain other endocommensal rhabdocoels. Similar exposures of Syndesmis sp. (from guts of the sea urchins, Strongylocentrotus purpuratus) and of Collastoma sp. (from guts of sipunculids, Dendrostoma sp.) resulted in death of the worms in three to five days. The well developed eyes and the uniformly ciliated body surface also suggests that Paravortex sp. nov. is capable of considerable independence from Macoma nasuta since these structures are

subject to considerable reduction or total loss in more highly specialized parasites.

SUMMARY

The morphology of Paravortex sp. nov., a parasite of Macoma nasuta, has been described. It was compared to the other species of the genus.

Host clams were collected and examined each month for one year. Size frequency analysis of the clam population indicated at least two age groups. The medium sized clams were found to have a substantially higher incidence of infection during all collecting periods. Infections were never found in clams less than 14 mm long.

Incidence of infection, the percentage of immature worms and the incidence of multiple infections reached a peak during April, May, and June of 1968. These data suggest a seasonal periodicity in the reproduction of the worm population. Reproduction of the rhabdocoels continued at a lower level during the other months of the year.

The data did not indicate any correlation between sex of the clam and the degree of incidence of infection. Male clams and female clams were found to be infected in approximately equal numbers.

Paravortex sp. nov. was found only in Macoma nasuta and only in the pericardial cavity of this clam. Bivalves of twelve other species were found to be uninfected with this worm. It is postulated that this rhabdocoel enters the host clam by passing up the excurrent siphon, through the suprabranchial space, through the kidney and into the pericardial space.

Physical abnormalities of the pericardial cavity could not be directly related to the presence of rhabdocoels. Any abnormalities

that were found were present as often in uninfected as in infected clams.

Single collections of clams from Coos Bay, Oregon, and from Penrose Point in Puget Sound, Washington, contained no rhabdocoels.

Survival time of Paravortex sp. nov. in sea water was compared to two other endoparasitic rhabdocoels. Fifty percent of the worms from Macoma nasuta survived for 37 days and the longest for 50 days. Paravortex sp. nov. does not have highly specialized morphological adaptations to fit it to a parasitic existence. These data suggest a relatively newly established relationship between rhabdocoel and host.

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APPENDIX

Table 1. The occurrence of Paravortex sp. nov. in Macoma nasuta from Yaquina Bay, Lincoln County, Oregon. The results are summed for each month.

Month	Year	Number clams examined	Number clams infected	Percent clams infected	Rhabdocoels found	Rhabdocoels per infected clam	Number single infections	Percent single infections	Number multiple infections	Percent multiple infections	Maximum infections	Percent immature Rhabdocoels
July	1967	110	46	41.8%	134	2.92	22	47.8%	24	52.5%	17	37%
August	1967	118	37	31.4%	130	3.52	18	48.7%	19	51.3%	14	39%
September	1967	133	50	37.6%	121	2.42	26	52.0%	24	48.0%	9	29%
October	1967	101	28	27.8%	61	2.14	15	53.5%	13	46.5%	9	28%
November	1967	86	19	22.2%	39	2.05	8	42.0%	11	58.0%	5	33%
December	1967	97	24	24.5%	48	2.00	12	50.0%	12	50.0%	5	35%
January	1968	120	23	19.2%	72	3.13	10	43.5%	13	56.5%	16	26%
February	1968	86	16	18.5%	41	2.56	6	37.5%	10	62.5%	8	30%
March	1968	101	17	16.8%	43	2.53	3	17.5%	14	82.5%	5	31%
April	1968	96	20	20.8%	63	3.15	7	35.0%	13	65.0%	13	61%
May	1968	84	33	39.3%	154	4.67	6	18.2%	27	81.8%	21	64%
June	1968	117	60	51.3%	119	1.99	36	60.0%	24	40.0%	10	46%

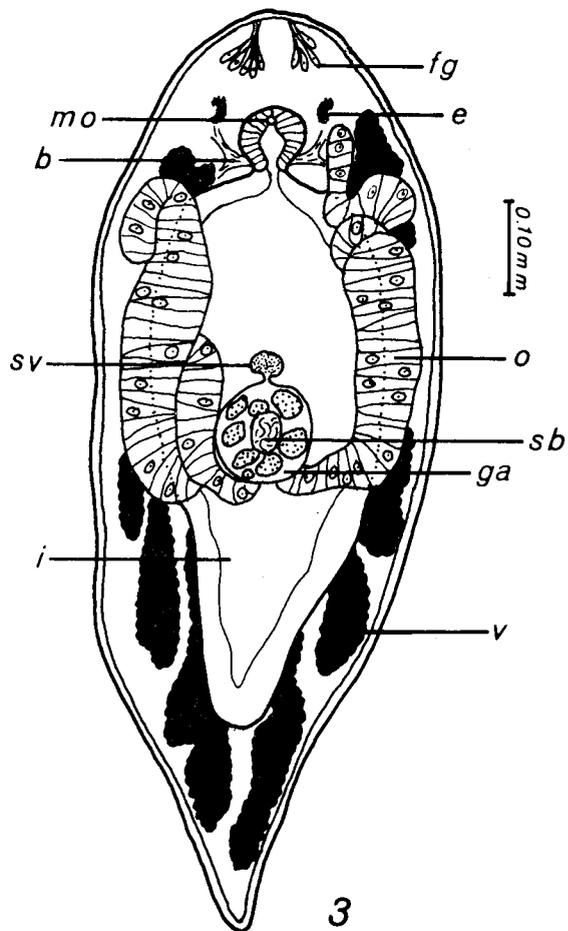
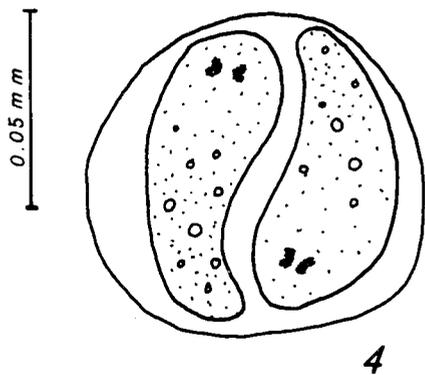
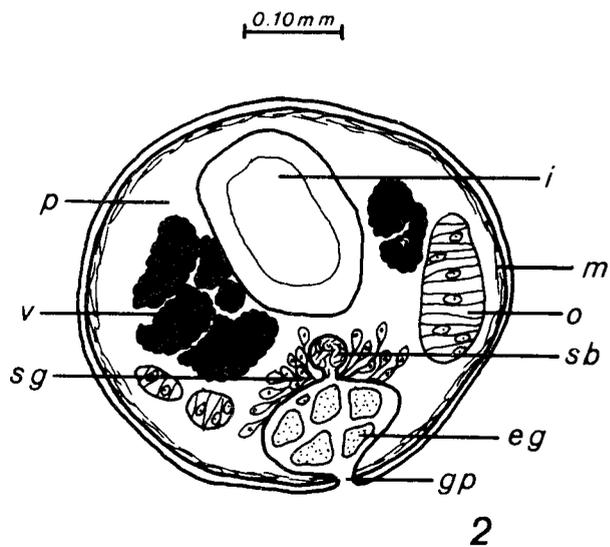
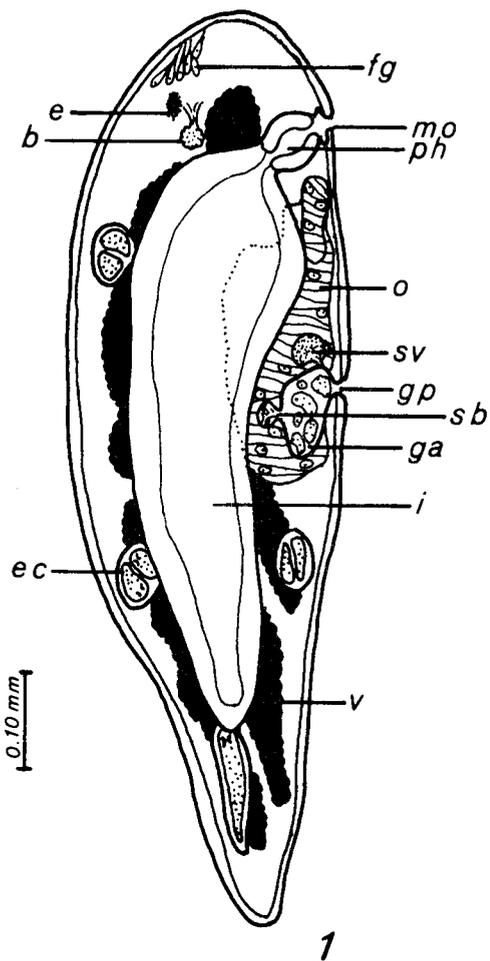
Table 2. Morphological comparisons of the four species of the genus *Paravortex*.

	<i>P. scrobiculariae</i> Wahl (1906)	<i>P. cardii</i> Hallez (1909)	<i>P. gamellipara</i> Linton (1910)	<i>Paravortex</i> Sp. Nov.
Length	1.0 to 1.28 mm	1.0 mm max.	1.30 to 1.54 mm (To 2.0 mm)	To 1.5 mm (1.45 mm)
Width	0.35 to 0.45 mm	0.3 to 0.4 mm	0.36 to 0.65 mm (To 0.80 mm)	To 0.5 mm
Breadth at eyes	0.22 to 0.30 mm	0.19 mm	0.28 mm	To 0.30 mm
Distance between eyes	0.10 mm	0.11 mm	0.10 mm	To 0.16 mm
Pharynx	Spherical 0.06 mm	Doliiform 0.06 mm	Spherical 0.07 to 0.09 mm	Spherical 0.10 mm
Esophagus	Absent	Long	Short 0.05 mm	Absent
Intestine	Cylindrical, extends to posterior	Cylindrical, extends to posterior	Cylindrical, extends to posterior	Slightly tapered, extends to posterior
Vitellaria	Paired, extensive "handlike, an- terior 1/4 to posterior	Paired, strand- ed, posterior to genital pore	Stranded, from anterior 1/4 to posterior	"Handlike" from an- terior 1/4 to posterior
Genital pore	Ventral, median 0.33 to 0.42 mm from an- terior	Ventral, median 0.28 mm from anterior	Ventral, median 0.06 to 0.25 mm from an- terior	Ventral, median, 0.6 mm from anterior
Testes	Paired, lateral to eyes, oval 0.08 x 0.05 mm	Paired, postero- lateral to G. P. oval 0.10 x 0.15 mm	(Anterior, lateral to eyes oval 0.05 x 0.09)	Paired, posterior
Ovaries	Anterior directed, not convoluted, tapered 0.25 mm long	Slightly anterior to midline, oval 0.19 mm long	Anterior from midline to near testes 0.04 mm long	Middle an- terior to level of eyes. Con- voluted 1.0 mm long
Seminal vesicle	Spherical, 0.10 mm in anterior 1/3	Spherical 0.06 mm in anterior 1/4	Pyriiform 0.048 x 0.051, 0.034	Spherical 0.05, in an- terior 1/3
Mouth	Subterminal	Subterminal	Subterminal	Subterminal

EXPLANATION OF PLATES

- Figure 1. Semidiagrammatic median sagittal section of Paravortex sp. nov.
- Figure 2. Transverse section through seminal bursa of Paravortex sp. nov.
- Figure 3. Paravortex sp. nov., entire worm, ventral view.
- Figure 4. Semidiagrammatic representation of egg capsule from parenchyma showing relationship of paired embryos.

Abbreviations for all figures: b, brain; e, eye; ec, embryo capsule; eg, embryo capsule in genital antrum; fg, frontal glands; ga, genital antrum; gp, genital pore; i, intestine; m, muscle layer; mo, mouth; o, ovary; p, parenchyma; ph, pharynx; sb, seminal bursa; sg, shell gland; sv, seminal vesicle; v, vitellaria.



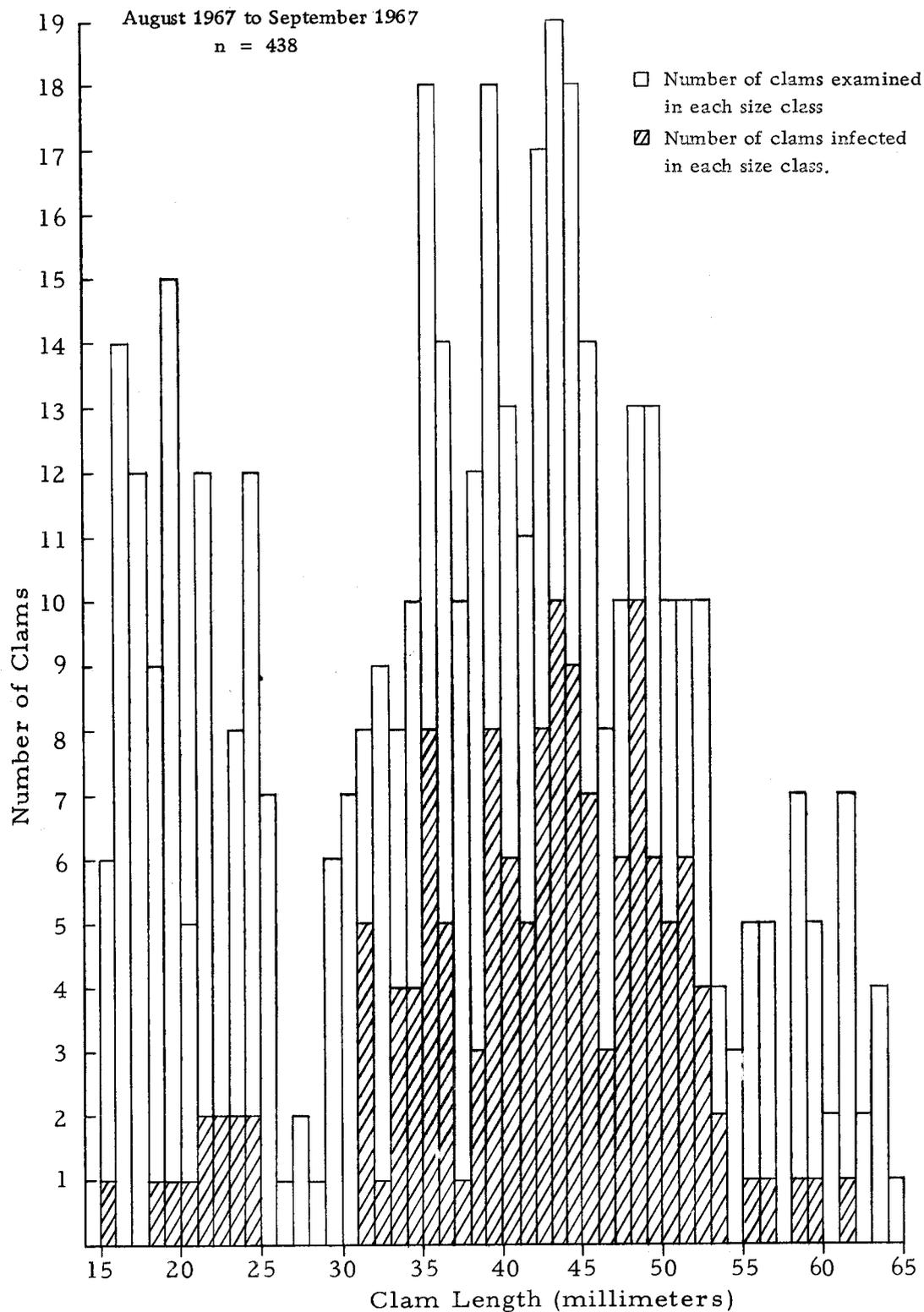


Figure 5. Histogram showing the size distribution of a large sample of clams taken during a two month period in 1967. It also illustrates the numbers of infected clams in each size class.

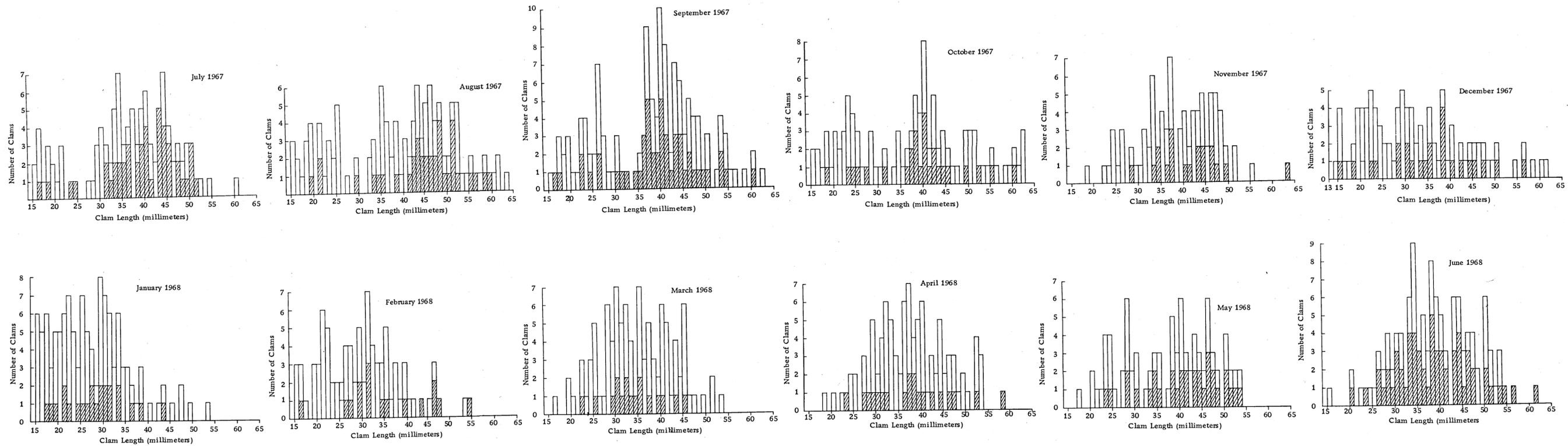


Figure 6. Summary of monthly changes in population size distribution of clams and in infection rates for the size categories.
 □ number of clams examined in each size class.
 ▨ number of clams infected in each size class.

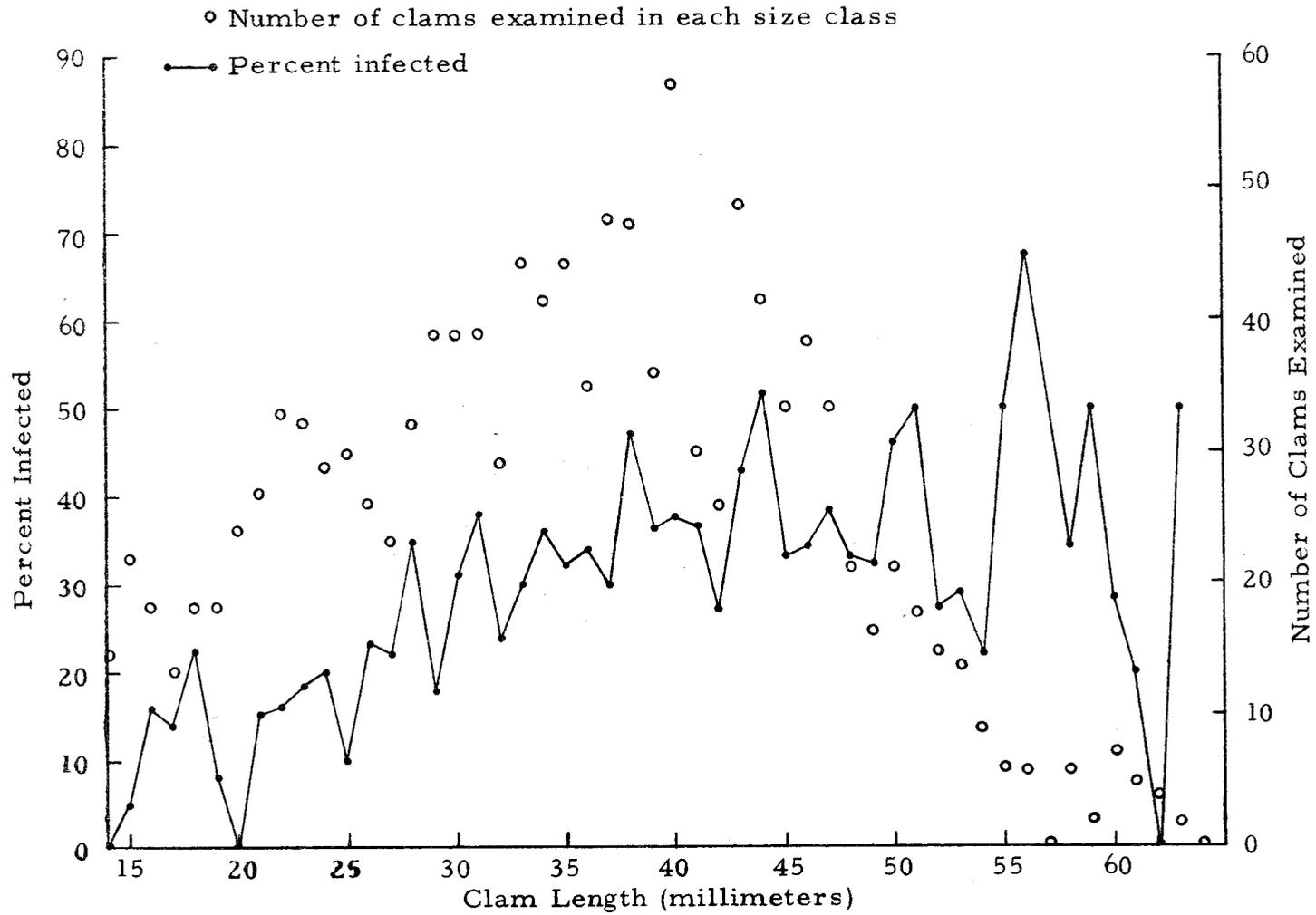


Figure 7. The relationship between size of host clam and rate of infection by Paravortex sp. nov.

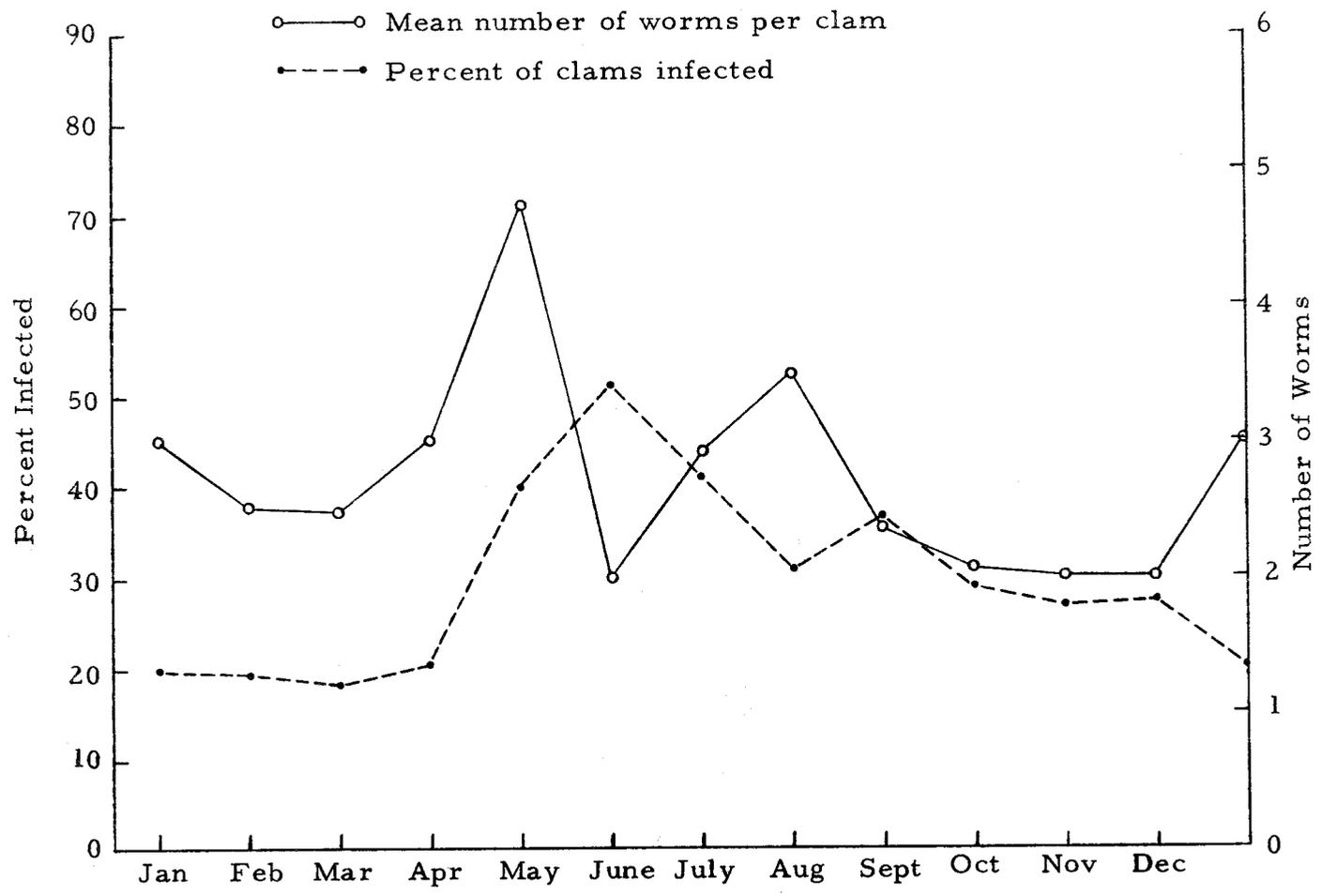


Figure 8. The monthly variation in rates of infection of Maccoma nasuta and in the mean number of worms per infected clam.