MEMOIRS OF THE COLLEGE OF SCIENCE, KYOTO IMPERIAL UNIVERSITY, SERIES B
Vol. VII. No. 2, Article 3, 1931.

Studies on the Modification of Sexual Characters in *Eupagurus samuelis* caused by a Rhizocephalan Parasite *Peltogaster sp.*

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With 15 Text-figures

(Received June 26, 1931)

Introduction

It is a well known fact that the sexuality of various arthropods is modified by the presence of certain parasites. This phenomenon, "parasitic castration" as it was called by A. GIARD (1886), was first described by him, and he gave in a series of papers pertaining to this phenomenon various instances of parasites and hosts. He found a tendency for the secondary sexual character in either sex of the host to be modified and approach the type of the other sex under the influence of the parasite. Next G. SMITH (1906), on examination of the same phenomenon in *Inachus scorpio* effected by *Sacculina neglecta*, came to the conclusion that the alteration in the female consists merely in the atrophy of the gonad, while in the male the atrophy of the gonad is coupled with the assumption of the secondary sexual character proper to the female.

The parasitic castration in the hermit-crab caused by the rhizocephalan parasite *Peltogaster* was studied by GIARD (1887) himself with *Eupagurus bernhardus* as material. In 1906 F. A. POTTS studied this phenomenon in *E. meticulosus* and *E. prideauxii*, and came to the same conclusion as SMITH, while J. GUÉRIN-GANIVET (1911), formed the opinion, based on his rather insufficient material, that the females of *E. cuanensis* and *E. prideauxii* change their secondary sexual character, which approaches that of the male. However, a more recent study by C. A. NILSSON-CANTELL (1926) working with a much more adequate supply of material, proved that this is not the case in *E. cuanensis*

and *Anapagurus chiroacanthus*.

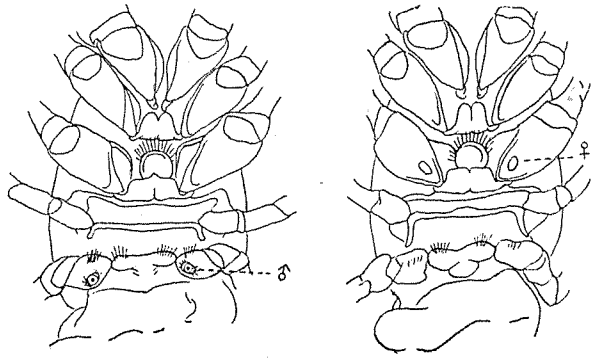
Since the spring of 1929 I have been carrying on an investigation on the modification of the sexual character in *Eupagurus samuelis* caused by *Peltogaster. sp.*, and obtained results which differ somewhat from those of the previous authors. In this paper I propose to give a brief account of the investigation and the results obtained.

My thanks are due to Prof. T. KOMAI for his kind instruction and valuable suggestions, and also to the staff of the laboratory, who helped my research work in various ways.

The Hermit-Crab and its Secondary Sexual Character.

Eupagurus samuelis is one of the commonest species of hermit-crab in the neighbourhood of the laboratory; nearly 30—40 per cent. of the individuals are infested with a species of *Peltogaster*.

In this hermit-crab the sexes may be distinguished by the differences in the gonopore and in the abdominal appendages. In the female the gonopore is situated on the internal corner of the basal joint of the third pereiopod, and is noticeable as an oval aperture (text-fig. 1, b). In the male on the other hand, the pore is found on the basal joint of the fifth pereiopod on the apex of a papilla which is bordered with setae (text-fig. 1, a).



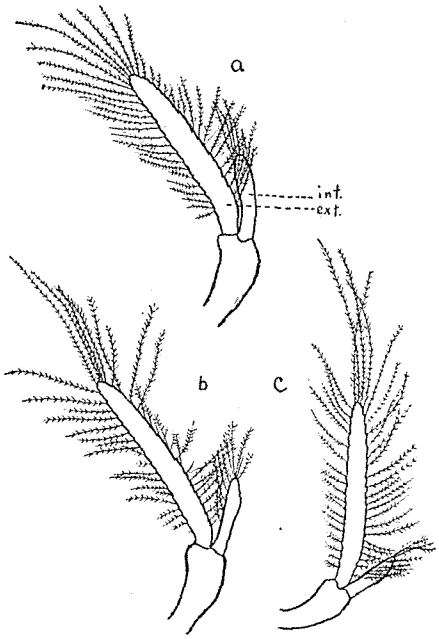
a b

Fig. 1.

Thoracic region of normal male (a) and female (b).
♂, male gonopore. ♀, female gonopore.

The abdominal appendages in the female are present on abdominal segments 2, 3, 4, 5 and 6, while in the male segment 2 is devoid of the appendage. These appendages are unpaired, and present on

the left side only, except those of segment 6 which are paired and form uropods. In the male each of the unpaired appendages consists of a protopodite and two rami, of which the external ramus is longer, flattened and bordered with plumose hairs; while the internal ramus is much shorter, flattened



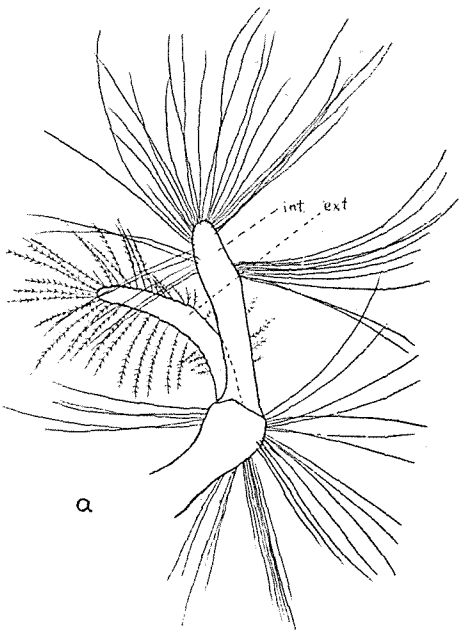
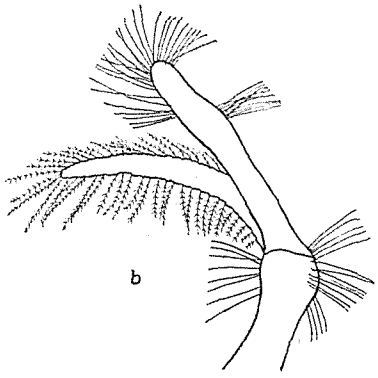


Fig. 2.

Abdominal appendages of normal male. a, first appendage of third segment: b, second appendage of fourth segment: c, third appendage of fifth segment. *int.*: internal ramus; *ext.*: external ramus.



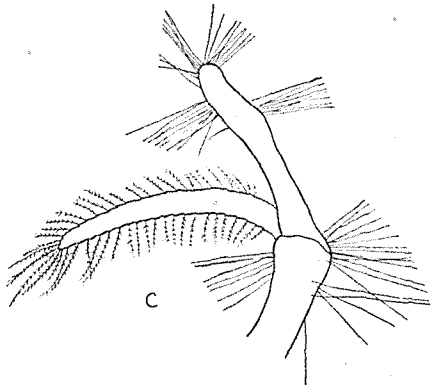


Fig. 3.

Abdominal appendages of normal female. a. first appendage of second segment; b, second appendage of third segment; c, third appendage of fourth segment. Fourth appendage of fifth segment not figured, being identical with fig. 2, c. *int.*: internal ramus; *ext.*: external ramus.

and sparsely provided with plumose hairs (text-fig. 2). In the female the internal rami of the appendages of segments 2, 3, and 4 are longer than in the male, club-shaped and furnished with long stiff setae to which the eggs are attached in the breeding season (text-fig. 3). The external rami of these appendages as well as the appendage of the fifth segment do not show any sexual difference.

Modification in the Secondary Sexual Character

(A) Proportional Length of the Two Rami of the Abdominal Appendages.

As stated above, in *E. samuelis* the internal rami of the abdominal appendages are relatively longer in the female than in the male; the relative length of these rami is modified in both sexes by the parasitism of *Peltogaster*. In order to make a crucial study on this point the ratio of the length of the internal ramus to that of the external ramus of the same appendage was taken and examined statistically. The lengths of the two rami were measured and the ratio, (length of internal ramus × 100) : (length of external ramus), was obtained as shown in tables 1—5. (Also see diagrams 1—7).

The facts disclosed in tables 1—5 are:

The ratio of the lengths of the rami in each of the first, second and third appendages is larger in the female than in the male, whereas there exists no sexual difference in the ratio of the rami in the appendage of the fifth segment (the third appendage in the male and the fourth appendage in the female).

In the first and second appendages of the male the ratio is greater in infected individuals than in uninfected, while in the first, second and third appendages of the female it is smaller in infected than in uninfected.

The ratio in the appendage of the fifth segment is not modified by parasitism in either sex.

(B) True Nature of Modification in Abdominal Appendage.

In order to enter deeper into the problem, the length of the ramus in relation to the carapace length was examined, the latter length being taken as an index of the general size of the body. The data have been obtained from all the appendages of infected and uninfected

TABLES 1—4: Showing the distribution of normal and infected individuals according to the relative length of the two rami of abdominal appendages: (length of internal ramus × 100): (length of external ramus).

TABLE 1.

Appendage of abdominal segment II.

Abd. app.	I in female	
Class	Norm.	Inf.
46.5—48.5	—	1
48.5—50.5	—	2
50.5—52.5	—	1
52.5—54.5	—	2
54.5—56.5	—	0
56.5—58.5	—	1
58.5—60.5	—	0
60.5—62.5	—	2
62.5—64.5	—	2
64.5—66.5	—	5
66.5—68.5	2	11
68.5—70.5	1	4
70.5—72.5	0	7
72.5—74.5	2	4
74.5—76.5	2	6
76.5—78.5	2	12
78.5—80.5	6	8
80.5—82.5	12	7
82.5—84.5	6	5
84.5—86.5	5	4
86.5—88.5	10	5
88.5—90.5	16	3
90.5—92.5	9	1
92.5—94.5	7	1
94.5—96.5	6	0
96.5—98.5	6	0
98.5—100.5	7	2
100.5—102.5	1	—
102.5—104.5	1	—
104.5—106.5	2	—
Total	103	96

TABLE 2.

Appendage of abdominal segment III.

Abd. app.	I in male		II in female	
Class	Norm.	Inf.	Norm.	Inf.
26.5—28.5	1	2	—	—
28.5—30.5	4	0	—	—
30.5—32.5	2	2	—	—
32.5—34.5	3	3	—	—
34.5—36.5	21	6	—	—
36.5—38.5	43	7	—	—
38.5—40.5	49	16	—	—
40.5—42.5	56	30	—	—
42.5—44.5	48	44	—	—
44.5—46.5	16	38	—	2
46.5—48.5	6	28	—	2
48.5—50.5	4	22	—	2
50.5—52.5	1	18	—	5
52.5—54.5	0	9	1	2
54.5—56.5	2	4	0	5
56.5—58.5	0	2	1	4
58.5—60.5	1	4	0	8
60.5—62.5	1	0	3	8
62.5—64.5	—	1	2	6
64.5—66.5	—	—	3	9
66.5—68.5	—	—	3	3
68.5—70.5	—	—	9	2
70.5—72.5	—	—	11	6
72.5—74.5	—	—	10	8
74.5—76.5	—	—	6	3
76.5—78.5	—	—	12	4
78.5—80.5	—	—	8	5
80.5—82.5	—	—	9	2
82.5—84.5	—	—	7	1
84.5—86.5	—	—	4	2
86.5—88.5	—	—	6	0
88.5—90.5	—	—	2	1
90.5—92.5	—	—	1	—
92.5—94.5	—	—	1	—
94.5—96.5	—	—	3	—
96.5—98.5	—	—	0	—
98.5—100.5	—	—	1	—
100.5—102.5	—	—	0	—
102.5—104.5	—	—	2	—
Total	258	236	105	96

Table 3.

Appendage of abdominal segment IV.

Abd. app.	II in male		III in female	
Class	Norm.	Inf.	Norm.	Inf.
24.5—26.5	1	—	—	—
26.5—28.5	4	—	—	—
28.5—30.5	7	—	—	—
30.5—32.5	19	—	—	—
32.5—34.5	35	3	—	—
34.5—36.5	67	14	—	1
36.5—38.5	57	25	—	1
38.5—40.5	27	29	—	2
40.5—42.5	22	44	—	1
42.5—44.5	11	52	—	5
44.5—46.5	4	29	1	4
46.5—48.5	2	18	1	10
48.5—50.5	1	9	2	9
50.5—52.5	—	3	5	7
52.5—54.5	—	7	3	9
54.5—56.5	—	3	4	11
56.5—58.5	—	3	6	5
58.5—60.5	—	—	10	5
60.5—62.5	—	—	15	5
62.5—64.5	—	—	14	6
64.5—66.5	—	—	6	3
66.5—68.5	—	—	6	8
68.5—70.5	—	—	6	2
70.5—72.5	—	—	10	0
72.5—74.5	—	—	2	1
74.5—76.5	—	—	5	—
76.5—78.5	—	—	1	—
78.5—80.5	—	—	1	—
80.5—82.5	—	—	1	—
82.5—84.5	—	—	1	—
Total	257	239	100	95

Table 4.

Appendage of abdominal segment V.

Abd. app.	III in male		IV in female	
Class	Norm.	Inf.	Norm.	Inf.
20.5—22.5	1	—	—	—
22.5—24.5	3	—	—	1
24.5—26.5	2	7	4	4
26.5—28.5	11	10	8	8
28.5—30.5	20	21	18	15
30.5—32.5	38	45	22	18
32.5—34.5	56	56	18	20
34.5—36.5	51	40	15	18
36.5—38.5	38	38	6	10
38.5—40.5	17	12	3	2
40.5—42.5	5	4	2	—
42.5—44.5	2	1	—	—
Total	244	234	96	91

Table 5.

Arithmetical means with probable errors calculated from Table 1—4.

		abd. seg. II	abd. seg. III	abd. seg. IV	abd. seg. V
			app. I	app. II	app. III
male	normal	—	40.73±0.175	36.63±0.344	34.06±0.159
	infected	—	45.25±0.243	42.92±0.205	33.70±0.167
		app. I	app. II	app. III	app. IV
female	normal	88.5±0.51	77.4±0.60	63.6±0.53	32.4±0.254
	infected	73.7±0.74	65.4±0.71	54.6±0.58	32.3±0.248

individuals of both sexes. The results are shown in tables 6—33. (Also see diagrams 8—14).

The facts that can be deduced from these tables are:

The external ramus of the first appendage of the male is shorter in infected individuals than in uninfected, whereas the internal ramus shows no difference between uninfected and infected. In the second appendage of the male, however, the internal ramus is longer in infected individuals than in uninfected, whereas the external ramus shows no difference whatever.

The internal ramus of each appendage of the female, except that of the fourth appendage, is shorter in infected individuals than in uninfected, whereas the external ramus is substantially equal in both classes, though not exactly so.

In the appendage of the fifth segment of either sex the internal ramus as well as the external ramus is unmodified.

(C) Appearance of an Extra Appendage in Male and Modification in the Structure of Abdominal Appendages.

As mentioned before, the appendage is normally absent from the second abdominal segment of the male. But, of the 260 normal males examined, 5 were found to be provided with an extra appendage in segment 2 like the female. One of these abnormal individuals was provided with a small finger-shaped unramified rudimentary appendage, while the remaining 4 had a biramous appendage. It is not known whether these males with an extra appendage had been infested by a parasite or not, but neither external nor internal anatomy shows any trace of previous infection in these individuals.

In infected males this appendage appears rather often: of the 246 infected males which I examined, 3 were provided with an unramified rudimentary appendage in this segment, and 26 had a biramous appendage.

TABLES 6—33: Correlation tables, showing the length of the ramus of the abdominal appendages in relation to the carapace length. For the carapace length the actual length and for the ramus length 22.5 times the actual length in mm. are given.

TABLE 6.

External ramus of abd. app. I of normal male

Ramus length in mm. × 22.5	Carapace length in mm.									
	2.5–3.5	3.5–4.5	4.5–5.5	5.5–6.5	6.5–7.5	7.5–8.5	8.5–9.5	9.5–10.5	10.5–11.5	
12.5–14.5	—	1	—	—	—	—	—	—	—	
14.5–16.5	—	—	—	—	—	—	—	—	—	
16.5–18.5	1	0.5	—	—	—	—	—	—	—	
18.5–20.5	—	0.5	—	—	—	—	—	—	—	
20.5–22.5	0.5	1	—	—	—	—	—	—	—	
22.5–24.5	—	2.5	—	—	—	—	—	—	—	
24.5–26.5	—	2.5	1.5	—	—	—	—	—	—	
26.5–28.5	—	0.5	7	—	—	—	—	—	—	
28.5–30.5	—	—	6.75	1.75	—	—	—	—	—	
30.5–32.5	—	—	2.75	4.75	—	—	—	—	—	
32.5–34.5	—	—	1	10.75	1.75	0.5	—	—	—	
34.5–36.5	—	—	—	13	4	—	—	—	—	
36.5–38.5	—	—	—	14.5	5	1	—	—	—	
38.5–40.5	—	—	—	6.25	11.75	1	—	—	—	
40.5–42.5	—	—	—	5.5	14.5	4.5	—	—	—	
42.5–44.5	—	—	—	1	14	5	—	—	—	
44.5–46.5	—	—	—	—	8.5	9.5	1	—	—	
46.5–48.5	—	—	—	—	12.5	10.5	2.5	—	—	
48.5–50.5	—	—	—	—	6	10	1	—	—	
50.5–52.5	—	—	—	—	0.75	9.25	1.5	—	—	
52.5–54.5	—	—	—	—	0.25	6.25	4.5	—	—	
54.5–56.5	—	—	—	—	—	4	3.5	1	—	
56.5–58.5	—	—	—	—	—	—	5	—	—	
58.5–60.5	—	—	—	—	—	—	—	3	—	
60.5–62.5	—	—	—	—	—	—	0.5	—	—	
62.5–64.5	—	—	—	—	—	—	1.5	—	—	
64.5–66.5	—	—	—	—	—	—	—	0.5	0.5	
Total	1.5	8.5	19	57.5	79	61.5	21	4.5	0.5	253
Mean	18.8	22.8	28.9	36.9	42.9	48.1	54.2	59.3	65.5	

TABLE 7.

Internal ramus of abd. app. 1 of normal male

Ramus length in mm. × 22.5	Carapace length in mm.								
	2.5–3.5	3.5–4.5	4.5–5.5	5.5–6.5	6.5–7.5	7.5–8.5	8.5–9.5	9.5–10.5	
4.5– 6.5	0.5	—	—	—	—	—	—	—	
6.5– 8.5	0.5	0.5	—	—	—	—	—	—	
8.5–10.5	0.5	4.5	1.5	1	—	—	—	—	
10.5–12.5	—	3.5	9	5	0.5	—	—	—	
12.5–14.5	—	—	6.5	22	5.5	—	—	—	
14.5–16.5	—	—	1	21.25	17.75	4	—	—	
16.5–18.5	—	—	—	9.75	35.5	14.5	0.75	—	
18.5–20.5	—	—	—	—	16.75	25.5	5.75	—	
20.5–22.5	—	—	—	—	3.5	13	10.5	2	
22.5–24.5	—	—	—	—	0.5	3.5	4	1	
24.5–26.5	—	—	—	—	—	1	0.5	1	
26.5–28.5	—	—	—	—	—	—	1	—	
Total	1.5	8.5	18	59	80	61.5	22.5	4	255
Mean	7.5	10.2	12.3	14.6	17.4	19.5	21.6	23.0	

TABLE 8.

External ramus of abd. app. 1 of infected male.

Ramus length in mm. × 22.5	Carapace length in mm. 3.5–4.5	4.5–5.5	5.5–6.5	6.5–7.5	7.5–8.5	8.5–9.5	9.5–10.5	10.5–11.5	
14.5–16.5	1	—	—	—	—	—	—	—	
16.5–18.5	—	2	—	—	—	—	—	—	
18.5–20.5	0.5	1.5	—	—	—	—	—	—	
20.5–22.5	1.5	1.5	—	—	—	—	—	—	
22.5–24.5	1.25	3.75	—	—	—	—	—	—	
24.5–26.5	1.25	5.25	—	—	—	—	—	—	
26.5–28.5	0.75	4.75	4	0.5	—	—	—	—	
28.5–30.5	0.25	9.75	9.5	0.5	—	—	—	—	
30.5–32.5	—	3.5	17.5	5.5	—	—	—	—	
32.5–34.5	—	—	19.75	8.25	—	—	—	—	
34.5–36.5	—	—	10.75	4.75	—	—	—	—	
36.5–38.5	—	—	7.5	5.5	2	—	—	—	
38.5–40.5	—	—	3	10.5	4	—	—	—	
40.5–42.5	—	—	1.5	10.5	2.5	0.5	—	—	
42.5–44.5	—	—	1	11.5	3.25	0.25	—	—	
44.5–46.5	—	—	1	10.5	8.25	0.25	—	—	
46.5–48.5	—	—	—	2.5	5.5	3	—	—	
48.5–50.5	—	—	—	—	9.5	1.5	—	—	
50.5–52.5	—	—	—	0.5	3	1	—	—	
52.5–54.5	—	—	—	—	2	1	1	—	
54.5–56.5	—	—	—	0.5	1	1	—	—	
56.5–58.5	—	—	—	—	0.5	1	1	—	
58.5–60.5	—	—	—	—	1	1.5	—	—	
60.5–62.5	—	—	—	—	—	—	—	—	
62.5–64.5	—	—	—	—	—	—	—	—	
64.5–66.5	—	—	—	—	—	—	—	1	
66.5–68.5	—	—	—	—	—	—	—	—	
68.5–70.5	—	—	—	—	—	—	—	—	
70.5–72.5	—	—	—	—	—	—	—	1	
Total	6.5	32	65.5	71.5	42.5	11	2	2	233
Mean	22.6	26.5	33.6	39.9	46.6	51.5	55.5	68.5	

TABLE 9.

Internal ramus of abd. app. 1 of infected male.

Ramus length in mm. × 22.5	Carapace length in mm. 3.5–4.5	4.5–5.5	5.5–6.5	6.5–7.5	7.5–8.5	8.5–9.5	9.5–10.5	10.5–11.5	
6.5– 8.5	2.5	—	1	—	—	—	—	—	
8.5–10.5	2.25	4.7	0.5	1	—	—	—	—	
10.5–12.5	1.25	11.75	8.5	1	—	—	—	—	
12.5–14.5	0.5	9.5	19.5	8.5	1.5	—	—	—	
14.5–16.5	—	4.5	22.25	9.75	0.5	—	—	—	
16.5–18.5	—	—	12.75	16.25	6	1.5	—	—	
18.5–20.5	—	—	4.5	20.25	13.75	2	1	—	
20.5–22.5	—	—	1.25	7.5	8.25	1.5	—	—	
22.5–24.5	—	—	0.25	2.75	6	4	—	—	
24.5–26.5	—	—	—	1.5	5.5	0.5	—	—	
26.5–28.5	—	—	—	0.5	0.5	2	—	—	
28.5–30.5	—	—	—	—	0.5	1.5	—	1	
30.5–32.5	—	—	—	—	1	0.5	—	1	
32.5–34.5	—	—	—	—	—	0.5	—	—	
Total	6.5	30.5	70.5	69	43.5	14	1	2	237
Mean	9.4	12.4	15.1	18.0	21.1	24.0	19.5	30.5	

TABLE 10.

External ramus of abd. app. II of normal male.

Ramus length in mm. × 22.5	Carapace length in mm. 2.5–3.5	3.5–4.5	4.5–5.5	5.5–6.5	6.5–7.5	7.5–8.5	8.5–9.5	9.5–10.5	
18.5—20.5	1	1	—	—	—	—	—	—	
20.5—22.5	—	1	—	—	—	—	—	—	
22.5—24.5	0.5	1.5	—	—	—	—	—	—	
24.5—26.5	—	1.5	—	—	—	—	—	—	
26.5—28.5	—	3.75	2.75	—	—	—	—	—	
28.5—30.5	—	0.25	6.25	—	—	—	—	—	
30.5—32.5	—	—	6	2	—	—	—	—	
32.5—34.5	—	—	4.5	4.5	—	—	—	—	
34.5—36.5	—	—	1	12.5	1.5	1	—	—	
36.5—38.5	—	—	—	11.5	4.5	—	—	—	
38.5—40.5	—	—	—	13.75	7.75	—	—	—	
40.5—42.5	—	—	—	7	10.5	2.5	—	—	
42.5—44.5	—	—	—	2.5	14.5	3.5	—	—	
44.5—46.5	—	—	—	1.75	11	7.25	1.5	—	
46.5—48.5	—	—	—	0.25	15	9	0.25	—	
48.5—50.5	—	—	—	—	6	7.5	1.75	—	
50.5—52.5	—	—	—	—	4.25	12.25	2	—	
52.5—54.5	—	—	—	—	1	2.5	3	—	
54.5—56.5	—	—	—	—	1	4.25	4.75	—	
56.5—58.5	—	—	—	—	—	4.75	4.25	—	
58.5—60.5	—	—	—	—	—	—	1	3	
60.5—62.5	—	—	—	—	—	1	2.5	1	
62.5—64.5	—	—	—	—	—	—	0.5	—	
64.5—66.5	—	—	—	—	—	—	1	—	
66.5—68.5	—	—	—	—	—	—	—	—	
68.5—70.5	—	—	—	—	—	—	1	—	
Total	1.5	9	20.5	56	77	55.5	23.5	4	247
Mean	20.8	25.0	31.0	38.1	44.6	49.6	56.1	60.0	

TABLE 11.

Internal ramus of abd. app. II of normal male.

Ramus length in mm. × 22.5	Carapace length in mm. 2.5–3.5	3.5–4.5	4.5–5.5	5.5–6.5	6.5–7.5	7.5–8.5	8.5–9.5	9.5–10.5	
4.5— 6.5	1	—	—	—	—	—	—	—	
6.5— 8.5	—	1.5	—	—	—	—	—	—	
8.5—10.5	0.5	3.5	3	1	—	—	—	—	
10.5—12.5	—	3.5	11.75	11.5	1.75	1.5	—	—	
12.5—14.5	—	—	6.25	22	13.25	1	—	—	
14.5—16.5	—	—	—	19.5	25.75	6.25	0.5	—	
16.5—18.5	—	—	—	2	29	27	—	—	
18.5—20.5	—	—	—	—	9.25	26.5	7.75	1.5	
20.5—22.5	—	—	—	—	—	2.25	10.75	1.5	
22.5—24.5	—	—	—	—	—	—	1	—	
24.5—26.5	—	—	—	—	—	—	1.5	1	
Total	1.5	8.5	21	56	79	64.5	21.5	4	256
Mean	6.8	10.0	11.8	13.9	16.3	17.8	21.0	21.8	

TABLE 12.

External ramus of abd. app. II of infected male.

Ramus length in mm. × 22.5	Carapace length in mm.							
	3.5–4.5	4.5–5.5	5.5–6.5	6.5–7.5	7.5–8.5	8.5–9.5	9.5–10.5	
20.5—22.5	2	—	—	—	—	—	—	
22.5—24.5	—	1	—	—	—	—	—	
24.5—26.5	2	2	—	—	—	—	—	
26.5—28.5	1	7	1	—	—	—	—	
28.5—30.5	0.5	8.5	2.5	—	—	—	—	
30.5—32.5	—	6.75	4.25	—	—	—	—	
32.5—34.5	—	2.25	7.25	1	—	—	—	
34.5—36.5	—	2	18.5	1.5	—	—	—	
36.5—38.5	—	1.5	11.5	2.5	—	—	—	
38.5—40.5	—	—	12	6.5	—	—	—	
40.5—42.5	—	—	3.25	6.25	—	—	—	
42.5—44.5	—	—	3.75	17	0.75	—	—	
44.5—46.5	—	—	2.5	19.25	4.75	—	—	
46.5—48.5	—	—	1.5	7.75	6.75	—	—	
48.5—50.5	—	—	0.5	5.25	9	0.25	—	
50.5—52.5	—	—	0.5	3.5	9.75	0.75	—	
52.5—54.5	—	—	—	2	2	1	—	
54.5—56.5	—	—	—	0.5	4.5	2	—	
56.5—58.5	—	—	—	0.25	3.25	4.5	—	
58.5—60.5	—	—	—	0.25	1.25	0.5	—	
60.5—62.5	—	—	—	—	—	—	—	
62.5—64.5	—	—	—	—	—	1	1	
64.5—66.5	—	—	—	—	—	—	—	
66.5—68.5	—	—	—	—	—	0.5	—	
68.5—70.5	—	—	—	—	—	0.5	—	
Total	5.5	31	69	73.5	42	11	1	233
Mean	24.8	30.1	37.4	44.7	50.6	57.8	63.5	

TABLE 13.

Internal ramus of abd. app. II of infected male.

Ramus length in mm. × 22.5	Carapace length in mm.								
	3.5–4.5	4.5–5.5	5.5–6.5	6.5–7.5	7.5–8.5	8.5–9.5	9.5–10.5	10.5–11.5	
6.5— 8.5	0.5	1	—	—	—	—	—	—	
8.5—10.5	3.5	2	—	—	—	—	—	—	
10.5—12.5	1	10.5	4.5	—	—	—	—	—	
12.5—14.5	0.5	14	11	—	—	—	—	—	
14.5—16.5	—	3.5	27.75	6.25	1.5	—	—	—	
16.5—18.5	—	—	16.25	19.75	1	—	—	—	
18.5—20.5	—	1	9	30	18.25	0.25	—	—	
20.5—22.5	—	—	0.5	13	12.25	4.25	—	—	
22.5—24.5	—	—	—	2.5	6.5	6	1	—	
24.5—26.5	—	—	—	2	3.5	3	—	—	
26.5—28.5	—	—	—	—	0.5	—	—	1	
28.5—30.5	—	—	—	—	1	0.5	1	0.5	
Total	5.5	32	69	73.5	44.5	14	2	1.5	242
Mean	10.4	12.8	16.0	19.3	21.2	23.5	26.5	28.2	

TABLE 14.

External ramus of abd. app. III of normal male.

Ramus length in mm. × 22.5	Carapace length in mm. 2.5–3.5	3.5–4.5	4.5–5.5	5.5–6.5	6.5–7.5	7.5–8.5	8.5–9.5	9.5–10.5	
16.5—18.5	1	—	—	—	—	—	—	—	
18.5—20.5	—	—	—	—	—	—	—	—	
20.5—22.5	0.5	3.5	—	—	—	—	—	—	
22.5—24.5	—	1.5	0.5	—	—	—	—	—	
24.5—26.5	—	3	3.5	1	—	—	—	—	
26.5—28.5	—	—	6.5	—	—	—	—	—	
28.5—30.5	—	—	5.25	1.75	—	—	—	—	
30.5—32.5	—	—	5.25	8.25	0.5	—	—	—	
32.5—34.5	—	—	—	14	4.5	—	—	—	
34.5—36.5	—	—	—	10.5	4	2	—	—	
36.5—38.5	—	—	—	13.5	10.5	0.5	—	—	
38.5—40.5	—	—	—	2.75	15	3.25	—	—	
40.5—42.5	—	—	—	2.25	20	7	0.75	—	
42.5—44.5	—	—	—	0.5	12.5	9.25	0.25	—	
44.5—46.5	—	—	—	—	4	12.75	1.75	—	
46.5—48.5	—	—	—	0.5	5	10.25	3.25	—	
48.5—50.5	—	—	—	0.5	3	8.5	0.5	—	
50.5—52.5	—	—	—	—	—	2	6	—	
52.5—54.5	—	—	—	—	—	0.5	1	1	
54.5—56.5	—	—	—	—	—	0.5	2	2	
56.5—58.5	—	—	—	—	—	1	2	1	
58.5—60.5	—	—	—	—	—	—	1	—	
60.5—62.5	—	—	—	—	—	—	1	—	
Total	1.5	8	21	55.5	79	57.5	19.5	4	246
Mean	18.8	23.4	28.6	35.3	41.0	45.5	51.8	53.5	

TABLE 15.

Internal ramus of abd. app. III of normal male.

Ramus length in mm. × 22.5	Carapace length in mm. 2.5–3.5	3.5–4.5	4.5–5.5	5.5–6.5	6.5–7.5	7.5–8.5	8.5–9.5	9.5–10.5	
4.5— 6.5	1	—	—	—	—	—	—	—	
6.5— 8.5	0.5	3	0.5	—	2	—	—	—	
8.5—10.5	—	5.5	12.25	8.75	1	—	—	—	
10.5—12.5	—	—	7.25	24.5	14.5	3.75	—	—	
12.5—14.5	—	—	—	21.25	31.75	15.25	2.25	—	
14.5—16.5	—	—	—	0.5	21.25	22.25	4.5	—	
165.—18.5	—	—	—	—	6	14.25	10.25	2	
18.5—20.5	—	—	—	—	1	0.5	3	0.5	
20.5—22.5	—	—	—	—	—	1.5	—	1.5	
Total	1.5	8.5	20	55	77.5	57.5	20	4	244
Mean	6.2	8.8	10.2	12.0	13.9	15.6	16.9	19.2	

TABLE 16.

External ramus of abd. app. III of infected male.

Ramus length in mm. ×22.5	Carapace length in mm.							
	3.5–4.5	4.5–5.5	5.5–6.5	6.5–7.5	7.5–8.5	8.5–9.5	9.5–10.5	
18.5–20.5	1	—	—	—	—	—	—	
20.5–22.5	1.25	0.25	—	—	—	—	—	
22.5–24.5	2.25	1.75	—	—	—	—	—	
24.5–26.5	2	5.5	0.5	—	—	—	—	
26.5–28.5	—	9	1.5	—	—	—	—	
28.5–30.5	—	7.5	7.5	1	—	—	—	
30.5–32.5	—	5	9.5	1	—	—	—	
32.5–34.5	—	1	14	2.5	—	—	—	
34.5–36.5	—	1.5	18.25	4.25	1	—	—	
36.5–38.5	—	—	7.5	9	—	—	—	
38.5–40.5	—	—	3.25	11.25	1	—	—	
40.5–42.5	—	—	1.5	15.5	4	—	—	
42.5–44.5	—	—	—	6.5	6.5	—	—	
44 5–46.5	—	—	3.5	14	7.5	—	—	
46.5–48.5	—	—	0.5	3.5	7.25	1.25	—	
48.5–50.5	—	—	—	1	9.5	2	—	
50.5–52.5	—	—	—	—	2.25	2.75	—	
52.5–54.5	—	—	—	0.5	0.5	2	—	
54.5–56.5	—	—	—	—	2.5	0.5	1	
56.5–58.5	—	—	—	—	1.5	0.5	0.5	
58.5–60.5	—	—	—	—	—	2.5	—	
60.5–62.5	—	—	—	—	—	1	—	
Total	6.5	31.5	67.5	70	43.5	12.5	1.5	233
Mean	23.1	28.6	34.8	41.2	47.1	53.9	56.2	

TABLE 17.

Internal ramus of abd. app. III of infected male.

Ramus length in mm. ×22.5	Carapace length in mm.								
	3.5–4.5	4.5–5.5	5.5–6.5	6.5–7.5	7.5–8.5	8.5–9.5	9.5–10.5	10.5–11.5	
6.5– 8.5	4.5	4	—	—	—	—	—	—	
8.5–10.5	2	17.5	10.5	1	1	—	—	—	
10.5–12.5	—	9	37	17.5	2	1	—	—	
12.5–14.5	—	1	15.75	34.25	7.5	0.5	—	—	
14.5–16.5	—	—	2.75	16.25	19.75	3.25	—	—	
16.5–18.5	—	—	0.5	5	13.75	6.25	0.5	0.5	
18.5–20.5	—	—	—	—	0.75	0.25	1	—	
20.5–22.5	—	—	—	—	0.25	1.25	—	1	
Total	6.5	31.5	66.5	74	45	12.5	1.5	1.5	239
Mean	8.1	9.9	11.9	13.7	15.4	16.8	18.2	20.1	

TABLE 18.

External ramus of abd. app. I of normal female.

		Carapace length in mm.						
		2.5–3.5	3.5–4.5	4.5–5.5	5.5–6.5	6.5–7.5	7.5–8.5	
Ramus length in mm. ×22.5	14.5–16.5	0.25	0.75	—	—	—	—	
	16.5–18.5	0.25	4.75	1.5	—	—	—	
	18.5–20.5	—	4.5	5.5	—	—	—	
	20.5–22.5	—	0.5	5.25	3.25	—	—	
	22.5–24.5	—	—	10.75	6.75	—	—	
	24.5–26.5	—	—	4.25	8.25	1	—	
	26.5–28.5	—	—	1.25	10.75	0.5	0.5	
	28.5–30.5	—	—	0.5	7	1.5	—	
	30.5–32.5	—	—	—	9.5	1.5	1	
	32.5–34.5	—	—	—	—	1	—	
	34.5–36.5	—	—	—	—	4	0.5	
	36.5–38.5	—	—	—	—	3	1	
	38.5–40.5	—	—	—	—	1	—	
	40.5–42.5	—	—	—	—	1.5	0.5	
	Total	0.5	10.5	29	45.5	15	3.5	104
	Mean	16.5	18.4	22.6	28.3	34.7	34.6	

TABLE 19.

Internal ramus of abd. app. I of normal female.

		Carapace length in mm.						
		2.5–3.5	3.5–4.5	4.5–5.5	5.5–6.5	6.5–7.5	7.5–8.5	
Carapace length in mm. × 22.5	10.5–12.5	0.25	0.75	0.5	—	—	—	
	12.5–14.5	0.25	1.75	—	—	—	—	
	14.5–16.5	—	2	1.5	—	—	—	
	16.5–18.5	—	3.75	3.75	1	—	—	
	18.5–20.5	—	2.75	8.25	2.5	—	—	
	20.5–22.5	—	—	4.5	7	—	—	
	22.5–24.5	—	—	8	16.5	—	—	
	24.5–26.5	—	—	1.5	7	2.5	—	
	26.5–28.5	—	—	0.5	7.5	1.5	1	
	28.5–30.5	—	—	0.5	4	0.5	—	
	30.5–32.5	—	—	—	—	2.5	0.5	
	32.5–34.5	—	—	—	—	4	0.5	
	34.5–36.5	—	—	—	—	2.5	0.5	
	36.5–38.5	—	—	—	—	—	—	
	38.5–40.5	—	—	—	—	0.5	0.5	
	Total	0.5	11	29	45.5	14	3	103
	Mean	12.5	16.6	20.9	24.3	31.5	32.5	

TABLE 20.

External ramus of abd. app. I of infected female.

Ramus length in mm. × 22.5	Carapace length in mm.						
	3.5–4.5	4.5–5.5	5.5–6.5	6.5–7.5	7.5–8.5	8.5–9.5	
10.5–12.5	1	1	—	—	—	—	
12.5–14.5	1.5	0.5	—	—	—	—	
14.5–16.5	1.5	0.5	—	—	—	—	
16.5–18.5	1	3.5	—	—	—	—	
18.5–20.5	—	6.5	1.5	—	—	—	
20.5–22.5	1	1.5	3	—	—	—	
22.5–24.5	—	3.5	3.5	—	—	—	
24.5–26.5	—	2.5	4.5	0.5	—	—	
26.5–28.5	—	1.5	8.25	3.25	0.5	—	
28.5–30.5	—	—	7.75	5.25	1	—	
30.5–32.5	—	—	3	7	0.5	—	
32.5–34.5	—	—	1.5	3	0.5	—	
34.5–36.5	—	—	0.5	2.5	1.5	1	
36.5–38.5	—	—	—	2	4.5	—	
38.5–40.5	—	—	—	—	1.5	—	
40.5–42.5	—	—	—	—	1.5	—	
42.5–44.5	—	—	—	—	0.5	—	
Total	6	21	33.5	23.5	12	1	97
Mean	15.6	20.7	27.1	31.6	36.8	35.5	

TABLE 21.

Internal ramus of abd. app. I of infected female.

Ramus length in mm. × 22.5	Carapace length in mm.						
	3.5–4.5	4.5–5.5	5.5–6.5	6.5–7.5	7.5–8.5	8.5–9.5	
4.5– 6.5	0.5	—	—	—	—	—	
6.5– 8.5	0.5	—	—	—	—	—	
8.5–10.5	2	0.5	—	—	—	—	
10.5–12.5	0.5	2	—	—	—	—	
12.5–14.5	2	5	4.5	—	—	—	
14.5–16.5	1.5	3	3.5	2	—	—	
16.5–18.5	0.5	5	6	1.5	—	—	
18.5–20.5	0.5	2	4	1	1	—	
20.5–22.5	—	1	7	4.5	—	—	
22.5–24.5	—	1	5	5.5	1.5	—	
24.5–26.5	—	—	2	0.5	2	0.5	
26.5–28.5	—	—	1.5	2	1	—	
28.5–30.5	—	—	—	4.5	0.5	—	
30.5–32.5	—	—	—	2	4	—	
32.5–34.5	—	—	—	—	1	—	
34.5–36.5	—	—	—	1	1	—	
Total	8	19.5	33.5	24.5	12	0.5	98
Mean	12.5	16.1	19.6	24.6	28.6	25.5	

Table 22.

External ramus of abd. app. II of normal female.

Ramus length in mm. × 22.5	Carapace length in mm.						
	2.5—3.5	3.5—4.5	4.5—5.5	5.5—6.5	6.5—7.5	7.5—8.5	
18.5—20.5	0.25	0.25	—	—	—	—	
20.5—22.5	0.75	0.75	—	—	—	—	
22.5—24.5	—	3.25	0.75	—	—	—	
24.5—26.5	—	2.75	2.75	—	—	—	
26.5—28.5	—	3	6	—	—	—	
28.5—30.5	—	1	3.5	1.5	—	—	
30.5—32.5	—	0.5	8	4.5	0.5	—	
32.5—34.5	—	—	5.5	10	1	—	
34.5—36.5	—	—	0.5	4	0.5	—	
36.5—38.5	—	—	1.5	14.5	0.5	—	
38.5—40.5	—	—	0.5	7	0.5	—	
40.5—42.5	—	—	—	1	1.5	1	
42.5—44.5	—	—	—	2	4.5	—	
44.5—46.5	—	—	—	—	1	—	
46.5—48.5	—	—	—	0.5	1.5	—	
48.5—50.5	—	—	—	—	0.5	0.5	
50.5—52.5	—	—	—	—	2.75	0.75	
52.5—54.5	—	—	—	—	0.25	0.25	
Total	1	11.5	29	45	15	2.5	104
Mean	21.0	25.7	30.5	36.3	44.0	47.3	

Table 23.

Internal ramus of abd. app. II of normal female.

Ramus length in mm. × 22.5	Carapace length in mm.						
	2.5—3.5	3.5—4.5	4.5—5.5	5.5—6.5	6.5—7.5	7.5—8.5	
8.5—10.5	0.5	0.5	—	—	—	—	
10.5—12.5	—	—	—	—	—	—	
12.5—14.5	0.5	1	0.5	—	—	—	
14.5—16.5	—	3.5	0.5	—	—	—	
16.5—18.5	—	—	2	—	—	—	
18.5—20.5	—	3.5	1	1	—	—	
20.5—22.5	—	2	2.75	1.75	—	—	
22.5—24.5	—	0.5	10.25	3.75	—	—	
24.5—26.5	—	0.5	7	10	0.5	—	
26.5—28.5	—	—	3.5	9.5	0.5	—	
28.5—30.5	—	—	1.5	8.25	1.25	—	
30.5—32.5	—	—	—	5.25	1.25	0.5	
32.5—34.5	—	—	—	2.75	3.75	1	
34.5—36.5	—	—	—	2.25	1.25	—	
36.5—38.5	—	—	—	—	1	0.5	
38.5—40.5	—	—	—	0.5	4	1	
40.5—42.5	—	—	—	—	—	—	
42.5—44.5	—	—	—	—	1	1	
44.5—46.5	—	—	—	—	—	—	
46.5—48.5	—	—	—	—	1.5	0.5	
Total	1	11.5	29	45	16	4.5	104
Mean	11.5	18.1	23.7	27.7	36.4	38.8	

TABLE 24.

External ramus of abd. app. II of infected female.

Ramus length in mm. × 22.5	Carapace length in mm. 3.5–4.5	4.5–5.5	5.5–6.5	6.5–7.5	7.5–8.5	8.5–9.5	
18.5–20.5	2	—	—	—	—	—	
20.5–22.5	0.5	0.5	—	—	—	—	
22.5–24.5	2	—	—	—	—	—	
24.5–26.5	0.5	3.5	—	—	—	—	
26.5–28.5	—	4	—	—	—	—	
28.5–30.5	1	4.5	0.5	—	—	—	
30.5–32.5	—	2	4	0.5	—	—	
32.5–34.5	—	3.5	7.5	—	—	—	
34.5–36.5	—	1	3.5	3	—	—	
36.5–38.5	—	—	6.25	4	0.25	—	
38.5–40.5	—	—	6	1.25	1.75	1	
40.5–42.5	—	—	1.75	8.25	—	—	
42.5–44.5	—	—	1.5	2.5	—	—	
44.5–46.5	—	—	—	4	0.5	—	
46.5–48.5	—	—	—	—	3	—	
48.5–50.5	—	—	—	—	2	—	
50.5–52.5	—	—	—	—	3	—	
Total	6	19	31	23.5	10.5	1	91
Mean	23.2	29.4	36.3	40.6	47.4	39.5	

TABLE 25.

Internal ramus of abd. app. II of infected female.

Ramus length in mm. × 22.5	Carapace length in mm. 3.5–4.5	4.5–5.5	5.5–6.5	6.5–7.5	7.5–8.5	8.5–9.5	
8.5–10.5	0.5	1.5	—	—	—	—	
10.5–12.5	1	—	1	—	—	—	
12.5–14.5	—	2	3	—	—	—	
14.5–16.5	2	4	1	—	—	—	
16.5–18.5	1	2	4	1	—	—	
18.5–20.5	0.5	5.25	3.25	1.5	1	—	
20.5–22.5	1	3.25	4.25	2	—	—	
22.5–24.5	—	2	4.25	5.25	2	—	
24.5–26.5	—	—	3.25	2.75	1	1	
26.5–28.5	—	—	4	2.5	1	—	
28.5–30.5	—	—	3	1	—	—	
30.5–32.5	—	—	2	0.5	—	—	
32.5–34.5	—	—	—	4	—	—	
34.5–36.5	—	—	—	3	0.5	—	
36.5–38.5	—	—	—	—	0.5	—	
38.5–40.5	—	—	—	—	2.5	—	
40.5–42.5	—	—	—	—	0.5	—	
42.5–44.5	—	—	—	—	2.5	—	
Total	6	20	33	26.5	11.5	1	98
Mean	16.0	17.9	22.3	27.0	33.4	25.5	

TABLE 26.

External ramus of abd. app. III of normal female.

		Carapace length in mm.						
		2.5—3.5	3.5—4.5	4.5—5.5	5.5—6.5	6.5—7.5	7.5—8.5	
Ramus length in mm × 22.5	22.5—24.5	1	3	2	—	—	—	
	24.5—26.5	—	2	—	—	—	—	
	26.5—28.5	—	3.75	3.25	—	—	—	
	28.5—30.5	—	1.25	8.5	0.25	—	—	
	30.5—32.5	—	0.5	4.25	2.75	—	—	
	32.5—34.5	—	—	6.25	8.25	—	—	
	34.5—36.5	—	—	2.25	6.75	0.5	—	
	36.5—38.5	—	—	1.5	12.5	0.5	—	
	38.5—40.5	—	—	1	8	—	—	
	40.5—42.5	—	—	—	4.5	2	—	
	42.5—44.5	—	—	—	2	4	—	
	44.5—46.5	—	—	—	0.25	1.25	—	
	46.5—48.5	—	—	—	0.25	2.25	1	
	48.5—50.5	—	—	—	0.5	0.5	0.5	
	50.5—52.5	—	—	—	—	2.5	0.5	
	52.5—54.5	—	—	—	—	0.75	0.75	
	54.5—56.5	—	—	—	—	0.25	0.25	
	Total	1	10.5	29	46	14.5	3	104
	Mean	23.5	26.4	31.2	37.3	45.8	51.2	

TABLE 27.

Internal ramus of abd. app. III of normal female.

		Carapace length in mm.						
		2.5—3.5	3.5—4.5	4.5—5.5	5.5—6.5	6.5—7.5	7.5—8.5	
Ramus length in mm. × 22.5	8.5—10.5	—	0.5	0.5	—	—	—	
	10.5—12.5	0.75	1.75	—	—	—	—	
	12.5—14.5	0.25	1.25	—	1	—	—	
	14.5—16.5	—	1.5	3	—	—	—	
	16.5—18.5	—	4	5.5	2	—	—	
	18.5—20.5	—	0.5	8	6.5	—	—	
	20.5—22.5	—	—	6	10.5	0.5	—	
	22.5—24.5	—	—	3.25	9.75	0.5	—	
	24.5—26.5	—	—	2.25	8.75	3	—	
	26.5—28.5	—	—	—	2.25	1.75	1.5	
	28.5—30.5	—	—	—	2.75	1.25	—	
	30.5—32.5	—	—	—	1	2.5	—	
	32.5—34.5	—	—	—	1	2	1	
	34.5—36.5	—	—	—	0.5	0.5	—	
	36.5—38.5	—	—	—	—	1.5	0.5	
	38.5—40.5	—	—	—	—	1.5	1	
	Total	1	9.5	28.5	46	15	4	104
	Mean	12.0	15.2	19.9	23.5	30.9	33.2	

TABLE 28.

External ramus of abd. app. III of infected female.

Ramus length in mm. × 22.5	Carapace length in mm.						
	3.5—4.5	4.5—5.5	5.5—6 5	6.5—7.5	7.5—8.5	8.5—9.5	
20.5—22.5	1	—	—	—	—	—	
22.5—24.5	0.5	0.5	—	—	—	—	
24.5—26.5	0.5	1	0.5	—	—	—	
26.5—28.5	1.5	3	—	—	—	—	
28.5—30.5	—	6	1	—	—	—	
30.5—32.5	1	4.5	1.5	—	—	—	
32.5—34.5	—	2	3.5	—	—	—	
34.5—36.5	—	3	3.5	0.5	—	—	
36.5—38.5	—	—	8.5	1.5	—	—	
38.5—40.5	—	—	7	5	—	—	
40.5—42.5	—	—	4	3.75	0.25	—	
42.5—44.5	—	—	2	3.75	0.25	—	
44.5—46.5	—	—	1	2.5	0.5	—	
46.5—48.5	—	—	—	5	1	—	
48.5—50.5	—	—	1	1.5	2	—	
50.5—52.5	—	—	—	—	4.5	—	
52.5—54.5	—	—	—	—	—	—	
54.5—56.5	—	—	—	—	1	—	
56.5—58.5	—	—	—	1	—	—	
58.5—60.5	—	—	—	—	2	1	
Total	4.5	20	33.5	24.5	11.5	1	95
Mean	26.4	30.6	38.0	43.8	50.7	59.5	

TABLE 29.

Internal ramus of abd. app. III of infected female.

Ramus length in mm. × 22.5	Carapace length in mm.						
	3.5—4.5	4.5—5.5	5.5—6.5	6.5—7.5	7.5—8.5	8.5—9.5	
8.5—10.5	1	1	—	—	—	—	
10.5—12.5	0.5	0.5	—	—	—	—	
12.5—14.5	0.5	4.5	2	—	—	—	
14.5—16.5	1.25	6.5	3.25	0.5	—	—	
16.5—18.5	1.25	3.5	7.25	1	—	—	
18.5—20.5	1	2	4.25	2.75	—	—	
20.5—22.5	—	2.5	8	6.5	2	—	
22.5—24.5	—	0.5	3.25	2.75	0.5	—	
24.5—26.5	—	—	3	2.5	—	—	
26.5—28.5	—	—	2.5	1.75	1.75	—	
28.5—30.5	—	—	—	5.75	1.25	1	
30.5—32.5	—	—	—	—	—	—	
32.5—34.5	—	—	—	—	2.5	—	
34.5—36.5	—	—	—	1	1.5	—	
36.5—38.5	—	—	—	—	2	—	
Total	5.5	21	33.5	24.5	11.5	1	97
Mean	15.1	16.3	20.3	24.5	30.6	29.5	

TABLE 30.

External ramus of abd. app. IV of normal female.

		Carapace length in mm.						
		2.5—3.5	3.5—4.5	4.5—5.5	5.5—6.5	6.5—7.5	7.5—8.5	
Ramus length in mm. × 22.5	18.5—20.5	—	0.5	—	—	—	—	
	20.5—22.5	1	2	—	—	—	—	
	22.5—24.5	—	1	0.5	—	—	—	
	24.5—26.5	—	3.5	3.5	—	—	—	
	26.5—28.5	—	2	5.75	1.25	—	—	
	28.5—30.5	—	—	6.75	5.75	—	—	
	30.5—32.5	—	—	7.75	2.75	—	—	
	32.5—34.5	—	—	2.75	8.75	—	—	
	34.5—36.5	—	—	1.25	8.75	1.5	—	
	36.5—38.5	—	—	0.75	7.5	1.25	—	
	38.5—40.5	—	—	—	4.25	0.25	—	
	40.5—42.5	—	—	—	2	4	—	
	42.5—44.5	—	—	—	2	3	1.5	
	44.5—46.5	—	—	—	0.5	2	—	
	46.5—48.5	—	—	—	—	0.5	0.5	
	48.5—50.5	—	—	—	—	0.5	0.5	
	50.5—52.5	—	—	—	—	0.25	0.25	
	52.5—54.5	—	—	—	—	0.25	0.75	
	54.5—56.5	—	—	—	—	—	0.5	
	Total	1	9	29	43.5	13.5	4	100
	Mean	21.5	24.5	29.9	35.3	42.4	48.4	

TABLE 31.

Internal ramus of abd. app. IV of normal female.

		Carapace length in mm.						
		2.5—3.5	3.5—4.5	4.5—5.5	5.5—6.5	6.5—7.5	7.5—8.5	
Ramus length in mm. × 22.5	4.5— 6.5	—	1	1	—	—	—	
	6.5— 8.5	1	4	3.5	—	—	—	
	8.5—10.5	—	2.5	14.75	12.5	0.25	—	
	10.5—12.5	—	—	8.75	24.5	6.75	0.5	
	12.5—14.5	—	1	1	5	3.5	2	
	14.5—16.5	—	—	—	1.75	2.75	1.5	
	16.5—18.5	—	—	—	0.25	0.25	—	
	Total	1	8.5	29	44	13.5	4	100
	Mean	7.5	8.6	9.9	11.4	12.9	14.0	

TABLE 32.

External ramus of abd. app. IV of infected female.

Ramus length in mm. × 22.5		Carapace length in mm.						
		3.5—4.5	4.5—5.5	5.5—6.5	6.5—7.5	7.5—8.5	8.5—9.5	
	22.5—24.5	2	1	—	—	—	—	
	24.5—26.5	0.5	1.5	—	—	—	—	
	26.5—28.5	1	3.5	0.5	—	—	—	
	28.5—30.5	1	3.5	1.5	—	—	—	
	30.5—32.5	—	4.5	1	—	—	—	
	32.5—34.5	—	4	6.5	0.5	—	—	
	34.5—36.5	—	—	6.75	3.25	—	—	
	36.5—38.5	—	1	8.25	2.75	—	—	
	38.5—40.5	—	—	4	2	—	—	
	40.5—42.5	—	—	1	7	0.5	—	
	42.5—44.5	—	—	1	3.5	1	—	
	44.5—46.5	—	—	—	3.5	2.5	—	
	46.5—48.5	—	—	—	0.25	2.25	—	
	48.5—50.5	—	—	—	0.25	2.25	—	
	50.5—52.5	—	—	—	1	—	—	
	52.5—54.5	—	—	—	—	1	0.5	
	54.5—56.5	—	—	—	—	0.5	0.5	
	56.5—58.5	—	—	—	—	0.5	—	
	58.5—60.5	—	—	—	—	1	—	
	Total	4.5	19	30	24	11.5	1	90
	Mean	25.9	29.9	36.1	41.3	49.2	54.5	

TABLE 33.

Internal ramus of abd. app. IV of infected female.

Ramus length in mm. × 22.5		Carapace length in mm.						
		3.5—4.5	4.5—5.5	5.5—6.5	6.5—7.5	7.5—8.5	8.5—9.5	
	6.5— 8.5	3.25	3.25	—	—	—	—	
	8.5—10.5	1.25	10.5	5.25	0.5	—	—	
	10.5—12.5	—	4.25	15.75	6	1	—	
	12.5—14.5	—	1	10	11.75	3.25	—	
	14.5—16.5	—	—	—	4.25	5.75	0.5	
	16.5—18.5	—	—	—	1.5	0.5	0.5	
	18.5—20.5	—	—	—	—	1	—	
	Total	4.5	19	31	24	11.5	1	91
	Mean	8.1	9.8	11.8	13.5	15.0	16.5	

This extra appendage, as well as the other appendage, of the infected male does not possess the club-like stout internal ramus typical of the appendage of the female nor the long and unbranched hairs which serve for the attachment of eggs in the normal female.

The appendage of the infected male is in no way different from the appendage of the normal male at first sight. A minute examination, however, reveals that the appendage of the infected male has a few simple unbranched setae on the protopodite which are absent from the protopodite of the appendage of the normal male (text-figs. 2 & 4).

The appendage of the infected female, on the other hand, shows a marked difference from the appendage of the normal female. The decrease in the length of the internal ramus is usually considerable. Moreover, the setae on that ramus are very different from the normal (text-figs. 3 & 5). While the normal female has many, long and stiff setae in the distal parts of the protopodite and endopodite of the appendage in the infected female these setae are very few and much shorter. Besides, the infected female has developed along the inner edge of its internal ramus a few plumose setae which occur in

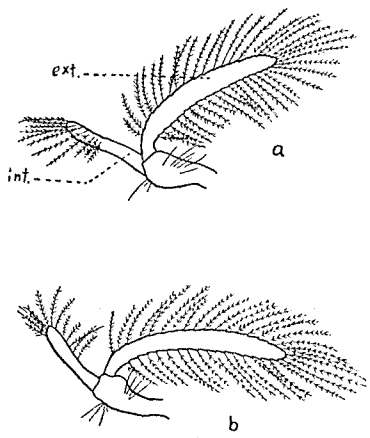


Fig. 4.
Abdominal appendages of infected male. a, first appendage; b, second appendage. Third appendage not figured, being identical with fig. 2, c. *int.*: internal ramus; *ext.*: external ramus.

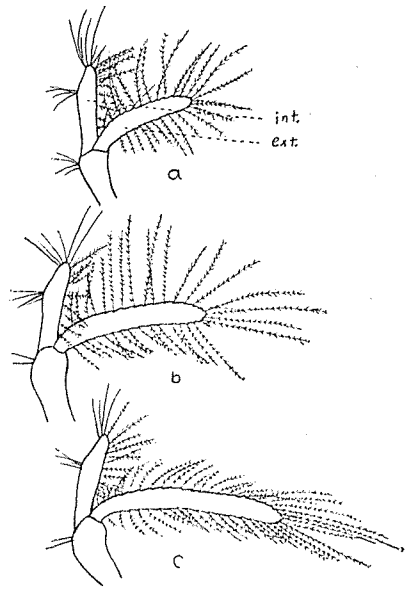


Fig. 5.
Abdominal appendages of infected female. a, first appendage; b, second appendage; c, third appendage; Fourth appendage not figured, being identical with fig. 2, c. *int.*: internal ramus; *ext.*: external ramus.

the corresponding part of the male, but are never found in the normal female. The internal ramus of the infected female is not elliptical in transverse section like that of the normal female, but is flat and sabre-like, like that of the male.

Thus in both male and female the appendages of the infected individuals are modified so as to approach the state of the other sex. The only differences which may be perceived as differentiating the sexes are the absence of the stiff simple setae from the internal ramus of the infected male, and that the length of the internal ramus relative to that of the external ramus is still greater in the infected female than in the infected male.

The structure of the appendage of the fifth abdominal segment is identical in both sexes, and not modified by the parasitism.

From the facts that have been stated above, it seems to be safe to conclude that the parasitic castration of *Eupagurus samuelis* brings about a change in both sexes causing one sex to approach the normal state of the opposite sex: the male is feminized, and the female masculinized.

Modification in Generative System

(A) Effect on the Gonopore of the Sexes.

Of 455 infected individuals 109 were entirely without any genital opening. 46 individuals of these were provided with three appendages and the rest with four appendages. It is obvious that the individuals

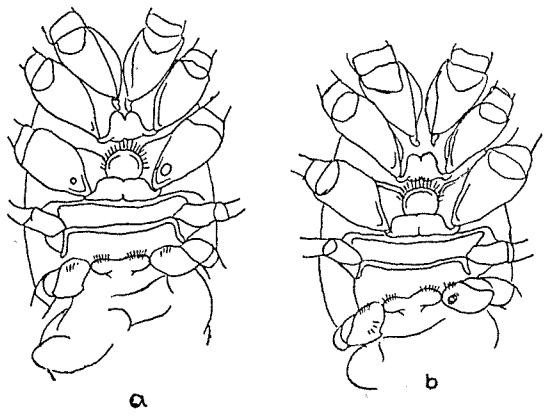


Fig. 6.
Two examples of the transitional stages to the complete closure of gonopores. a, Female with left gonopore normal, right gonopore rudimentary. b, Male with left gonopore rudimentary, right gonopore absent.

TABLE 34.

Number of indwiduals in the transitional stages to the complete degeneration of gonopores.

Size of gonopore	Left gonopore	Right gonopore	Male	Female
Left smaller than right	rudimentary	normal	5	1
	absent	normal	5	0
	absent	rudimentary	1	0
Left=Right	rudimentary	rudimentary	13	5
Left larger than right	normal	rudimentary	1	1
	normal	absent	1	2
	rudimentary	absent	4	1
		Total	30	10

with three appendages are males; but it can not be readily decided whether those with four appendages are males or females.

Some transitional stages between the normal individuals and those without gonopores are represented by certain individuals in which only one of the gonopores is closed, or one or both of them are in a rudimentary condition (text-fig. 6). In Table 34 are shown the number of such individuals.

PORTS (1906) remarked in connection with *E. meticulosus* that the disappearance of the gonopore occurs first on the left side, but this is not the case with *E. samuelis*.

(B) Effect on the Gonad.

By dissection of hermit-crabs, both infected and uninfected, I have found that the gonad of the host is modified in some way or other by the parasitism, without exception.

The testis and the vas deferens of the infected male are greatly reduced in comparison with those of the uninfected male. In many cases, on account of the greater or less reduction in length of the vas deferens, the testis is situated higher in the abdominal cavity than in normal individuals. The ovary and the oviduct are also reduced in thickness and length. The effect of the parasitism on the ovary is most clearly perceived during the breeding season when the infected female contains, in place of the large ovary stuffed with deeply pigmented eggs, only a small whitish and shrunken ovary.

PORTS (1906) has reported that in the male of *E. meticulosus* parasitized by *Peltogaster curvatus* ova appear in the testis while the

parasite is still present. In order to ascertain whether this is the case with *E. samuelis* or not, more than a hundred gonads of infected individuals of both sexes, as well as about the same number of gonads of normal individuals, were cut into serial sections and examined. All the gonads of the infected individuals, whether testes or ovaries, showed marked reduction of sexual cells, but in none of the testes was any trace of the formation of ova perceived.

Before commencing the description of the abnormal gonads it will be well to give a brief account of the structure of the normal gonad of *E. samuelis*.

The testis proper (text-fig. 7, A, *t*) is a narrow lobulated tubule, which is so thickly convoluted as to appear as a solid mass. The sexual elements arise from the epithelial lining of this tubule (text-fig. 8). In serial sections of a testis various stages of the development of sexual cells may be found spermatogonia, spermatocytes, spermatids and spermatosomes, as well as many intermediate stages of these.

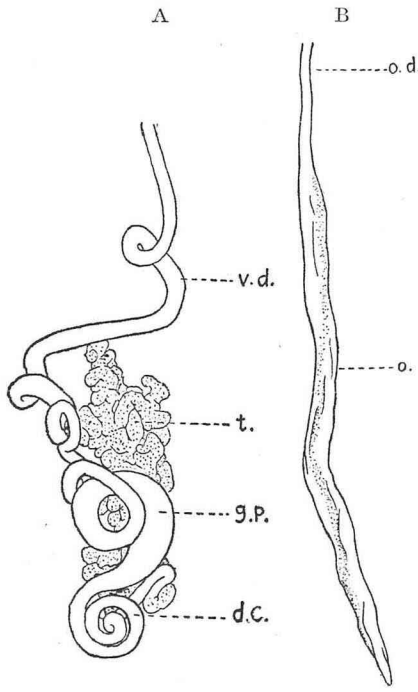


Fig. 7.

A, Male generative gland. B, Female generative gland. *d. c.*, dorsal coil of vas deferens; *g. p.*, glandular portion of vas deferens; *o.*, ovary; *o. d.*, oviduct; *t.*, testis proper; *v. d.* vas deferens.

The spermatogonia (text-figs. 8 & 9, *spg*) are larger than any other cells of more advanced stages; the nuclei stain somewhat more faintly than those of the spermatocytes, and the cytoplasm contains many small granules which have been considered by GROBBEN to be protein bodies. The spermatogonia always are found at the periphery of the testicular tubule. The spermatocytes (*spc*) are somewhat smaller than the spermatogonia, but with relatively large nuclei which are seen in various phases of maturation divisions. In the distal part of the testicular tubule the spermatocytes are replaced by smaller cells, the spermatids (*spt*). They have small and concentrated nuclei and very little cyto-

plasm. Various stages of development from the spermatid to the spermatosome are easily recognized. However, the minute structure of the spermatosome as well as the spermatogenesis and spermiogenesis has not been studied, as these are hardly necessary for the aim of the present work.

Another element which is contained in the testicular tubule is the nutritive cell —"Ersatzkeim" of GROBBEN— (*ntc*), which is known to arise also from the germinal epithelium. The nutritive cells are scattered about among sexual cells, adjoining cells fusing together to form a nutritive syncytium; the nuclei stain comparatively uniformly and deeply, and have an irregular contour.

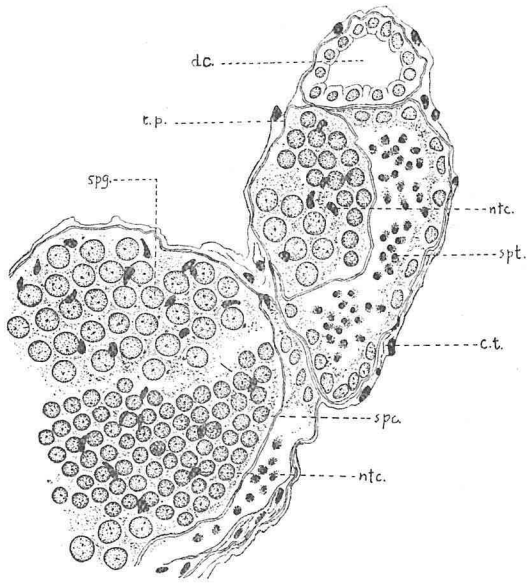


Fig. 8.

Section of testis of normal male. *c. t.*, connective tissue sheath; *d. c.*, dorsal coil of vas deferens; *ntc.*, nuclei of nutritive cells; *spc.*, resting spermatocyte; *spg.*, spermatogonium; *spt.*, spermatid transforming into spermatosome; *t. p.*, tunica propria.

The vas deferens is a much convoluted tube. The portion which is connected with the testis is coiled very tightly and is called the dorsal coil of vas deferens. This portion is lined with cubic epithelial cells (text-figs. 7, 8 & 9, *d. c.*), and in its lumen the initial step of the formation of the spermatophore is probably carried on. Next comes the glandular portion (text-figs. 7 & 9, *g. p.*, text-fig. 10, a), a smooth thick-walled portion which consists of tall glandular epithelial cells (text-fig. 10, a, *g. c.*). These cells secrete a chitinous substance which forms the spermatophores (*spph*). This portion describes a large coil and the inner cavity is mushroom-shaped in the transverse section. The secretory activity is apparently most vigorous in the cells found in the portion which forms the cap of the mushroom. Next comes the vas deferens proper (text-figs. 7 & 10, b), a thin-walled tube lined with low epithelial cells (*e. c.*) and circumscribed with circular and longitudinal muscles (*c. m.*, *c. l.*). The portion of the duct close to the external opening is provided with strong musculature and may be called ductus ejaculatorius.

The testis is enclosed by a thin membrane, the tunica propria (*t. p.*) derived from connective tissue which also envelopes the testis and its duct.

The ovaries in the breeding season occupy a large part of the abdominal cavity, both the right and left ovaries extending throughout the length of the cavity. They are a pair of sausage-shaped bags of a deep black colour, with the surface presenting a granulated appearance owing to the developing ova. In other seasons they shrink to very thin and inconspicuous tubes (text-fig. 7, B) difficult to make out, which continue to the oviducts (*o. d.*) without any demarcation. The oviducts show no convolution whatever.

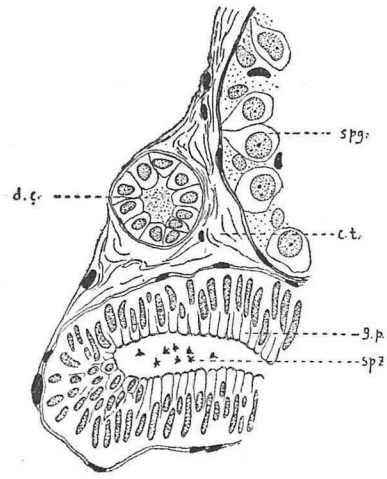


Fig. 9.

Section of normal testis and duct. *c. t.*, connective tissue sheath; *d. c.* dorsal coil of vas deferens; *g. p.*, glandular portion of vas deferens; *spg.*, spermatogonium; *spz.*, spermatosome.

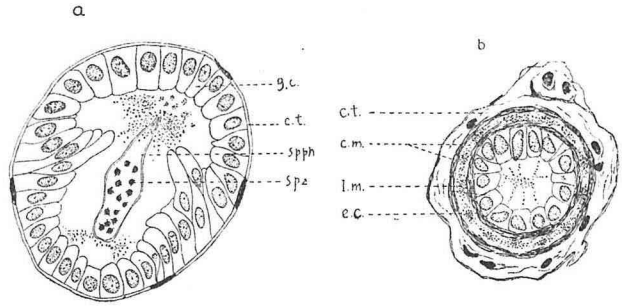


Fig. 10.

Cross section of vas deferens; a, glandular portion; b, vas deferens near ductus ejaculatorius.
c. m. circular muscle layers; *c. t.*, connective tissue sheath; *e. c.* epithelial cell layer; *g.c.*, glandular cell of epithelial layer; *l. m.*, longitudinal muscle layer; *spph.*, spermatophore; *spz.*, spermatosome.

The internal structure of the ovary shows little difference from that found in other decapods. At one point of the periphery of the ovarian tube there is a proliferating zone of egg-cells —"Keimbahn" (text-fig. 11, *Km*) which extends throughout the entire length of the ovary. From this narrow band of epithelial cells young egg-cells which resemble the spermatogonia in appearance are budded off. The larger eggs occupy the more central position of the cavity. They are crowded

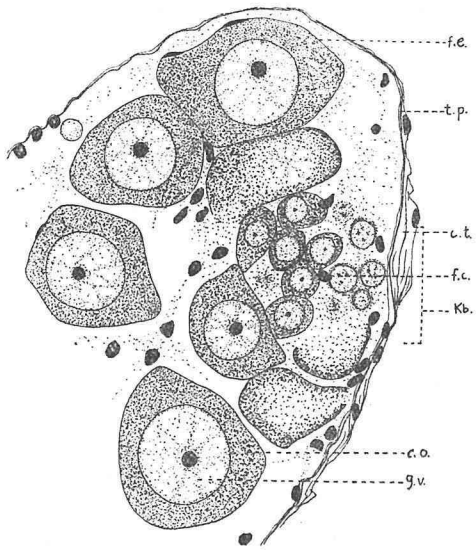


Fig. 11.

Section of younger normal ovary.
c. o., cytoplasm of ovum; *c. t.*, connective tissue sheath; *f. c.* nucleus of follicle cell; *f. e.*, follicle epithelium of ovum; *g. v.*, germinal vesicle of ovum; *Kb.*, "Keimbahn"; *t. p.*, tunica propria.

so close together that they come to assume a polygonal shape through mutual pressure. Such eggs enclose each a large germinal vesicle (*g. v.*), the ground substance of which stains faintly with dyes. A conspicuous nucleolus is found in the middle of the network of chromatin substance.

The element corresponding to the nutritive cell of the testis is the follicle cell (*f. c.*) which supplies yolk substance to the ovum. It is amoeboid in form and the cytoplasm of adjoining cells fuses with it into a kind of syncytium; older ova are surrounded by a thin membrane derived from follicle cells (*f. c.*).

The ovary is enclosed by the tunica propria (*t. p.*), and a thin layer of connective tissue (c. t.). The oviduct is also enclosed by the connectiue tissue which is traversed by muscle fibres.

The effect of the parasite on the male and female gonads of the host is briefly as follows:

The gonad of either sex undergoes degeneration to a greater or smaller extent through the influence of the parasitism.

The size of the testis of the infected male is commonly much smaller than that of the normal male which has the same carapace length. In the testis where the effect of the parasitism is relatively profound, the vas deferens is greatly reduced in thickness and length; the coil of the glandular portion is diminished more or less. In some cases, owing to the great reduction of the testis, it is difficult to distinguish externally the testis proper from the vas deferens, which is found in the form of a simple thin straight duct. Finally, there are some individuals where even the vas deferens has disappeared entirely so that no trace of reproductive organs remains.

The ovary of the infected female is also reduced greatly. It is much thinner and shorter than the normal. The posterior end is found

somewhere near the middle of the abdominal cavity or slightly anteaiorly, while in the normal female it reaches the posterior end of the abdominal cavity. In the more profoundly affected female, the ovary is found in the shape of a small vessel very hard to make out. Finally in the extreme cases, the ovaries may be entirely absent.

In most of the cases where the gonopores are closed, the testes and ovaries with their ducts are altogether absent, though in rare cases they may be found in a highly degenerated condition. In those cases where one of the gonopores is closed, the gonad is much reduced or entirely absent on the side where the gonopore is closed, while on the other side where the gonopore is in the normal condition, the gonad is less affected. Parallelism between the degree of degeneration of the gonad and that of the gonopore can be found clearly.

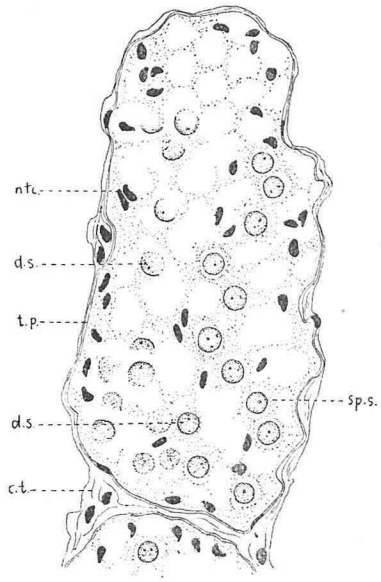


Fig. 12.
Section of testis of infected male, showing the degeneration of sperm cells. Abbreviations as fig. 8. *d. s.* degenerating sperm cell; *sp. s.* survived sperm cell.

From the examination of the serial sections of the infected gonads it has become clear that:

In the male on which the effect is slight the testis is not very different from the normal testis in the cellular constitution, except for the reduced size of the testicular tubule. In such a testis on account of the small size of the testicular tubule, the sexual cells contained are very few, though the cavity is stuffed with those cells as in the normal tubule. In such a tubule, the sperm cells may continue to develop into mature spermatosomes, and in some cases even the spermatophores were actually found to be in course of formation.

In the testis where the effect is more profound, the testicular tubule is much thinner and shorter, and its convolution is looser than in the normal testis. The internal cavity (text-fig. 12) contains incomparably fewer sperm cells than the normal, evidently on account of the degeneration of the sexual cells. There occur many sperm cells which are evidently in course of degeneration. The cells which have

survived the effect of the parasitism lie scattered about in the cavity enclosed in the syncytial mass of nutritive cells which are apparently quite immune to the effect. There are also some testes where the tubules are almost destitute of sexual cells and surrounded by an abnormally thick coat of connective tissue (text-fig. 13).

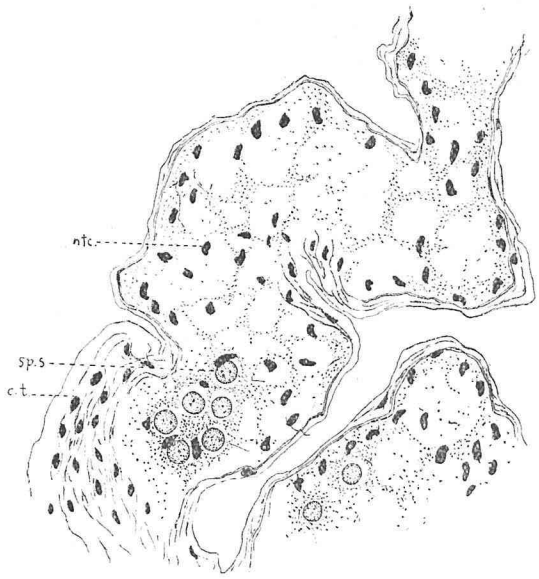


Fig. 13.
More advanced stage of degeneration of infected testis. Abbreviations as before.

In the case where the testis proper is externally indistinguishable from the vas deferens, the section shows that the posterior extremity is occupied by an apparently young germinal layer whence sexual cells are being budded off into the lumen of the tube. In such a gonad the vas deferens is very thin and short and its convolution is inconspicuous, and the cross section of the glandular portion shows that the inner cavity has an elliptical shape instead of the mushroom-shape of the normal duct. The caliber of the vas deferens is much smaller than normal and the number of the epithelial cells which line the duct has decreased.

The ovary of the infected female is also greatly reduced, and the degeneration of sexual cells is very apparent. Even in a slightly affected ovary (text-fig. 14) ova provided with much yolk substance are very few; most of them being much smaller than those in the normal female collected in the same season. Not only the quantity of plasm, but also the size of the germinal vesicle, is smaller. Even

the ova with a larger germinal vesicle are manifestly in course of degeneration. It seems that when the ovum develops to a certain limited extent the degenerating process always sets in. This is probably due to the insufficiency of the nutritive material provided for further development of the ova; thus no egg could attain maturity. In fact, I have never seen a female bearing *Peltogaster* spawn in the breeding season.

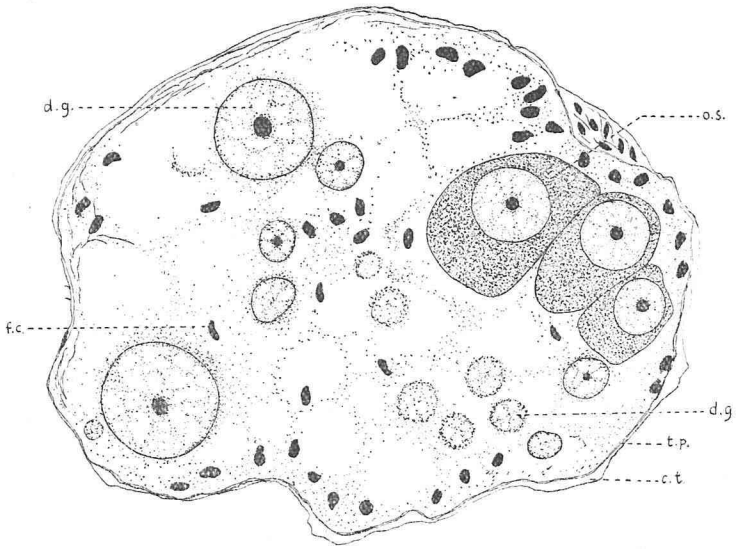


Fig. 14.

Cross section of ovary of infected female, showing the degeneration of ova. *d. g.* decomposing germinal vesicle of degenerating ovum. *o. s* survived ovum. Other abbreviations as before.

In more serious cases of affection (text-fig. 15), the ovary contains no larger ovum, and there occur only younger and smaller cells, much like spermatogonia in appearance, in the proliferating band of the wall of the ovarian tube. The greater part of the ovarian cavity is occupied by the follicle syncytium enclosing hollow cavities which have been formed by the degeneration of ova. A more profoundly affected ovary has developed a thick coat of connective tissue around it, and retains only a few small younger ova in the lumen.

Thus the effect of the parasitism on the gonad of the host is different in the testis and the ovary. In all the ovaries of infected females ova cannot develop into mature and fertile eggs. They all degenerate in the course of development, evidently on account of the lack of nourishment. In the testis, on the other hand, some of the sperm cells may develop into spermatosomes though there are some

cases where the testis has completely degenerated. A complete transitional series can be traced from the only slightly affected state to the entirely degenerate state.

To sum up the effect of the parasitism on the gonad, it appears that in the degeneration of the gonads two apparently different processes take part in both sexes: One of them consists in the retardation of the development of the gonad, or to put it more appropriately, the checking of the multiplication of sexual cells to a greater or less degree. This is shown by the facts that the size of the gonad of the affected individual is usually smaller than normal, and that the sexual cells are much fewer in number even in the gonad where the degeneration of sexual cells is seemingly only slight, and that the gonoduct is short and thin. The other effect of the parasitism on the gonad consists in the degeneration of sexual cells, which may result in the complete reduction of the gonad.

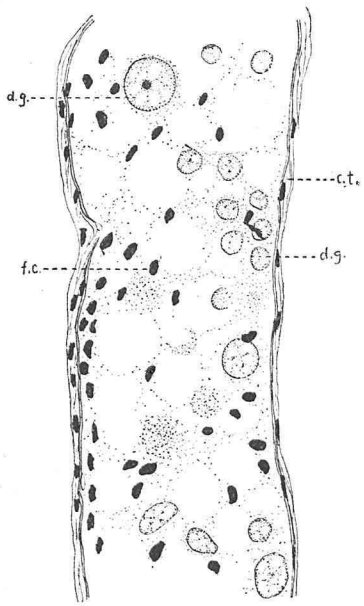


Fig. 15.
More advanced stage of degeneration of infected ovary. (longitudinal section) Abbreviations as before.

These twofold effects which seemingly differ from each other may be due to a common cause—that the parasite draws nourishment from the host which is necessary for the normal development of sexual cells.

The number of the affected gonads which I have examined is very considerable, nevertheless I have never met with any ovum or ovumlike cell in the testis of the infected male nor any sperm cell in the ovary of infected female. No case like that described by POTTS (1906) in *E. meticulosus*, in which egg-cells appear in the testis of the infected male, while bearing *Peltogaster*, occurs in *E. samuelis* so far as my observation goes.

Summary

The effects of *Peltogaster sp.* on its host *Eupagurus samuelis* may be summarized as follows:—

1) The ratio of the length of the internal ramus of an abdominal

appendage to that of the external ramus of the same appendage is greater in the normal female than in the normal male except in the case of the appendage of the fifth segment, where the ratio is equal in both sexes. The effect of the parasite on the abdominal appendage is to bring about an increase in this ratio in the male, and a decrease in the female.

2) The increase of the ratio in the first appendage of the male is due to the retardation of the development of the external ramus, while in the second appendage it is due to the acceleration of the development of the internal ramus. In the female this is principally due to the retardation of the development of the internal ramus in all the appendages except the fourth.

3) The appendage of the fifth segment of both sexes is absolutely unmodified.

4) The parasite also brings about a change in the structure of the abdominal appendage: masculinization of the female and feminization of the male.

5) Another effect of the parasite on the external character is to cause the development of an extra appendage on the second abdominal segment of the male in some cases.

6) In many cases of infected individuals of both sexes the gonopores are closed.

7) The effect of the parasite on the gonad of the host is always to bring about the greater or less reduction of the gonad in both sexes or even complete degeneration of it.

8) The effect of the parasite on the gonad of the host is different in the testis and the ovary. In the testis the degeneration may be complete, but may also be incomplete and spermatosomes are formed. None of the ovaries, however, can produce mature ova.

9) In the degeneration of the gonad two processes take part: the retardation of the development of the gonad, and the degeneration of the sexual cells.

10) In no case had an individual a hermaphroditic gland, while the parasite was still present.

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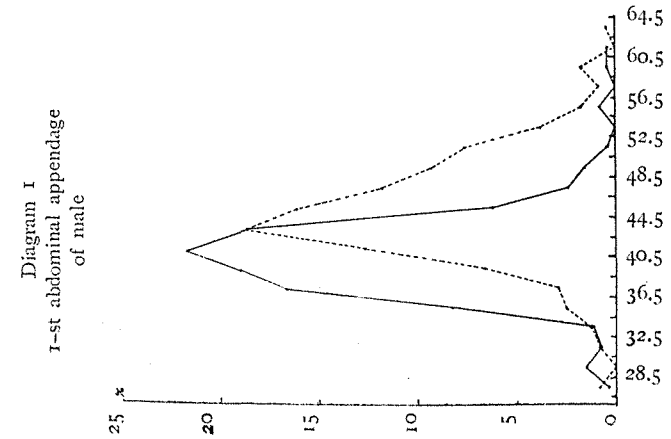
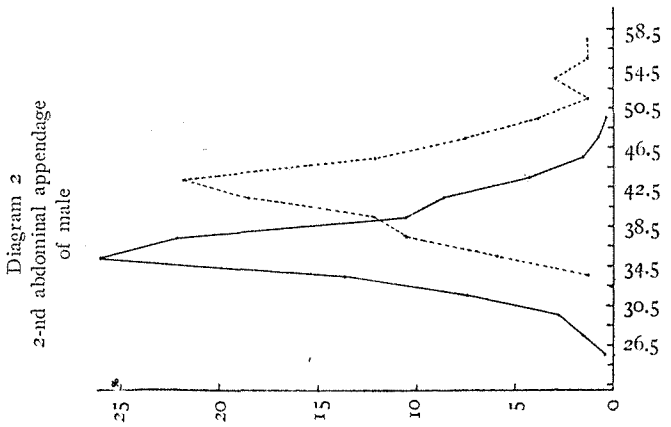
Explanation of Diagrams.

Diagrams 1—7: A series of frequency curves composed from tables 1—4. In the horizontal line are taken the classes of the ratio of two rami. (See text) The height of knot of curve exhibits the number of individuals represented by the percentage of the total number which is used for making each table. The complete line refers to the normal individual, broken line refers to the infected individual.

Diagrams 8—14: A series of diagrams composed from tables 6—33. The diagrams are constructed by drawing the line through the average condition of ramus length (vertical axis) associated with carapace length (horizontal axis). The complete line refers to the normal individual and broken line refers to the infected individual. *ext.*—external ramus; *int.*—internal ramus.





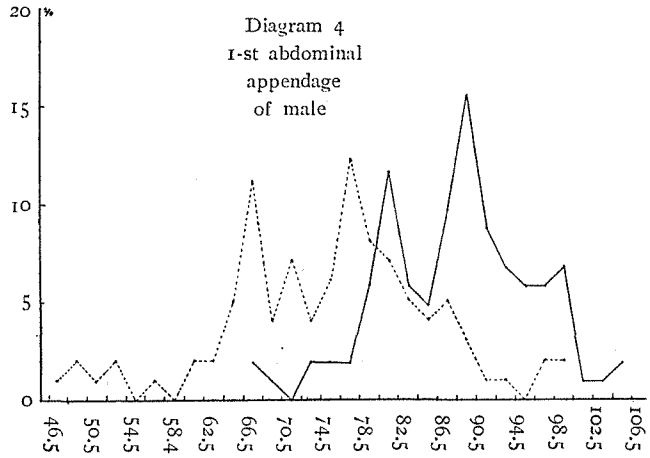


Diagram 4
1-st abdominal
appendage
of male

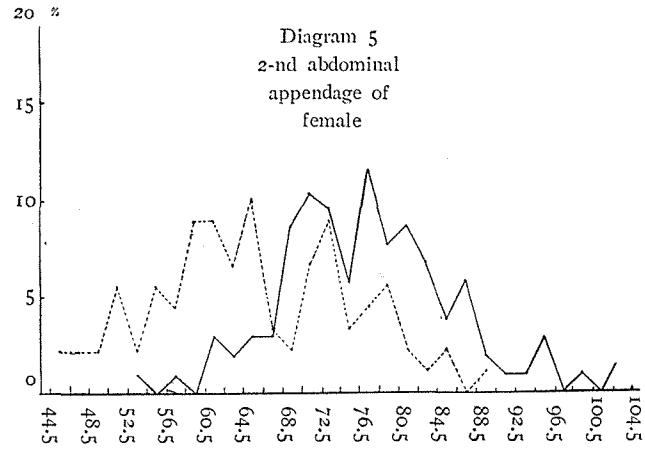


Diagram 5
2-nd abdominal
appendage of
female

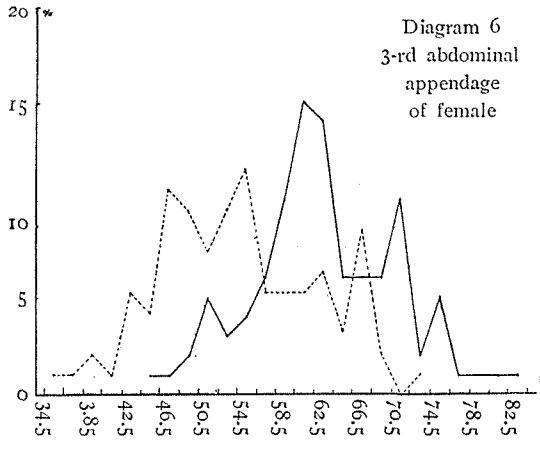


Diagram 6
3-rd abdominal
appendage
of female

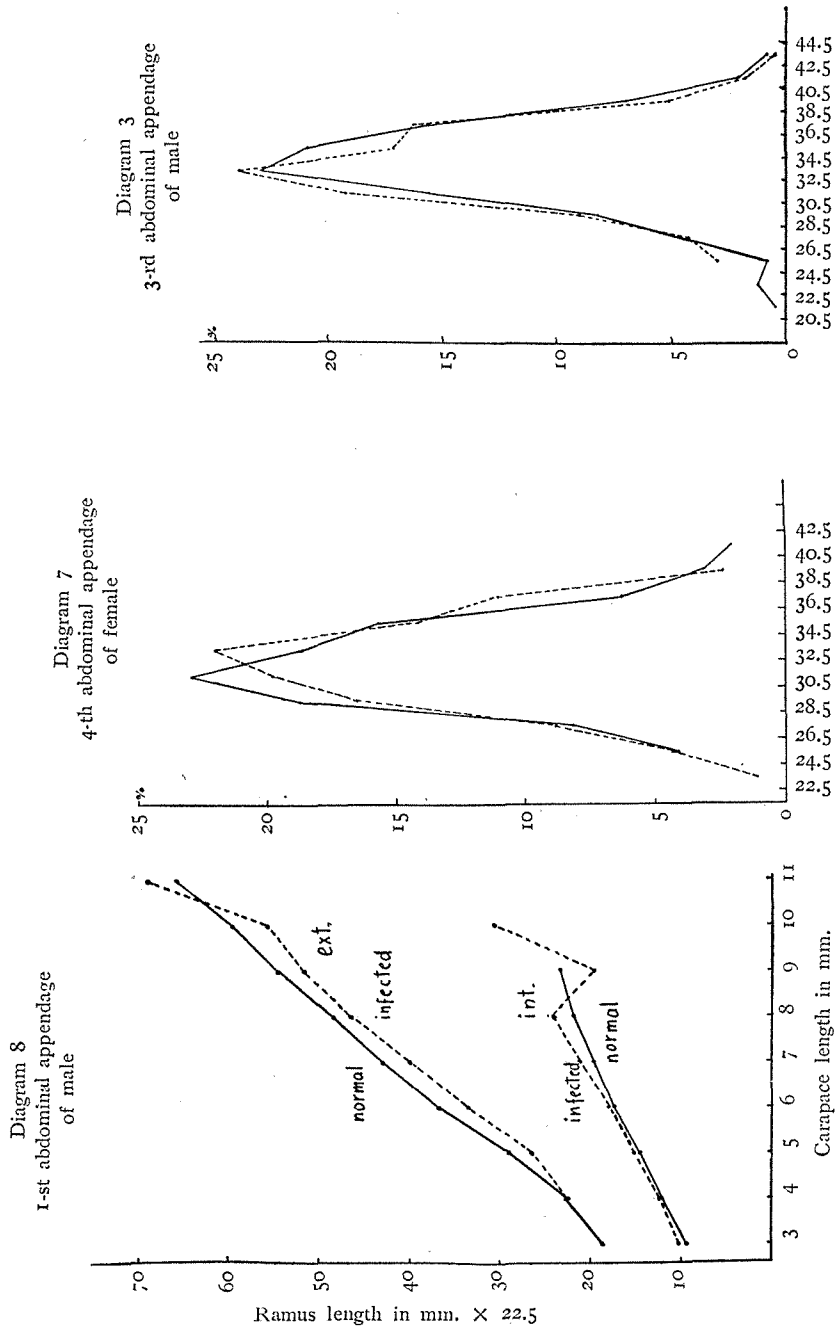


Diagram 3
3-rd abdominal appendage
of male
%
25
20
15
10
5
0
44.5
42.5
40.5
38.5
36.5
34.5
32.5
30.5
28.5
26.5
24.5
22.5
20.5
Diagram 7
4-th abdominal appendage
of female
%
25
20
15
10
5
0
42.5
40.5
38.5
36.5
34.5
32.5
30.5
28.5
26.5
24.5
22.5
Diagram 8
1-st abdominal appendage
of male
ext.
infected
normal
int.
infected
normal
70
60
50
40
30
20
10
Ramus length in mm. × 22.5
3
4
5
6
7
8
9
10
11
Carapace length in mm.

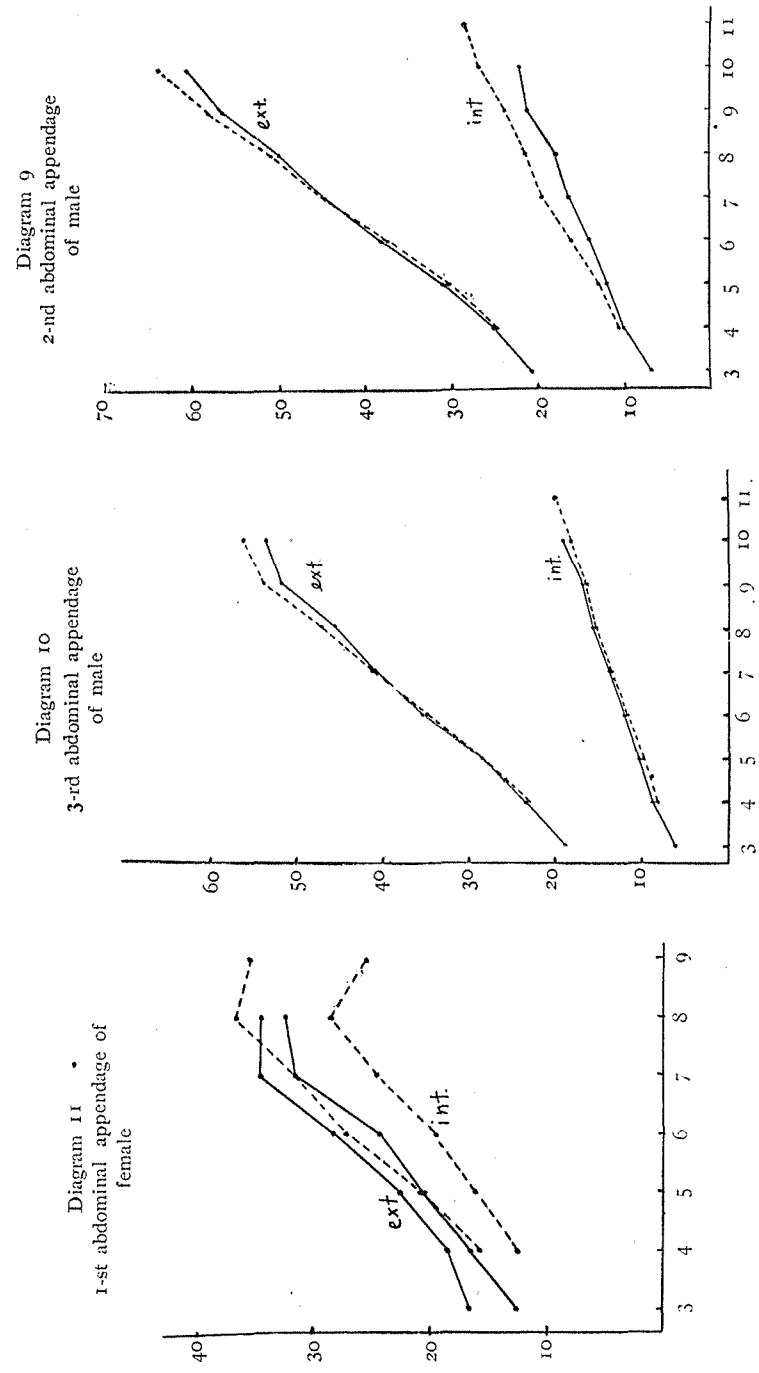


Diagram 9
2-nd abdominal appendage of male
ext.
int.
Diagram 10
3-rd abdominal appendage of male
ext.
int.
Diagram 11
1-st abdominal appendage of female
ext.
int.

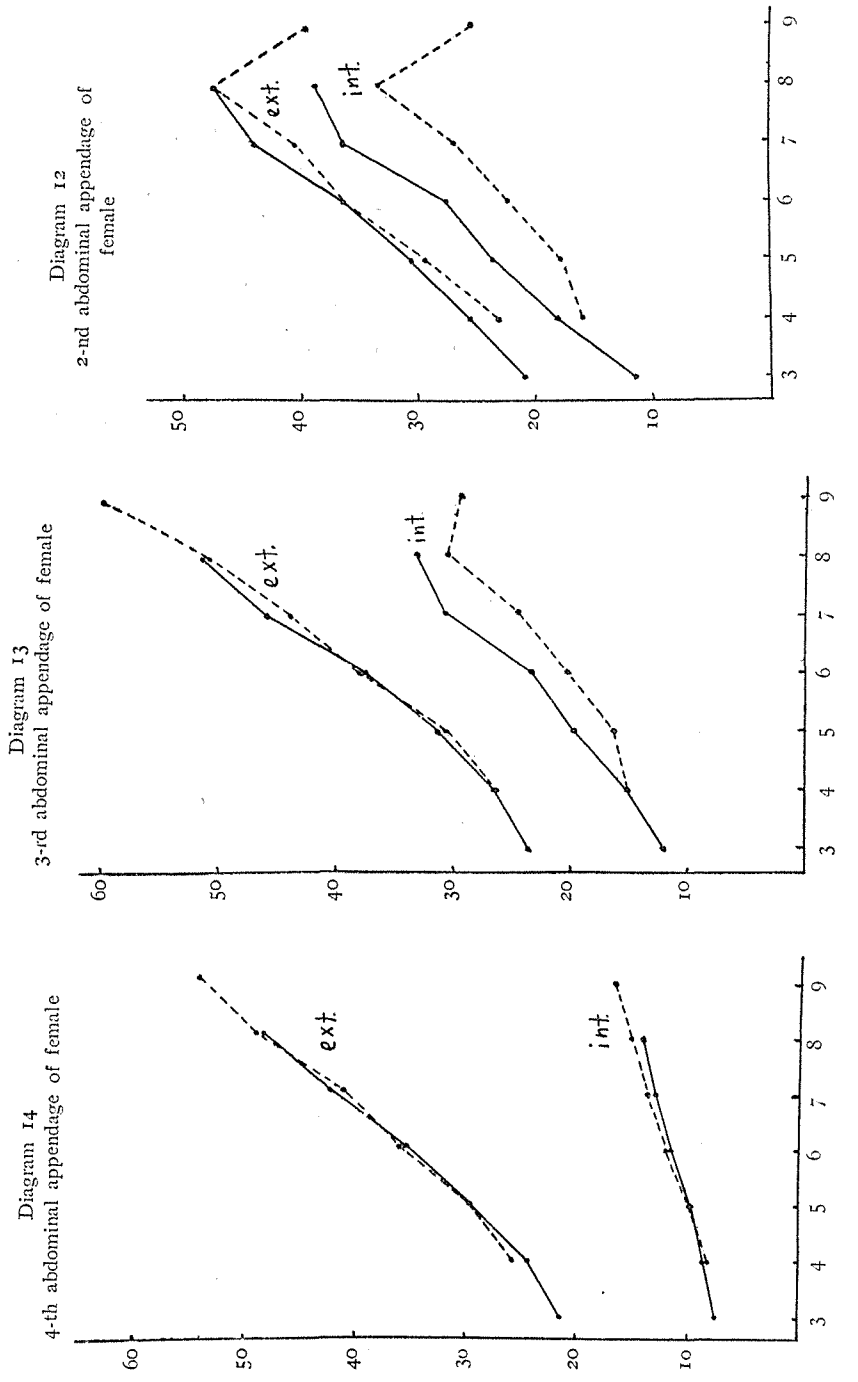


Diagram 12
2-nd abdominal appendage of female
ext.
int.
Diagram 13
3-rd abdominal appendage of female
ext.
int.
Diagram 14
4-th abdominal appendage of female
ext.
int.