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Sacculinization in *Eriocheir japonicus* de HAAN,
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Sex-reversal in Parasitized Male Crabs.

By

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With Plates VIII & IX and 18 Text-figures

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Introduction

Eriocheir japonicus de HAAN is a Grapsoid crab widely distributed in Japanese territories. The crab seems to be an extraordinarily euryhaline animal, being found most abundantly in estuaries but often coming up the river a long distance, sometimes making its way even into mountain brooks; it is also recorded at the sea-bottom. These facts show its unusual resistance to milieu-changes.

While the junior author was living in Tango Province by the River Yura (on the Japan Sea slope), his attention was directed to a peculiar Rhizocephala infesting the crabs captured in the river. The parasite was always found in gregarious condition upon the ventral side of the host's abdomen (fig. 1). During the autumn of 1932, having collected a large number of crabs carrying the parasite, he visited the senior author at his laboratory to work together on these interesting specimens.

The Rhizocephala in question was small in size, discoidal in shape and without mantle opening. Moreover, its gregarious occurrence at first led us to believe it to be a form allied to the genus *Thompsonia*. The supposition, however, soon revealed itself deceptive, for early in the next year we obtained crabs carrying grown-up parasites having a fully formed mantle opening. Examining the external and internal structures of these specimens we soon became aware that the Rhizocephala is no other than a species of *Sacculina*, which is distinguishable from other known forms by its constantly

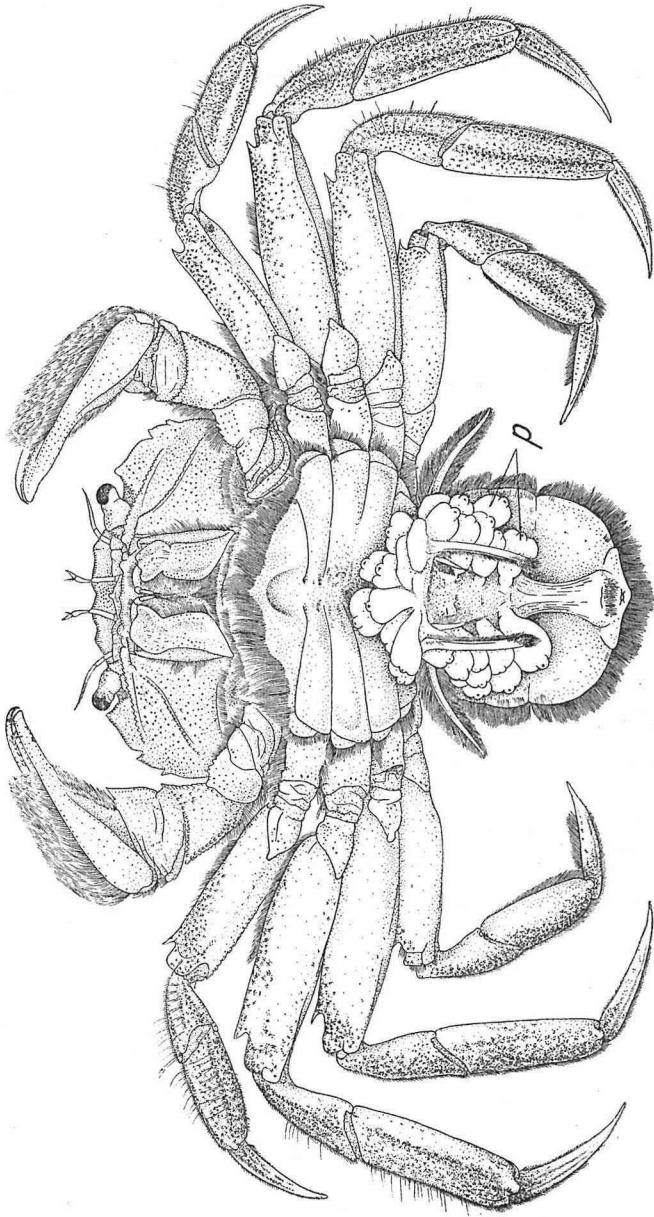


Fig. 1. *Eriochelone japonicus* de HAAN (δ) carrying a cluster of *Saccuinae externae* (p), seen from the ventral side, the abdomen being turned over. The specimen is represented in about natural size. Note the broadened abdomen and well-developed exopodite of the pleopod II.

gregarious occurrence. Beside these specimens of external stages we could also obtain younger crabs containing the parasite of internal stages. All male crabs infected by the *Sacculina*, either externa or interna, exhibited unmistakable signs of feminization and in some extremely strong cases of so-called parasitic castration one could hardly discriminate them from normal females.

In the following pages we shall first describe the parasite and then its effects upon the host animal. The observations on the phenomena of sacculinization in the large Grapsoid crab will in many ways supplement the classical study of G. SMITH (1910-'13) in *Inachus mauretanicus*.

Part I, the Parasite

Sacculina gregaria sp. nov.

The grown-up parasite has usually a flat oval shape, sometimes more or less elongated in the longitudinal axis (fig. 2). The large individuals measure 13-17 mm in breadth, 10-15 mm in height, and 5-6 mm in thickness. Those which have not spawned are much

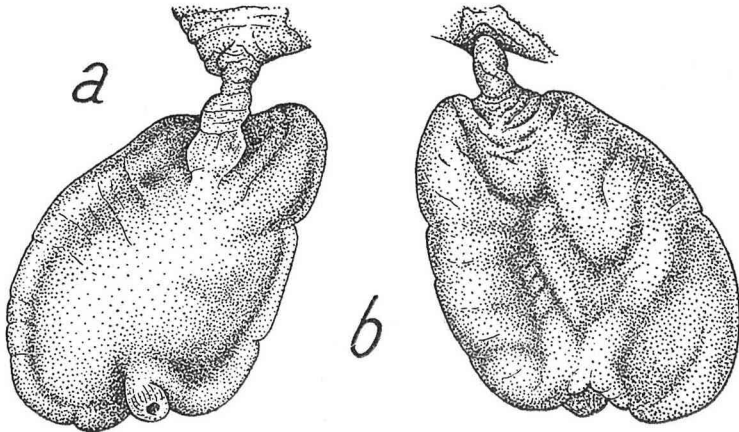


Fig. 2. An example of *Sacculina gregaria* n. sp.; (a) through surface, (b) the same specimen in abdominal surface. $\times 4$

flattened, the thickness being only 2-3 mm. The mantle opening is situated exactly at the median anterior end of the body. The mantle is smooth and devoid of any sort of excrescences on the external surface, but much wrinkled on the internal cuticula. The retinacula, (fig. 3) which can be detected only in grown-up specimens, consist of separated spindles having a length of 14-20 μ with a diameter of ca. 6 μ . Each spindle is smooth, bearing no trace of barbs.

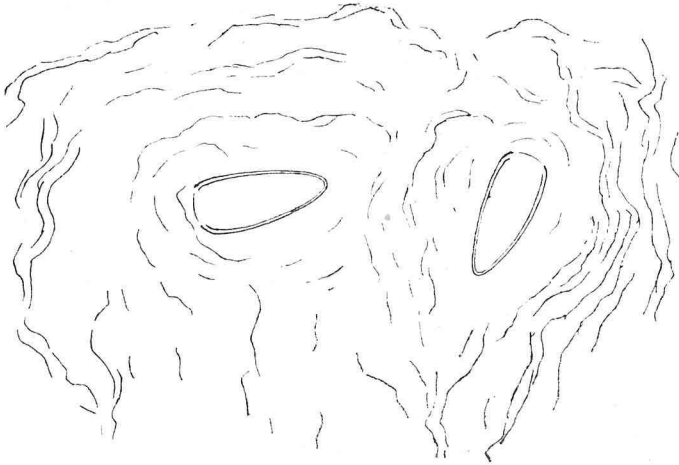


Fig. 3. Retinaculae. $\times 1000$.

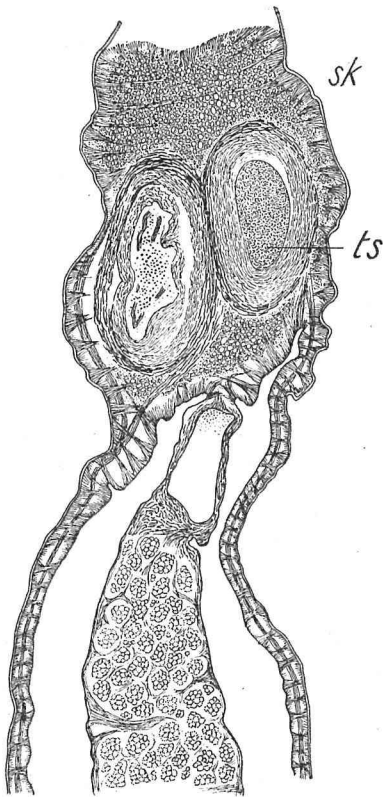


Fig. 4 a. Posterior part of a longitudinal section of *Sacculina gregaria* n. sp. through the stalk (*sk*); *ts*, testis.

The internal structures (fig. 4) show no peculiar features. The testes (fig. 4 a, *ts*) are situated outside the visceral mass in the distal part of the stalk. They are oval in shape, about uniform in size (ca. 1 mm in length), and distinctly separated one from the other. From very young stages of externa the testes can be detected as small white bodies which can be easily pressed out by a slight pressure upon the upper part of the body. The colleteric glands (fig. 4 b, *cg*) are situated at the usual place, nearer to the mantle opening than to the stalk. When the mantle is removed the gland can be perceived as a white spot of about 3 mm in diameter on the surface of the visceral mass.

The most characteristic point to the present species is as mentioned already the gregariousness of its occurrence. Altogether 20–40 individuals can be counted in a single crab,

being distributed upon the abdomen from the first to the fifth segment. As noted by E. DELAGE (1884) in *Sacculina carcini* that the external part comes out always by penetrating the cuticle of intersegmental portions, so also in this species peduncles of the parasite are always situated on softer intersegmental areas. But the external parts are rarely found hanging to the hard part of segments. In some exceptional cases they are also found beneath the carapace. These stray individuals come to the exterior breaking through the hypodermis of the visceral mass instead of penetrating the abdominal cuticle of the host as usual. In one specimen an externa was on the middle part of the inner ramus of a pleopod. The manner of distribution of individual parasite (external part) in 5 specimens is shown in Table I.

The external part of *Sacculina* found on the same host show almost the same state of development except some special cases in which, as will be described later, the parasites vary in their development, some remaining within while others are external and have already attained a remarkable size. In these cases only a few individuals seem to be capable of normal growth at the cost of the rest. It is interesting to note that in spite of their

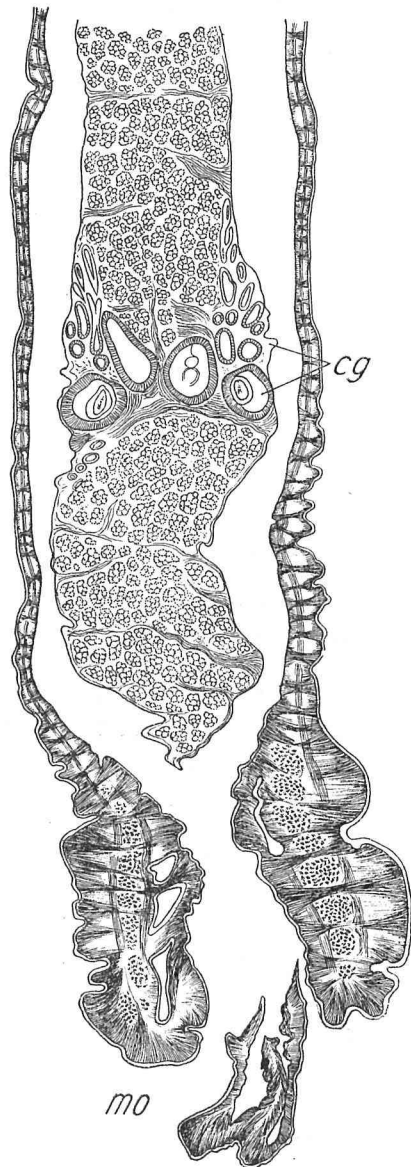


Fig. 4 b. Anterior part of another longitudinal section of the same specimen from the median region to the mantle opening (*mo*); *cg*, colleteric gland. \times ca. 30

Table I

Abd. segment \ Specimen	no. 1	no. 2	no. 3	no. 4	no. 5
I	13	5	8	5	8
II	6	7	8	5	6
III	9	8	9	4	9
IV	8	4	6	2	7
V	4	3	4	—	4
VI	1	—	—	1	—
total	41	27	35	17	34

gregariousness the orientation of the external parts of the parasite relative to the host is always constant, the mesentery of *Sacculina* invariably running on the right side of the crab just as in solitary forms.

Among Rhizocephala the genus *Thompsonia* is known to be constantly gregarious. Beside this the parasites of hermit-crabs, such as *Peltogaster socialis* and *Peltogastrella socialis* afford instances of gregarious occurrence (F. A. POTTS, 1915). In the Sacculinidae, however, no species has yet been described to be constantly gregarious, though it is by no means rare to find a plural number of parasites upon one and the same host. Consequently we see in the present species the first example of *Sacculina* which is truly gregarious. This condition is probably brought about by way of polyembryonic process at a certain period of its development but the problem still remains to be elucidated.

Remarks on the life-history of *Sacculina gregaria*

The life-history of the present species of *Sacculina* is not yet sufficiently studied. Our knowledge about the habit of the host crab in this case is also far from being satisfactory. Some fragmental data which we could obtain so far will at least provide a few necessary clues to work out the problem in future.

The youngest specimens of *Eriocheir* obtained in the River Yura are of the size from 10 to 20 mm in carapace measurement. They were captured under submerged stones during summer months. Of them about 10 per cent are found infected with *Sacculina* of internal stages, the presence of which can be easily detected by inspecting the ventral side of the crab. The abdomen of infected specimens bears a white tumor at its basal part, as a consequence of which

it does not meet exactly to the thorax, a narrow slit-like space being formed between them. Moreover, there is often a slight distortion to one side of the abdomen, and the tips of pleopods are often seen through the slit (fig. 5).

In larger crabs measuring from 30 to 40 mm in carapace length, the parasite is still internal. In these specimens the presence of the internal parasite is readily revealed to the observer by the general swelling up of the basal part of the abdomen.

In normal crabs the passage of the intestine and the posterior extension of the liver in the abdomen can well be recognized through the transparent cuticle. In parasitized specimens these structures become obscured by the development of milky white tissue beneath the cuticle. The tissue consists chiefly of the rampant root-system of *Sacculina interna*. An appearance of the young externae is initiated by the formation of translucent round spots just beneath the cuticle. Complete emergence of the young externae is often observed in crabs of about 40-50 mm carapace length.

As DELAGE confirms, the parasite becomes external by the simple disintegration of the cuticle just above its own body and does not wait for the intervention of a moult as SMITH supposes. Prior to the extrusion of the parasite a thick brown ring is formed around the spot through which each individual part comes out to the exterior. This ring persists as a boundary line between the host's cuticle and that of the parasite representing the "anneau chitineux" of DELAGE. Many crabs carrying the parasite in such transitional stages were found during September and October about 30 km from the mouth of Yura River. The youngest externa measures ca. 2 mm in diameter.

The young externae of 5 mm in breadth still lack the mantle opening, which is perforated at the stage of ca. 8 mm. However, large *Sacculinae* provided with the mantle opening are exceedingly rare among those specimens of crab collected in the autumn, while they are first met with in those specimens obtained in January of

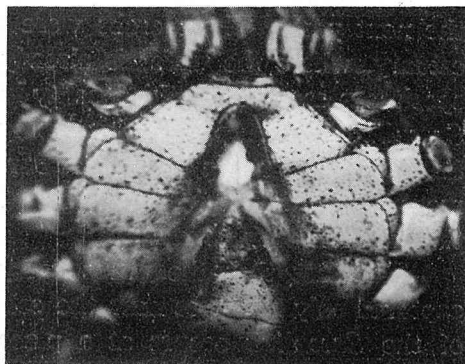


Fig. 5. Crab containing internal parasite, seen from the ventral side; about 3 times in magnification. Notice the deformed abdomen not tightly fitted to the thoracic plastron.

the next year. These crabs were captured about 10 km from the estuary, where the water is already rather brackish. Among these specimens captured at this locality in April, some are found carrying *Sacculinae* filled up with developing embryos. In this condition the *Sacculina* becomes purple in colour owing to the formation of pigment in the developing embryos. The Nauplius is very similar to that of *Sacculina carcini*.

The fact that the crabs carrying grown-up *Sacculinae* were captured only at places near the estuary suggests that the breeding of the *Sacculina* occurs at a place not far from the river-mouth. It would take place at least in brackish water though not in the sea. As to this breeding habit of the parasite, it is important to note that the breeding of the host crab is said to take place also on the bottom of the sea in spring time. Although we have yet no direct observation on this point, it is sure that the crab does not breed in places very far up the river-mouth. Sexually mature crabs are therefore supposed to migrate down the river before the approach of the breeding season. In the River Yura there are evidences that the migration really takes place in the last half of autumn. In October and November a large number of crabs are captured by setting up a simple trap in the shallows of the river. The trap consists of a bamboo basket fastened at the bottom of coarse wire net. Crabs that come into contact with the net during their course down the river are led into the basket. Especially at a time when the river swells after a heavy rainfall an unusually large amount of crabs can thus be captured. Such migration of *Eriocheir*, according to Mr. T. URITA, a carcinologist, can be observed also in rivers of Kagoshima Prefecture. Beside this the following circumstance may further be taken as evidence of the migration of the crab. With the approach of winter it becomes gradually more difficult to obtain crabs in localities distantly upward from the estuary, though lower down the river they are still obtainable in large numbers. Thus before the approach of breeding the majority of mature crabs seem to be assembled in the region of the estuary where the water is more saline. Hence it is inferred that the reproduction as well as the new infection of the parasite takes place in this locality where the reproduction of the host also occurs.

The active upward migration of the latter begins at a very young stage of development. As noted above, small crabs measuring from 10 to 20 mm carapace length are commonly found in summer

under stones at places more than 20 km distant from the river-mouth. They are presumably 3-4 months old and still in the process of active migration up the river. The *Sacculina interna* found in these young crabs has already occupied the final place of its development, i. e. the basal part of the host's abdomen. If we assume that the new infection took place in May, the age of the parasite is estimated to be about 3 months old. By the next spring the crab has grown to a size of 30-40 mm carapace length, and 40-50 mm in autumn when the *Sacculinae* become external. Thus it is surmised that it takes about one and half years for the parasite to become external. The *Sacculina externa* formed in autumn is considered to attain maturity in the next spring so that it takes about 2 years for the parasite to grow to sexual maturity. These estimations are on the whole in accord with the data furnished by the classical study of DELAGE on the life-history of *Sacculina carcini*. The fate of *Sacculina* as well as of its host after reproduction is unknown. Probably the parasite would die out as in the case of *Sacculina carcini*.

Remarks on freshwater species of Rhizocephala

Rhizocephala are known almost exclusively as marine organisms. We know only two exceptional cases in which they were found upon freshwater crabs. In 1911 N. ANNANDALE described a *Sacculina*-like parasite on a specimen of *Sesarma thelxinoe* obtained in the mountain district of Andaman and named it *Sesarmaxenos monticola*. His description based on a single preserved specimen was naturally quite incomplete but he could confirm the fact that the embryos develop directly into Cypris larvae. Quite recently J. B. FEUERBORN (1932) obtained several specimens of similar parasite infesting *Sesarma nodulifera* from the mountainland of Java. The parasite described by this author is perhaps identical with *S. monticola* of ANNANDALE but owing to the imperfect description of the latter it is treated as a new species and called *S. gedehensis*. Structures of the adult as well as of the Cypris larva were studied in detail and it was concluded that *Sesarmaxenos* is a Rhizocephalan form especially well adapted to freshwater life. The direct development of embryos into Cypris and the folding-up of the mesentery are features pointed out as specially adapted for freshwater environment.

The present species of *Sacculina* is not strictly a freshwater animal and consequently is not so profoundly modified as in *Sesarmaxenos*. Except for its gregarious occurrence it conforms quite

well in structure with purely marine allies. The curious point is that the greater part of its developmental cycle is passed through while the host crab sojourns in freshwater environment. But the adaptation to freshwater is in this case facultative because there is every reason to believe that the parasite as well as the host is capable of reproduction only in brackish or even in saline water. The harmony between the host and the parasite appears to be particularly remarkable here because of the unusual environmental changes to which the host is subjected. Anyhow the present species of *Sacculina* affords an interesting example of so-called "marine animals in freshwater" (K. SEMPER, 1880).¹⁾

Part II, Effects upon the host

Since the discovery of the phenomena of so-called parasitic castration the effects of parasite on the sexual organization of its host in different groups of Arthropods have been studied by many investigators. Especially the effects of *Sacculina* upon its Brachyuran host are the best known to us by a series of classical works of G. SMITH (1911-1913) on *Inachus mauretanicus* LUCAS.

On the other hand, by the recent advances in the field of experimental analysis of sex-problems much clear insight is now gained also into this curious phenomena, of which the following facts may be considered to be well established: 1) Anomalies in the sexual organization caused by the parasite (sacculinization, stylopization etc.) can be included in the phenomena of intersexuality. It has nothing to do with castration as one would assume from the unhappy term "parasitic castration". Intersexes are produced here not by an abnormal hereditary constitution of genes but by the sudden physiological changes aroused by the invasion of parasite. As to what the nature of this change is we are still wrapped in mystery. 2) So far as the Crustaceans are concerned it is only male intersexes that are produced by the effects of parasite. No comparable changes are brought about in the female sex.

The results of our observation on sacculinized individuals of *Eriocheir japonicus* verify these facts. But the chief interest in the present instance lies in the fact that all possible stages of male intersexes can be secured with comparative easiness. Moreover, the unusually large size of the crab much facilitates the examination

1) SEMPER, K., 1880: Die natürlichen Existenzbedingungen der Tiere. Leipzig.

and at the same time serves to diminish the probable errors which may lead to false conclusion.

Between August, 1932, and April of the next year more than 300 infected crabs out of many thousands of specimens caught by fishermen were examined. Generally speaking, infected crabs, both male and female, can be readily distinguished from healthy ones by simply examining the external appearance of the abdomen. The exoskeleton of the abdomen appears thickened and is very often accompanied with numerous brown spots which give the surface a coarse appearance. Besides, the abdomen is not so tightly fitted to the thorax as in normal specimens and the distal part of pleopods are often thrust out from the slit to the exterior (see fig. 5). If the abdomen of such crabs is turned over, a cluster of *Sacculinae externae*, or else a swelling of the intestinal wall betraying the presence of still internal parasite beneath the cuticle is invariably recognized. In some cases it is almost impossible to discriminate infected crabs from normal ones merely from their external appearance. But usually a slight degree of shrinkage or wrinkles can be perceived in the abdomen and in some extreme cases it is highly teratologic as in the examples described later. On the whole, infected crabs are rather smaller in size than normal ones; in fact, teratological abdomens are limited to smaller crabs. But among infected males it is by no means rare to find large specimens of more than 70 mm carapace length. Thus, the general effects of the parasite on the host are extremely variable.

The secondary sexual characters of the host crab

Differences in the secondary sexual characters of *Eriocheir japonicus* are as follows. In normal males the chelae are very stout, and each is adorned with a tuft of luxuriant hairs. The size of the chelae enormously increases with the growth of the body: in crabs of more than 70 mm carapace length, the chela length (to be more precise, the total length of propodite of the cheliped) often exceeds the carapace length. The abdomen (fig. 6) is narrowed up from the base towards the tip showing concave outline at both lateral sides. The 5th segment, which is the broadest in the opposite sex, is here the narrowest except for the last one. The appendages consist of two pairs. The first are stout rod-like copulatory styles, the tip of which reaches the 6th abdominal segment. The basipodite of each copulatory style elongate inwards forming a strong

calcified bridge (*br*) which is arched over the basal portion of the intestinal tract. The male genital opening is situated on the 5th thoracic segment, just opposite the base of the copulatory style. At this aperture is situated a flexible papilla (*gp*), at the pointed tip of which opens the ejaculatory duct.

The female crabs are on average smaller than males, rarely exceeding 70 mm in carapace measurement. Chalae are always below 70 per cent of the carapace length. The abdomen (fig. 7) is broad and trough-like and bears 4 pairs of well-developed biramous appendages (pleopods II-V).

The important question as to the development of the sexual characters is not well worked out in the present species. So far as the observations on very young crabs kindly sent by Mr. T. SAKAI of the M. B. Laboratory (Tokyo Literature and Science College) at Simoda, Izu Province, are concerned, in those specimens of less

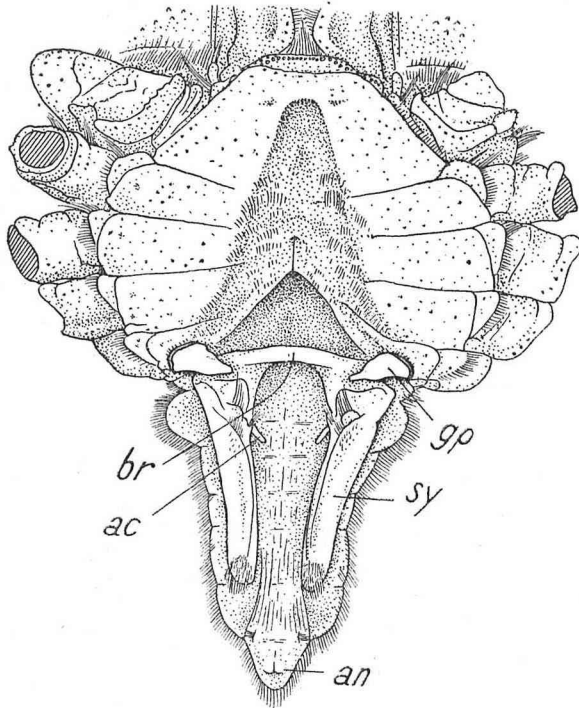


Fig. 6. Male thorax and abdomen seen from the ventral side, the latter being turned over; *ac* accessory copulatory organ; *an*, anus; *br*, calcified bridge; *gp*, genital papilla; *sy*, copulatory style.

than 10 mm carapace length the difference in abdominal shape according to sex is not yet marked as in larger specimens. In the male as well as in the female the abdomen is narrowly triangular, the lateral sides of which are almost straight or only slightly concave in the male sex. Unfortunately we lack male specimens below 6 mm. The female appendages (fig. 8) begin to appear at the carapace length of 5 mm. There are 4 pairs from the beginning, with slight developmental differences from proximal side to the distal end. The genital apertures become visible from the stage onward when the carapace measures more than 6 mm. They are situated on the 3rd thoracic segment. In this length of carapace the 1st pair of male abdominal appendages (fig. 9) are distinctly elongated, the tips already reaching the middle of the 4th abdominal segment. The 2nd pair of appendages are also formed; they are simple instead of

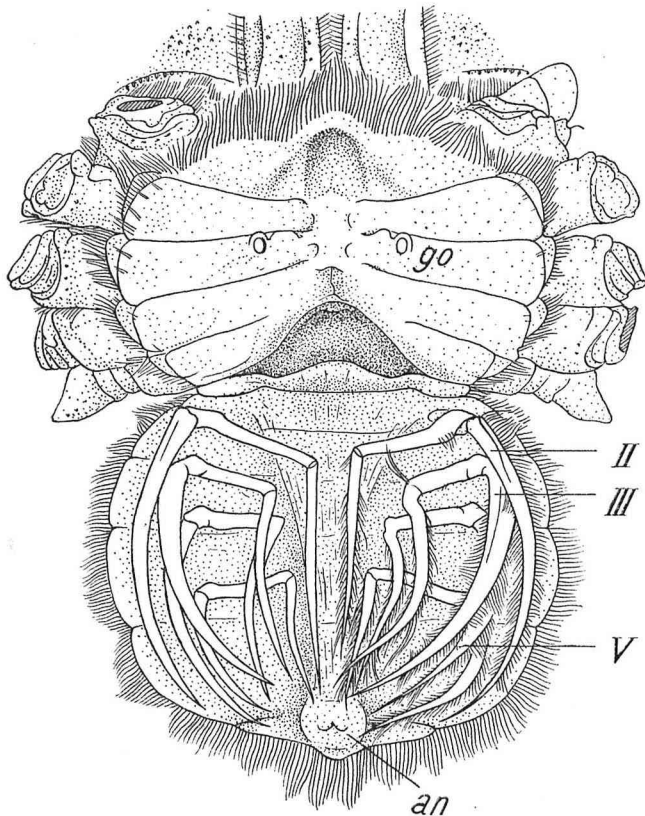


Fig. 7. Female thorax and abdomen in the same representation as in the preceding figure; *go*, genital opening; II-V, ovigerous appendages.

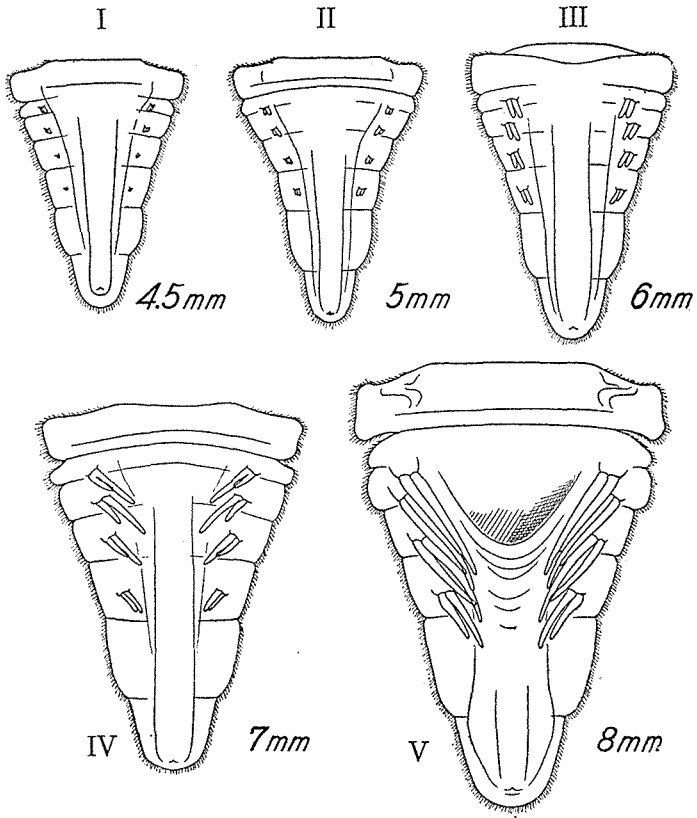


Fig. 8. Female abdomens in developmental series (\times ca. 10). Stages measured by the carapace length are indicated for each abdomen.

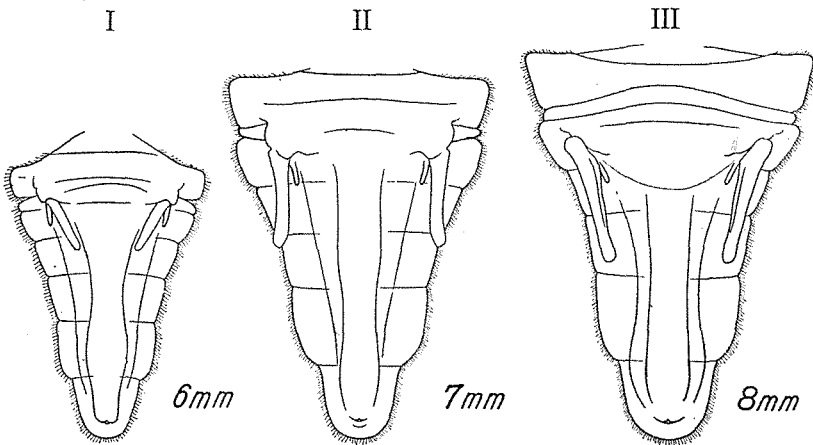


Fig. 9. Male abdomens in developmental series (\times ca. 10). Stages measured by the carapace length are noted for each abdomen.

biramous as in the other sex. The 3rd, 4th and 5th segments are entirely without appendages. In the subsequent stages the 1st pair of appendages gradually elongates to the male copulatory organs with the growth of the animal and becomes already typical in structure when the young crabs attain about 8 mm carapace length. They differ from the adult organs only in shortness of the length and without a tuft of hair at the tip (fig. 9 III). The male genital papillae are also formed from very early stages of development on the postero-lateral edges of the 5th thoracic segment.

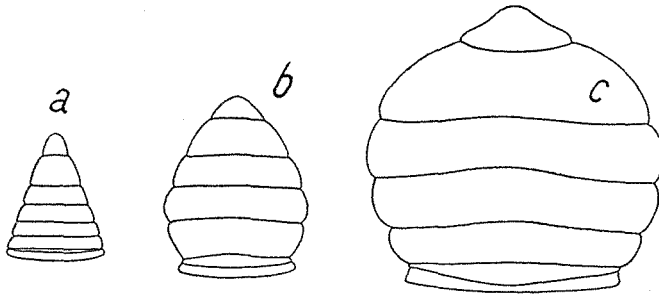


Fig. 10. Change of shape that takes place during the growth of normal female abdomen, seen from the outer surface: (a) The abdomen of crabs of ca. 10-20 mm carapace length, (b) the female abdomen of so-called juvenile type (crabs of ca. 30 mm carapace length), (c) the adult trough-like abdomen (over 40 mm carapace length).

Contrary to the male in which the shape of the abdomen remains almost constant, the female abdomen (fig. 10) is subjected to gradual change of shape during the growth of the animal. In crabs of about 30 mm carapace length the abdomen (fig. 10 a) is still nearly triangular but the lateral sides are no longer straight but more or less convexed, the 4th segment being the broadest. The pleopods are still quite thin, and with no marked growth of hairs. The abdomen remains juvenile-shaped (fig. 10 b) until the crab attains ca. 40 mm carapace length. From this stage onward the female abdomen assumes the trough-like adult type (fig. 10 c) and the pleopods as well as segmental margin are adorned with a thick growth of hairs (fig. 9).

Effects of sacculinization on the female

As is anticipated from comparable cases in other Crustaceans, there is in the infected females no perceptible change towards the opposite sex. According to G. SMITH in sacculinized specimens

of female *Inachus* the reduction of abdominal appendages is quite prevalent and in extreme cases appendages are rudimentary or absent. In the case of *Eriocheir* although no such reduction of abdominal appendages is, as a rule, observed, yet it occurs in some special cases where the phenomenon is always associated with the malformation of the abdomen. In the specimens having undeformed abdomen the development of pleopods is almost the same as in the normal females.

SMITH found in *Inachus* that the infected females prematurely assume the adult-type abdomen, a fact, according to him, of great theoretical importance. It is to be regretted that we could not corroborate the fact in the present case owing to the lack of smaller specimens available for statistical studies.

Effects on the male

In *Eriocheir japonicus* the male individuals are without exception affected by sacculinization, showing more or less marked degrees of external changes. In this respect the present case gives a noteworthy contrast to the case of *Inachus* where only about 70 per cent of infected males showed external modifications. The present case of

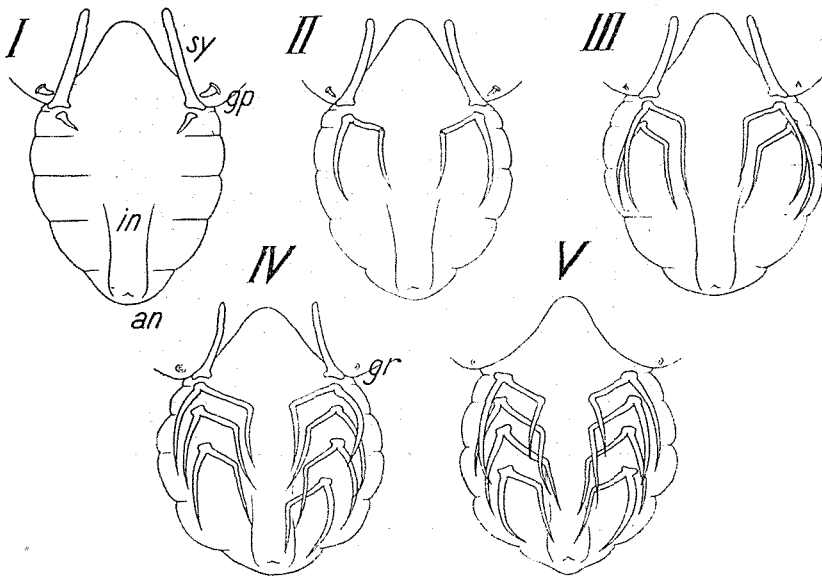


Fig. 11. Diagrammatic illustration of the abdomens of male intersex classified in 5 categories (types I-V); *an*, anus; *gp*, genital papilla; *gr*, rudimentary gonopore; *in*, intestine; *sy*, copulatory style.

Eriocheir is thus comparable to the result of B. W. TUCKER's observations (1930) on *Urogebia littoralis* parasitized by *Gyge branchialis*, where all individuals infected showed modifications.

Modifications invariably occurring to infected males are as follows: 1) The abdomen takes on the female character and becomes broad and trough-like. But in many cases modified abdomens are somewhat different from the normal female abdomen in being perceptively narrower than the latter. 2) The copulatory styles are in greater or less degree reduced. Instead of being stout and straight as in the normal male they are always thinner and usually curved inwards. In most highly feminized specimens they are wholly rudimentary or entirely wanting. 3) The calcified bridge formed by fusion of inward extensions of basipodites of each copulatory style becomes invariably obliterated.

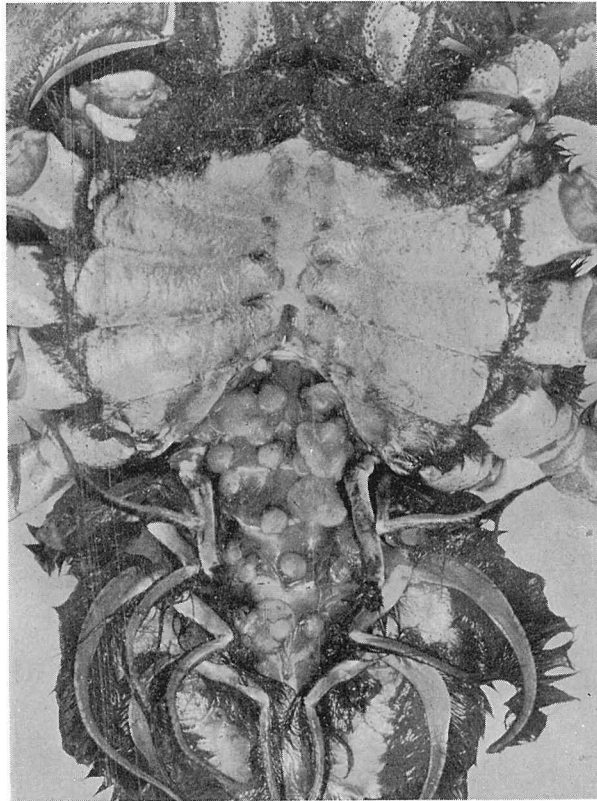


Fig. 12. Photographic representation (in natural size) of a male intersex in the class of 4th category (type IV), copulatory style still remaining, seen from the ventral side, the abdomen being turned over.

Since the development of biramous appendages manifests itself in all possible intermediate stages from almost normal male type to completely feminized type, the infected male crabs may be classified into the following 5 categories :

Type I (fig. 11 *I*). Appendages on the second segment rudimentary or slightly enlarged ; copulatory styles slender.

Type II (fig. 11 *II*). The second abdominal appendages assumed the form of biramous female ones ; copulatory styles slender and reduced.

Type III (fig. 11 *III*). Two pairs of female appendages developed ; copulatory styles reduced.

Type IV (fig. 11 *IV*, fig. 12). Three or four pairs of biramous appendages developed ; copulatory styles reduced or rudimentary.

Type V (fig. 11 *V*, fig. 13). Four pairs of female appendages complete ; copulatory styles entirely absent.

In this last category the abdomen is perfectly feminized and there is no more male character associated.

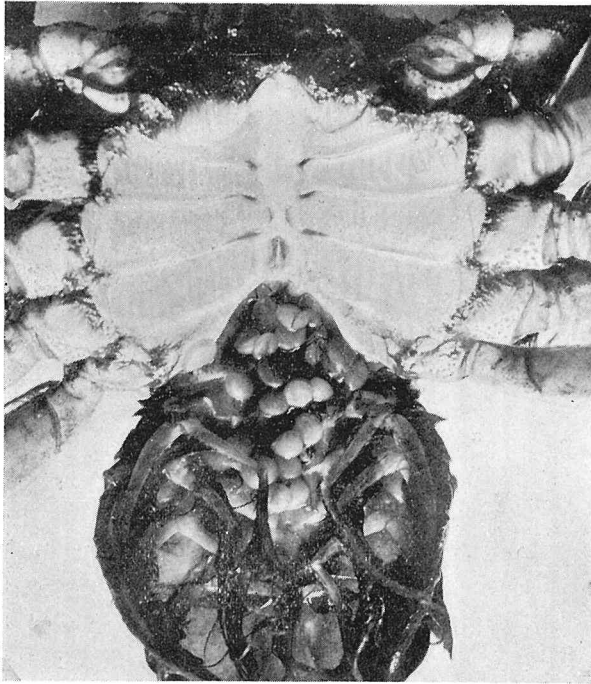


Fig. 13. Male intersex in the class of 5th category (type V), where no trace of copulatory style is visible. Notice the absence of female genital openings on the 3rd plastron.

Between these 5 categories there exist all series of intermediate types as we often meet with specimens having asymmetrically developed appendages. Male genital apertures show also a complete series of reduction which is apparently parallel to the degree of feminization in the appendages. In slightly feminized specimens as "type I" or "type II" the reduction of genital papillae is very slight. Generally speaking the higher the degree of feminization of the abdomen the more intense is the reduction of genital apertures and papillae. In specimens of "type IV" and "type V" the papillae are usually completely obliterated and the apertures often blocked up. In extreme cases the genital apertures are quite vestigial leaving only depressions surrounded by a ring of short bristles. The extremely feminized specimens (type V) can be referable to the original sex only by the presence of rudimentary genital pores on the 5th thoracic segment and by the absence of female genital apertures on the 3rd abdominal segment (cf. figs. 13 and 14). In such highly feminized crabs the

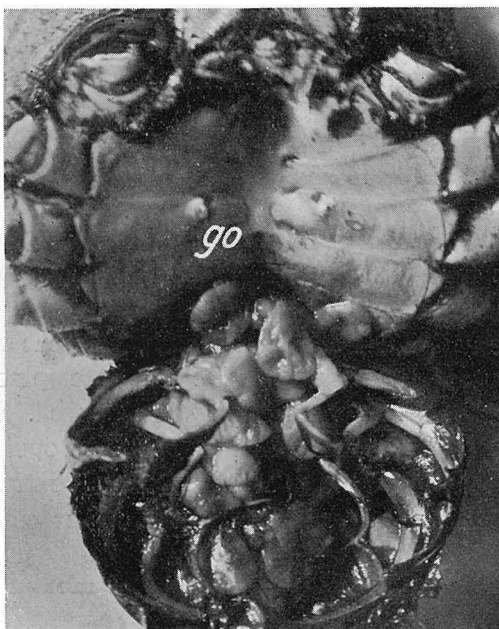


Fig. 14. Ventral view of a female specimen infected by *Sacculina gregaria*, the abdomen being turned over. Notice the presence of genital openings (go) on the 3rd plastron.

abdomen is of perfectly normal adult female type. On the other hand the abdomen of less modified males is peculiarly intermediate in shape between the juvenile female and the trough-like adult female types, the lateral sides being only slightly bulged.

The distribution of these 5 categories among infected male specimens of different sizes is shown in Table II:

As is obvious from the above table, slightly modified crabs of type I are rather frequent especially in larger specimens exceeding 60 mm carapace length. Highly modified males are also not infrequent among middle-sized specimens. If we compare these results

Table II
Categories of modification in parasitized males

Carapace length	I	II	III	IV	V	Total
30--39	—	—	—	2	—	2
40--49	3	3	1	5	8	20
50--59	10	5	4	11	6	36
60--69	10	4	3	1	—	18
70--79	4	1	1	—	—	6
Total	27	13	9	19	14	82

with those obtained by G. SMITH in *Inachus mauretanicus* we notice at once that the frequency of profoundly modified males is far greater in *Eriocheir* than in *Inachus*. Consequently in the present case it is far easier to obtain a complete series of male intersex. In *Inachus* only 11 individuals out of 140 infected males showed one or more female biramous appendages, whereas in *Eriocheir* in 55 individuals out of 82 infected males the development of one or more female appendages (types. II-V) was observed. Moreover, SMITH was unable to find a specimen in which the copulatory style was completely absent. In the present case such extremely modified examples (belonging to the type V) were rather common.

Results of measurement

We could take measurement of 240 specimens of *Eriocheir* of which 122 were infected with *Sacculina gregaria*, 52 were infected with an Epicaridan parasite of the family Entoniscidae and 79 were normal individuals. When we consider the range of variation in size, the numbers measured are naturally too small to allow of statistic analysis of any kind. But it may at least serve to show the general tendency in the growth of *Eriocheir*, especially as it pertains to the influence of the parasite on the size of chelae and abdomen. For this purpose carapace length, that of chelae (the length of propodite of the chelliped) and the breadth of the 5th abdominal segment (the broadest segment in the female) were measured. The results of measurement are summarized in Table III and IV, and graphs (figs. 15 and 16) were constructed from these measurements to demonstrate the relative growth of chelae and the 5th abdominal segment.

Table III

Chela length

Classification of animals	carapace length	number of animals measured	mean of each group	mean chela length for each group	$\frac{\text{chela length}}{\text{carapace length}} \times 100$
normal males	30—39	1	38.0	26.0	68.4
	40—49	6	45.5	32.7	71.6
	50—59	7	54.4	45.7	84.0
	60—69	14	63.9	59.0	92.3
	70—79	9	73.3	72.1	98.3
	80—89	1	80.0	82.0	103.0
normal females	30—39	2	36.3	20.8	57.3
	40—49	11	46.2	28.4	61.3
	50—59	20	54.3	34.8	64.1
	60—69	6	65.1	43.3	66.6
sacculinized males	40—49	20	46.4	29.4	63.5
	50—59	33	54.5	35.2	64.6
	60—69	14	64.4	45.1	70.3
	70—79	4	74.0	53.0	71.6
sacculinized females	30—39	3	36.7	21.3	58.0
	40—49	8	45.0	27.5	61.1
	50—59	16	55.1	34.2	62.1
	60—69	4	65.4	41.3	63.1
epicaridized males	30—39	3	37.7	23.7	62.8
	40—49	7	44.7	30.5	68.3
	50—59	1	53.0	38.0	71.7
epicaridized females	30—39	2	37.3	22.0	59.0
	40—49	14	43.7	25.7	58.8
	50—59	6	52.5	32.1	61.1

a) Relative growth of chelae (fig. 15). The growth of chelae in length in normal males is very remarkable. In smaller crabs the chela length is less than 70 per cent of the carapace length, whereas in large specimens of over 70 mm carapace length it often exceeds the carapace length. In normal females the curve is decidedly lower than the male curve, the chela length being always less than 70 per cent of the carapace length. The curves for sacculinized females and for females parasitized by the Entoniscid show only insignificant deviations from that of the normal female. The curve

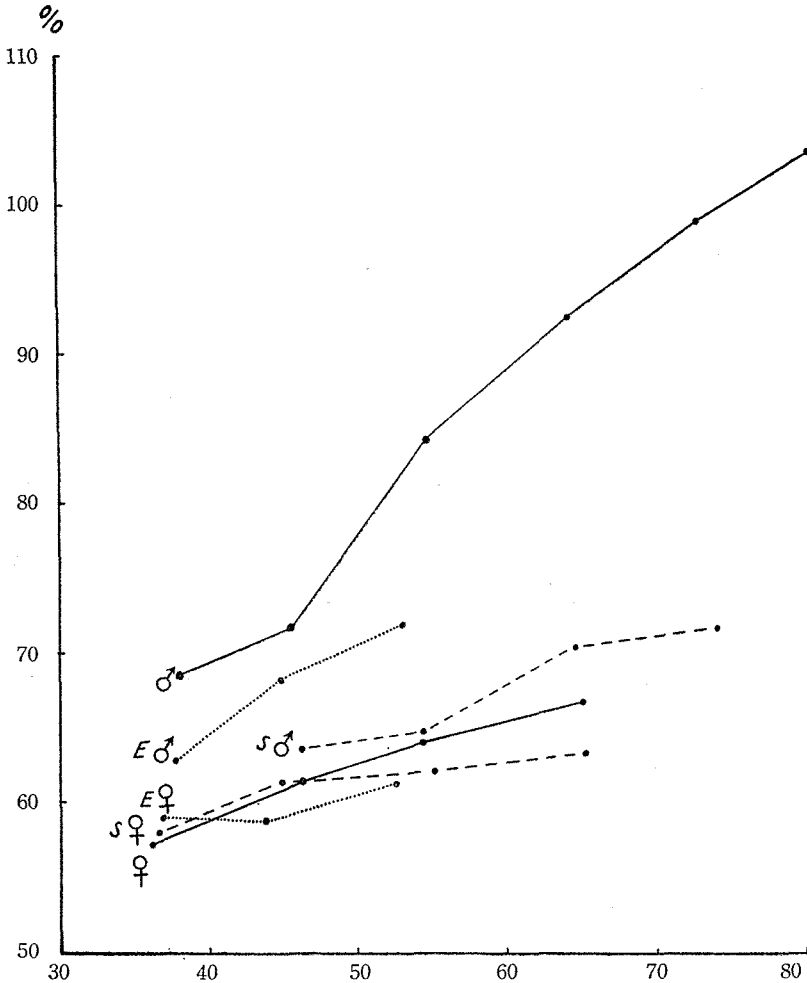


Fig. 15. Graphic representation of chela length in normal and parasitized males and females, expressed in percentages of the carapace length; to show relative growth in length of the chelae. —normal, ----sacculinized,parasitized by Epicarid (Entoniscidae).

for sacculinized males is unmistakably nearer to the female curve than to the normal male curve, showing clearly the feminizing influence of the parasite. As to the male crabs parasitized by the Entoniscid the growth of chelae is less affected than in the case of sacculinization; the curve approaches to that of the normal male, though it is appreciably lower than the latter.

b) Breadth of the 5th abdominal segment (fig. 16). In normal males the 5th abdominal segment is the narrowest except for the

Table IV

Breadth of the 5th abdominal segment

classification of animals	carapace length in groups	number of animals measured	mean of each group	mean breadth of the V. segment	br. of the V. seg. $\times 100$ / carapace length
normal males	30-39	1	38.0	11.0	26.0
	40-49	6	45.5	12.8	28.1
	50-59	7	54.4	15.4	28.3
	60-69	14	63.9	17.7	27.7
	70-79	9	73.3	19.8	27.0
	80-89	1	80.0	21.0	26.3
normal females	30-39	2	36.3	21.0	57.8
	40-49	11	46.3	32.9	71.1
	50-59	21	54.5	43.6	80.0
	60-69	6	65.1	52.3	80.5
sacculinized males	40-49	21	46.3	28.1	60.7
	50-59	32	54.5	36.6	67.2
	60-69	14	64.4	44.4	69.1
	70-79	4	74.0	55.8	75.4
sacculinized females	30-39	3	36.7	17.3	47.1
	40-49	8	45.0	30.1	66.9
	50-59	16	55.1	39.1	71.0
	60-69	4	65.4	50.0	76.5
epicardized males	30-39	3	37.7	10.5	27.9
	40-49	9	44.2	12.1	27.4
	50-59	1	53.0	15.0	28.3
epicardized females	30-39	4	36.8	16.8	45.6
	40-49	14	43.7	22.8	52.2
	50-59	6	52.5	28.8	54.9

last one. It remains always below 30 per cent of the carapace length. Males parasitized by the Entoniscid differ little in the measurement of the segment from normal males. In normal females the breadth of the abdomen steadily increases until it reaches about 80 per cent of the carapace length. The curve for sacculinized females is slightly lower than that of the normal individuals. This is probably due to the fact that the abdomen of infected females is arched so that the actual diameter measured is narrower than that of the normal flat abdomen. In sacculinized males the curve is found very near

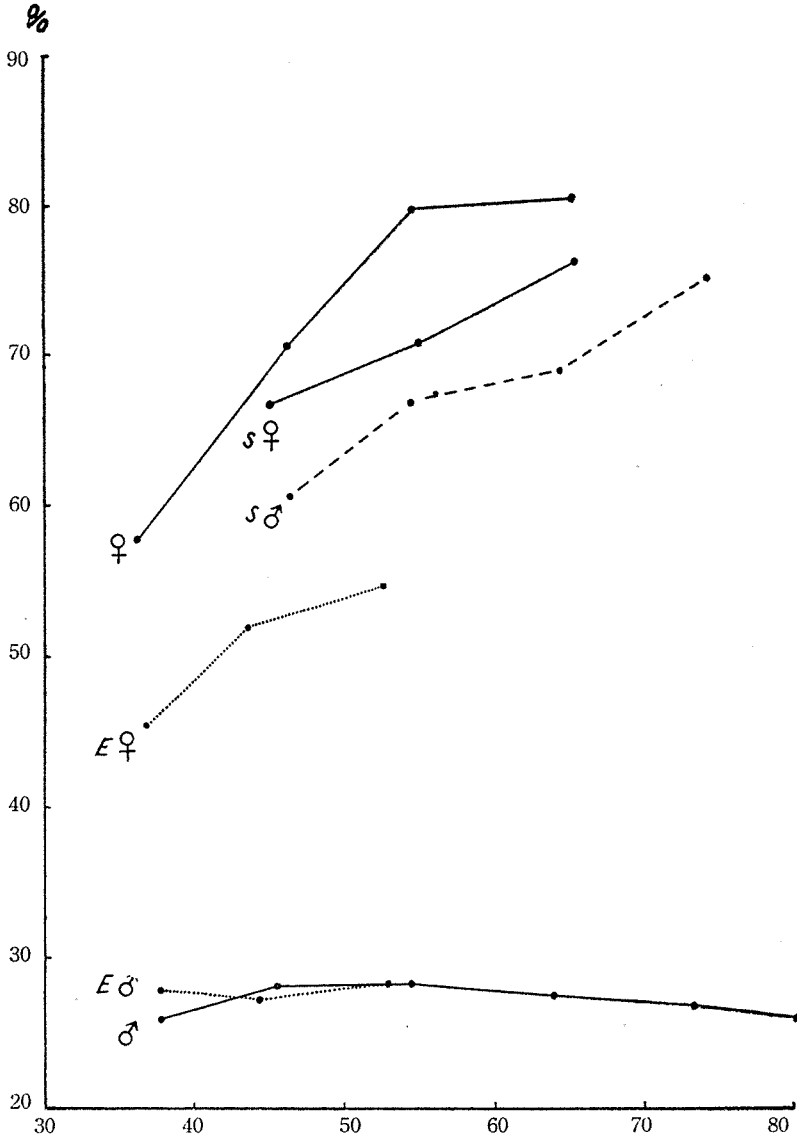


Fig. 16. Graphic representation of the breadth of 5th abdominal segment in normal and parasitized males and females, expressed in percentages of the carapace length; to show relative increase in width of the abdomen.

to the female curve, though slightly lower. Here also the feminizing influence of the parasite is quite distinctly manifested. Females parasitized by the Entoniscid show decidedly narrower abdomen than in the normal crabs. This is due to the fact that the abdomen

of female crabs containing the parasite remains in juvenile condition. The matter was discussed in a former paper (1933) by the junior author.

Specimens with deformed abdomen

Among large number of infected crabs we sometimes find specimens having a more or less deformed abdomen. Often it is unusually arched at the middle part, with the resulting production of a wide space between the abdomen and thorax, and tips of pleopods are frequently thrust out to the exterior. Besides, the inside of such abdomens is usually coated with muddy sediment. Distortion of the abdomen to one side is not infrequent in younger specimens. The degree of malformation is variable and there are specimens in which the abdomen is so much deformed as deserves to be better called teratological. Two such examples are shown in the fig. 17, one belonging to a highly modified male of the type IV and the other to a female. In both cases the 5th and 6th abdominal segments are greatly shrunken, and the appendages are all deformed in a manner summarized in the following:

Specimen in fig. 17 *a* and *b*; infected male of type IV

	right	left
Copulatory style	rudimentary	much reduced and strongly curved inwards
Pleopod II	biramous, stunted	same as the right
Pleopod III	rudimentary, only a small protuberance	only endopodite?
Pleopod IV	biramous, stunted	same as the right
Pleopod V	biramous, stunted	same as the right
Male gonopore	closed	closed

Specimen in fig. 17 *c* and *d*; infected female

	right	left
Pleopod II	basal part only	exopodite broken off
Pleopod III	exopodite only	endopodite only
Pleopod IV	biramous, crooked	biramous, basal parts only
Pleopod V	exopodite amputated	biramous, crooked

These teratological structures are in our opinion produced by the disharmony between the growth of the host and the development of the internal stage of the parasite. In very young crabs the

distortion of the abdomen caused by the tumor of *Sacculina interna* is rather frequent. If, however, the subsequent development of the parasite is in harmony with the growth of the host, this deformation of the abdomen may afterward be remedied to some extent. If, on the contrary, the development of the parasite is very active in comparison with the growth of the host, the tendency to deform will be accentuated with the lapse of

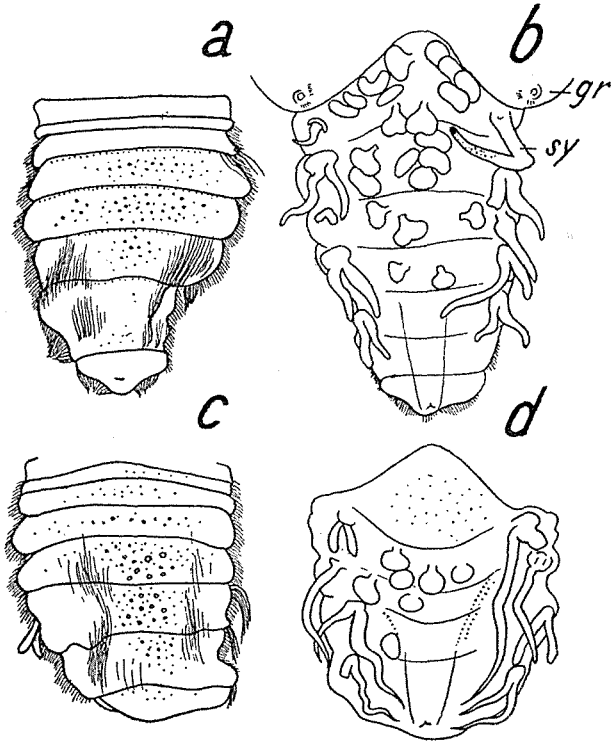


Fig. 17. Deformed abdomens: (a) dorsal; (b) ventral view of a male specimen; (c) dorsal; (d) ventral view of a female specimen.

time, leading to various types of malformed abdomens. But when the abdomen is severely deformed the later development of the parasite seems to be affected in its turn, for seldom is the luxuriant growth of the external parts of *Sacculina* found in such specimens. The abdominal wall is unusually swollen and oedematic and upon such abdomens only a few *Sacculinae externae* show uneven growth. In short the malformation of the abdomen seems to call forth abnormal conditions on the part of the parasite, too. It must be pointed out, however, that these malformations are only of secondary nature and should be treated as belonging to pathologic changes unrelated to the phenomena of intersexuality due to parasitism.

Simultaneous parasitism of Entoniscidae and Rhizocephala

The curious phenomenon that the Entoniscid and Rhizocephala occur simultaneously in one and the same host can also be observed in *Eriocheir japonicus* from Yura River. The junior author collected

altogether 85 specimens of the crab infected with an Entoniscidan parasite, the presence of which can be recognized from exterior by the slight asymmetry of the carapace. Of them 26 were found infected also with the Rhizocephala. By the data at hand the rate of infection with each parasite separately can be estimated to be not more than 10 per cent so that the frequency of simultaneous occurrence of two different parasites (ca. 30%) is actually far greater than the number expected assuming the infection to take place merely by chance.

A. GIARD and J. BONNIER (1887) accounted for this curious association by supposing that the Entoniscid had descended from a group of Epicaridan ancestor which was the parasite of Rhizocephala. But there is no positive ground for this assumption.

G. SMITH (1906) put forward an alternative explanation based on the fact that the presence of *Sacculina* in a crab retards the growth and consequently diminishes the number of moults of the host. He states that "the larvae of Entoniscid which penetrate into the crab by way of gills, would be liable to removal or injury by the constant moulting of the host. But if the larvae were to enter a crab containing *Sacculina interna* its liability to removal or injury through moulting of the host would be greatly diminished and so a greater number of the Entoniscid would survive when associated with *Sacculina* than in crabs uninfected."

This account of SMITH is very convincing and probable but so far as our experience in *Eriocheir* goes, we are still in doubt whether the number of moults of the crab is really diminished in such an early stage at which the infection by the Entoniscid would take place. At least in very young crabs which are found under submerged stones in summer there seems to be hardly any noticeable difference in growth-rate whether it contains *Sacculina interna* or not. Moreover, we have found several moulted skins of young *Eriocheir* which bear signs of being parasitized by *Sacculina* (showing distortion or vaulting of the abdomen). Anyhow, a more thorough study of the actual mode of penetration of these parasites into the host is necessary for an adequate explanation of the phenomenon.

A further noteworthy feature concerning the simultaneous parasitism in *Eriocheir* is that the *Sacculina* associated with the Entoniscid was in all observed cases of internal stages. This is first of all due to the smallness of the majority of infected crabs. But even in larger specimens of over 50 mm carapace length, at which stage

Sacculina is usually external, when associated with the Entoniscid the Rhizocephala remained always internal. It seems, therefore, to be certain that *Sacculina* is delayed in its development by the presence of the other parasite, which will naturally greatly restrict the distribution of the ramifying root-system of *Sacculina*, causing malnutrition of the latter.

Effects on the gonad

The effect of sacculinization upon the gonad of the host varies greatly in the present case. In the majority of infected crabs not even a trace of gonad is detected upon dissection. The place normally occupied by the organ is filled up with a soft grayish mass consisting mainly of a highly intricate root-system of the parasite. But in larger male specimens we sometimes encounter a testis which invariably shows marked reduction in size. Presence or absence of the gonad is, however, not exactly correlated with the modification of external characters. It depends very likely upon the degree of the drain caused by the parasite on the general nutrition of the crab, because of the fact that the gonad is more often found in specimens in which the parasite is obviously retarded in development in comparison with the size of the host.

a) The testis of parasitized males (pl. figs. 1 and 2). In slightly affected cases, the root-system of the parasite envelops only the superficial layer of the testis proper which in itself does not show much degeneration. Some irregularities may creep into the arrangement of seminal tubules, and interstitial connective tissue is markedly thickened. In many cases, contrary to the statement of G. SMITH in *Inachus*, the root-system actually penetrates into the testicular tissue ramifying among the tubules in a manner as if the roots were a proper constituent of the tissue (pl. fig. 1 *rt*). By this intrusion of the root-system and the thickening of interstitial connective tissue, the seminal tubules become highly reduced and separated widely from one another. In highly degenerated cases (pl. fig. 2) the seminal tubules are often broken in pieces and irregularly occupy the central part, being embedded in a cartilagenous substance which is perhaps the product of the hypertrophied connective tissue that normally enclothes the tubules. The thick peripheral part is irregularly penetrated by the ramifying root-system of the parasite. Even in such extremely reduced tubules ripe spermatozoa and apparently healthy spermatocytes can be perceived. It may therefore be con-

cluded that the spermatogenesis itself is least affected by the parasite; it proceeds normally in spite of highly degenerated condition of the testis, so long as there remain seminal tubules, unconcerned whether they are highly deformed in shape or torn into pieces.

b) The ovary of parasitized females (pl. fig. 3). The gonad is much more rarely detected in infected female specimens than in the male. When it is present it is usually nothing more than an inconspicuous white lamellar body quite different from the normal ovary, which is a very extensive organ of deep purple colour. The sections of such a reduced ovary (pl. fig. 3) show naturally highly degenerated condition. The oocytes appear to be incapable of growth beyond a certain extent. The larger oocytes are quite irregular in shape and in most part (especially in the central part) fused together. So in the last condition we can only discern large nuclei of oocytes scattered in the finely granulous mass of yolky cytoplasm. While the central part of the ovary is thus occupied by the fused mass of degenerated oocytes, in the peripheral region oocytes more often retain their cellular boundaries, but their shape and arrangement are very irregular. There we notice at once that the interstitial connective tissue is unusually thick and seemingly tends to enclose the deformed oocytes. The root-system of the parasite, so far as our observation goes, does not penetrate into the ovarian tissue. In *Inachus*, according to the observation of G. SMITH it is into the ovary and not into the testis that the absorbing roots of the parasite penetrate. The matter is quite reversed in our case of *Eriocheir*.

In very rare instances the ovary was found to be thick and of a light purple colour. In such cases the histology of the organ presented the aspect of a normal moderately developed ovary. Such a condition would be established when the demand of the parasite for the nutrition of the host has been unusually slight.

c) The gonad in highly feminized males (pl. figs. 4-10). In the case of highly feminized males we could confirm a theoretically important fact that development of the ovary is by no means infrequent, in spite of the presence of the parasite *in situ*. We have even met with 7 such cases. All of them were highly modified males with 4 pairs of well-developed ovigerous appendages. Three of them had the copulatory styles (type IV of our classification) while the rest were without them (type V, *i. e.*, extremely feminized type).

Ovaries were much smaller in extent than in normal females but they were coloured in light purple or brownish, and ova contained

in them could be well perceived even with unaided eyes. In two cases we could confirm the hermaphroditic condition of the gonad and in the remaining five cases a complete inversion into the ovary. In the first cases the surface of the gonad is mottled with small white streaks or patches and in some parts small white protuberances are recognized. Upon sectioning it was revealed that these white spots are no other than the testicular portions of the hermaphroditic organ, the main bulk of which consists of moderately developed ovary. In both of these cases the testicular portion (pl. figs. 4 and 5 *ts*) is disproportionately smaller than the ovarian portion and in places where no white spot is discerned the gonad is pure ovary

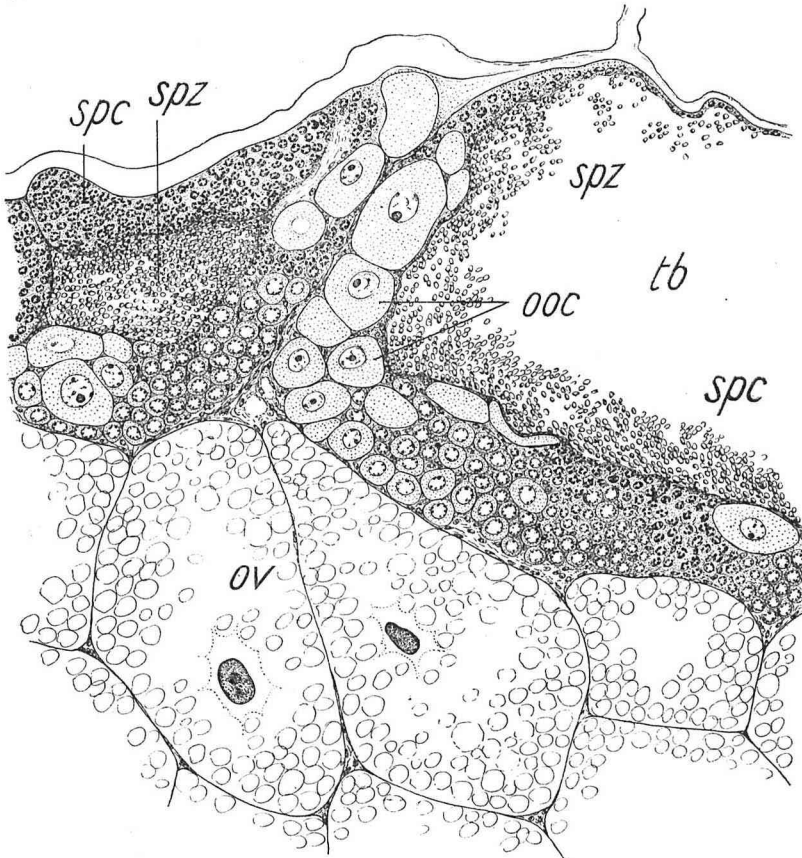


Fig. 18. Typical section of the hermaphroditic gonad of a male intersex, showing the development of eggs and sperms in one and the same tubules; $\times 186$. This figure can be compared with the photograph reproduced in Pl. fig. 6. *ooc*, Oocytes; *ov*, ova; *spc*, spermatocytes; *spz*, spermatozoa; *tb*, seminal tubule.

without any testicular element. Fig. 18 gives a very instructive figure of the hermaphroditic structure of the gonad in which eggs (*ooc*) and sperms (*spz*) are in development in the wall of one and the same tubules.

So far we have found no case in which the sexual glands of both sexes were equally developed. Such a condition would probably be found in younger crabs.

In five other cases the gonad contained no testicular element. The histological structure of these transformed ovaries (pl. figs. 7-9) is of quite normal aspect with large egg-cells laden with rich yolk at the periphery and younger oocytes in the central part.

From these observations it is obvious that in highly intersexual male specimens the gonad can develop not only as a hermaphroditic organ but as a normal ovary, provided that the demand of the parasite for the host's nutrition is not so drastic as to inhibit the development of the sexual gland at all. The condition of the gonad is, however, quite variable and even in highly feminized crabs of the type IV or V, we have a few examples in which there is a degenerated testis instead of a hermaphroditic organ or an ovary. This fact indicates that the correspondency of the modification of the gonad to that of the external characters is not of a very definite nature but is liable to vary to a certain extent. But in no case is inversion to an ovary found among slightly feminized specimens of the types I-III.

Some general considerations

The phenomenon of so-called parasitic castration in higher Crustacea can be explained as the formation of intersexes under the influence of *Sacculina* and other parasites. From this point of view the problem was fully discussed in a former and a recent work of R. GOLDSCHMIDT (1920, '31) and by G. SALT (1926) as well. As pointed out by these authors the classic hypothesis of G. SMITH can also be incorporated in this theory of intersexuality, which agrees with the observed facts so well that there is hardly any room to doubt its validity as the explanation of the phenomenon. The foregoing accounts of the sacculinized *Eriocheir* are, of course, in accord with this explanation in every respect.

When we look through the modifications of sacculinized male crabs we see progressive development of female characters together with the reduction of male characters. Among the changes, the

broadening of the abdomen is common to all specimens which came under observation.

In the normal development of the abdomen in female *Eriocheir* we have distinguished nearly triangular "juvenile type" and broad trough-like "adult type", and have suggested that the attainment of the latter type is very likely conditioned by the ripening of the ovary. But in the sacculinized specimens not only the female but also the male abdomen is usually trough-like in spite of the absence of mature ovary. We submit that this apparent contradiction may be explained by the local stimulating effect of the parasite, which from its very early stage occupies the upper part of the abdomen and there accomplishes its development. However, the local stimuli would not be the sole agent for the broadening of the abdomen. It would be effective only when accompanied with the feminizing effect of the parasite that produces other modifications of the sexual characters. When this influence is weak the abdominal shape does not perfectly show the adult female type. In fact, the abdomen of slightly intersexual male crabs of the type I or II is usually intermediate in shape between juvenile and adult types, i. e., the lateral sides running almost in parallel lines. Thus weakly feminizing influence in these cases is presented in the shape of the abdomen. But in highly intersexual specimens the abdomen is of perfectly adult female shape. We see from these cases that for the complete achievement of the adult type the stimulating action of the parasite, assuming its existence, must be at work on the sufficiently feminized soma. In other words the shape of the abdomen seems to be determined by the double action of the stimulating effect of the parasite plus the feminizing influence due to the parasitism in very early period of development.

To explain the feminizing action of *Sacculina*, G. SMITH assumed that the sexual formative substance was produced as the result of changed metabolism, and so far his hypothesis is substantially in accord with the modern theory of intersexuality. But his theory that the root-system of *Sacculina* acts like developing ovary and thus changes the general metabolism of infected male crabs to the female type is quite doubtful, since the formation of male intersexes well comparable to the result of sacculinization seems to be brought about by the infection of the Bopyrids. H. OHSHIMA (1930) and K. SHÔJI (1930) have reported cases of male intersex in *Philyra pisum* de HAAN parasitized by a branchial Bopyrid, in which there is no

penetration of the root-system into the viscera of the host animal and blood of the latter is simply sucked from without. From this example we may well suspect that the physiological changes due to the simple loss of blood at a critical period in early development are not sufficient to produce male intersexes? Finally, SMITH's interesting observation that the parasitized female *Inachus* prematurely assumes the adult type abdomen, can also be explained simply, without recourse to his elaborate theory, by taking into account the stimulating effect of the parasite acting upon the abdomen which is *sui generis* female in constitution.

Next, the development of biramous female appendages always proceeds from proximal to distal according to the degree of intersexuality. The total disappearance of the male copulatory styles is always met with in those individuals provided with 4 pairs of biramous appendages. The facts agree to a certain extent with the embryological procedure in the differentiation of pleopods which proceeds also from proximal side to the distal end, the male gonopod being formed the earliest. With the progressive development of pleopods, the male genital papillae tend to be reduced, often completely disappearing in the intersexes of types IV and V. In spite of the closure of the opening, the gonopore itself is always indicated by some unmistakable trace of it. This fact may indicate that the male gonopores differentiate before the influence of sacculinization is commenced. However, we know very little of the developmental sequence of the modification of these characters in the infected specimens and we are especially demanded to find out at what stage of development young crabs are infected.

Thirdly, the most important question concerning the so-called parasitic castration is the sexual gland and its relation to the modification of the external characters. We are informed in the case of *Inachus* that the functional hermaphrodite organ is regenerated when the highly modified male host is freed from *Sacculina*, hence it is supposed that the highly feminized crabs are capable of producing hermaphroditic organs. F. A. POTTS (1907) found in *Eupagurus* parasitized by *Peltogaster* that egg-cells are produced in the testis, in spite of the presence of parasite *in situ*. Analogous observation was made also by B. W. TUCKER (1930) in *Urogebia* parasitized by a Bopyrid, *Gyge*. (But in this last example the production of ova in the testis is of normal occurrence and this tendency seems to be emphasized in the parasitized condition.) Thus the tendency of

reversal of the sexual nature in the gonad seems to be by no means rare among parasitized Decapods. In *Eriocheir* we have also confirmed the fact by finding ovaries of almost normal structure in highly feminized intersexual specimens.

The possibility to produce ovary in the gonad of highly intersexual male crabs is definitely demonstrated in our 7 specimens above mentioned. Thus, under favourable conditions the sexual nature of the gonad can be perfectly reversed by parasitism. On the other hand, R. COURRIER in his study of *Carcinus maenas* parasitized by *Sacculina*, (1921) claims that in spite of highly feminized abdomen, the existence of normal functional testis is a proof that there is in the Crustaceans as in the insects no correlation between the somatic changes and the sexual gland. In view of our results in *Eriocheir*, COURRIER's observation is too limited to allow of general application. Especially in his case the variability of the conditions of the gonad is quite neglected. As we have already shown testes may be found at times even in highly feminized male crabs whereas in other cases almost normal ovaries are discovered. It is also very probable that in *Carcinus* the intersexuality due to sacculinization may be decidedly lower in degree than in *Eriocheir* as we know from POTT's observation that in this shore-crab the effect of sacculinization is not so marked as in *Inachus*. From the fact that the ovary is capable of development in the male intersexes of *Eriocheir* it may further be considered that the sexual nature of the gonad is also a character determined not *a priori* but only in the early phase of development just as other modifiable external characters. In other words, the sexual nature of the gonad represents one set of sexual characters which become differentiated in the course of development and can be influenced when the invasion of the parasite takes place before the critical period of their determination. This does not necessarily presuppose a direct correlation between the gonad and those external characters that can be influenced by sacculinization. On the contrary it is more reasonable to consider that the sexual nature of the gonad as well as somatic characters are modified by the common influence of the parasite which is comparable to the action of sex-controlling gene. Hence there is only parallel changes and not a correlation between somatic changes and the gonad. So far, the relation is just as we know of in Insecta.

There is, however, another set of sexual characters in the

Brachyura, namely those which become manifest in the later period of life and perhaps with the maturation of the gonad. These are the trough-like abdomen in the female and the enlarged chalae in the male, both of which are probably under the control of the sexual gland. Local stimulating effect of the parasite may substitute or intensify the possible influence of the maturation of the ovary in modelling the abdomen into adult type. As to the chelae their growth beyond the female type seems to be caused by the activity of the male gonad but there is as yet no experimental proof to settle this point.

Generally speaking the male intersexes of the Brachyura produced as the result of sacculinization, taking those of *Eriocheir japonicus* as an example, show no essential difference in the mode of modifications of sexual characters from the well known cases of genetic intersexes of gipsy moth and other insects. There seems to be, however, a few additional complications which are perhaps peculiar to the Crustaceans namely probable conditionment of some characters by the gonad. But exact proof for this can be furnished only by experimental work in the future.

As to the cause of production of male intersexes as the result of succulization we are still wrapped in a cloud of mystery, and only a few working hypotheses are put forward by R. GOLDSCHMIDT (1931). For the solution of the problem it would first of all be necessary to investigate the conditions in the early phase of development of the host crab at which the infection of the parasite takes place.

Summary

1) A typically gregarious *Sacculina* (*S. gregaria* n. sp.) is here described for the first time, the host animal being *Eriocheir japonicus* de HAAN which is very common in the streams of Japan. The crabs are infected by the parasite at the estuary or in the sea where the breeding both of the host and the parasite takes place and come up the river together with the non-infected sound ones. When they attain the size of ca. 40-50 mm carapace length, the parasite becomes external. Subsequent growth and maturation of the parasite is accomplished again in the region of the river-mouth.

2) Even very small crabs (10-20 mm) which contain the internal stages of *Sacculina* can be distinguished from the normal ones by the presence of a white tumor in the abdomen. In the subsequent

stages the presence of internal parasite is revealed by the general swelling of the wall of hind-gut.

3) All parasitized male crabs are affected in their sexual characters with the resulting production of intersexes of varying degrees. The change common to all is the broadening of the abdomen and the loss of the stout calcified bridge at the base of the abdomen. Female biramous appendages are produced in most cases.

4) The intersexual male crabs can be classified in 5 categories according to the degree of development of pleopods. In the highest intersex of the type V copulatory styles are completely obliterated and 4 pairs of ovigerous appendages are well developed. The male gonopores are observed as mere traces. The female crabs are not much affected by the parasite and the reduction of pleopods does not occur. Both in male and female the abdomen of infected crabs is in some cases highly deformed.

5) The relation of the growth of chelae and of the breadth of the 5th abdominal segment to the carapace length has been measured in normal and parasitized individuals (tables III and IV).

6) Simultaneous parasitism of Rhizocephala and Entoniscid can be met with also in this case of *Eriocheir japonicus*.

7) In both infected males and females the gonad is often difficult to find. When present it is usually very much affected and presents the aspect of great abnormality. The root-system of the parasite penetrates into the testicular tissue but not into the ovary.

8) Seven cases of inversion of the male gonad into the ovary, of which five were complete and two slightly hermaphroditic, were discovered in highly modified intersexes belonging to the types IV and V. This is perhaps the first instance in the male intersex produced by the parasitism in which complete sex-reversal of the gonad is definitely demonstrated.

9) Among the characters affected by the parasite those which differentiate in a very early period of development are quite independent of the gonad, whereas the broadening of the abdomen to the adult type in the female seems to be dependent on the maturation of the ovary. In the sacculinized specimens this broadening of the abdomen is held to be the result of cooperation of the stimulating effect of *Sacculina* and feminizing influence due to the early infection of the parasite.

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Explanation of plates

All figures except the 6th are of the same magnification, viz. 35 times as large as the original size.

- Pl. VIII Fig. 1. Section of a median affected testis, in which seminal tubules are still regularly arranged, but the peripheral portions are highly invaded by ramifying roots (*rt*) of the parasite.
- Fig. 2. Section of a highly affected testis, in which extensive degeneration has taken place. The seminal tubules are greatly reduced; those remaining are broken and the matrix is almost replaced by a cartilagenous substance.
- Fig. 3. Ovary of a parasitized female. The oocytes appear to be incapable of growth beyond a certain extent. Larger ones are quite irregular and in most part fused together.
- Fig. 4. Section of a hermaphroditic organ, showing smaller testicular portion (*ts*) and a part of larger ovarian portion.
- Fig. 5. Section of a similar organ of another specimen.
- Fig. 6. Testicular portion of the same preparation as in the preceding figure shown in higher magnification, $\times 120$ times.
- Pl. IX Fig. 7-10. Four sections of gonads, each belonging to different male intersexes, in which a complete inversion into ovary has taken place.

Postscript

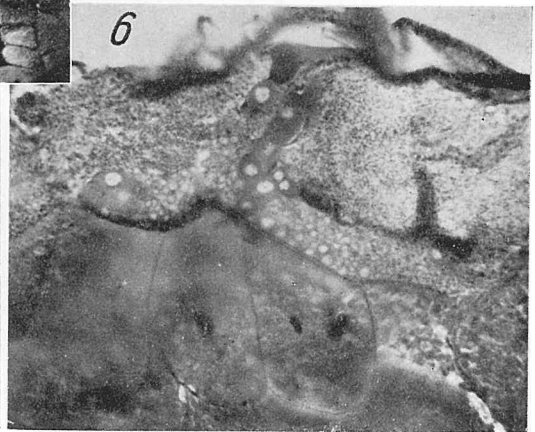
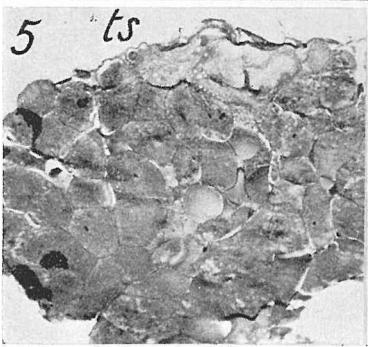
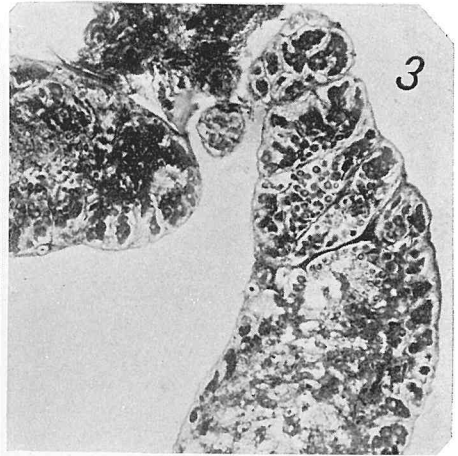
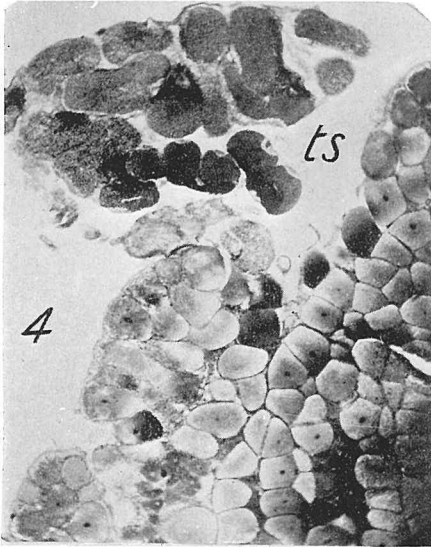
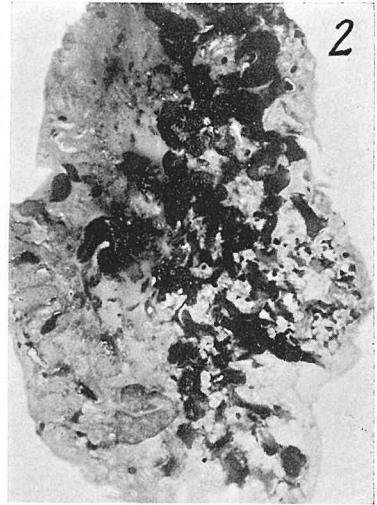
It was only during the redaction of the present work that we could make access to the highly interesting work of N. PETERS and A. PANNING: "Die chinesische Wollhandkrabbe (*Eriocheir*

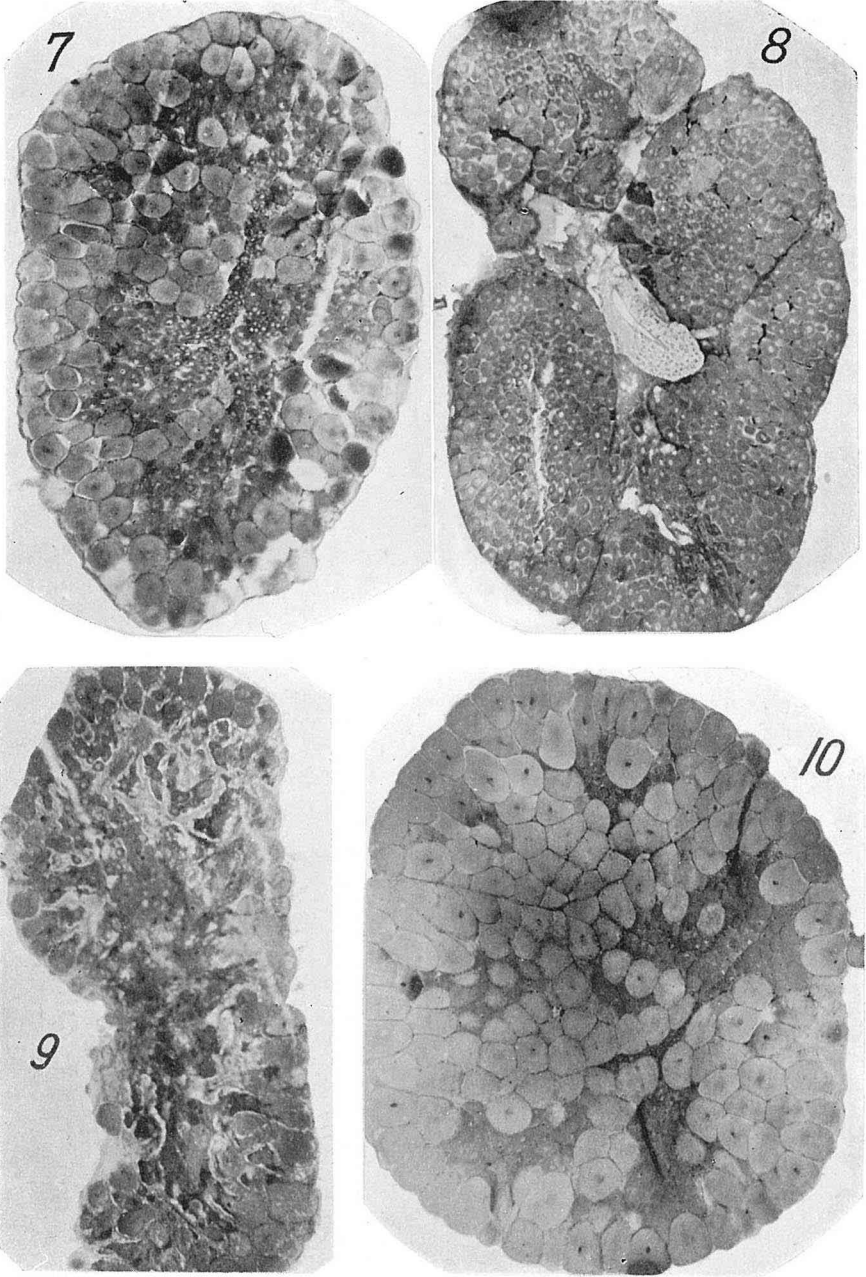
sinensis MILNE-EDW.) in Deutschland".* Very thorough descriptions of morphology and ecology of the Chinese crab are for the first time given in the work. What is most striking is that the habit of *E. chinensis* in Germany is surprisingly well in accord with that of Japanese species in its native habitat. We have stated in the present work that the breeding of *E. japonicus* as well as its parasite should occur only in the region of estuary and given some evidences of the migrating habit of the crab. Now that the migration and the breeding of the Chinese species are very well worked out by PETERS in Elbe, we can safely assert that almost the same thing would take place in our species also. Especial interest is added in the Japanese species by the association of parasitic organisms of purely marine characters, i. e. Rhizocephala and Entoniscidae.

Besides, the burrowing habit of the crab as well as its injuries to fishermen are notorious also in Japan. But the crab is not regarded merely as a troublesome creature. A large amount of them is captured especially in autumn and sent to Osaka districts, where people are fond of eating them boiled. Liver and ovary of the crab are said to be particularly tasteful.

In view of the striking similarities of these two species of *Eriocheir*, it is very likely, as is mentioned in the referred work (p. 8), that these are simply geographical varieties rather than two distinct species. It is, therefore, very desirable to gain more exact data concerning the distribution of these two forms in the Far East.

* Zool. Anz. Ergänzungsband zu Bd. 104. (1933). pp. 1-180.





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