NOTES ON THE LIFE HISTORY OF *SACCULINA CARCINI* THOMPSON

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Introduction

The present paper is the outcome of the suggestion made to me some years ago by Prof. Edward Hindle that the life history of *Sacculina* would repay further study. Observations on living specimens of *S. carcini* parasitic on *Carcinus maenas* were commenced at the Zoological Laboratory in the University of Glasgow and at the Marine Station, Millport. Later it became apparent that, in order to make certain points clear, a collection of parasitized crabs representative of a whole year would be necessary. Thus such a collection was formed, and it is this collection which forms the basis of this paper, the previous observations being introduced only when they serve to amplify or to confirm the deductions drawn from the study of the collection. This study has been carried out in the Department of Zoology, University College, Cardiff.

I desire to express my thanks to Prof. E. Hindle for the suggestion referred to above, to Prof. W. M. Tattersall for the facilities for my work at Cardiff, to Mr R. Elmhirst for ensuring a regular supply of material from Millport, and to the University of Wales for a grant towards the expenses of forming the collection.

The life history of *Sacculina*, first worked out by Delage (1884), has recently been the subject of further investigation by Day (1935), and Orton (1936) has elucidated additional details.

Whilst Delage's classical observations were made at Roscoff on *S. carcini* parasitic on *Carcinus maenas*, Day, in the Mersey area, worked on the same species of parasite but parasitizing *Portunus holsatus*. It seemed, therefore, that some of the differences between Day's account and that of Delage might be due to the fact that observations were made on a different species of host, and that others might be associated with the more northerly latitude from which Day's material was obtained. It thus appeared that, if observations were made on *Sacculina carcini* parasitic on *Carcinus maenas* in the Clyde Sea area, it might be possible to detect the effect of latitude on the life history of the parasite, and it might, at the same time, give some indication as to whether the parasite showed any modification correlated with its occurrence on a different host species.

It was decided to pay particular attention to the following points: (*a*) the breeding season of the *Sacculina*, (*b*) the date of the appearance of the young *Sacculina* externa, (*c*) the fate of the *Sacculina* externa.

Before turning to the details of the collection it is necessary to draw attention to two important points which will not be discussed further. First, Day has clearly shown that the *Sacculina* externa does not become external at a moult of the host, as was previously thought, but when the exoskeleton of the crab is hard. Secondly, the time that elapses between the infection of a crab by the *Sacculina* cypris larva and the emergence of the externa is approximately 9 months, as shown by Day for *Portunus holsatus* and Orton (1936) for *Carcinus maenas*, and not 21 months as postulated by Delage.

The Collection

The collection of parasitized crabs was made by the Marine Station, Millport; the majority of specimens were collected at a point near the pier at Fairlie, Ayrshire, but some were obtained near Millport itself. These localities are, however, only some 2 miles apart, so that there seems to be no objection to dealing with crabs from the two sources together.

It should be made clear that the collection is one of parasitized crabs; that is, of crabs which, on collection, showed some visible sign of parasitization by *Sacculina*. It may be pointed out that this method does not follow that of Day who worked on a collection of crabs and began by finding the percentage infection of the crab population.

The exact dates on which the collection was made varied from month to month according to weather conditions; these were particularly unfavourable in October 1938, when the number of specimens obtained was very small.

The collection extends over the 12 months commencing in June 1938, the total number of crabs bearing *Sacculina* externa was 181, and, owing to multiple infections, the number of externa was 188. The distribution of the specimens over the months of the year is shown in Table I.

Table I. Summary of the Collection

Month	No. of crabs	No. of *Sacculina* externa	No. of double infections	No. of triple infections
1938				
June	15	15	..	..
July	11	11	..	..
Aug.	18	18	..	..
Sept.	25	25	..	..
Oct.	7	9	..	1
Nov.	24	25	1	..
Dec.	18	19	1	..
1939				
Jan.	12	12	..	..
Feb.	9	10	1	..
Mar.	12	13	1	..
Apr.	13	14	1	..
May	17	17	..	..
Total	181	188	5	1

It will be noted that double infection occurred in 2·8 % of parasitized crabs, and that the one case of triple infection, if expressed as a percentage, works out at 0·6.

The Breeding Season of *Sacculina carcini*

One of the chief objects of the investigation was to fix, if possible, the time and duration of the breeding season of the parasite. Day had found that, in the Mersey area, *Sacculina carcini*, parasitic on *Portunus holsatus*, bred in March, April and May; whereas Delage had found at Roscoff that *Sacculina carcini*, parasitic on *Carcinus maenas*, produced the greatest numbers of ripe externa and nauplii in June, July and August. Orton (1936) gives March or April to September or November as the breeding season of *Sacculina carcini* at Plymouth. Day postulated that the difference observed by him was caused by a different species of crab being the host, and made some suggestions, which will be touched on later, as to why this should be so.

In any attempt to fix a breeding season for *Sacculina* a point which would appear to be of great importance is the presence of eggs or nauplii in the mantle cavity of the externa. Delage pointed out that the eggs, when laid, are passed into the mantle cavity which is used as an incubatory pouch, and the ovary then becomes engaged in producing the next batch of eggs. After each batch of larvae is cast out the lining of the mantle cavity is also shed—thus the finding of a partially cast mantle lining protruding from the opening of the *Sacculina* externa is also of great importance. Indeed it may be of greater significance than the finding of nauplii in the mantle cavity for we have no accurate knowledge of the possibility, or otherwise, of the nauplii being retained in the mantle cavity pending the onset of favourable conditions. In this connexion Day remarks "...the examination of the samples from the Mersey area indicated that the externa is able to retain the larvae for some considerable time should conditions not be suitable for the survival of the larvae".

It seems convenient to call the presence of nauplii in the mantle cavity and the incompletely shed mantle lining "signs of ripeness", and the occurrence of these signs throughout the year is shown in Table II. In this table only *Sacculina* externa of over 12 mm.* in breadth have been included as it was concluded from the study of the collection that this is the smallest size at which breeding normally takes place. It may also be noted that, as in some cases it is difficult to determine whether a given specimen should be included as "eggs" or "nauplii", it was decided to include as nauplii all those embryos in which the eye pigment had appeared.

* This table omits one specimen of 11 mm. breadth which from its colour and internal organization resembled larger specimens. As it contained neither eggs nor nauplii its omission does not affect the results. Altogether this specimen was small for its colour and degree of development; it is one of a pair in a case of double infection (February 1939) and, as its partner was 23 mm. in breadth, suggests that, when two parasites are in competition on one host, one may be dwarfed, particularly if infection was not simultaneous. For it may be supposed that the first parasite to infect a host would succeed in establishing a more extensive root system than a later arrival.

An inspection of Table II shows that if the presence of the partially shed mantle lining be taken as the chief indication that breeding is taking place then we have an indication that the breeding season extends from July to December. It must be noted, however, that during some of these months nauplii were not found. On the other hand, nauplii were found in several

TABLE II. DETAILS OF THE *SACCULINA* EXTERNA SHOWING "SIGNS OF RIPENESS"

	Sacculina externa				
Month	Total	No. over 12 mm. broad	No. eggs in mantle cavity	No. nauplii in mantle cavity	No. with mantle lining partly extruded
1938					
June	15	15	10	2	0
July	11	11	5	1	1
Aug.	18	16	8	0	2
Sept.	25	13	7	0	1
Oct.	9	7	2	0	1
Nov.	25	21	11	5	2
Dec.	19	18	5	3	1
1939					
Jan.	12	11	6	0	0
Feb.	10	8	5	3	0
Mar.	13	12	6	0	0
Apr.	14	14	5	1	0
May	17	17	13	1	0

months when the cast mantle linings were not obtained; thus if we take the two "signs of ripeness" together the breeding season would extend to the whole year excluding January and March. When keeping parasitized crabs in captivity in earlier years it was found that it was relatively common for the nauplii to be shed in the warmer months, notes about this were made in August 1936 and 1937, but no records were made in the cooler months although the crabs survived well. The earliest date of which I have record of *Sacculina* larvae being liberated in the laboratory at Glasgow was on May 17, but, on this occasion, the host had just arrived from Millport and many unripe eggs were also extruded, so that it appears likely that the emission of the larvae was slightly premature and was probably due to the increase in temperature to which the specimen was submitted on being brought into the laboratory.

Additional evidence as to the duration of the breeding season can be obtained from the time of emergence of the young externa now that it is known that this takes place approximately 9 months after the infection of the host. The young externa, when they appear, are a few (up to four) millimetres in breadth and quite white; they grow quickly, keeping their white colour, and are believed to be in a breeding condition some 6 weeks or 2 months after their appearance. Table III shows the number of the small white externa and their distribution through the year. Those of 12 mm. maximum breadth and under are included in this table.

A study of Table III shows a preponderance of small white externa in September and a smaller number in August and during the months October to February. Counting back 9 months, the appearance in September indicates breeding in the previous December, August, in the previous November, and October to February in the previous January to May. This extends the breeding season to nearly the whole year; but there are certain points which must be mentioned.

TABLE III. DETAILS OF THE DISTRIBUTION THROUGH THE YEAR OF SMALL WHITE EXTERNA

		Sacculina externa		
Month	Total	12 mm. and under not white	12 mm. and under white	Total 12 mm. and under
1938				
June	15	..	..	0
July	11	..	..	0
Aug.	18	..	2	2
Sept.	25	..	12	12
Oct.	9	..	2	2
Nov.	25*	2	1	3
Dec.	19	..	..	0
1939				
Jan.	12	..	1	1
Feb.	10	1†	1	2
Mar.	13	..	..	0
Apr.	14	..	..	0
May	17	..	..	0

* In addition to the specimens tabulated for this month another with small white externa may be included. It was forwarded to me from Millport and consisted of an isolated crab abdomen with a note to the effect that it had been taken from the tanks during this month.

† This is the smaller of two externa in a double infection and is referred to in the footnote on p. 255.

Although small white externa are to be found during several months of the year, as is shown in Table III, they are seen to be most common in September. The appearance of a large number of small white externa had been noted in August in 1936 and 1937 and there can be no doubt that it is a common feature in August and September. Attention may be drawn here to Table IV which deals with the colour of the externa and this shows that white predominates in the months August to November and also that breeding size (over 12 mm. in breadth) is reached by white specimens in late summer.

From all the foregoing considerations it is obviously not possible to name any two or three months of the year as a "breeding season". Rather the conclusion must be drawn that breeding takes place under favourable conditions during most months of the year and that a maximum is reached in the late summer and autumn (August to December) and that there is probably a minimum in the winter (January to March).

A further point to which consideration should be given is that the time taken by the parasite over its internal development has been assumed in the

paragraph above to be 9 months, but there seems a possibility that it might be affected by temperature, and might be slightly slower when infection takes place during the colder months; however, no evidence in support of this view can be offered.

If we compare these deductions with the findings of Day it seems conclusive that the difference in the breeding season of *Sacculina carcini* when parasitizing *Carcinus maenas* and when parasitizing *Portunus holsatus* is caused by the different host, and is not due to any cause of geographical origin. Day suspected this and put forward an hypothesis to account for it. He suggests that the difference is due to variation in the breeding season of the host. Day says "Thus Delage's seasonal table which is true for *Carcinus maenas* from Roscoff does not hold for *Portunus holsatus* from the Mersey, but in both cases the nauplii appear a little earlier than the zoea; and the young internae become evident when the ovaries of the uninfected crabs are beginning to ripen. The growing parasite in the female is thus able to absorb nourishment that would normally be stored as yolk."

The breeding season of *Carcinus maenas* in the Clyde has been summarized by Elmhirst (1922) as follows: "full" females are found in October and November, spawning November to May, hatching of zoeas late March to late August. Here, then, if we accept the late summer and autumn as the chief breeding period of *Sacculina*, the nauplii will be appearing later than the crab zoeas, not earlier as found by Day. This may indicate that Day's explanation is not complete, for the breeding seasons of host and parasite do not bear the constant relationship which Day's explanation seems to demand.

There is no doubt, however, that the breeding period of the parasite is greatly influenced by its host, and, in particular, the breeding periods of host and parasite bear a marked resemblance in duration, as has been noted by Orton (1936, p. 624).

While it is clear that the difference in host species accounts for the chief differences between the time and duration of the breeding period of *Sacculina carcini* when parasitizing *Carcinus maenas* on the one hand and *Portunus holsatus* on the other hand, if the results of the observations made on the material from the Clyde are compared with Delage's from Roscoff it is possible to detect a distinct effect of latitude. Delage found the young externa common in April and May, in the Clyde they are most frequent in August and September; again, while at Roscoff most ripe externa are found in July (primiparous August–October), in the Clyde they are to be found from August to December. Thus in the Clyde the seasonal sequence of events appears to take place some two to three months later than at Roscoff.

Plymouth occupies a somewhat intermediate position between Roscoff and the Clyde and it is perhaps worth noting that Orton (1936) gives the breeding season of *Sacculina* at Plymouth as from March to November, thus it probably begins somewhat earlier here than at Millport. It may also be noted that the host (*Carcinus maenas*) appears to have a more restricted breeding season

in the Clyde than at Plymouth where it is stated to continue all the year round with a maximum number of larvae in the spring (*Plymouth Marine Fauna*, 1931).

The Fate of the *Sacculina* Externa

Day found, after the breeding season, a large number of crabs present in the collections which bore the blackened stump of former *Sacculina* externa. He concluded that it was a general phenomenon for the externa to shrivel and fall off after the comparatively short breeding season. This is, of course, in marked contrast to the older beliefs that the normal life of the *Sacculina* externa was approximately equal to that of the host, see for instance Tattersall (1920). Delage noted that in November "on trouve un certain nombre de Crabes portant les traces d'une Sacculine détruite". As the collection at my disposal was of parasitized crabs no numerical evidence of a general falling off of the externa can be available; but from the fact that abundant material was available all the year round it did not appear that when *Carcinus maenas* is the host there is any general falling off of the externa. In fact the presence of some very dark brown externa on crabs bearing heavy incrustations of epizootic organisms directly suggested that in some *Carcinus*, and perhaps the majority, the externa persist for a considerable time producing larvae when conditions are favourable. For this reason the colours of the various externa were noted and also the degree of the incrustation of the host by epizootic organisms.

As regards colour it is interesting to note that Day does not remark on any darkening of the externa, whereas Delage noted that the ripe externa were violet, this coloration being caused by the pigmentation of the nauplii within.

Table IV. Showing the Colours of the *Sacculina* Externa of 12 mm. in Breadth and over

Month	White	Grey	Yellow	Brown	Total
1938					
June	6	1	2	6	15
July	1	0	3	7	11
Aug.	14	0	0	3	17
Sept.	12	0	0	2	14
Oct.	8	0	0	0	8
Nov.	12	1	4	6	23
Dec.	2	0	5	12	19
1939					
Jan.	2	0	2	7	11
Feb.	1	0	2	5	8
Mar.	5	0	3	4	12
Apr.	5	0	4	5	14
May	4	0	5	8	17

The colours of externa with a breadth of 12 mm. and over have been recorded in Table IV. The numbers are not sufficiently large for statistical treatment but justify the conclusion, which has been reached in working through the collection and in previous years' work, that the small white

externa appearing in August rapidly enlarge and produce larvae. The externa then gradually darken either through varying shades of yellow, or of grey, to brown, and finally to dark brown. Thus the age of the externa can be judged to some extent by their colour, those which are brown having probably been in position for at least some 6 months.

Additional evidence as to the age of the externa can be obtained from a study of the epizootic organisms which the host may bear. Before proceeding to discuss this point it may be noted that Day remarks "...crabs bearing barnacles and serpulid tubes have not much vitality..."; but I do not think that this is always a justifiable statement. Rather the presence of incrusting organisms indicates an absence of moulting; in support of this it may be noted that I have had a berried female, living in the laboratory, which carried several barnacles on the carapace; also Table V shows that there were always crabs with epizootic organisms found in each month's collection.

In Table V the total number of crabs for each month is given and then the number with no epizootic organisms. Those bearing incrustations other than balanids and serpulids are not further mentioned. The balanids and serpulids have each been divided into three groups, small, unspecified and large, according to any notes made about them when working through the collection.

TABLE V. SUMMARY OF THE INCRUSTING ORGANISMS FOUND ON THE CRABS IN THE COLLECTION

(For full explanation see text)

Month	No. of crabs	No. without epizootics	No. with balanids			No. with serpulids		
			Small	Unspec.	Large	Small	Unspec.	Large
1938								
June	15	7	4	..	..	4	2	1
July	11	3	1	3	2	2	5	..
Aug.	18	9	1	..	..	5	1	..
Sept.	25	16	1	..	3	6	..	..
Oct.	7	4	..	..	..	3	..	..
Nov.	24	8	..	8	..	3	10	2
Dec.	18	6	4	1	1	9	1	..
1939								
Jan.	12	4	..	..	1	2	4	..
Feb.	9	2	1	..	1	4	2	..
Mar.	12	8	1	..	..	2	..	1
Apr.	13	4	6	..	..	2	1	..
May	17	8	8	..	2	..	3	1

Before proceeding to the deductions to be drawn from Table V one point must be made clear. It was not ascertained that the epizootic organisms were living at the time of collection and the grouping has been made from the hard parts only. There is thus room for considerable error, as if a young serpulid settled in the autumn and then died after only a short existence its tube would remain and the young serpulid worm would be recorded in the month in which the crab that bore it was collected. However, allowing for

this large error, small freshly spatted barnacles were prominent in April, May and June, and the young serpulids from June onwards in increasing numbers towards the autumn. This, of course, is what would be expected from our knowledge of the breeding seasons of these animals.

This aspect of the study becomes of greater interest when it is correlated with the probable history of the moults of the host. It has been shown that the greatest number of new externa appear in the late summer and autumn, and it has also been established by Day that the emergence of the externa takes place when the exoskeleton of the host is hard and not at a moult. It is well known that in *Carcinus* moulting of the host ceases when the externa of the parasite has appeared. Thus the last moult previous to the appearance of the externa would probably take place in May or June, and the crab with the new externa would be more likely to carry a serpulid than a barnacle as the young balanids would have been cast at the moult; this point is clear in the table. Thus it seems likely that a crab carrying externa which appeared in the summer would not acquire barnacles until the following spring. If this were quite certain we could then say that every crab carrying a barnacle had had the externa for some 6 months before it acquired the barnacle. However we cannot be quite sure, particularly in large crabs (which may only moult once a year), that the host would moult in the spring of the year in which the externa appeared, and, in some therefore, the barnacle might be some 3 months older than the externa. Thus although it is probable that the externa are some 6 months older than the barnacle it cannot be said that they are always so.

There is, however, the additional point that sometimes a crab will bear two generations of barnacles. Two such crabs were obtained in August 1937; Mr H. G. Stubbings has kindly identified these for me and finds them to be the smooth variety of *Balanus crenatus* Brug. Mr Stubbings pointed out that there were two generations of barnacles present, and, that, according to the views of H. B. Moore, *Balanus* spp. breed only once per annum, and the two generations would therefore belong to the spattings of 1936 and 1937. Here it seems certain that the crab had not moulted since early in 1936, and there is a possibility that the last moult was in 1935; it therefore appears that the externa on this crab had been in place at least a year and perhaps longer. Another case is that of a specimen picked up at Dawlish, Devon, in September 1938; the externa was dark brown, the carapace of the host bore a barnacle which from its size must have been spatted in 1937; the barnacle was smothered by a young frond of *Laminaria* the holdfast of which grasped the barnacle. The crab thus gave every indication of not having moulted since the spring of 1937 and it was again concluded that the externa had been in position for at least a year. In the collection of 1938–9 there were several crabs bearing two generations of barnacles.

Taking the evidence of colour and the incrusting organisms together it is impossible to avoid the conclusion that there is no evidence of any definite

allotted span of life for the externa when the parasite occurs on *Carcinus maenas*. It is true that "scarred" crabs are met with and that sometimes a crab with externa bears the scar of former externa. This, of course, may be due either to the regeneration of the parasite or to a second infection. When keeping crabs in captivity it was found that damage to externa usually resulted in their disintegration and also in the death of the host. No evidence has been obtained to suggest that the shrivelling and dropping of the externa is a normal part of the life history when *Sacculina* is affecting this host. The "scarred" crabs which are found may easily have lost the externa by suffering accidental damage.

Note on the Modification of Male Hosts

There has been much controversy as to whether there is any correlation between the size of the male host and the degree of modification of its secondary sexual characters caused by the presence of the parasite. Potts (1909), working on *Carcinus maenas*, failed to find any such correlation, whereas Day, working on *Portunus holsatus*, found a degree of correlation which he summed up thus: "This shows quite clearly that among externally parasitized crabs... the smaller the crab the greater the liability to be modified to a maximum extent. This is not the same as saying that the smaller the crab the greater the degree of modification...."

In the present work the degree of modification of the male hosts has been noted by a method rather similar to that used by Day but which differs in certain details. The males have been divided into three groups. In group 1 were placed those males which had undergone little or no modification of the abdomen and redivision of the fourth and fifth abdominal segments was not complete; in group 2 were placed all those which showed moderate modification; and, in group 3, were placed the few that showed closest approximation of the abdomen to the female condition. The results are tabulated in Table VI. The carapace breadth was measured to the nearest millimetre and is the distance between the postero-lateral spines.

Table VI. Modification of Abdomen in Male Crabs

	Group 1	Group 2	Group 3
No. of males occurring in group	22	63	6
Width in mm. of carapace of smallest and largest crabs in group	48–77	39–68	38–52
Average width of carapace in group in mm.	63·5	51	48

These results are closely comparable with those of Day and show that while the degree of modification of a crab does not depend on its size, the larger the host the less liable it is to modification, and the smaller it is the greater the amount of modification which may take place. Thus *Carcinus maenas* behaves here in the same way as *Portunus holsatus*.

Discussion

The life history of *Sacculina carcini* as it occurs in the Clyde sea area, where *Carcinus maenas* is the host species of crab, shows two important differences from the life history which has been recorded for it when *Portunus holsatus* is the host. These differences are: (1) The breeding season on *Carcinus maenas* is long and in the Clyde probably extends from late spring until late autumn (June or July to December), whereas, on *Portunus holsatus* in the Mersey area, the breeding season is comparatively short and is at a maximum in the early spring, at a time when the breeding in the Clyde is almost minimal. Correlated with this difference in the breeding season the young *Sacculina* externa appear at different times in the two localities. (2) When *Carcinus maenas* is the host the evidence suggests that there is no definite limit to the longevity of the externa; on *Portunus holsatus* the persistence of externa after a short breeding period was considered by Day to be abnormal.

When the breeding period of *Sacculina carcini* on *Carcinus maenas* in the Clyde is compared with what has been found at Roscoff and Plymouth a geographical effect can be noted, and, as would be expected, the phases of the life cycle occur somewhat later in the year in the more northerly locality. Thus it is clear that the differences found when *Sacculina carcini* is parasitizing *Portunus holsatus* are not geographical in origin but can be ascribed to a difference in the host-parasite relationship.

It has been shown that the length of the breeding period of the parasite bears a close relationship to the length of that of the host, and it has also been noted that while it is considered abnormal for the externa to be retained on *Portunus holsatus* after the breeding season, there is evidence that, on *Carcinus maenas*, the externa may persist for the remainder of the life of the host. Thus it might be said that *Sacculina carcini*, with its longer breeding period and longer external life, is more perfectly adapted to parasitizing *Carcinus maenas* than *Portunus holsatus*.

These points might be more acceptable if the parasites of the two species of crab were to be regarded as different species, but, according to Boschma (1937), there are no constant differences of sufficient magnitude between the parasites to warrant their separation into two species on morphological grounds. However, it may not be without significance that, in the Clyde area, although *Portunus holsatus* is not an uncommon species, there are as yet no records of it being parasitized by *Sacculina* in this locality. If we accept the view that variation in host species is the sole cause of the variations met with in the life history of the parasite we might reasonably expect some proportion of the *Portunus holsatus* in the Clyde area to be parasitized.

In the present state of our knowledge it seems best to regard the parasites of the two species of crab as identical, but it may be suggested that we are seeing a division into biological races. It may well be that *Sacculina carcini* is primarily

a parasite of *Carcinus maenas*, but that, under certain circumstances, it can adapt itself to parasitize *Portunus holsatus* and that in so doing its life history undergoes some modification.

Summary

The life history of *Sacculina carcini* parasitic on *Carcinus maenas* in the Clyde sea area is discussed and the breeding period and the time of the emergence of the young externa are indicated. The time and duration of the breeding season are compared both with what has been found at Plymouth and Roscoff for the same species of parasite on the same host crab, and also with what was found by Day (1935) who worked in the Mersey area on *Sacculina carcini* but parasitizing *Portunus holsatus*.

The length of life of the *Sacculina* externa and their ultimate fate are discussed. It is shown that in male crabs which act as hosts the liability of the secondary sexual characters to modification is correlated with size.

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