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THE EFFECTS OF PARASITIC AND OTHER KINDS
OF CASTRATION IN INSECTS

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THE EFFECTS OF PARASITIC AND OTHER KINDS OF CASTRATION IN INSECTS¹

WILLIAM MORTON WHEELER

WITH EIGHT FIGURES

I. THE EFFECTS OF STYLOPIZATION IN WASPS AND BEES

The perusal several years ago of a very interesting paper by Pérez ('86) on bees of the genus *Andrena* infested with *Stylops* led me to undertake a similar study of our North American wasps of the genus *Polistes* parasitized by *Xenos*. I began to collect stylopiized *P. variatus* during the autumns of 1898 and 1899, while I was living in Chicago, but the wasps proved to be too scarce to serve my purpose. During the summer of 1900, however, while I was spending my vacation at Colebrook, in the Litchfield Hills, Connecticut, I noticed many specimens of *Polistes metricus* Say infested with *Xenos* (*Acroschismus*) *wheeleri* Pierce and I at once began to collect them.²

In ten days during the latter part of August I gathered one thousand specimens of the *Polistes* from flowers of the golden

¹ Contributions from the Entomological Laboratory of the Bussey Institution, Harvard University No. 20.

² There may be some doubt about the specific names of the host and parasite here mentioned. I have called the wasp *P. metricus* as this is the name under which it is commonly known and because our extremely variable species of *Polistes* are in a state of great taxonomic confusion. Miss Enteman, who has studied them very extensively ('04), would probably refer my specimens to *P. pallipes* Lepelletier, while others would be inclined to regard them as belonging to *P. fuscatus* Fabricius. Brues ('09) and I had identified the parasite as *Xenos peckii* Kirby, but Pierce ('08), regards it not only as specifically, but also as generically distinct. He has given it the name *wheeleri* and placed it in a new genus (*Acroschismus*) because it has the œdeagus "considerably dilated at the base, arising between two claws," whereas Kirby's species is placed in another new genus, *Schistosiphon*, because it has the œdeagus "cleft at the apex." The old genus *Xenos* of Rossi he restricts to the European species (*vesparum* Rossi and *jurinei* Saunders). Although these generic distinctions may prove to be valid, I shall use the old name *Xenos* in the present paper.)

rod (*Solidago canadensis*) within an area of less than a square mile and noted the sex of each individual and the number, sex and position of the *Xenos* parasites which had protruded their heads between the gastric sclerites of the wasps. A further study of the form and coloration of the hosts was undertaken in the hope of detecting modifications, like those seen by Pérez in stylopized *Andrenæ*. My observations, however, gave much less interesting results than those obtained by the French naturalist, and I therefore refrained from publishing them and awaited an opportunity to continue them on additional material. This opportunity, however, has not presented itself, so that I have decided to give my observations for what they are worth, in the hope that they may be amplified by some other more fortunate observer. My preserved *Xenos* material was turned over partly to Miss Enteman, who published a short paper on the genital ducts of the females ('99), and partly to Mr. C. T. Brues who published a brief account of the embryology of the parasite ('03). The table on the page opposite contains the results of counting the sexes of both host and parasite on the different dates of collecting.

From this table the following conclusions, valid only, of course, for the particular summer and locality in which the insects were collected, may be drawn:

1. Of the total number (1000) of *Polistes metricus*, 251 or fully 25 per cent were stylopized. This is a high percentage, though as will be shown, it has been exceeded in the statistics of other observers. It may be regarded as too great, first because the parasitized individuals, being more sluggish, would be more easily caught, and second, because my interest in such specimens would lead me to exercise greater care in capturing them. I would say, however, in answer to such objections, that I attempted to collect the wasps at random without noticing whether they bore parasites or not, that a long handled net was used in capturing them, and that the table contains only specimens in which *Xenos* had already protruded their heads between the gastric segments of the wasps. A number of apparently unfested wasps were dissected and were found to contain larval parasites, so that the actual percentage of parasitism was even greater than that indicated in the table.

Number of Collection	Date	Total Number of Polistes Taken	Male Polistes	Female Polistes	Total Number of Infested Polistes	Number of Males Infested	Number of Females Infested	Total Number of Xenos	Number of Male Xenos	Number of Female Xenos
	August									
1	14	60	4	56	33	0	33	85	71	14
2	16	72	3	69	31	0	31	67	58	9
3	19	31	5	26	14	2	12	55	49	6
4	20	108	5	103	43	3	40	89	73	16
5	21	73	6	67	18	0	18	36	24	12
6	22	143	6	137	12	3	9	19	10	9
7	23	66	15	51	20	2	18	50	36	14
8	24	137	36	101	21	5	16	40	32	8
9	27	167	50	117	29	8	21	55	34	21
10	29	143	7	136	30	2	28	66	56	10
Totals:		1000	137	863	251	25	226	562	443	119
Aver. and per cent		100	13.7	86.3	25.1	2.5	22.6	56.2	44.3	11.9

2. The number of male *Polistes* increased very suddenly August 23 to 27 and then fell off still more abruptly. Apparently these collections were made at the time of the emergence of the male brood for the particular locality.

3. The greater difference in the ratio of male to female *Polistes* (1 : 6.3) is to be accounted for partly by this temporary appearance of the males and partly, perhaps, by the fact that this sex is much more wary and therefore more difficult to capture than the females.

4. While the total number of females examined was somewhat more than six times as great as that of the males, the number of females stylopized was fully nine times as great as that of the stylopized males. As the male brood of the wasp appears late in the season this may be due to a partial immunity of this sex from the attacks of the parasites, since Brues ('05) has shown that the triungulin *Xenos* must enter the wasp larvæ in the spring or early summer (*vide infra*, p. 393.)

5. The table shows that the sexual ratio of the *Xenos* (3.7 males to 1 female) was almost the reverse of that of the sexual ratio of the *Polistes*. That the male parasites should be nearly four times as numerous as the females is easily explained, however, from the fact that the males are so much smaller than the females that more of them can develop to maturity in a single host.

In addition to these more general conclusion, a number of more

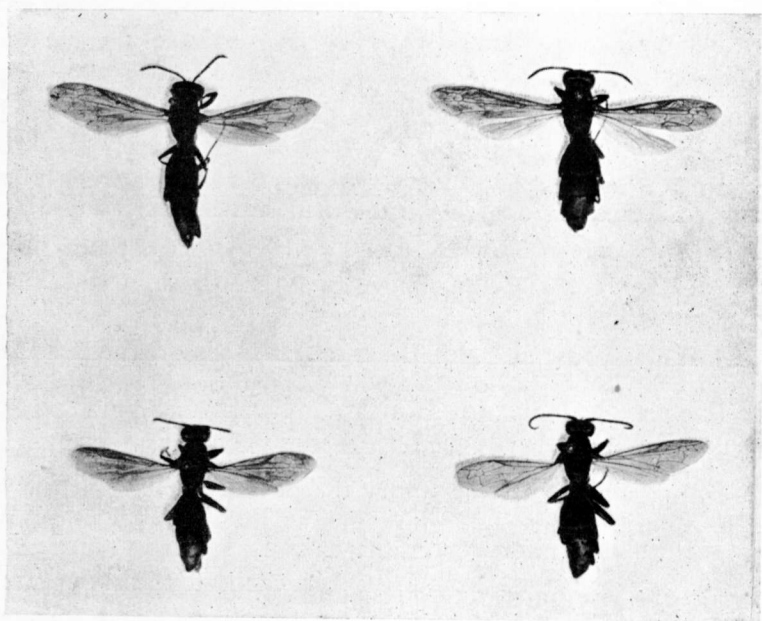


Fig. 1. Specimens of *Polistes metrica* heavily parasitized by *Xenos* (*Acroschismus*) *wheeleri*.

special deductions may be mentioned, based on the daily tables which are too long and complicated to be inserted here:

1. The number of *Xenos* in a single *Polistes* varied from 1 to 11. The latter number was taken from only three wasps and these were all females. Ten *Xenos* were taken from a single individual, also a female, and as a rule the higher numbers, *i.e.*, 5 to 9 were all taken from wasps of this sex, but one male contained 8 of the parasites. In the great majority of infested specimens only one

or two *Xenos* were present. The table shows that the average number in all the infested wasps was about 2.4. These numbers probably represent the few survivors of an originally much greater number which had lived as larvæ in the individual larval wasps. Brues ('03) took as many as 31 larvæ of *X. pallidus* of both sexes from a single larva of the Texan *P. annularis*!

2. Both sexes of the *Xenos* may occur in the same *Polistes*, but when the number exceeds 4, the *Xenos* are all males. In only one case did I find as many as 3 female *Xenos* in the same host; in all other cases there were only one or two. In 45 of the 251 infested *Polistes*, or in nearly 18 per cent, *Xenos* of both sexes occurred. Hence while there is undoubtedly a tendency, as Brues has observed ('03), for the sexes to be the same in the same host, this is so far from being a general rule, that the sex of the parasite cannot be supposed to be determined by its host.

3. When more than one female *Xenos* is present in the same *Polistes*, they are of the same size but each is smaller than the females occurring singly in a wasp.

4. When both sexes inhabit the same *Polistes* the heads of the females protrude between the more posterior segments, whereas the cephalic ends of the male puparia may protrude between any of the segments behind the first. The heads of the females therefore usually appear from under the posterior edges of the fourth or fifth abdominal segments. This is obviously an adaptation to the greater length of the female parasite, which has to lie stretched out in the abdomen of its host and could not protrude its head between the more anterior segments without bending its body. Sometimes both sexes protrude their heads side by side from under the tergite or sternite of the same segment. Sometimes one sex is on the dorsal, the other on the ventral side of the same wasp, but protruding from the same segment.

5. When the female *Xenos* protrudes its head between two tergites, it lies with its ventral surface uppermost, *i.e.*, its dorso-ventral orientation is the reverse of that of its host: when it protrudes its head between two sternites, it lies with its ventral surface downward, *i.e.*, with the same dorso-ventral orientation as the wasp. This is obviously an adaptation to copulation with the winged

male; for the latter must have to insert its penis along the ventral surface of the head of the female and immediately under the overlapping sternite or tergite of the host.

That several of the conclusions drawn from the table on page 379 cannot have general validity is shown by comparing them with the statistics of other observers. Horne ('72) says that the specimens of *Polistes hebraeus* which he observed in India were "extremely troubled with *Stylops* (*Xenos*), every fifth or sixth one taken having a female of one under one of the segments of the abdomen." Theobald ('92) found that among 180 *Andrena lapponica* taken in England during 1887, 105 or 58 per cent contained *Stylops*; of 60 bees of the same species, taken in 1888, 54 or 90 per cent were badly stylopized. He believes that the female *Andrenæ* are more afflicted with the parasites than the males, and he records the number of *Stylops* found in the 54 bees taken during 1888 as comprising 33 females and 21 males; 2 females each contained 2, 3 males contained 2, 25 females and 18 males 1 each. The corresponding numbers for 40 stylopized specimens of *Andrena nigroænea* were 3 females each with 3 *Stylops*, 1 male with 3, 3 females with 2, 5 males with 2, 16 females with 1 and 12 males with 1, making 22 females and 18 males. On the basis of these figures Theobald differs from Perkins ('92), who found the males of various *Andrenæ* and *Halicti* more frequently stylopized than the females. This author says that he has seen hundreds of stylopized male *Halictus tumulorum*, but has never seen a female in this condition. Although Theobald's conclusions agree with my own, his data do not furnish very strong support in favor of his contention, since in *A. lapponica* the ratio of parasitized males to females is 1:1.5 and in *A. nigroænea* only 1:1.2. Skinner ('03) counted 34 stylopized individuals among 140 *Polistes texanus*, which he found at Pecos, Texas. He says that "most of the *Xenos* appeared to be females and only 4 males were secured."

The percentage in this case is very similar to that which I found in *P. metricus*. Brues ('05) has published some statistics on two colonies of the Texan *P. annularis* infested with *Xenos nigrescens* Brues and *X. pallidus* Brues. In these cases the amount of para-

sitization was very great. In one nest there were 86 wasps, 44 or 51 percent of which contained *X. nigrescens*. There were from one to seven in each wasp (an average of 2.6 per host), and of the total number of *Xenos* (94), 91 were males and only 3 females. In the other nest there were 42 wasps, and 36 or more than 85 per cent were stylopized. The total number of the parasites—in this case *X. pallidus*—was 125 (81 males and 44 females); the highest number in a single wasp being 10, the average per host 3.6.

Fuller consideration must be given to the effects of the stylopids on their hosts. This may properly begin with a résumé of the excellent work of Pérez (1886) who examined stylopized specimens of 47 species of *Andrena*. The effects produced by *Stylops* in these bees is so considerable as to render their specific determination difficult. This is not surprising perhaps, when we consider the vast number of closely related species in the genus. All the known specimens of certain "species" (*F. Smith's Andrena insolita, separata and victima*) have been found to be stylopized, which gives force to Pérez's opinion that these are not true species but merely parasitized individuals of forms that are already known under other specific names. Pérez describes minutely the following modifications as characteristic of stylopized *Andrenæ*: (1) The abdomen is shortened and swollen and therefore more globular, the shortening being due to an attenuation of the terminal segments. (2) The head is usually smaller than that of normal specimens. (3) The villosity of the abdomen is more abundant, longer and more silky, especially on the terminal segments, and its color is often greatly altered, becoming lighter and more reddish or fulvous. The villosity of the thorax may undergo similar but less pronounced changes. (4) The punctuation of the body becomes finer, denser and more superficial in correlation with the pilosity, which arises from the punctures. These changes are common to both sexes and therefore affect specific characters. They give the specimens a peculiar pseudo-specific facies. Pérez therefore rightly warns against basing new species of *Andrena* on stylopized individuals.

The following changes affect the secondary sexual characters:

(1) The normal males of the genus *Andrena*, as in many other

genera of bees, have a greater amount of yellow or white on the face or clypeus or on both than the conspecific females. Stylopization tends to diminish this light color very perceptibly and hence to make the face of the male resemble that of the female. In the female the parasites produce the reverse effect, making the face resemble that of the male. "It is difficult to find a stylopized male of *A. labialis*, e.g., whose face is normally colored and, on the other hand, it is quite as rare to find a stylopized female of this species having the face entirely black." (2) The normal female *Andrena* differs from the normal male in the structure of its hind legs, the tibiae of which are modified for collecting pollen. They are always robust and incrassated and have a brush of long, curved hairs, especially on their internal surfaces. Similar hairs are found also on the femora, coxae and metapleuræ. The metatarsal joint of the hind legs is also kilated or enlarged and is furnished with rows of stiff hairs on its lower surface. In the male the hind tibiae and metatarsi are slender and bear only short, sparse, straight hairs and this is true also of the coxae and metapleuræ. The presence of *Stylops* in the abdomen of the female diminishes the development of the pollen-collecting apparatus to such a degree that the hind legs become like those of the male. The reverse occurs in stylopized males, the organs under consideration becoming more enlarged and approximating to the female type in their pilosity. The modifications in this sex, however, are rarer than in the female and in both sexes they vary greatly in different stylopized individuals. (3) The frontal furrow near the internal orbit of the eyes, which is filled with velvety pubescence, is well-developed in the normal female, but feeble or absent in the normal male. In stylopized *Andrenæ* this furrow may undergo diminution of development in the female and becomes accentuated in the male. (4) Although the female *Andrena* has 12-jointed, the male 13-jointed antennæ, there is no modification of the number of joint in parasitized individuals. The antennæ of the normal sexes may differ in the length of the second funicular joint. In one species, *A. Trimmeriana*, the second funicular of the normal female is as long as the two succeeding joints taken together, whereas in the normal male this joint is at most half as long as the succeeding

joint. In the stylopized male of this species Pérez found the second funicular attaining to two-thirds the length of the third joint and to this extent approximating to the conditions in the female. (5) The normal female *Andrena* bears a fringe of long hairs, the ana fimbria, on the edge of the fifth abdominal sternite, but this fringe is lacking in the normal male. Stylopization tends to suppress the development of the fimbria or causes it to disappear completely in the female and more rarely has the reverse effect on the male. (6) The sting, which is peculiar to the female, is reduced in size in the parasitized individuals, the copulatory organ of the male is also reduced in length and becomes narrower and less curved, while the paramera tend to become atrophied.

Pérez concludes from these observations that, so far as the secondary sexual characters of *Andrena* are concerned, the modifications induced by the Stylops are not merely attenuations, but actual inversions of development. "The stylopized *Andrena*, male or female, is not merely a diminished male or female; it is a female which takes on male attributes; a male that takes on the characters of the female."

The intimate correlation which exists between the structure and instincts of all organisms, leads one to look for instinct peculiarities corresponding with the morphological inversions described above. Pérez found only one stylopized female *Andrena* which had its hind legs charged with pollen, and he therefore concludes that the stylopized bees rarely or never forage or build nests like the normal females. Normal and parasitized bees of both sexes, however, visit flowers as this is not a unisexual instinct, and hence the triungulins produced by the Stylops have an opportunity to move off onto the plants, climb onto normal foraging bees and thus get transferred to the brood in incipient nests. In this way the perpetuation of the parasites is insured through a line of bees capable of nourishing them.

The internal changes due to stylopization have been studied by Newport (48), Pérez and Perkins (92). All of these authors find that the testes and ovaries are not destroyed by the parasite but are more or less reduced in size, in the male sometimes only on the side of the body bearing the Stylops. In the female the oöcytes

or ova degenerate in their follicles and are evidently quite incapable of development, in the male there may be ripe spermatozoa in at least one of the testes. Perkins found motile spermatozoa in all the stylopized males which he dissected, and Pérez mentions a male of *Andrena decipiens* taken *in copula*, so that this sex may retain, at least occasionally, not only the normal mating instincts, but the ability to fecundate normal females. The parasites before maturity live on the fat-body and blood-tissue of their hosts and do not attack the other organs directly. These undergo partial atrophy through lack of nutrition. Observations similar to those of Pérez have been published by Saunders ('82) and Schmiedeknecht ('83).³

Turning now to *Polistes*, we find that in this genus the secondary sexual characters are in certain respects quite as clearly developed as in the andrenine bees, but as wasps do not collect pollen, the hind legs show no special modifications in the female. The following are the main external sexual differences observable in *Polistes metricus*: The male has a slender thorax and long, narrow abdomen. The antennæ are 13-jointed, with a long, slender funiculus, not enlarging towards its tip; the second funicular joint is little if any longer than the two succeeding joints taken together. The face is long and narrow, with a pair of longitudinal grooves running from the antennal insertions to the clypeus and separated by a prominent longitudinal welt or elevation. The clypeus is flat or even slightly concave and its surface is impunctate. The whole face and clypeus, the anterior surface of the antennæ to within a few joints of the tip of the funiculus, the anterior surface of the coxæ, femora and tibiæ, a series of transverse bands or spots on the abdominal sternites behind as well as including the first segment, are sulphur yellow. The two large ferruginous spots on the first abdominal segment are usually well-developed.

In the female the thorax is proportionally stouter and the

³ Though the publications of these authors antedate the article above reviewed, we are not to infer that this implies priority of discovery. Pérez says that he originally called the attention of these investigators to the facts and had himself published a preliminary account of his researches as early as 1880 in the *Revue Internationale des Sciences*, Tome I.

abdomen is decidedly shorter. The antennæ are 12-jointed, with a shorter funiculus slightly enlarging towards its tip; the second funicular joint is nearly as long as the three succeeding joints taken together. The face is decidedly shorter than that of the male, the grooves and welt much less pronounced and the clypeus is convex and coarsely punctate. The face is black, with the internal orbit and sometimes portions of the clypeus, the anterior surface of the scape and of the two first funicular joints, the anterior surfaces of the tibiæ and apical portions of the femora, ferruginous. The sulphur yellow is restricted to the tarsi and the posterior border of the first abdominal tergite, and the ferruginous spots on the first abdominal segment are obscure or wanting. The wings are often somewhat more deeply infuscated than in the male.

In stylopized *Polistes metricus* of either sex I fail to find any modifications of a morphological character which could be definitely attributed to the presence of the parasites. A few of the more heavily stylopized females were abnormally small, but with these exceptions, all the wasps were of normal stature. No modifications of the antennæ nor of the structure and proportions of the face could be detected. A study of the coloration, however, yielded more positive results, but even here, owing to the great range of color variation to which *P. metricus* like all our other species of the genus, is subject, the results are not capable of very precise formulation. In the coloration of the face stylopized males show no tendency to approach the female. In 14 out of 25 heavily stylopized females I find the clypeus of the usual black or dark brown color; in the remaining 11 it is more or less ferruginous or yellow. Some specimens have the free border of this sclerite sulphur yellow or its whole surface ferruginous, or only its posterior border or sides of this color. One specimen has the clypeus ferruginous with a small black spot in the center. It would be possible to regard these cases as approximations to the male type of coloration due to parasitism, were it not that perfectly normal, unstylopized females not infrequently exhibit the same erythrism of the clypeus. I have not seen a sufficient number of *P. metricus* from different localities to be able to determine

whether the percentage of this modification is so much greater among stylopized than among unstylopized individuals as to show that it must be attributable to the influence of the parasites. I am inclined to believe, however, that it is part of a more general erythrism which affects also the abdomen of many parasitized individuals. This region, to a varying degree in such specimens, but undoubtedly to a greater degree in those that are most heavily stylopized, takes on in both sexes alike a distinct ferruginous tinge which is usually most pronounced towards the posterior borders of the tergites and sternites. Sometimes it may be very strongly developed as in one rather small female taken August 29, and bearing three male *Xenos*. In this case the second gastric segment is entirely ferruginous, with the exception of a black anteromedian triangle, and the posterior half of each of the remaining segments and the whole clypeus, except its anterolateral corners, are rich ferruginous. I have failed to notice in the legs, wings and antennæ of either sex in stylopized specimens any color modifications that could not be regarded as falling within the wide limits of normal specific variability.

The color modification here described is not confined to stylopized specimens of *P. metricus*. It has also been observed by Brues ('03) in two of the Texan species, *P. rubiginosus* and *annularis*. "The stylopized *Polistes*," he says, "can be recognized even before the heads of the pupa cases begin to appear between the sclerites of the abdomen, by their paler color. They seem never to become as darkly colored as normal specimens. This lighter color of parasitized specimens seems to apply only to the originally dark species, in *P. rubiginosus* there seems to be but slightly if any lighter coloration. In the specimens of *P. annularis* from which I raised *Xenos*, all of them females, the faded appearance is especially noticeable upon the dorsum of the abdomen. The first abdominal which is normally piceous with a narrow apical yellow band is in this case almost entirely bright ferruginous, or is ferruginous with the border yellow. The remainder of the abdomen is normally piceous, but the posterior margins of the segments, especially the second and third tend to become more or less broadly dull ferruginous in stylopized specimens."

There is also a modification of behavior in stylized *Polistes*. Several observers have noticed that such individuals are more sluggish, that they fly about less actively, and Brues ('03) has found that they are less inclined to use their sting, probably because the voluminous parasites interfere with the exertion of this organ. A similar inability is observed in queen honey-bees with ripe ovaries and in worker honey-bees with their crops full of honey. The peculiarities of behavior in stylized wasps are such as would be expected in parasitized organisms for these almost invariably exhibit a general reduction of vitality due to malnutrition.

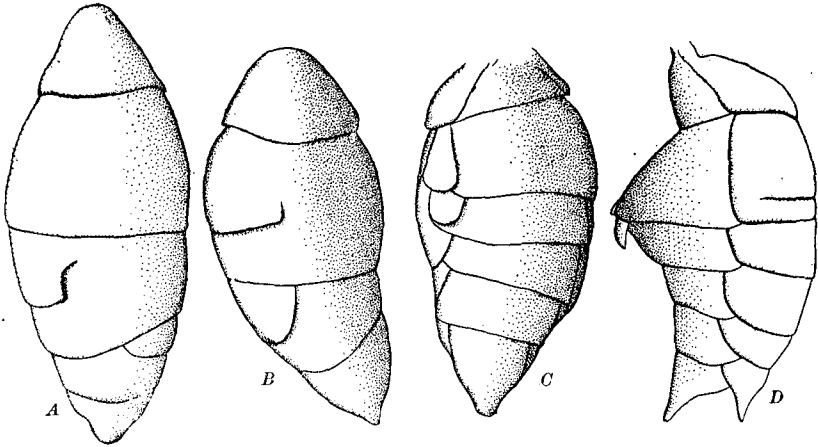


Fig. 2. Abnormal abdomens of *Polistes metrica*; A and B, dorsal; C, ventral; D, lateral view.

Among the unstylized female *Polistes* taken at Colebrook there were three specimens with abnormal abdomens. Sketches of these are shown in Fig. 2. The segments in some cases were partially divided on either the right or left side, and in one case there were several supernumerary sclerites. It might be inferred that these abnormalities were the result of stylization, for although no *Xenos* were found in the specimens, these parasites may have been present in the larvæ from which the anomalous individuals developed. I doubt this, however. At any rate, the anomaly in question is not peculiar to wasps that are subject to

stylopization or indeed to insects. Janet ('03) describes and figures a very similar abnormality in *Vespa rufa*, an insect that is not afflicted with *Stylops* or *Xenos*, and Cori and Morgan ('92) show that similar abnormalities are not uncommon in earthworms and cestodes. In the case of *Polistes* the abnormality must be produced either in the early embryonic stages while the metameres are forming or at the time of the formation of the abdominal sclerites in the pupa.

We may conclude, therefore, that *Xenos* produces no modifications of the secondary sexual characters of its *Polistes* host comparable to those produced by *Stylops* in the bees of the genus *Andrena*, but merely a tendency to a reddish coloration of the abdomen and face, a tendency which, so far as the abdomen is concerned, is manifested equally by both sexes.

This general lightening of color in stylopized *Polistes* and its reddish tinge remind one at once of the similar changes observed by Pérez in *Andrenæ*, although in the latter insects it seems to be confined to the pilosity. Pierce ('09, p. 32), cites the following observations, which show that a similar change of color was long ago observed by Saunders in stylopized bees of the genera *Prosopis* and *Hylæus*: "*Prosopis gibba* occasionally exhibits irregular rufous patches on the abdomens of affected individuals (Saunders, '50). *Prosopis rubicola* exhibits color changes regularly. The nymphs of those *Hylæi* which are likely to produce the pale-colored specimens (*H. versicolor*), which prove, as anticipated, to be only a variety of the *H. rubicola* consequent upon parasitic absorption, may usually be identified within one or two days of their final metamorphosis by assuming a yellow tinge, and may be set apart as certain to produce male parasites. (Saunders '52.)" It is not easy to account for this modification. Brues is inclined to believe that "the reason that the reddish *Polistes* are not affected, is that red is a more primitive color than piceous and that the color simply becomes arrested at this stage and does not tend to become so before the red stage." The question of the development of variations of color in the species of *Polistes* is a very complicated one, as Miss Enteman ('04) has shown, and a number of possible explanations of the erythrism of stylopized individuals might be

suggested. The ontogenetic explanation suggested by Brues is one of these, implying that a red stage precedes the brown or black of the mature form of dark species like *P. metricus*. This is borne out by the development of the color pattern in such species. On this view stylopization inhibits color development in an ontogenetically and presumably therefore in what corresponds to a phylogenetically earlier stage. A second explanation is, however, suggested by Miss Enteman's studies. These tend to show that the dark-colored races or species of *Polistes* are due to cold and moisture, the lighter yellow and red forms to heat and aridity. This seems to be clearly indicated in the distribution of the species, *e.g.*, in such extreme forms as the yellow *P. texanus* and the black *canadensis*. It is possible, therefore, that the erythrism of stylopized *P. metricus*, which in normal coloration is closely related to *P. canadensis*, is due to withdrawal of water from the tissues by the developing parasites. This does not contradict the ontogenetic and phylogenetic explanations but supplements them, if we suppose that the primitive yellow or red color cannot pass on to the piceous or black stage unless the tissues contain a sufficient amount of water. Miss Enteman has shown that the piceous or black color is in the form of pigment granules in the chitinous cuticle of the wasp's integument, whereas the yellow is deposited in the hypodermis. Erythrism is probably due, therefore, to a diminution in the cuticular pigment which permits the yellow hypodermal pigment to shine through. As both kinds of pigment are the result of metabolism in the pupa, we can see how a disturbance of metabolism either through withdrawal of water by the parasites or through other causes might lead to the deposition of a smaller amount of the black pigment and hence to erythrism.

It is more difficult to account for the absence of all modifications of the secondary sexual characters in stylopized *Polistes*, when such modifications are so evident in *Andrena*. We may, perhaps, account for this difference on one of the following hypotheses:

1. As will be shown in the sequel, complete extirpation of the gonads in young larval insects, has produced in the few species on which it has been performed, no appreciable effects on the development of the secondary sexual characters. This indicates that

these characters may be so fixed and so nearly independent of the gonads, except, perhaps, in the very earliest larval or late embryonic stages, as to remain quite unaffected in their development after the gonads have been completely removed. The degree of this independence may be supposed to differ in different insects and even in different individuals of the same species. It may be slight or almost absent in *Andrena* and very well marked in *Polistes* and this may account for the differences between the stylized specimens in the two genera.

2. The difference in the manifestation of changes in the secondary sexual characters may, however, be due to ethological differences between the two genera. *Andrena* has only male and female forms and both under normal conditions are adequately fed in their larval stages. In *Polistes* the larvæ of the earlier broods in the annual series, as Marchal has shown ('96, '97) are poorly fed and as a result become sterile females, or workers. As imagines they maintain themselves in a sterile condition by appropriating very little of the food they collect to their own use, since they at once lavish it in feeding the succeeding broods. Hence the females of these earlier broods become sterile, in the first place through alimentary castration of the larvæ from which they develop, and in the second place, maintain themselves in this condition as adults through the nursing or nutritive function (nutritive castration). These peculiar phenomena will be more fully discussed in the second part of this paper. Owing to these two forms of physiological castration inhibition of the development of the reproductive organs is a common and normal occurrence in *Polistes* females, and the parasitic castration induced by *Xenos* would not be expected to produce somatic changes of such magnitude or of such a nature as Pérez has observed in *Andrena*, all the females of which are normally fertile mothers. In other words, the effects of the *Xenos* on their hosts is of the same nature as the alimentary castration to which all the earlier broods during the seasonal development of the *Polistes* colony are normally subjected, and this probably accounts for the absence of any specific effects on stature and structure and the evident ease with which the voluminous parasites are borne and tolerated.

In the case of the male *Polistes* the matter is not so readily explained, since this sex is not subjected to the two forms of normal physiological castration just mentioned. But it should be noted that the effects of stylopization on the secondary sexual characters of the male even in *Andrena* are rarer than in the female (*vide*, p. 384), owing to the fact that castration is much less complete in this sex, as both Pérez and Perkins have shown. This is, no doubt, also the case in *Polistes*, for the development of the testes requires much less food than does that of the ovaries, and the presence of the *Xenos* probably, therefore, has much less effect on this sex.

It has long been known that male puparia and adult female *Xenos* are found only in the late summer or fall brood of *Polistes* in the brood, namely, which consists of fertile females and males that are to mate and provide, after hibernation, of individuals of the former sex, for the formation of new colonies during the ensuing spring. Brues ('05) captured on May 22 a large overwintered female of *P. rubiginosus* containing a female *Xenos nigrescens* that gave birth to a lot of triungulin larvæ. Evidently, therefore, the larvæ of the wasp must be infested with triungulins in the spring, soon after the colony is founded. How come it then, we are led to ask, that the adult *Xenos* appear only in wasps belonging to the last or autumn broods? If these wasps really belong to so late a brood they could not become infested, unless we suppose that the triungulins hang about the wasps' nest for a long period before entering the larvæ. As this assumption is very improbable, we seem to be forced to the conclusion that the wasps that bear the *Xenos* in the late summer really belong to early broods which have been greatly retarded in their larval and pupal development. Dodd ('06) and Howard ('08) have published some interesting observations which show that the larvæ of other insects (Lepidoptera, Formicidæ) parasitized by chalcidids are greatly retarded in their growth and development. If this occurs also in *Polistes* larvæ infested with *Xenos*, as seems probable, we may be able to account for the facts and understand how the single generation of *Xenos* manages to survive till the following spring to insure the perpetuation of the race in healthy,

incipient colonies of the wasps. The triungulins are, in all probability, carried to these colonies by healthy wasps from the flowers onto which they crawl from their mothers after hibernating in their hosts.

Since the foregoing paragraphs were written Pierce's fine monograph of the Strepsiptera has appeared ('09). This work contains such a full summary of all that has been published on this remarkable group of insects, together with so much new matter, that I should have thought it unnecessary to publish the preceding pages, but for the fact that they were written for the purpose of elucidating a problem which Pierce treats only incidentally. Of the many interesting facts contained in his paper I shall cite only a few which have an immediate bearing on the matters considered above.

The fullest statistics given by Pierce relate to two large colonies of *Polistes annularis* infested with *Xenos pallidus*. These colonies, which were collected at Rosser, Texas, September 23, together contained 1553 wasps, 1311 males and 242 females. Of these 266, or 17.1 per cent were stylopized, 259 being males and only 7 females. The highest number of *Xenos* observed in a single wasp was 15, and this occurred in a male specimen! Pierce also cites some statistics published by Austin (1882) on 50 *Polistes metricus* collected at Readville, near Boston, Mass., August 20, 1879. Of these wasps, 14 of which were males and 36 females, 9 or 18 per cent were stylopized (2 males and 7 females).

Pierce figures the abdomen of a male wasp (*Leionotus* (*Odynerus*) *annulatus* Say) which has the sclerites much distorted as in the *P. metricus* shown in Fig. 2. Concerning his specimen, which contained a female *Leionotoxenus hookeri* Pierce, he says: "It seems that in pushing itself out between the segments the parasite completely split the dorsal tergites of segments three, four and five and split segment two half way to the base. The parasite was located behind segment three." He cites the observations of Pérez on the effects of stylopization in *Andrena* and adds the following modifications observed by Crawford in specimens of *Andrena crawfordi* infested with *Stylops crawfordi*:

"1. Puncturation of abdomen less strong, punctures finer and sparser; especially noted on second segment.

"2. In females with male parasites the basal joint of the hind tarsi is narrower, approaching the shape of the corresponding joint of the male tarsi; this joint not noticeably narrowed in female with female parasites.

"3. Scopa of parasitized female thinner, plumosity shorter, not so silky.

"4. Out of six males with male parasites two show the second transverse cubital gone in both wings; one has stubs at each end, however, in right wing; one has the transverse cubital slightly interrupted in both wings. Out of about 110 nonparasitized males none show any variation.

"5. Out of 38 females with male parasites one has the left wing with three submarginals, the right wing with two submarginals; one has two submarginals in both wings but right wing with a stub of the nervure; one has first transverse cubital of the left wing one-half gone; forty-five nonparasitized females show no variation.

"None of the other salient alterations found by Pérez could be expected in this species because of the close resemblance of the two sexes. *Andrena crawfordi* is a very generalized bee."

Pierce also calls attention to a single parasitized specimen of *A. advarians* in his collection, with a spurious nervure in the third discoidal cell, and believes that parasitism may affect the tracheation of the wings, a modification not observed by Pérez.

II GENERAL CONSIDERATIONS.

By employing the word "castration" in a broad sense to mean any process that interferes with or inhibits the production of ripe ova or ripe spermatozoa in the gonads of an organism, and not merely in the concise original meaning as the sudden and complete extirpation of the gonads, we are enabled to bring together a number of interesting but hitherto rather scattered facts which have a bearing on the correlation of the primary and secondary sexual characters. An adequate consideration of these facts would go a long way, I believe, towards preparing us for a profitable study of the recondite problem of sex determination.

Owing to the limits of this paper and to the fact that the dependence of the secondary on the primary sexual characters in vertebrates has been recently analyzed by several authors, notably by Herbst ('01) and Cunningham ('08), I shall confine my remarks very largely to the arthropods. Taking the word "castration" in the broad sense suggested above, we may distinguish:

1. *Surgical, or true castration, i. e.*, the sudden and complete ablation of the male or female gonads, so that the organism is deprived of its primary sexual characters, if we do not include in this term also the gonad-ducts and copulatory organs. This operation is of the greatest experimental significance, since, when performed at the proper ontogenetic stage, it has been shown to lead in many animals to interesting modifications of the secondary characters of each sex.

2. *Physiological castration.* Under this head may be included at least three different forms of inhibition in the development of the gonads, leading to a failure of the individual to develop its primary sexual characters, or, in other words, to an inability to function as a male or a female. This inhibition is brought about by an insufficient supply of nutriment and appears as the result of a well-known law, according to which the organism provides in the first instance for the growth and differentiation of its soma and develops its gonads on the nourishment in excess of that required for normal growth in stature and the complete differentiation of the various tissues. The following three forms of physiological castration may be distinguished:

A. *Alimentary castration.* This term was originally given by Emery ('96) to the suppression of gonadic development through insufficient feeding of the organism during its larval life.

B. *Nutritional castration.* This term was first used by Marchal ('97) to designate the maintainance of the gonads in an undeveloped condition in the adult, owing to the latter's devoting itself to nursing the brood of other fertile individuals instead of itself taking on the reproductive function.

C. *Phasic castration.* I use this term, for lack of a better, to include all the cases in which the gonads are inhibited in their development by seasonal or ontogenetic (growth) conditions. This

form of castration is not sharply marked off from the two preceding but may be made to include them, since both alimentary and nutritial castration can be suspended during the life time of the individual and normal reproduction supervene.

3. *Parasitic castration.* This term was first introduced by Giard ('87, etc.) in a series of studies on crustacea. It refers to the suppression or destruction of the gonads by parasites. By enlarging the scope of Giard's definition we can distinguish two forms of parasitic castration:

A. Individual parasitic castration, which is induced in certain organisms when they contain parasites, and

B. Social parasitic castration, which occurs in ants when one colony in becoming parasitic on a colony of a different species eliminates the sexual individuals of its host.

A number of illustrations will bring out the fundamental resemblances between these different methods of suppressing the reproductive function and the resulting modifications of the somatic characters of the individual or of their equivalents in animal societies.

1. Surgical castration.

The pronounced modifications of the secondary sexual characters observed in vertebrates, especially in birds and mammals, from which the gonads have been removed during early life, or in which these organs have become diseased, have led some investigators to look for corresponding modifications in the secondary sexual characters of insects subjected to a similar operation.

One observer, Hegner ('08), has succeeded in castrating the embryos of a chrysomelid beetle (*Calligrapha multipunctata*) by removing the very young sex-cells as soon as they are segregated in the protoplasmic accumulation at the posterior pole of the egg during the formation of the blastoderm. Although Hegner's experiment, which consisted in pricking the chorion at the posterior pole and allowing the sex-cells to flow out, was successful to the extent of demonstrating that the embryo may continue its development after the operation, nothing but a few young larvæ

were obtained. The experiment therefore, throws no light on the question with which we are here concerned.

Much more important are the results of experiments performed by Oudemans, Kellogg, Meisenheimer and Regen in castrating larvæ.

Oudemans ('99) was the first to attempt surgical castration in insects. He removed one or both gonads from male and female caterpillars of the gypsy moth (*Ocneria dispar*) before the last and second last moults. About one-third of the caterpillars (30 out of 86) survived the operation and produced moths. From a study of these, the Dutch investigator concluded that castration has no influence, either on the external appearance, *i.e.*, on the secondary sexual characters, or on the behavior of the moths, since the castrated males copulated, though they had no spermatozoa, and the females, though they had no eggs, nevertheless stripped from their abdomens the mass of long hairs in which they normally oviposit. Females castrated only on one side laid eggs, and three normal females that copulated with castrated males, laid eggs which developed parthenogenetically.

Kellogg ('04) succeeded in castrating silk-worm caterpillars (*Bombyx mori*) after the second, third and fourth moults by burning out the gonads with a hot needle. This method was very inferior to that employed by Oudemans. Not only was the mortality of the caterpillars greater, to judge from Kellogg's remarks, but the complete destruction of the gonads was obviously much less certain. Like Oudemans, he failed to detect any modifications of the secondary characters of either sex in cases in which dissection of the adult moths proved that the gonads had been completely destroyed.

More recently Meisenheimer ('07) has carried out much more elaborate experiments than either of his predecessors, on about 600 *Ocneria dispar* caterpillars, of which 186 yielded imagines. The smallest caterpillars castrated were between the second and third moults, and about $\frac{3}{4}$ cm. long, but he also used those between the third and fourth and between the fourth and fifth moults. He was able to remove the gonads even before the second moult but the larvæ were too delicate to survive the operation.

Three series of operations were performed: first, the removal of both gonads; second, the removal of the gonads together with the gonad-ducts; and third, the transplantation of testes into female and of ovaries into male caterpillars. The transplantation of ovaries was more easily performed than that of the testes. In these cases the transplanted organs not only developed to their normal size, but the ovaries in some cases even united with the male vasa deferentia. In one case a single transplanted ovary united with one of the vasa deferentia, and as the testes of the opposite side developed, an artificial hermaphrodite was produced. Meisenheimer describes the results of his operations as follows: "Oudemans' and Kellogg's experiments established the fact that the removal of the gonads exerts no influence on the secondary sexual characters. My results agree with these to the extent that in my experiments the originally male caterpillar always produced a male moth, the female caterpillar a female moth. The general habitus of the respective sex was always perfectly preserved, both in the form of the body, the structure of the antennæ and the coloration of the wings, and this was true of the operations, both in the case of the castrated moths and of the artificial hermaphrodites. But on examining, in a comparative way, the material obtained, a certain effect of the operations seems, nevertheless, to be noticeable. The moths subjected to the two kinds of operation may be arranged in series, which in the males vary from dark to light forms and pass over in the females from a whitish to a darker color." But, as Meisenheimer observed, there is considerable color variation in both sexes of normal gypsy moths, and this was true also of his control series, though he believed the variations to be greater in those developed from operated caterpillars. The specimens with transplanted organs, however, showed no greater modification than those of the castrated series. It is especially noteworthy that in the cases of transplantation there was no change in the copulatory or other organs, though these had not yet developed at the time of operating. Hence, although Meisenheimer made artificial hermaphrodites, he did not succeed in producing artificial gynandromorphs.⁴

⁴ Unfortunately I was unable to secure a copy of the first part of Meisenheimer's final monograph ('09) till after the manuscript of my paper had gone to press. The review here given of his experiments is, therefore, inadequate.

It will be noticed that the preceding experiments were performed only on holometabolic insects of the order Lepidoptera. As such experiments on ametabolic insects might be expected to yield different results, it is interesting to record that Regen ('09, '10) has recently succeeded in castrating crickets (*Gryllus campestris* L). In his first paper he gives us little more than an orientation experiment performed for the sake of determining whether the insects would survive the operation, but his second contribution brings ampler and more satisfactory data. In order to perform the operation he narcotized the crickets with CO₂. The testes were removed from 40 males (20 in the second last and 20 in the last larval instar), and the ovaries were removed from 10 females in the last instar. These 50 individuals were released in the open field and each returned to the burrow which it is in the habit of occupying throughout its larval life. The operated individuals were marked by cutting off portions of their wings, and near their burrows stakes were placed with records of the necessary data. After the crickets had reached maturity Regen recovered 9 males that had been castrated in the second last, 13 of those castrated in the last larval instar, and 6 females. The insects were left in their burrows. Ten days later he found that the crickets had changed burrows and there was a tendency for them to associate in pairs, each consisting of a male and female occupying a hole in common. Several individuals had migrated to other parts of the meadow in which Regen experimented, but he succeeded in capturing and placing in a terrarium 10 males (4 castrated in the second last and 6 in the last larval instar) and one female. On these specimens he made the following observations:

"1. Nine imaginal males, part of which had been castrated during the last and part during the second last larval instar, chirped throughout the remainder of their lives in as lively and shrill a manner as normal males. Only one of the males, which had been castrated in the last larval instar, chirped feebly and at rare intervals.

"2. The behavior of the castrated males towards the females was the same as that of normal individuals. They enticed the females with their shrill stridulation and when a female approached,

emitted a soft, whirring sound, and tried to affix their spermatophores to her, for

"3. The glands which secrete the spermatophore envelopes produced these structures up to within a short time of the death of the crickets and therefore performed their function independently of the testes.

"4. In external appearance the spermatophore envelopes of castrated males were in all respects like those of normal males (in some cases they were somewhat smaller), and contained a white secretion, which was less abundant than in normal spermatophores.

"5. The markings of the anterior wings, or tegmina and the development of the stridulatory organ showed no modifications.

"6. The females were unable to distinguish between normal and castrated males. They followed the call of the latter, mounted their backs and permitted them, as if they were normal males, to affix their spermatophore envelopes near the genital orifice.

"7. The castrated female behaved like one that had not been castrated. She thrust her ovipositor into the earth and made motions like a normal female, so that she had every appearance of desiring to oviposit. As time went on this "oviposition" became abnormal, as the female kept on thrusting her ovipositor into the earth but only to a slight depth."

Regen assured himself of the completeness of castration in these crickets by dissection and by examination of the spermatophores, which were found to contain no spermatozoa. He also kept a series of castrated individuals in captivity from the time of operation, and when these reached maturity they were found to behave exactly like the individuals that had been permitted to mature in the field. His experiments, therefore, gave results in complete harmony with those of Oudemans, Kellogg and Meisenheimer. It must be admitted that his insects were all castrated in rather late stages. He informs us, however, that during the summer of 1909 he successfully castrated a number of much younger larvæ, measuring only 5 to 8 mm., and that these had grown to a length of 20 mm., by December 1909 when he wrote his second paper. At that time the females were readily distinguishable

from the males by their ovipositors. He intends to remove the spermatophore glands from some of the males of this series and also from some uncastrated males and to report on the results in a further publication.

2. *Alimentary Castration*

The best examples of this form of castration are to be found among the social Hymenoptera, *i.e.*, among the social wasps, bees and ants. In these insects the majority of the female larvæ in each colony become what are called workers, because they are fed on a limited diet, grow very slowly, pupate more or less prematurely and hence as adults, or imagines are smaller in stature than the normal females of their respective species. These workers are also distinguished by other morphological and ethological peculiarities. Owing to their inadequate nourishment as larvæ, their ovaries are, as a rule, in a very rudimentary condition. Very striking examples of this alimentary castration are seen in the incipient colonies of ants, while the mother queen is bringing up her first diminutive brood of workers, in the species of *Carebara*, the queens of which are more than 1000 times as large as their sterile offspring, and in *Pheidologeton*, in which there is nearly as great a difference between the stature of the queen and that of the smallest workers. In bumblebees, honey-bees, social wasps, and most ants this difference is less pronounced, but it is nevertheless perceptible and clearly traceable to larval starvation. Opinions differ as to whether the other characters peculiar to the worker forms of these insects are the result of underfeeding, but it is evident that none of these can be regarded as an approach to the male type of structure. In other words, notwithstanding the very decided inhibitory effect of larval starvation on the development of the ovaries in the adult workers of the social Hymenoptera, the soma does not tend to become like that of the male, but merely departs to a greater or less degree from that of the female type. This departure is usually in the direction of greater simplification and is most pronounced in the ants, the workers of which are wingless, have a smaller and much simpler thorax and smaller eyes and ocelli.

The social Hymenoptera, however, are not the only insects which practice alimentary castration. A very interesting case is also seen in certain aphids of the genus *Phylloxera*, *e.g.*, in the *Ph. caryæ-fallax* recently studied by Morgan ('09). The stem-mother, or fundatrix of this insect makes and inhabits a hollow gall on hickory leaves. She lays numerous eggs which may give rise to two kinds of offspring. The eggs first deposited produce individuals that grow up to form the wingless sexuparæ, (Fig. 3*A*),

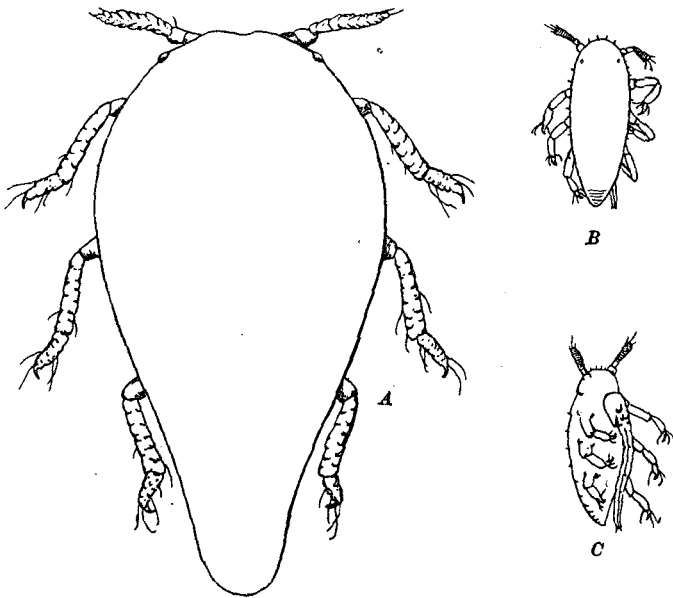


Fig. 3. Large wingless female of *Phylloxera caryæ-fallax*; B and C, dwarf females of same, drawn to same scale as A. (After T. H. Morgan.)

while the eggs laid later give rise abruptly to very small females, (Figs. 3*B* and *C*), which Morgan calls "supernumerary or dwarf females." These he describes as follows: "In the larger galls as many as 46 eggs may produce the large individuals, and then the smaller series abruptly begins; while in the smallest galls only one to three or four or more large individuals are produced when the small series begins. There seems to be here not a predetermined number of large and dwarf females, but the conditions

of life determine when the one kind ceases to be produced and the other begins. The two types of individuals must, however, be predetermined by alternative possibilities possessed by each egg. The supernumerary or dwarf females differ from their large wingless sister-forms, and from the young of the latter in a number of points. The shape of the body is entirely different and resembles that of the sexual male; but it differs from the male in two important respects; first, the dwarf individuals have a very long proboscis which in this species is absent in the male; second, there are no testes within the abdomen as in the males, where they form a relatively enormous mass. Otherwise the dwarfs are so similar in external form to the sexual males that their true nature was uncertain until they were studied in serial sections. These showed the absence of the testes and the presence of rudimentary ovaries and ducts resembling those of immature parthenogenetic females. There was nothing to indicate that the dwarfs could become sexual females. In fact the latter contain each an enormous egg when they hatch." Morgan believes that the dwarf females "are destined to a brief existence, and die without progeny," and he gives good reasons for supposing that they owe their origin to inadequate feeding of their parents. In other words, we have here a case of alimentary castration differing from that of the social Hymenoptera only to the extent that the mother insect provides her egg with an inadequate amount of yolk instead of feeding the larva from day to day on an insufficient amount of food. The resemblance of the dwarf females of *Phylloxera caryæ-fallax* to the workers of ants and other social insects is very striking, although it seems not to have been noticed by Morgan.

Perhaps the well-known "high" and "low" types of male in many insects, notably of the Scarabæidæ and Lucanidæ are to be regarded as the results of larval feeding. If this is the case, the low males may present examples of alimentary castration. This peculiar male dimorphism certainly bears more than a superficial resemblance to the female dimorphism of the social Hymenoptera. These may, indeed, be said to have high and low females, which, like the corresponding forms of the opposite sex in Scarabæidæ,

are sometimes connected by intermediates. In ants the soldiers and desmergates represent the intermediate forms.⁵

But no one, to my knowledge, has studied the testes of beetles with dimorphic males, with a view to ascertaining whether these organs are more imperfectly developed in the low than in the high individuals. The low males undoubtedly approach the female in form, and might, therefore, be said to assume the secondary characters of this sex, were it not for the consideration that in a large number of scarabæid and lucanid species and genera both sexes have the same simple form. This indicates that the low male simply fails to develop its secondary sexual characters and hence returns to the ancestral type of the species in which these characters were either very feebly manifested or were altogether absent. G. Smith ('05a) has shown that in the Scarabæidæ and Lucanidæ, as well as in certain crustacea (Tanaidæ), "the differentiation into high and low males within the limits of a species has widely influenced the progressive differentiation among the different closely related species of many groups." This is somewhat more clearly expressed by saying that there are also high and low species in certain groups, the larger species of certain genera having a more pronounced male dimorphism than the smaller closely allied species. This is also true of the sexual dimorphism of female ants, as is seen in such genera as *Solenopsis* and *Camponotus* and among the genera of the subfamilies *Dolichoderinæ*, *Camponotinæ* and *Mymicinæ*. It will be shown in the sequel that there is also another way of accounting for the "high" and "low" forms of some insects.

In this connection, I may briefly consider two cases which, if correctly reported, would appear to represent a complete loss of the reproductive organs by alimentary castration carried back into the early larval or embryonic period. Adlerz ('86) and Miss Bickford ('95) failed to find any traces of ovarian tubules in workers of the common pavement ant, *Tetramorium cespitum*. If this negative observation be correct, the workers of this ant must be regarded as utterly sexless. In my opinion, however, renewed investigation

⁵ For a fuller account of the conditions in these insects the reader is referred to my paper on polymorphism ('07).

is required to establish the truth of this statement. The other case is even more doubtful. Silvestri ('06) recently described *Copidosoma truncatellum*, a chalcidid which is polyembryonic and infests the eggs and caterpillars of moths belonging to the genus *Plusia*, as possessing two very different larval forms. One of these he designates as "asexual" and states that it lacks every trace of the reproductive organs. It is very unlike the ordinary sexual larva in having a large head, well-developed mandibles and a very slender nematode-like body, and never lives beyond the larval stage. Silvestri believes that it has been developed for the purpose of breaking down the tissues of the host caterpillar and of thus rendering them more easily assimilable by the sexual larvæ which alone develop into imagines. The following considerations seem to me to cast considerable doubt on this interpretation: First, the asexual larvæ figured and described by this investigator are suspiciously like certain very young ichneumonid larvæ, and as their development is not satisfactorily traced to the same cell-masses from which the sexual *Copidosoma* larvæ arise, it is not improbable that the two larval forms really belong to two very different parasites. In other words, Silvestri's *Plusia* caterpillars were probably infested with ichneumonid in addition to *Copidosoma* larvæ. Second, I have been unable to find any larvæ of the asexual type in a number of American *Plusia gamma* caterpillars which were heavily infested with *Copidosoma truncatellum*. Third, as in many species of Chalcididæ larvæ of Silvestri's sexual type are able by their own endeavors to break down and assimilate the tissues of their host, it seems improbable that a single species should have developed a peculiar sexless and moribund larva for this particular purpose.

3. *Nutritional castration*

The abortive or rudimental condition of the sexual organs seen in the cases of alimentary castration may be normally prolonged and maintained throughout the adult life of the workers among the social Hymenoptera, when these insects are compelled to live on the slender remnant of food that remains to them after

they have satiated their queens and the young broods which are continually hatching from her eggs. Marchal ('97) has called attention to this condition in the wasps, and it has long been known to obtain in ants and the social bees, though the causal connection between the protracted immaturity of the ovaries in adult workers and their primary function as nurses had not been sufficiently emphasized. The form of castration which is thus produced is, however, not necessarily permanent. If the trophic status of a colony becomes highly favorable, or if the queen dies, the ovaries of one or of a number of the workers may undergo active growth and produce eggs capable of normal development. In such cases the workers may be said to usurp or to supplement the function of the queen, but owing to the fact that the adult insect cannot modify its external characters, there is no visible difference between the sterile and fertile workers, except in the size of the abdomen, and even this may be so slight as to escape observation. The primary cause of nutritive castration is to be sought in the instincts of the individual itself, whereas alimentary castration would seem to be attributable to the instincts of the individual's living environment, *i.e.*, to its nurses. This distinction, however, is probably more apparent than real, since as I have suggested in a former paper ('07), it is possible that the worker larva is from the beginning an organism predisposed to assimilate only a portion of the nourishment with which it is provided by its nurses. The growth and development of the larva obviously does not depend on the amount of food administered to it but on the character and rate of operation of its assimilating mechanism. A larva may be very voracious, but its tissues may be constitutionally unable to appropriate more than a limited portion of the food which enters its alimentary tract. The administration of highly assimilable food, as in the case of the "royal jelly" which is fed to the larval queen bee, may be, as I have maintained ('07), primarily for the purpose of accelerating the development of her ovaries, and the secondary characters of this insect, which are mostly of an abortive character (smaller sting, shorter wings, smaller hind legs) may be the result of this development.

Nutritional castration is not confined to the social insects but occurs also in mammals during the periods of gestation and lactation and in birds during incubation, as the result of a very similar inability of the organism to expend in reproduction the energies demanded by the exigencies of the nursing function.

4. *Phasic Castration.*

The forms of sterility which I include under this term, though temporary, cannot be sharply distinguished from the cases of alimentary and nutritional castration, since both of these may be abolished during ontogenetic development and yield to a fertile phase, as, *e.g.*, when worker ants become gynæcoid and nymphal termites become supplemental males and females. We may, indeed, say that the great majority of animals exhibit alimentary castration during their embryonic, larval and juvenile stages, but that this is not universally true is shown by the many examples of neotenia and pædogenesis scattered through the animal kingdom. There are, however, several cases of temporary castration which, though intimately dependent on the trophic condition of the individual nevertheless do not properly fall in the categories previously considered. The following may serve as examples:

A. Many hermaphroditic animals are protandric, *i. e.*, develop only their male reproductive organs at a very early stage and do not mature their female reproductive organs till after the testes are partly or wholly exhausted. Some of the most extreme cases of this phenomenon are seen in the epicarid crustacea and in the singular parasitic worms of the genus *Myzostoma*. In the crustacean *Danalia* the individual becomes a functional male while it is still a minute and active larva. Later this form attaches itself to the abdomen of a crab, loses its limbs, and develops a long proboscis which penetrates the tissues of its host. The abundant nutriment thus acquired enables the parasite to grow rapidly. Its ovaries then begin to enlarge, while the remains of its testes degenerate and are devoured by phagocytes, and the creature becomes a female. A very similar condition occurs, as I showed several years ago ('96) in certain species of Myzo-

stoma (e.g., in *M. pulvinar* von Graff). In these striking examples the animal is only potentially hermaphroditic, since functionally it exhibits seasonal gonochorism through phasic castration of the ovaries during its youth and of the testes during its adult stages.

B. Geoffrey Smith ('05 a, '09) has called attention to a very striking form of phasic castration in decapod crustacea: "During the breeding season the males of *Inachus mauritanicus* fall

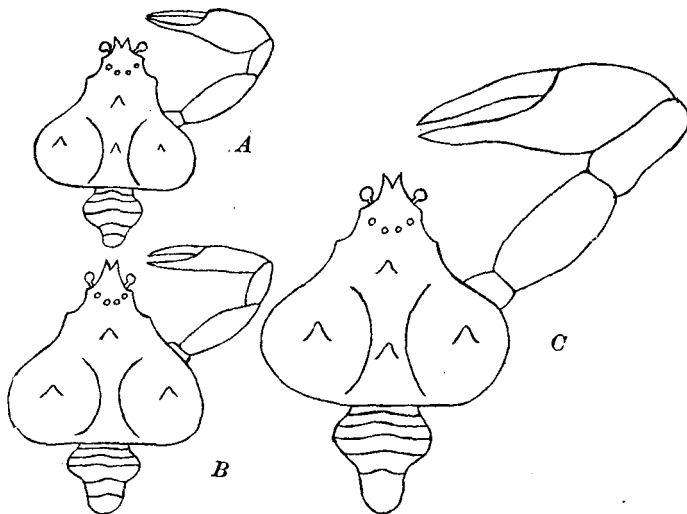


Fig. 4. Males of *Inachus mauritanicus*. *A* small breeding male with swollen chelæ; *B* non-breeding male, with slender chelæ; *C*, large breeding male with swollen chelæ. (After Geoffrey Smith.)

into three chief categories: Small males with swollen chelæ (Fig. 4*A*), middle sized males with flattened chelæ (*B*), and large males with enormously swollen chelæ (*C*). On dissecting specimens of the first and third categories it is found that the testes occupy a large part of the thoracic cavity and are full of spermatozoa, while in the middle-sized males with female-like chelæ the testes appear shrivelled and contain few spermatozoa. These non-breeding crabs are, in fact, undergoing a period of active growth and sexual suppression before attaining the final stage of devel-

opment exhibited by the large breeding crabs." This same condition was previously observed by Faxon ('85) in male crayfish belonging to the American genus *Cambarus*. Of course, the three stages distinguished by Smith are separated by moults. Obviously we have here a condition like that observed in many male fishes, amphibians and birds, which lose their secondary sexual characters during the seasons when they are not breeding. Smith regards the phenomenon as "obviously parallel to the 'high and low dimorphism,' so common in lamellicorn beetles," but this is a mistake, as Cunningham ('08) has shown, for we are here confronted with a case of seasonal sexual dimorphism. Nothing comparable to the condition described above is seen in insects, for the reason that these animals either do not mature their gonads till after they have attained their fixed and final imaginal instar, or if they become sexually mature as larvæ or pupæ (neotenic and pædogenetic aphids, cecidomyids, chironomids, etc.) they do not develop beyond this stage. It is not improbable, however, that insects which live several years in the adult stage and have seasons of sexual activity alternating with seasons of infertility, may exhibit great periodical changes in the size and development of the reproductive organs. I have been unable to find any observations on this subject in the entomological literature.

5. *Individual Parasitic Castration.*

The first zoölogist fully to appreciate the importance of parasites in suppressing the reproductive function and in incidentally affecting the somatic characters of their hosts was Giard. He published some twenty papers ('69-'02) on a great variety of cases which he observed not only among animals but also among plants. The cases to which he devoted most attention were the decapod crustacea, especially species of *Stenorhynchus*, *Portunus*, *Carcinus*, *Cancer*, *Platyonychus*, *Eupagurus*, *Palæmon*, *Gebia* and *Hippolyte*, which are infested with extraordinary cirriped and bopyrid parasites of the genera *Sacculina*, *Portunion*, *Bopyrus*, *Probopyrus*, etc. Within more recent years these studies have

been continued and deepened by Geoffrey Smith ('06, '09) on the spider crab *Inachus mauritanicus* infested with the cirriped *Sacculina neglecta* and by Potts ('06, '09) on hermit crabs (*Eupagurus meticulosus*) infested with the cirriped *Peltogaster curvatus*. A summary of the work of these two authors will not be out of place here, since they have reached rather definite con-

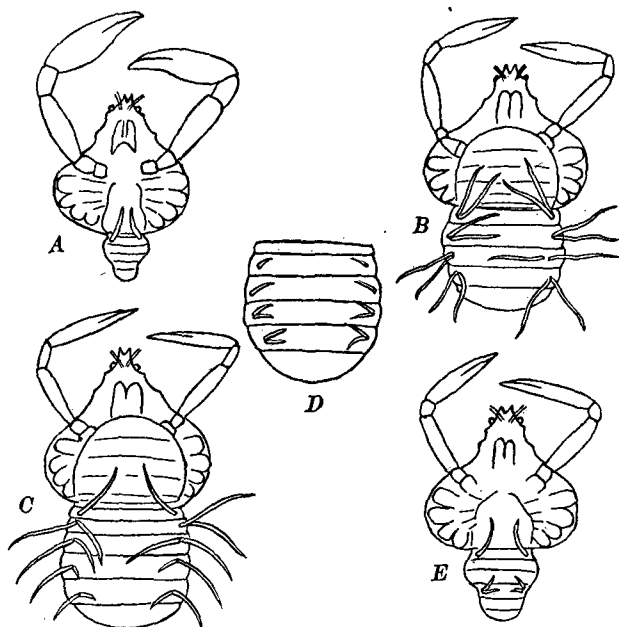


Fig. 5. Specimens of *Inachus mauritanicus* to show effects of parasitic *Sacculina neglecta*. *A* normal male; *B*, normal female; *C*, male infested with *Sacculina* (final stage); *D*, abdomen of infested female; *E*, infested male in an early stage of its modification. (After Geoffrey Smith.)

clusions not without a bearing on the various cases of parasitic castration in insects and other organisms to which I shall have occasion to refer.

According to Geoffrey Smith ('09) the abdomen of the normal male of *Inachus mauritanicus* "is small and bears a pair of copulatory styles, while the chelipeds are long and swollen (Fig. 5*A*). In the female (Fig. 5*B*) the abdomen is much larger and trough-

shaped, and carries four pairs of ovigerous appendages; the chelæ are small and narrow.

"Now it is found that in about 70 per cent of males infected with *Sacculina* the body takes on to varying degrees the female characters, the abdomen becoming broad as in the female, with a tendency to develop the ovigerous appendages, while the chelæ become reduced (Fig. 5C). This assumption of the female characteristics by the male under the influence of the parasite may be so perfect that the abdomen and chelæ become typically female in dimensions, while the abdomen develops not only the copulatory styles typical of the male, but also the four pairs of ovigerous appendages typical of the female. The parasitized females, on the other hand, though they may show a degenerate condition of the ovigerous appendages (Fig. 5D), never develop a single positively male characteristic. On dissecting crabs of these varying categories it is found that the generative organs are in varying conditions of degeneration and disintegration.

"The most remarkable fact in this history is the subsequent behavior of males which have assumed perfect female external characters, if the *Sacculina* drops off and the crabs recover from the disease. It is found that under these circumstances these males may regenerate from the remains of their gonad a perfect hermaphrodite gland, capable of producing mature ova and spermatozoa. The females appear quite incapable, on the other hand, of producing the male primary elements of sex on recovery any more than they can produce the secondary."

The following account is quoted from Pott's summary ('09) of his own studies on the modifications induced in *Eupagurus* by *Peltogaster* and of Smith's observations:

"The difference between the sexes of *Eupagurus* is shown only in a couple of external characters, the position of the generative apertures (as in all Decapods) and the character of the abdominal appendages. The abdomen of the hermit crab is furnished on one side only with a few appendages, insignificant, but with definite functions. It is in the female that we see the full development of the appendage as a swimmeret with two equal branches, the inner one provided with long hairs affording a secure anchorage for

countless eggs while the outer one is of equal size in both sexes, and in both by its paddle-movement maintains respiration currents in the shell. No use has been found for the outer branch in the male and so has become quite rudimentary, but the effect of the parasite *Peltogaster* is to stimulate the growth of this rudiment. There is of course great variability of response to this stimulus but those individuals which experience the maximum amount of change possess swimmerets exactly similar to those of a mature female, even in the assumption of the curious branched or barbed hairs which in this case can never bear eggs. As in the spider crabs so here, the female appeared incapable of the reverse change, and the large number of hermit crabs with typical female appendages and sealed genital apertures are undoubtedly to be regarded in part as modified males.

"A protest will conceivably be uttered against the attribution of a special sexual significance to the development of typical swimmerets in the male in both spider crabs and hermit crabs. It is of course well known that in the larval stages of these Crustacea biramous abdominal appendages are found in both sexes to be subsequently reduced or lost in the male. Lest this, then, be deemed a happy opportunity for applying the term "reversion" to this phenomenon I hasten once more to point out that when the male develops biramous abdominal swimmerets they are of the type associated with female maturity, and that the specialized nature of their nursing-hairs cannot well be associated with ancestral conditions.

"Both *Sacculina* and *Peltogaster* inflict sterility upon their host and apparently entire abortion of the gonad generally is the final consequence. On the external appearance of the parasite the eggs of the female shrink through absorption of their yolk and the formation of spermatozoa is after a time suspended in the male. The testis of the spider crab dwindles and disappears without undergoing any particular histological change; but in the hermit crab it is curious to note the presence of large cells with large nucleus and abundant protoplasm in sections of the testis. These instantly suggest ova in their appearance and call to mind the instances of the occurrence of such cytological elements as a nor-

mal experience in the testes of many animals. In sand-hoppers (*Orchestia*) to quote a well-known case (and there are many others in the Crustacea) spermatozoa are produced in the anterior part of the young testis while posteriorly the whole space is occupied by two or three large ova (*vide* Boulenger '08).

"The particular interest of the phenomenon in this case is its association with a definite cause, that is, parasitism. We are also able to come to some conclusion as to the degree in which such a condition can be called true hermaphroditism. Some striking evidence is offered by spider crabs which were once infected by *Sacculina* but which have outlived their parasite and recovered from its influence. Such crabs occur in nature in fair frequency and the only reminder of their former condition is the chitinous ring on the abdomen which surrounded the peduncle of the parasite. After the death of the external part of the *Sacculina* the root system may continue to exist in the host and it is only when this has disintegrated and been absorbed that regeneration of the gonads becomes rapid, for the still living roots repress the development of the sexual organs as effectually as the living parasite. A few crabs however were found in which the gonads had again attained full size and maturity. One was a female with a well-developed ovary and four were males only slightly modified externally, with glands producing large quantities of spermatozoa. The remaining four cases were remarkable for the crabs showed with a complete external hermaphroditism the corresponding gonads. In all four animals the reproductive gland consisted of a male part with ripe spermatozoa, and a female division with large pigmented ova. The ducts were usually absent, but one individual possessed both vasa deferentia and oviducts. The sequel to these observations is given by the experimental evidence which Smith then obtained. It was attempted to destroy the parasite by removing the external part and the crabs so freed were kept under comfortable conditions for several months and the few survivors then killed. Regeneration had obviously occurred to a considerable extent, but the gonads were nearly always unisexual. In one individual alone, which was externally a hermaphrodite there was a gonad similar to those just described. In spite of the

comparatively small number of cases with fully formed hermaphrodite glands we are not going too far in definitely asserting a connection between their occurrence and parasitic influence, for bisexual gonads have to my knowledge never been met with in Decapod Crustacea under normal conditions.⁶ But it thus appears that the curious condition in the hermit crab is an incipient stage corresponding to the perfect hermaphroditism of the "recovered" spider crabs, and if the action of the parasite in absorbing surplus nutrition were withdrawn the young ova in the testis of the hermit crab would become large and pigmented like those in the spider crab.

"These two cases have been described at some length as examples of *extreme modification*. In other Decapod Crustacea which are infected by the same parasite an effect is observable which is similar in kind but not in degree. The common shore crab of England (*Carcinus*) is commonly afflicted (if affliction it be) by *Sacculina*. Here again the male undergoes modification while the reverse change never occurs in the female. The narrow abdomen of the male is often exchanged at the moult after infection for one much broader but never attaining the full female width. One may look in vain, however, for any reduction of the copulatory styles or for the appearance of the smallest rudiments of swimmerets. The closure of the genital apertures nearly always follows parasitic attack in spider crab and hermit crab; but they never become blocked up in shore crabs with *Sacculina*. Yet the external change is apparently greater than that produced in the reproductive glands. Dissection in every parasitized male showed vasa deferentia of the characteristic milky white color due to countless masses of spermatophores all packed with spermatozoa. The testes though reduced, then, always remain in reproductive activity. The parasites which infect spider crab and shore crab are practically identical and presumably exert a very similar stimulus yet the results are markedly different. It is obviously the host which offers a different reaction in the two cases. In another

⁶ In a footnote Potts states that "Calman in the recently appeared volume *Crustacea* of Ray Lankester's *Treatise on Zoölogy* refers to the unpublished observations of Wolleback on normal hermaphroditism in certain deep-water Decapoda."

crab (*Eriphia*) examined by Smith there was infection both by *Sacculina* and by a parasitic Isopod crustacean. Here the nature of the parasite governs the result, and crabs with *Sacculina* alone never showed the least trace of modification, while changes closely similar to those described above occurred in those which harboured the Isopod."

Geoffrey Smith ('05 *b*) has also described parasitic castration in *Inachus dorsettensis* by a sporozoön (*Aggregata inachi*) which lives in the intestine of the crab and induces modifications not unlike those induced by *Sacculina*. Smith says that of fifty males of *I. dorsettensis* examined, "seven specimens were clearly distinguished by having the flat chelæ characteristic of the females, while the abdomen was much broader than is the case in normal males of a corresponding size, thus converging on the female condition. In one specimen there was present on the under side of the abdomen a pair of swimmerets which are characteristic of the female, these appendages being altogether absent in the normal males." Dissection of these crabs showed the intestine "to be covered with cysts of *Aggregata inachi*, the body cavity was also full of liberated sporozoites, the hæmolymph having a milky appearance due to the crowded presence of these bodies. The testes were in all cases disintegrated, only the vesiculæ seminales remaining. Two modified males were also found to contain the cysts of *Aggregata inachi*, but in none of these males were there larger quantities of sporozoites in the hæmolymph, so that it appears that the hermaphrodite external characters are assumed by the infected male at the moult which follows the liberation of a large quantity of sporozoites." Smith made no observations on the infected female *Inachus*, as this sex is much rarer than the male.

The foregoing examples of parasitic castration in crustacea have been reviewed at some length, because they show the phenomenon in its most striking manifestation. Giard as early as 1888 (*b*) published a long list of other animals and plants known to be castrated by what he calls "gonotomic" parasites. The most interesting examples, apart from *Andrena* and the crustacea just considered, are the castration of the nemertean *Lineus obscurus* by the orthonectid *Intoshia lineæ*, of the planarian *Leptoplana tremellaris*

by *Intoshia kefersteini*, of the brittle, star *Amphiura squamata* by the orthonectid *Rhopalura giardi* and by a copepod (Fewkes '88), of the snails of the genera *Paludina*, *Lymnæa* and *Planorbis* by distome sporocysts (*Distomum militare*, *retusum*, etc.), of the crustacean *Cyclops tenuirostris* by larval distomes (Herrick '83), of the bumble bees (*Bombus*) by the extraordinary nematode *Sphæularia bombi*, and of the males of various North American squirrels and chipmunks (*Tamias lysteri*, *Sciurus hudsonius* and *leucotis*) by the bot-fly *Cuterebra emasculator* as described by Fitch ('59), Riley and Howard ('89) and Osborn ('96). Among plants Giard cites the castration of the fig by *Blastophaga grossorum*, of *Melandryum album* (*Lychnis dioica*) by *Ustilago antherarum* and various grasses by smuts, ergots, rusts, etc. The case of *Melandryum* and *Ustilago* which was repeatedly studied by Giard ('69, '87a, '88d, '89a) bears a curious resemblance to that of the male crab infested with *Sacculina*. The *Melandryum* is "normally dioecious. The young flower is hermaphrodite but in certain individuals the ovaries abort, in others the stamens remain rudimentary. When the parasitic fungus develops on a male plant, it fructifies in the stamens, but when it falls on a female plant, it seems at first as though it could not fructify and that the infested plant must profit accordingly. But this is not the case, for the plant develops its rudimentary stamens completely in order to permit the fructification of the parasite, just as the male *Stenorhynchus* enlarges its abdomen in order to protect the *Sacculina fraisei*."

Castration frequently occurs in plants through petalody, or petalomania, *i. e.* the conversion of stamens or carpels into petals, producing the well-known "double" flowers. Molliard ('01) has produced petalody experimentally in *Scabiosa columbaria* by artificially infecting the plant with the nematode *Heterodera radicolica*. And this investigator, Meehan ('00), Giard ('02) and Cramer ('07) cite a number of observations which indicate that petalody is often the result of infection of a plant with root-fungi. Veuillemin ('07) has observed in *Lonicera* infested with aphids a suppression of the carpels and a distinct androgeny of a certain number of the flowers.

Instead of stopping to review the various examples of parasitic castration cited by Giard in his paper of 1888, and in many of his later publications, it will be preferable to describe as briefly as possible a number of selected examples, especially some that have come to light more recently among insects. The stylopized *Polistes* and *Andrenæ*, having been adequately described in the first part of this paper, will be omitted.

Grassi and Sandias ('93) describe a remarkable case of parasitic castration in termites. They find that worker and soldier termites have the intestinal cæcum, which occupies much of the abdominal cavity, distended with enormous numbers of parasitic Protozoa belonging both to the Ciliata (*Dinonympha*, *Pyrsonympha*, *Trichonympha*) and to the Gregarinida. The Ciliata have been studied by several authors, notably by Leidy ('77, '81), Grassi ('85), Kent ('85), Porter ('97), and Dodd ('06). In termites infested with these parasites the reproductive organs, both male and female, remain small and undeveloped, apparently as the result of the pressure exerted on them by the distension of the cæcum. The parasites are absent in the very young termites and in the sexual forms, which are fed on saliva. Grassi and Sandias infer that the Protozoa must either be killed off or, at any rate, prevented from living and growing in the alimentary tract of saliva-fed individuals. These investigators are inclined, therefore, with some reservations, to regard the development of the two sterile castes in termites as the result of infection with protozoan parasites. This infection is, of course, readily brought about as the workers and soldiers are not fed on saliva like the sexual forms but on dead wood and on the fæces of individuals belonging to the same castes.

The researches of Grassi and Sandias have received a certain amount of confirmation from Brunelli ('05), who finds that queens of *Calotermes flavicollis* and *Termes lucifugus* sometimes become infested with the parasitic Protozoa, and that when this happens the young oöcytes in their ovaries degenerate. *Calotermes* queens are more susceptible to this form of castration than the queens of *Termes*. Brunelli explains the winged soldier observed by Grassi and Silvestri's ('03) 48 workers of *Microcerotermes struncki* with

well-developed reproductive organs (40 females and 8 males), as being instances of fertility brought about by a disappearance of the Protozoa through some unknown cause. Such fertile soldiers and workers would be comparable to the "recovered" spider crabs above described, except that there is no tendency towards hermaphroditism.

It is not altogether improbable that the high and low males among the Scarabæidæ, Lucanidæ and Forficulidæ are produced

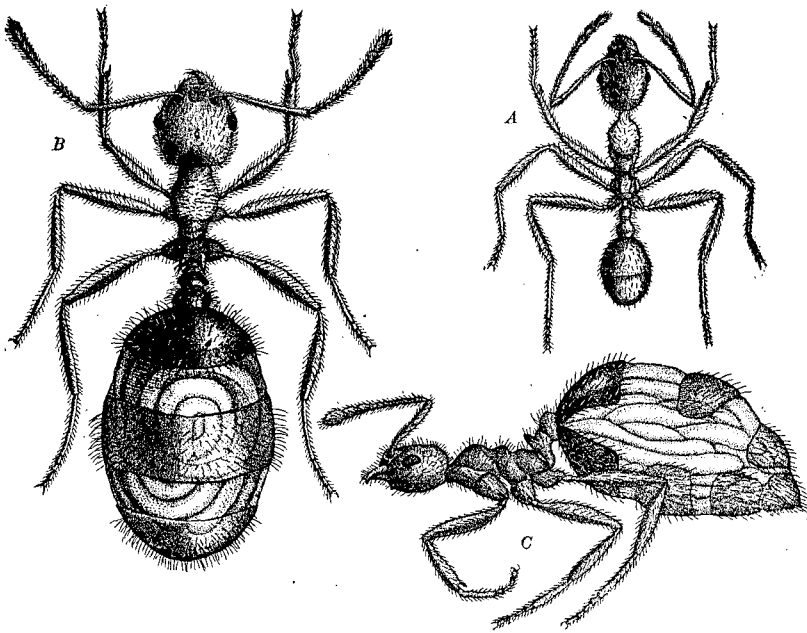


Fig 6. A, normal worker of *Pheidole commutata*; B and C mermithergate of same in dorsal and lateral view.

in some such manner as the workers and soldiers of termites. It is certainly suggestive that all three of these families of insects live on decomposing vegetable substances and in situations where they become very readily infected with gregarines. Giard ('94a) has given good reasons for supposing that the high and low males of *Forficula*, which were made the basis of a statistical study by Bateson (92), are produced by differences in the number of gregarines they harbor in their alimentary tract. The French

observer says: "It is, indeed, possible to predict from the length of its forceps whether or not a male *Forficula* possesses gregarines and whether these are present in greater or lesser numbers. Since these parasites produce a diminution of a secondary sexual character, that is, the length of the forceps, without bringing about absolute sterility (complete castration being exceptional), it not infrequently happens—and this is the case both on the beaches of Wimereux and on the Farne Islands—that the individuals with short forceps, namely, those containing parasites, are more numerous than the individuals with long forceps." Giard is inclined to believe that similar conditions may obtain in such beetles as *Xylotrypes gideon*, *Oryctes nasicornis* and other *Scarabæidæ* with high and low males. The low males of these beetles, however, are not to be regarded as having acquired female characters, but as having lost the male characters, so that, as Giard remarks, the "infested individuals are generally pædomorphic as compared with the normal form."

In two of my former papers ('01, '07) I described a peculiar case of parasitism in a Texan ant, *Pheidole commutata*. The larvæ of this insect are occasionally infected with nematodes of the genus *Mermis* and develop into peculiar forms, which I have called mermithergates (Figs. 6*B* and 6*C*). These are much larger than the normal workers (Fig. 6*A*), which they nevertheless resemble in the structure and small size of the head, although they possess small ocelli and in this respect resemble the queens. In thoracic structure they approach the soldier form while the gaster is enormously distended with *Mermis* and retains scarcely any vestiges of the fat-body, reproductive organs and other viscera. The behavior of these parasitized individuals is also peculiar, since they never excavate the soil, nor care for the brood like the normal workers, but run about in a state of chronic hunger, begging food from their uninfested nest-mates. Emery ('90, '04) has recorded the occurrence of mermithergates in quite a series of neotropical ants, including *Pheidole absurda* and several *Ponerinæ* of the genera *Odontomachus*, *Neoponera*, *Ectatomma*, *Pachycondyla* and *Paraponera*.

In the cases described by Emery and myself only the worker

forms were infested and modified by the *Mermis*, but Mrázek ('08) has recently shown that the virgin queens of the European *Lasius alienus* may become infested with this worm and that when this occurs the insects develop abnormally small wings (Fig. 7B). These individuals, or mermithogynes, as Mrázek calls them, have been seen by other investigators and described as brachypterous to distinguish them from the normal macropterous individuals of the species.

After seeing Mrázek's paper I examined a small collection of seven brachypterous and as many macropterous females of *Lasius neoniger* (a form closely related to *alienus*) which I had taken from a single colony near Manitou, Colorado, August 9, 1903. Three of the short winged individuals were dissected and each was found to contain a large coiled *Mermis*, 53 to 55 mm. long, which filled out the whole abdomen, so that in the living individuals there could have been little left of the reproductive organs and other viscera. There is nothing unusual in these females except the small size of their wings, which measure only 6 to 6.5 mm. in length, whereas those of normal *L. neoniger* females measure 10 to 11 mm. These observations show that the queens of our American *Lasius* may be affected by *Mermis* in exactly the same manner as the queens of the related European species.

The species of *Mermis* are not, however, the only known gonotomic nematodes. A much more extraordinary form is *Sphærolaris bombi*, which has been known ever since the days of Réaumur (1742) to produce sterility in the hibernating queens of bumble-bees. According to Leuckart ('87), who has written the best and apparently also the most recent account of *Sphærolaria*, infested bees are sometimes found, "which have not a single mature egg in their ovaries. Structurally these organs are perfectly developed and have ova in the blind ends of their ovarioles, but ripe eggs are lacking. In other specimens one may find in addition to the young, also some ova of perfectly normal dimensions." He says that he has "never seen an infested queen which had the ovarioles as uniformly and richly provided with eggs as are the ovaries of healthy bumble-bees at the same season. As a rule, one finds only a few eggs, sometimes only a single egg." These

bees are therefore unable to found colonies, according to Schneider and Leuckart. They keep flying about till late in June and then die, whereas uninfested queens have started their colonies and no longer fly at large after the beginning or middle of May. *Sphærolaria* occurs only in the queens, and has never been found in those that have become mothers of colonies. It would be interesting to know whether the colony-founding instincts of

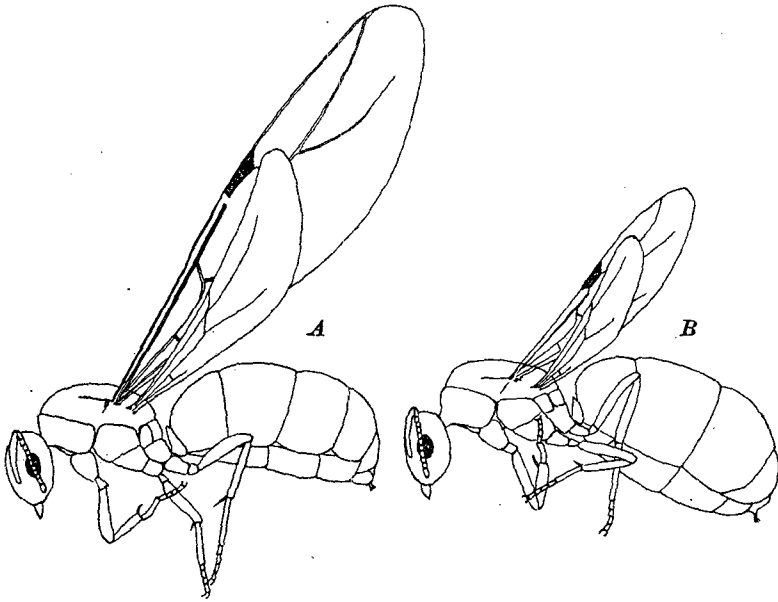


Fig. 7. A, normal female of *Lasius alienus*; B, mermithogyne of same species (After Mrázek.)

infested queens show the same tendency to atrophy as the ovaries. As the bees become infected in their imaginal instar, apparently while seeking their winter quarters, the parasites can produce no modifications in the external characters.

The *Lasius mermithogynes* described above recall some observations of Künckel d'Herculais ('94) on Algerian grass-hoppers (*Stauronotus maroccanus* and other species) infested with flies of the genus *Sarcophaga*. The maggots of the flies are entoparasitic, devouring the fat-body, and, according to Künckel d'Herculais, also absorbing the oxygen dissolved in the blood-plasma of

their hosts. The results are an atrophy of the reproductive organs (parasitic castration) and a weakening of the wing-muscles, so that the grasshoppers have a disinclination to fly. For this latter condition, which is described as a "kind of rhachitis," Künckel d'Herculais suggests the name "apteria." Like the brachyptery of the *Lasius mermithogynes*, it points to an intimate correlation between the development of the reproductive organs and the wings, a correlation which is also clearly demonstrated in most insects by the coincident maturation of the former and full development of the latter organs at the beginning of the imaginal instar.

The extensive literature on entoparasitic Diptera and Hymenoptera, if carefully searched, would probably yield a number of accounts of parasitic castration. Pantel ('09), in an important paper, distinguishes both direct and indirect parasitic castration as the result of the infestation of lepidopteran larvæ with the larvæ of tachinid flies. In the former case the fly larvæ live in the testes of the lepidopteron and destroy the gonadic elements directly. In the latter the gonads suffer atrophy through the action of the parasites on the other viscera. The only cases I have found in which the host shows a modification of its external sexual characters as the result of such castration, are the homoptera *Typhlocyba hippocastani* and *douglasi*, which are described by Giard ('89*b*, '89*d*) as being infested with a dryinid hymenopteron, *Aphelopus melaleucus* and a pipunculid dipteron, *Chalarus* (*Ateloneura*) *spuria*. The females of both species of *Typhlocyba*, when castrated by *Aphelopus*, have the ovipositor much reduced; the *Chalarus* alone seems to have less effect on this organ. The penis of the male *T. douglasi* is little modified by either of the parasites, but in *T. hippocastani* infested with *Chalarus*, this organ shows a decided reduction in size and simplification of structure so that the specific characters become profoundly modified. None of these modifications, however, indicates any tendency to take on the characters of the opposite sex.

6. *Social Parasitic Castration*

This category is not sharply marked off from the preceding, for if we define it as including those cases among social insects

in which the individuals that represent the reproductive organs (*i.e.*, the males and queens) of the colony considered as an organism of a higher order, are castrated by parasites, we should perhaps include also the *Lasius* colonies containing mermithogynes and the queens of *Bombus* infested with *Sphærolaria* described in the foregoing paragraphs. But in these cases it is merely prospective colonies, so to speak, which are castrated, since neither the mermithogynes nor the parasitized *Bombus* queens have as yet become mothers of colonies. For this reason I have treated them as cases of individual parasitic castration. Here belongs also the production of pseudogynes in *Formica* colonies infested with the peculiar myrmecophilous beetles of the staphylinid tribe *Lomechusini* (*Lomechusa* and *Xenodusa*) which I have considered at length in a former paper ('07). These beetles tend to suppress the development of the annual brood of virgin queens since the worker ants of parasitized colonies either neglect the queen larvæ or endeavor to convert them into workers, after the period during which this change can be successfully accomplished has passed. The results of this behavior is the production of the non-viable pseudogynes and the gradual degeneration of the colony. In this case also the colony is not castrated, but the mothers of prospective colonies may be said to suffer from misapplied alimentary castration.

Leaving all these cases out of account we have left only those in which a parasitic colony of insects prevents the development of or destroys the fertile sexual individuals of the host colony in which it lives. As parasites of this type I may mention the various slave-making ants (*Formica sanguinea* and *Polyergus rufescens* and their various varieties and subspecies), the temporary social parasites (*Formica rufa*, *exsecta*, *exsectoides*, etc.) and the permanent social parasites of the genera *Anergates*, *Wheeleriella*, *Epipheidole*, *Symphheidole* and *Epæcus*. There are other social parasites that do not destroy the reproductive individuals of the host colony, for example, the bees of the genus *Psithyrus*, which live in the nests of bumble-bees, and among ants such species as *Lepthorax emersoni*, *Formicoxenus nitidulus* and *Harpagoxenus sublevis*. Still other ants, such as the species of *Strongylognathus*,

do not destroy the queen of their host colony (*Tetramorium cespitum*), but since the workers of this colony prefer to rear the small sexual forms of the parasites instead of their own bulky males and females, the development of future colonies of the host species is rendered impossible and we have here again a case of prospective social castration.

The conclusion which we reach after marshaling this long series of illustrations of the various forms of castration is that among insects the only case in which destruction or inhibition of the reproductive function clearly results in any modifications of the secondary sexual characters comparable to the modifications observed in vertebrates under like conditions, is that of the stylopized andrenine bees as described by Pérez. In all the other cases extirpation of or injury to the gonads may indeed result in modifications of the somatic or secondary sexual characters, but the latter do not take on the peculiarities of the opposite sex. The most striking illustrations of the truth of this statement are the insects that have been surgically castrated. These show that the secondary sexual characters must be so independently and so immovably predetermined and at so early a period in the ontogeny that complete extirpation of the gonads during prepupal life fails to produce the slightest curtailment or modification either in the secondary sexual characters or in the sexual instincts of the adult insect. This conclusion renders it imperative to reinvestigate the cases of stylopization in the andrenine bees for the purpose of ascertaining whether Pérez's interpretation is the only one which they will yield, especially since it has been shown in the first part of this paper that the study of stylopization in *Polistes* leads to a very different view and one in complete harmony with the other cases of castration in insects.

It is interesting to note that castrated crustacea, to judge from the observations of Giard, Geoffrey Smith, and Potts, show modifications like those of castrated vertebrates and not like those of the insects. This is in all probability due to the fact that the development of the primary and secondary sexual characters is gradual and continuous in the Crustacea and vertebrates, whereas both these characters in insects are arrested in their develop-

ment and remain unaffected by the surrounding processes of growth and differentiation till the imaginal stage is attained. In holometabolic insects the secondary sexual characters are, of course, segregated in the imaginal discs, or histoblasts, and even in hemimetabolic and ametabolic insects there must be a similar isolation of the cell-materials which will produce the somatic sexual peculiarities of the adult.

The opinion here advocated, namely, that in insects the primary and secondary characters are very loosely correlated during ontogenetic development or in a very different manner from what they are in vertebrates or even in the crustacea, receives indirect support from two interesting classes of facts. One of these classes comprises the anomalies known as gynandromorphs, which, though always rare, are nevertheless much more frequently found among insects than among any other animals. These anomalies consist in combinations of male and female somatic characters in the same individual, usually in such a manner that the two lateral halves or the anterior and posterior portions of the body are of different sexes. In the former combination the reproductive organs may be hermaphroditic and correspond with the sex of the halves of the body in which they lie, but this is not always the case, and in anteroposterior, or frontal, or in mosaic, or decussating gynandromorphs, which exhibit an irregular mingling of the sexual characters, the gonads may nevertheless be unisexual. Herbst ('01) and Driesch ('07) have emphasized the obvious inference that these various arrangements of the male and female characters cannot owe their origin to internal secretions, or hormones, and indeed all those who have speculated on the origin of these anomalies are unanimous in holding that they must arise either from peculiarities in the structure of the egg or from irregularities in its fertilitation or early cleavage stages at the very latest. Among recent speculations on the origin of gynandromorphism those of Boveri ('02) and Morgan ('05, '09) may be mentioned. Boveri believes that the gynandromorph arises from an egg which has segmented prematurely, so that the male pronucleus unites with one of the cleavage nuclei. Morgan is of the opinion "that the results may be due to two (or more) spermatog-

zoa entering the same egg, one only fusing with the egg nucleus and the other not uniting, but developing without combining with any parts of the egg nucleus." These hypotheses have no very cogent facts to support them and I fail to see how they have any advantage over the hypothesis which was advanced by Dönhof as long ago as 1860, to the effect that the gynandromorph arises from the fusion of two eggs, only one of which, in the case of the honey bee, is fertilized. In its original form Dönhof's hypothesis is incomplete, but I believe that its plausibility is increased by addition of the following considerations. We may assume with Beard ('02), von Lenhossék ('03), Reuter ('07), Morgan ('09) and others that the gonochoristic Metazoa produce two kinds of eggs, male and female, which may or may not differ in size but differ in sex even as oöcytes. Now we know from zur Strassen's researches on *Ascaris* ('98) that two eggs may fuse and nevertheless give rise to a single embryo of perfectly normal structure though of twice the normal size. In *Ascaris* the fusion occurs after the oöcytes have reached their full growth, but a fusion of younger oöcytes would be, in all probability, not only more readily accomplished but lead to the formation of a single embryo of the normal size. The structure of the ovarioles of insects indicates that it would be a very easy matter for two young oöcytes to become enclosed in the same follicle, too easy, indeed, to accord, at first glance, with the fact that gynandromorphs are such rare anomalies. But if two female or two male oöcytes fused no gynandromorph would result, and the chances of either of these fusions of like oöcytes occurring would be quite as great as that of two oöcytes of opposite sex. If this be the way in which gynandromorphs arise, we should have to explain the occurrence of the lateral type of the anomaly by supposing that the plane of fusion of the two eggs be omes the median sagittal plane of the future insect, whereas in the frontal type this plane would be transverse to the longitudinal axis. Finally, in the mixed and decussating types we should have to suppose that the male and female egg-materials are mixed or interpenetrate one another to a variable degree. The hypothesis here sketched has the advantage of permitting of some slight cytological verification, for microscopic examination

of the ovarioles of a large number of Lepidoptera, which seem to present the anomaly in question more frequently than other insects, might reveal an occasional inclusion of two oöcytes in the same follicle or even various stages in their fusion. Or if hives are ever again found like the famous Eugster hive, in which so many gynandromorphous bees were produced, the cytologist will have an opportunity to test the hypothesis here advocated by a careful examination of the ovarioles of the queen.

But no matter what view we hold in regard to the origin of gynandromorphs, we are compelled to admit that they demonstrate the very early and rigid determination of the secondary sexual characters, the possibility of their complete development even when the gonads of the corresponding sex are lacking and their independence of internal secretions. To this extent they confirm the results obtained by Oudemans, Kellogg, Meisenheimer and Regen in their castration experiments. Indirectly they indicate that the insect egg not only has its primary sexual characters determined long before fertilization and independently of the later nuclear or chromosomal phenomena, but that even the secondary sexual characters are in some manner also predetermined at this early stage. Where great differences of stature are secondary sexual characters, as in phylloxerans, some aphids and rotifers, we find corresponding differences in the size of the male and female oöcytes. This is, of course, quite in harmony with the remarkable predetermination of the embryonic regions of the insect egg. Long ago Hallez ('86) and I ('89, '93) showed that in many insect eggs the regions corresponding to the ventral and dorsal, right and left, and cephalic and caudal portions of the embryo are clearly established long before the maturation divisions.

The second class of cases, which indicate that the primary and secondary sexual characters of insects may develop independently of one another, are found among certain species of ants, the males of which, though developing gonads and external genitalia of the usual type, have nevertheless become decidedly feminine in their secondary sexual characters. That this condition is an expression of degeneration seems to be indicated by the fact

that it occurs only in parasitic species of the genera *Anergates*, *Formicoxenus* and *Symmyrmica* or in species like those of the genera *Cardiocondyla*, *Technomyrmex* and *Ponera*, which form small, scattered colonies, often with a tendency to lead a secluded or subterranean life. In the three parasitic genera the males are always wingless and resemble the females and workers in the structure of their bodies. The resemblance to the worker is very great

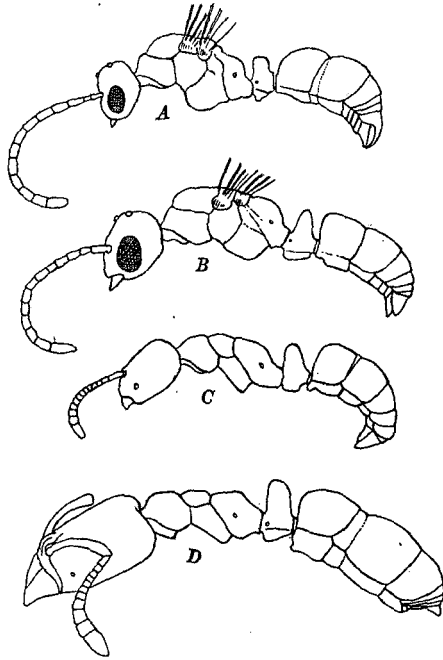


Fig. 8. *A*, winged male of *Ponera coarctata* in profile; *B*, winged male of *P. eduardi*; *C*, subergatomorphic male of the same species; *D*, ergatomorphic male of *P. punctatissima* (After Emery.)

in the case of *Formicoxenus*. In *Cardiocondyla* and *Ponera* we have a number of species whose males show a similar approximation to the worker and female type, and in one species of the latter genus, *P. punctatissima*, shown in the accompanying figure (Fig. 8*D*) the male is indistinguishable from the worker except in the structure of the genitalia. We have here, therefore, a true inversion of the male, so far as its secondary sexual characters are con-

cerned, apparently as an adaptation to ethological requirements, although the primary sexual characters have remained unaffected.

If it be true that the rudiments of the secondary sexual characters are set aside so early in the development of insects and remain uninfluenced by the internal secretions, we can understand why these characters exhibit no modification in cases of surgical castration and why the modifications induced by alimentary, nutritial and parasitic castration bear the aspect of inhibitions or retardations of growth. Normal imaginal development in insects, as is well known, depends on the amount of food accumulated during larval life and stored up in the fat-body. In insects surgically castrated during their younger stages there is nothing to hinder the accumulation of this reserve material, and all the imaginal characters, including the secondary sexual characters, are thereby enabled to develop normally and completely. But in insects that have been underfed or are infested with parasites the reserve materials are either prevented from accumulating or are consumed, so that the imago may have great difficulty in developing its imaginal characters. It is not surprising that under such conditions the secondary characters are more or less reduced or aborted, as we see in the forceps of parasitized *Forficula* males, the thoracic and cephalic horns of male *Scarabæidæ*, the mandibles of male *Lucanidæ*, the wings of female *Lasii*, and many of the other cases cited above. There is simply not enough nutriment to permit of the full growth of the characters under consideration. Their modification, therefore, is readily explained in insects as due to malnutrition and we are not compelled to invoke the internal secretions, or hormones, which play such an important and interesting rôle in the sexual physiology of vertebrates.

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