

VII. *An Investigation by Pedigree Breeding into the Polymorphism of Papilio polytes, Linn.*

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CHAPTER I.

Introduction. Notes on Larva and Pupa. General Notes on the Imago in Captivity with Special Reference to its Senses. Special Notes on the Mating of the Imagines. Sterility Phenomena.

The following paper gives an account of a series of breeding experiments which were made with the butterfly *Papilio polytes*, Linn., in the course of one and a half years' research on insect polymorphism in Ceylon. In the first instance the experiments on butterflies were not limited to this species, but unfortunately all others proved refractory in captivity and were one by one discarded. More time therefore could be given to this, the only amenable species, and it was possible to make a number of observations on the habits of the imago which are suggestive in several ways, and justify a more extensive reference than is usual in papers on heredity. The first chapter of this paper, therefore, is devoted to observations on the species in captivity, especially to the pairing habits of the imagines. The second chapter deals with the results obtained from the pedigree breeding and their Mendelian interpretation, and a final chapter may be added to allow of a comparison with similar work on other species and of a summary of the conclusions to be derived from the investigation as a whole.

P. polytes, as a classical example of mimicry, is too well known to need a full description here. As a subject for a detailed investigation it has peculiar advantages. It is trimorphic; this trimorphism is confined to the female sex; of the three forms of female, one resembles the male in general pattern, while the other two are mimetic, their models being *P. hector*, Linn., and *P. aristolochiæ*, Fabr. It would naturally be supposed that the female like the male would be known as the *polytes* ♀, but this is not the case, as one of the mimetic forms was first described under this name. To avoid confusion and to facilitate subsequent reference, the various forms of the species may be stated thus:—

P. polytes ♀ form *cyrus*, Fabr., resembles the male.

P. polytes ♀ form *romulus*, Cram., resembles *P. hector*, Linn.

P. polytes ♀ form *polytes*, Linn., resembles *P. aristolochiæ*, Fabr.

P. polytes ♀ s, *romulus* and *polytes*, are referred to collectively as the "mimetic" ♀ s.

(309.)

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According to ROTHSCHILD and JORDAN,* "this variable polymorphic *Papilio* has developed into a number of geographical forms which inhabit an area extending from Ceylon, North-west India, and Northern China, to the Moluccas and the Timor group of islands." Of these various races, this paper is only concerned with that which the above authors consider typical, and which ranges through Ceylon, India, the Andamans and Nicobars, Burma, Malay Peninsula, Sumatra, Siam, and Tonkin. The typical race of *P. polytes* does not produce the three forms of female throughout its range, the *romulus* ♀ being limited to Ceylon and India south of the Himalayas, though it has been recorded very occasionally from Burma. It is only in Ceylon and South India, however, that this form is really common. Of the "models," *P. hector* has a very similar range to that of *P. polytes* ♀ *romulus*, though it does not reach so far north; *P. aristolochiæ* is a very widely ranging species, and exists wherever *P. polytes* is found. All the material used for experiment was obtained in Ceylon, and so belonged to the typical race of the species from a locality in which all three forms of female are common.

As regards the early stages of *polytes*, no satisfactory account either of larva or pupa seems to have been written; BELL gives brief descriptions in his "Butterflies of the Plains of India,"† and a table of points by which the species may be distinguished from similar *Papilio* larvæ and pupæ in Ceylon can be found in 'Spolia Zeylanica.'‡ Of more importance to breeding work is the period occupied by the immature stages, for upon it depends the number of generations which can be obtained in a definite time. *Polytes* in its earlier stages was most accommodating, since it passed from egg to pupa in about four weeks. The pupal period, on the other hand, was very variable; sometimes a whole brood would emerge within a fortnight after pupation, but more often emergence would be spread over a much longer period, and, not uncommonly, a few individuals in each brood remained as pupæ for two or three months. In Ceylon the species has no fixed resting season, and this protracted pupal life, which occurs sporadically in most broods, may perhaps take its place. Whatever may be the cause, however, it was a disadvantage to breeding work, for, in the first place, it seldom allowed the experimenter much choice of individuals for the purpose of mating, while, in the second, pairings for the future generation had to be made before the composition of the various broods in use was known.

A more serious difficulty, however, was encountered in the larval mortality, which throughout the experiments was very high; a loss of 20 per cent. was frequent, and this often rose to 40 or 50 per cent., and, in spite of all attempts, no method of reducing it was discovered. The forms of death were two in number: the more usual occurred during the first two changes of skin; the affected larvæ spun for themselves

* "Revision of the Papilios of the Eastern Hemisphere exclusive of Africa," 'Novitat. Zool.,' 1895, vol. 2, p. 345.

† 'Bombay Nat. Hist. Soc. Journ.,' vol. 21, pp. 527-531.

‡ 'Spolia Zeylanica,' August, 1911, vol. 7, Part XXVIII, p. 218.

the usual attachment to a leaf or other support, but then, instead of casting their skins, gradually shrivelled up and died; it appeared, in fact, as if they had begun to change their skins before they had fed sufficiently, and that they starved during the process. The second form of death appeared after some fifty broods had been reared, and became gradually more severe until the experiments were abandoned. It was caused either by a bacterial or a protozoal disease and was almost certainly hereditary, as the most stringent measures failed to stamp it out. Theoretically, perhaps, a high larval mortality, exercising no selective function, ought not to affect the statistical results, but in practice this would only apply if the number of broods was sufficiently great; in the experiments to be detailed there is little doubt that the relative numbers in many broods have been seriously affected, and that they must all be looked on with suspicion.

Turning next to the imago in captivity, a few notes must be given on the cages which were found suitable. For the first 25 broods, medium-sized cages, 4 feet long by 3 feet 6 inches wide by 6 feet 6 inches high, of fine brass gauze were used. The male and female which were desired to pair were released in one of these cages, and were left permanently together unless a pairing was actually observed—a somewhat rare event. This proving unsatisfactory, a much larger cage, 16 feet long by 8 feet wide by 6 feet 6 inches high, was built, and the old cages were utilised for females which had been observed to pair and from which eggs were required. In the small cages the butterflies had evidently realised their captivity, but the large cage seemed almost to reproduce natural conditions—a statement which perhaps requires some justification. This may be found in the fact that an error was made in the mesh of the wire netting, and on the first occasion on which the cage was used the butterflies crawled through the netting and escaped; these individuals, however, had not been fed since their emergence—some 24 hours earlier—and it was found subsequently that, provided the insects were well fed, they made no determined efforts to escape. This appears to be distinct evidence that conditions in the large cage were sufficiently natural to cause the butterflies no positive discomfort.

Feeding was of paramount importance, for unless nourishment could be obtained whenever it was wanted no pairings occurred, and the females refused to oviposit; fortunately it presented no great difficulty; dilute syrup was placed on flowers, and the insects usually responded to the stimulus of bright colours and fed without trouble. Occasionally, however, a butterfly failed to show any response, and then it was necessary to introduce the proboscis by force into the syrup, after which there was usually no further difficulty.

The sense of smell seemed to have no connection with the discovery of food hidden in flowers; starved butterflies, however, would frequently discover a damp spot on the ground and obtain some moisture from it, just as most species in the dry northern regions of Ceylon may be found feeding on damp spots on the road or in beds of streams. In these cases it is probable that the initial discovery of water is made by

the sense of smell, but afterwards the crowd which usually collects on the damp spot is certainly due to the sense of sight, as may be proved by pinning a few dead butterflies on a dry spot, when a number of others will settle and explore the ground with their proboscides, as if searching for the food which attracted the first arrival. Finally, in connection with feeding, it may be of interest to record that sexual excitement in a female at rest, as, for instance, when a male was hovering near, usually caused an extension of the proboscis, which was introduced into any cranny exactly as if the female was seeking for food in a flower. It appears to show that psychologically the sensations of feeding and pairing are somewhat closely related, and this connection, though apparently purposeless in butterflies, may have resulted in the curious instinct in Empid flies,* which causes the male to catch some insect for the female to suck when pairing. The sense of sight as applied to the discovery of food seemed fairly keen, but when attempting to discover each other the butterflies were extraordinarily blind to any individual which was not in motion. In the cages one butterfly would observe another, if flying, at a distance of 4 or 5 feet, but an insect at rest was rarely noticed at a greater distance than 6 inches, and was frequently passed over altogether. Rapid movement also was required to produce a feeling of danger, so that the butterflies in the cages could be caught in the hand if approached slowly and with a regular motion. The only other sense of which definite evidence was obtained in the cages was that of touch. The female, when ovipositing, explored most carefully the shoots, leaves, or twigs with the tip of the abdomen before actually laying an egg; in this process the first pair of legs also seemed to be used as a sense organ, for the female always vibrated them rapidly on the surface of the leaf or twig under examination, making a quite audible tapping. It was concluded, though on very slight evidence, that a suitable food-plant was recognised by its scent, then the front legs were used for testing the age of the foliage, the female being very averse to laying on anything but soft young leaves and shoots, and finally the exact position for the egg was discovered by the sensory organs at the tip of the abdomen.

The next subject to be dealt with concerns the sexual life, and specially the possibility of selective mating in *polytes*. This is a difficult subject to deal with, for the reason that so little can be obtained in the way of definite facts on which to base conclusions, while, in addition, the observer is likely to be influenced in the interpretation of the few facts at his command by numerous small unrecorded and even subconscious observations absorbed in the course of the experiments. For this reason, perhaps, though numerous accounts are given of the courting habits of butterflies, no opinion is usually ventured as to their general bearing. In the present case it seems better to place on record the opinions formed during the experiments,

* HOWLETT, 'Ent. Mont. Mag.,' 1907, p. 229, "Note on Coupling of *Empis borealis*"; HAMM, 'Ent. Mont. Mag.,' 1908, p. 181, "*Empis livida*."

so that future observers may at least be on the watch for further facts on the subject to be obtained from other species.

In the case of *polytes*, both sexes emerge from the pupa in the morning, frequently about 8 o'clock, and the male is usually quiescent for the greater part of the day, possibly taking a short flight in the afternoon, but making no attempt to pair. On the following day the male is ready to pair, and, if well fed, is willing to do so on all occasions until death, which in captivity occurred seven or eight days after emergence. Only a single pairing was usually made by one male, though two pairings were not infrequent, and the record numbers were five pairings, of which two only were fertile, and four pairings, all of which were fertile.

In the case of the female, there were in captivity two distinct periods during which matings could be obtained. The first commenced as soon as the wings had expanded, and continued until they were sufficiently hardened to allow the insect to fly strongly, a period approximately from 9 A.M. to 12 NOON; then, for four, five, or even six days there was a very marked unwillingness to pair, and matings during this "period of refusal" were most exceptional; afterwards the females again became willing and remained so for three or four days, at the end of which they died, unless they had succeeded in pairing previously. The general impression was that the first period of acquiescence was due solely to the fact that the female was not in a position to resist effectively the advances of the male, while during the second there was an actual desire on the part of the female to pair. Cases in which a female paired twice were rare; in fact, they were only noticed on two occasions; it may, however, be a more common event in nature, for, in captivity, it was impossible to discover if the first mating was fertile until too late to attempt others. (See note at end, p. 254.)

A description of an absolutely typical mating may next be of interest, for it shows that this process in *polytes*, as in other butterflies, is not the simple affair found in many moths, in which the male is accepted by the female as soon as he arrives. In the case under consideration, the female was of the *polytes* form and was in the first "period of consent," and the notes are abstracted directly from the account written at the time. "The male first noticed the female when at rest, and immediately tried to pair, but was refused, the female flapping her wings to keep him at a distance; finally, however, she was knocked off her perch and then hovered in the air in the typical way, the body being held almost vertical and the wings moving rather slowly almost in a horizontal plane, so that she appeared to be swaying in the air at the end of an invisible thread. The male then hovered a few inches below the female, his wings moving more rapidly and his position practically horizontal; he usually turned his back on the female, but sometimes they faced the same way; at intervals he rose slightly and collided with the female, rebounding off again to the same distance. After four or five minutes of this aerial dance the female settled and the male followed her, but remained hovering just behind her, swaying from one side to the other as if fanning her; finally, getting closer, he attempted to pair, but the

female flew off again, closely pursued by the male, until she again alighted on the cage wall; this time, instead of sitting with the wings expanded, they were elevated and closed over the back, while the body, instead of being almost parallel to the surface of the cage, was raised almost at right angles to it. This is the attitude invariably assumed before pairing, which in this case immediately took place."

The aerial dance is always a great feature in the courting of the butterflies and is evidently appreciated by the females, for they were frequently observed to follow and hover behind an apathetic male which had settled before they were satisfied. A further feature in the female, which was quite unexpected, was that she seemed most attractive during the intermediate days between the two periods of consent; in fact, she was most attractive during the time when it was practically hopeless to attempt a pairing. These peculiarities in the female naturally made it more difficult to obtain reliable evidence of selective mating, and for the same reason observations had to be made rather on the male than the female. The following cases, abstracted directly from notes taken at the time, are typical:—

On January 10, 1912, a ♂ 37* was offered first a ♀ *cyrus* 37, then a ♀ *polytes* wild,† and then a ♀ *romulus* 39, but he showed no inclination to pair, though the females mentioned were all willing. Then he was given a ♀ *cyrus* wild and pairing immediately took place. On January 11 the same male 37 was offered a ♀ *cyrus* 37 but refused; then he was given a ♀ *cyrus* 39 and he paired at once.

A second ♂ 37 emerged on January 14, but refused to pair that day; on the 15th he paired with a ♀ *polytes* 36; on the 16th he paired with a ♀ *cyrus* 40; on the 17th he refused a ♀ *cyrus* 39, but took a ♀ *romulus* 39; on the 18th he paired with a ♀ *polytes* wild; on the 19th he refused a ♀ *cyrus* 39, a ♀ *cyrus* 40, a ♀ *romulus* 40, but took a ♀ *romulus* 41.

On January 26 a ♀ *cyrus* 41 which emerged on the 25th was given to two ♂ s 41, but, though these males were willing, the female refused; then two ♂ s 38 were tried, and these were so violent in their efforts to pair that one had to be removed to give the other a chance. The female, however, refused utterly and kept the male away by continually vibrating her wings. The wings were then secured by means of a small piece of tin foil and the male again did his best to pair, but the female foiled him by curling her abdomen underneath her thorax. The female's wings were then released, the male 38 was removed, and a male 34 was introduced, but, strange to say, this male was not attracted. The female was therefore removed and a ♀ *romulus* 41 was introduced, and the ♂ 34 was immediately attracted and pairing took place. Here, then, is a case in which a male refused a female, previously shown to be strongly attractive, but paired readily with another female.

On January 28 a ♂ 34 was given a ♀ *polytes* 36 which had emerged that morning,

* A number following the designation of any individual shows the brood from which it came. See table, p. 251.

† Shows that the female *polytes* was bred from wild larvæ.

but he refused her altogether, in spite of all attempts to bring her to his notice. He was then given a ♀ *cyrus* 41 which had also emerged that morning, and pairing took place at once.

On January 31 a ♀ *cyrus* 41—very old—paired with a ♂ 41; this female had had many previous chances but had always refused.

On February 2 a ♀ *romulus* 41 which had emerged on January 25 and was very old and worn, paired with a ♂ 34; she had refused all offers before.

On February 13 a ♂ 39 utterly refused a ♀ *polytes* wild (emerged February 13), examined, but was not strongly attracted by, a ♀ *cyrus* 37, which also had emerged that morning, and finally was much attracted by and attempted to pair with a ♀ *cyrus* 42 (emerged on February 12), but the female rejected him and no mating occurred.

On February 14 the ♂ 39, mentioned in the note on February 13, was again offered to three females which had been tried unsuccessfully the day before, but he exhibited no interest in them; then a freshly emerged ♀ *cyrus* 37 was introduced, and though she was noticed and examined, only very faint attempts at pairing were made. This female was then removed and a freshly emerged ♀ *polytes* wild substituted, when the male immediately became excited and pairing took place at once.

On February 27 a ♂ 39 was given two ♀ *cyrus* 47, which emerged on the 25th, and a ♀ *polytes* 46, freshly emerged. He refused the ♀ *polytes*, was feebly attracted by one of the ♀ *cyrus*, and strongly by the other, with whom he repeatedly tried to pair, but the female refused, probably because she was moribund.

Instances such as these occurred throughout the experiments in the case of the males: with the females also it seemed probable that something similar occurred, but it was never possible to obtain cases into which the sexual periods did not enter and, to a large extent, vitiate the results; there was no doubt, however, that a violent male was more likely to overcome the frequent reluctance of the females, and in consequence had a better chance of reproducing his kind.

In the case of the male there was absolutely no suggestion that the external form of the female was ever noticed, and, whatever the attraction between the sexes may be, it is most improbable that it is connected with sight; the behaviour of the butterflies favoured the opinion that scent is largely concerned in the phenomena of pairing, but there was no definite proof of this.

Taking the pairing phenomena as a whole, there seem to be grounds for the statements:—

- i. That all females are not equally attractive to all males.
- ii. That a female which is highly attractive to one male may be of no interest to a second.
- iii. That the attraction of the female is not raised during, and is probably unconnected with, the “periods of consent.”
- iv. That there is sufficient selection in the mating of the butterflies to have a possible influence on the course of evolution in the species.

The last section in this chapter may be devoted to a curious form of sterility which may ultimately prove of interest. When the experiments were first started, the insects were paired in the smaller cages, and it was assumed that if fertile ova were not obtained no pairing had taken place. The butterflies, then, as already stated, were left together permanently until they died, and though numerous pairings were obtained they were only occasionally observed; when the large pairing cage came into use, every pairing was noted, and it soon became evident that many matings were sterile. As this observation was first made on members of families which had been inbred for several generations, the cause seemed fairly obvious; later, however, fresh strains were obtained, and still there was a high percentage of sterile matings. The distribution of such matings can be most easily realised by following the table on p. 253. It begins with pairings made among broods 27-32, of which many were sterile, but four resulted in a further generation, comprising broods 33-36. It was then assumed that the strain was becoming degenerate, and a number of fertile wild females were caught, from which arose broods 37-42. Among these broods a large number of pairings were made, while there were also matings into which individuals from broods 33-36 entered, and others with insects reared from captured larvæ. In all, 34 pairings were recorded, and of these only 15 were fertile, so that the percentage of sterile matings exceeded 50 per cent., in spite of the fact that the individuals concerned were unrelated.

Of the 15 fertile matings, 4 were discarded and the remainder produced broods 43-53; 13 matings were made in this, the F_2 generation, in captivity,* and all were fertile, a very marked contrast to the preceding generation. In the F_3 generation, 17 matings were made, of which 2 were sterile, 1 pair escaped, and the remainder were fertile, giving broods 67-78.† In this generation 8 pairings were made, and of these 4 were sterile, the remainder yielding broods 79-82, which formed the last generation.

These statistics appear to show clearly that many of the sterile matings could not have been due to inbreeding. The next hypothesis considered was that they were due the effects of captivity. This again was unsatisfactory, for, in the first place, it has already been shown that captivity cannot have pressed on the butterflies severely, while, in the second place, it seems improbable that one generation should have been so affected that under 50 per cent. of the matings were fertile, while in the next the fertility rose to 100 per cent. under precisely similar conditions. A further curious feature is that the sterility was usually absolute, while finally it should be noted that when a male paired more than once all the pairings might be fertile or only a portion of them, and in the latter case it was not necessarily the earlier pairings which were fertile. There is not sufficient material to show whether this sterility can be attributed to the absence of some Mendelian factor or not. On the whole, the one

* It should be noticed that in one cross a late male from the F_1 generation was used, while in two others early males from the F_3 generation were used.

† Two matings were discarded.

point of theoretical importance suggested by these observations is that certain matings are normally "illegitimate," and can produce no offspring, and that this feature is possibly as prominent in nature as in captivity, though in the former case the evil results are probably counteracted by each sex being able to make several matings if required.

CHAPTER II.

Breeding Results and Inheritance. Hypothesis.

The high larval mortality, the long period during which emergence took place, combined with the selection and sterility phenomena indicated in the previous section, made any systematic Mendelian work most difficult, and it was frequently necessary, after attempting in vain to obtain desirable matings, to carry on the experiments by any pairings which proved fertile. This naturally resulted in the duplication of many of the less interesting crosses, while others likely to prove of value have been omitted. In spite of these difficulties, however, sufficient material has been obtained on which to base an hypothesis to explain the mode of inheritance of the three forms of female, though it must be admitted that the experimental numbers do not in all cases coincide with the hypothetical, a discrepancy probably due to the high larval mortality.

An inspection of the table of broods given at the end of this paper (p. 251) will show that each form of female gave certain alternative results, which may be tabulated as follows :—

The *cyrus* ♀ gave—

- i. *Cyrus* ♀ s alone.
- ii. *Cyrus* ♀ s and mimetic* ♀ s in about equal numbers.
- iii. Mimetic ♀ s alone.

The *romulus* ♀ gave—

- i. *Cyrus* ♀ s and mimetic ♀ s in about equal numbers.
- ii. *Cyrus* ♀ s and mimetic ♀ s, the latter greatly in excess, so that the ratio approaches 1 : 3.
- iii. Mimetic ♀ s alone.

The *polytes* ♀ gave—

- i. *Cyrus* ♀ s and mimetic ♀ s in about equal numbers.
- ii. *Cyrus* ♀ s and mimetic ♀ s, the latter greatly in excess, so that the ratio approaches 1 : 3.
- iii. Mimetic ♀ s alone.

* It may be recalled that a mimetic ♀ is either a *romulus* or a *polytes* female ; the number of mimetic females in a brood is the sum of the numbers of these two.

There is therefore a marked difference between the possible results to be obtained from a *cyrus* ♀ and those from either of the mimetic forms, while, as regards the latter, the potentiality of each appears to be alike. If, for the moment, the *cyrus* ♀ is disregarded, then the results obtained from the mimetic forms are as follows —

The *romulus* ♀ gave—

- i. *Romulus* ♀ s alone.
- ii. *Romulus* ♀ s and *polytes* ♀ s, the former greatly in preponderance.
- iii. *Romulus* ♀ s and *polytes* ♀ s in about equal numbers.

The *polytes* ♀ gave—

- i. *Romulus* ♀ s alone.
- ii. *Romulus* ♀ s and *polytes* ♀ s in about equal numbers.
- iii. *Polytes* ♀ s alone.

The problem of the various forms of female in *P. polytes* may therefore be divided into two distinct portions, the first being that which deals with the relations between the *cyrus* form and the mimetic forms, and the second dealing with the difference between the *romulus* ♀ and the *polytes* ♀, which, superficially at all events, does not affect the first part of the problem.

The Relationship between the cyrus ♀ and the Mimetic Forms.

Mention has already been made of the fact that there is only one form of ♂ in *P. polytes*, though, as has been pointed out by Prof. PUNNETT,* considerable variation is found in the colour and extent of the subterminal series of spots on the underside of the hind wing. The *cyrus* ♀ shows a similar variation, though its range is somewhat different, for the normal female coincides with those males which have the subterminal spots most developed and most highly coloured; variations from the normal in the female usually tend towards an accentuation of these features, and thus pass further from the normal type of male. As a whole, the material obtained seems to show that the variation is truly continuous, passing from a male with the spots barely discernible to a female in which they are much accentuated and are marked almost as strongly on the upper surface of the wing as on the lower. Efforts were made to trace some connection between this variation and the polymorphism of the female sex, but without success. Some such connection may exist, but as no suggestion whatever can be made on the subject, the mere statement of these facts is deemed sufficient.

As, externally, there is only one form of male, it becomes evident that the *cyrus* ♀ and the male must differ in constitution; further, as each form of female can give three distinct results, it is probable that there are at least three forms of male, two of which correspond to the mimetic females, though externally they resemble the other

* 'Spolia Zeylanica,' vol. 7, Part XXV, p. 1.

owing to some inhibitor intimately connected with the factors which must be supposed to produce the male sex. Thus, if the sex factors are represented as $Mmff$ in the male and $MMFf$ in the female, it may be supposed that there is a factor H , which causes any individual possessing it to take on a mimetic form, unless it is inhibited by a further factor P . This factor P may be considered to be present and heterozygous (Pp) in the male and absent (pp) in the female, while at segregation it is repelled by the sex factor M .

The following formulæ are then obtained for the two sexes: males are (i) $MmffPphh$, (ii) $MmffPpHh$, (iii) $MmffPpHH$; and females are (i) $MMFfpphh$, (ii) $MMFfppHh$, (iii) $MMFfppHH$. The males all appear alike as the factor H is inhibited by " P "; but in the females " P " is absent, and therefore females Nos. (ii) and (iii) take on a mimetic form, while female (i) alone is of the *cyrus* form since H also is absent.

These formulæ may be simplified in future by omitting altogether the sex factors, which are unnecessary since it is not proposed to enter into any discussion of the various methods of representing sex.* Males may be told at a glance by the possession of the factor P , the absence of which equally denotes a female.

The formulæ for the various individuals will therefore be as follows:—

The male will be: (i) $Pphh$, (ii) $PpHh$, (iii) $PpHH$.

The females of the *cyrus* form: $pphh$.

The females of a mimetic form: (i) $ppHh$, (ii) $ppHH$.

Among them there are nine possible matings.

Table of Matings.

Cyrus ♀ $pphh \times \delta_1 Pphh$ gives *cyrus* ♀ $pphh + \delta_1 Pphh$.

Cyrus ♀ $pphh \times \delta_2 PpHh$ gives *cyrus* ♀ $pphh + \text{mimetic } \delta_1 PpHh + \delta_2 PpHh$.

Cyrus ♀ $pphh \times \delta_3 PpHH$ gives *mimetic* ♀ $ppHh + \delta_2 PpHh$.

Mimetic ♀ $ppHh \times \delta_1 Pphh$ gives *cyrus* ♀ $pphh + \text{mimetic } \delta_1 PpHh + \delta_2 PpHh$.

Mimetic ♀ $ppHh \times \delta_2 PpHh$ gives *cyrus* ♀ $pphh + 2 \text{ mimetic } \delta_1 PpHh + \text{mimetic } \delta_2 PpHH + \delta_3 PpHH$.

Mimetic ♀ $ppHh \times \delta_3 PpHH$ gives *mimetic* ♀ $ppHh + \text{mimetic } \delta_2 PpHh + \delta_3 PpHH$.

Mimetic ♀ $ppHH \times \delta_1 Pphh$ gives *mimetic* ♀ $ppHh + \delta_2 PpHh$.

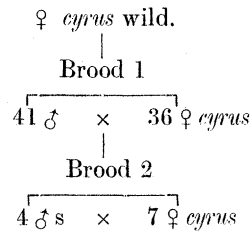
Mimetic ♀ $ppHH \times \delta_2 PpHh$ gives *mimetic* ♀ $ppHh + \text{mimetic } \delta_2 PpHh + \delta_3 PpHH$.

Mimetic ♀ $ppHH \times \delta_3 PpHH$ gives *mimetic* ♀ $ppHH + \delta_3 PpHH$.

This scheme may now be tested against the actual result obtained by experiment.

* If the formulæ for sex used above are considered too unwieldy, the more usual MM for the male and MF for the female may be employed, but it must then be supposed that the inhibitor " P " is homozygous

Broods 1 and 2.—*

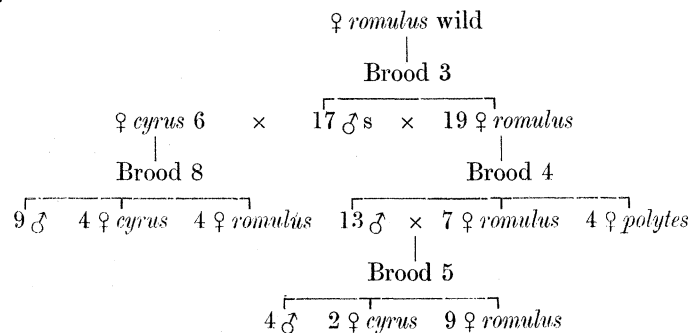


According to hypothesis, the *cyrus* ♀ is pphh, which can only be crossed by a male Pphh in order to give *cyrus* ♀ s alone. Represented in the form of an equation—

$$\text{♀ } \textit{cyrus} \text{ pphh} \times \text{♂ } \text{Pphh} = \text{♀ } \textit{cyrus} \text{ pphh} + \text{♂ } \text{Pphh}.$$

It is evident, therefore, that in the F_2 and all subsequent generations only *cyrus* ♀ s can be produced.

Broods 4, 5, 8.—



Broods 3, 4, 5 form the F_1 , F_2 , F_3 from a wild ♀ *romulus*. In the F_1 and F_2 only mimetic ♀ s were produced, but an interesting feature in the family is the appearance of *cyrus* ♀ s in the F_3 generation.

Brood 3 containing only mimetic ♀ s can be obtained by pairing a female of constitution ppHH with a male PpHH, or a female ppHH with any male. The cross ppHH \times PpHH, however, is evidently inadmissible, as it could never produce a *cyrus* ♀ in any subsequent generation, while the cross ppHH \times Pphh may also be neglected as it would produce *cyrus* ♀ s in the F_2 generation. Brood 3, therefore, may be represented either as

$$\left. \begin{array}{l}
 \text{ppHH} \times \text{PpHH} \\
 \text{or } \text{PpHh} \times \text{PpHH}
 \end{array} \right\} = \text{ppHH} + \text{ppHh} + \text{PpHH} + \text{PpHh}.$$

Brood 4 might also have been produced by either of these two alternatives, but in this case there is evidence that the mating ppHH \times PpHh occurred, for the male

in the male (MMPP) and heterozygous in the female (MFPp), and also that it requires the combination "PP" to inhibit "H." "P" is repelled by "F" at segregation.

* Mr. E. E. GREEN, Government Entomologist, reared these broods, and has kindly given me the result.

parent also paired with a *cyrus* ♀ from brood 6, giving brood 8, which contained equal numbers of *cyrus* and mimetic ♀s.

Brood 4, therefore, may be expressed—

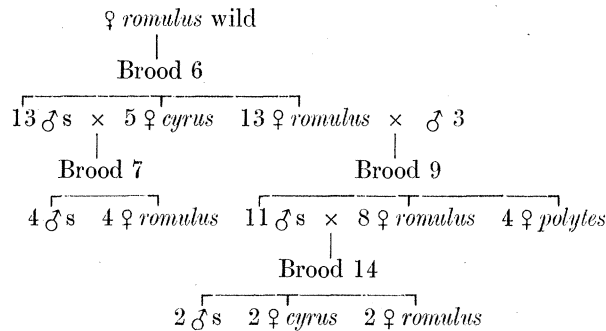
$$ppHH \times PpHh = ppHH + ppHh + PpHH + PpHh.$$

Brood 5 contained *cyrus* ♀s and was therefore produced by the cross $ppHh \times PpHh$ —

$$ppHh \times PpHh = 1 pphh + 2 ppHh + 1 ppHH \text{ (1 } cyrus : 3 \text{ mimetic)} + Pphh + 2 PpHh + 1 PpHH.$$

The actual numbers, 2 ♀ *cyrus* : 9 ♀ *romulus*, approximate sufficiently to the 1 : 3 ratio.

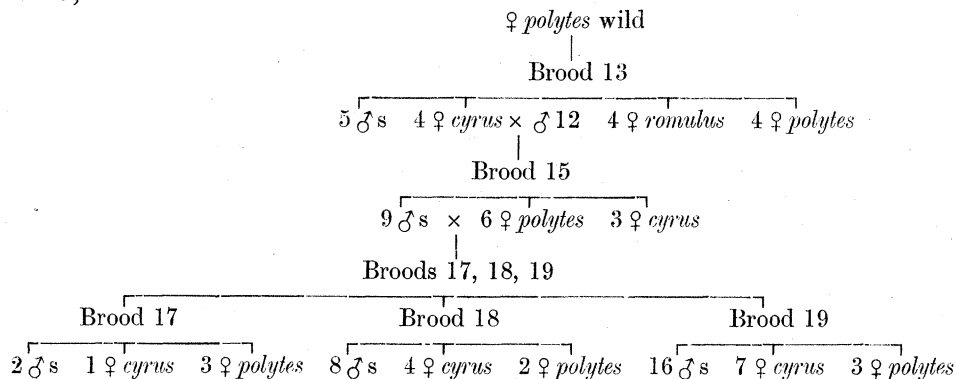
Broods 6–12, 14.—



Broods 6 and 7 form the F_1 and F_2 generations which arose from another wild ♀ *romulus*, while broods 9 and 14, also shown in the above table, resulted from the mating of a *romulus* ♀ of brood 6 with a ♂ of brood 3.

Brood 6 is evidently another instance of the mating $ppHh \times PpHh$ exemplified in brood 5; the ♂s of brood 6 therefore contain individuals of constitution $PpHH$, and if a *cyrus* ♀ $pphh$ is crossed by such a ♂, then the offspring will contain only ♀s of mimetic form, and this appears to be the explanation of brood 7. Broods 9 and 14 are analogous to broods 4 and 5. The remaining broods in this section, 8, 10, 11, 12, have either been discussed already (brood 8) or provide no evidence of value in testing the hypothesis.

Broods 13, 15–36.—



Brood 13 arose from a wild *polytes* ♀ and contained all three forms of female ; the *romulus* ♀s were neglected, and the *polytes* ♀s proved sterile when paired with males of their own brood, but two *cyrus* ♀s were crossed by ♂s of brood 12, about which little is known, save that, according to hypothesis, they were either PpHh or PpHH in constitution. These pairings gave broods 15 and 16 ; brood 15, containing 9 ♂s, 3 ♀ *cyrus* and 6 ♀ *polytes*, was presumably the result of a mating pphh × PpHh—

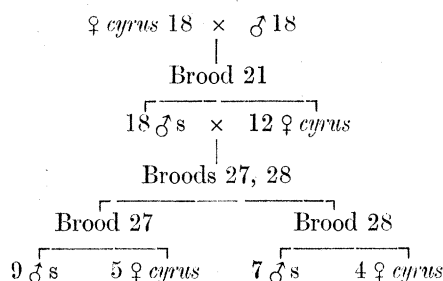
$$\text{pphh} \times \text{PpHh} = \text{pphh} + \text{ppHh} + \text{Pphh} + \text{PpHh}.$$

Brood 16 gave only 2 ♂s and 4 *polytes* ♀s, and was not continued further.

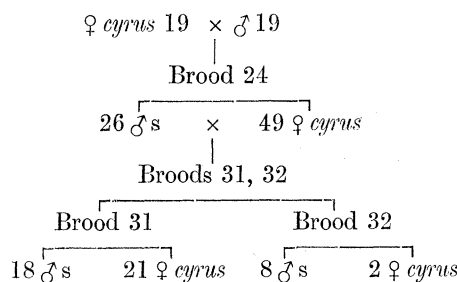
Brood 15 produced three F₂ broods, 17, 18, 19, all from *polytes* ♀s, and according to theory all of these should contain *cyrus* ♀s, since the female parent in each case was ppHh, and the male parent either PpHh or Pphh. The actual results can be seen from the pedigree table ; the *cyrus* ♀ appears in each brood but in excess of the calculated numbers, since there is a total of 12 *cyrus* ♀s to 8 *polytes* ♀s.

Among broods 17, 18, and 19 a large number of pairings were made, as it was hoped to obtain strains pure to both the *cyrus* and *polytes* forms of female. This hope was realised in the case of the *cyrus* ♀, but, as might have been expected in the light of the hypothesis, a strain which could be proved pure to a mimetic ♀ was not obtained.

A detailed analysis of every brood need not be given, for, though all find an explanation, many deal with individuals for whose constitutional formulæ there are several alternatives, and in consequence only negative evidence in favour of the hypotheses can be obtained. Special reference must be made, however, to those broods in which a *cyrus* ♀ yielded that form of ♀ alone, for in this case both the ♂s and the ♀s must have been homozygous for h, and if bred together should have given a strain pure to the *cyrus* form. An instance of this is to be found in broods 18, 21, 27, 28, the pedigree of which is given below :—



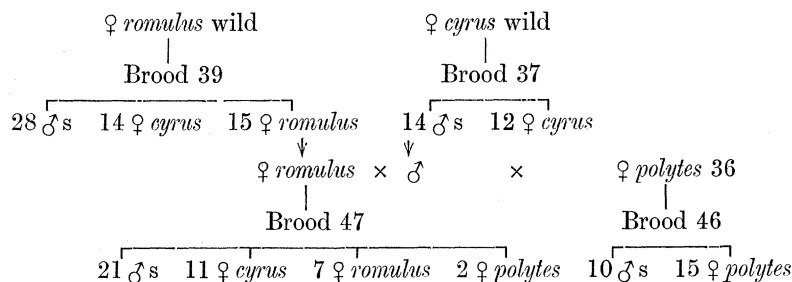
A further instance occurs in the same family in broods 19, 24, 31, 32, the pedigree of which may also be given :—



Broods 37-42 and Subsequent Generations.

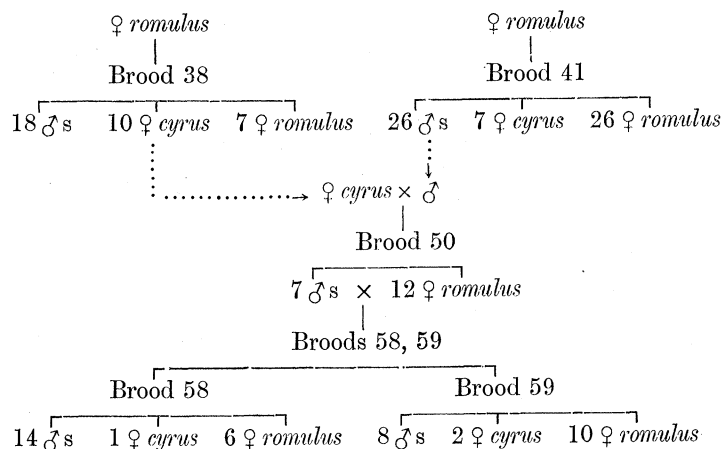
At this point in the experiments fresh blood was introduced, broods 37-42 all arising from wild females; as before, every effort was made to obtain individuals whose constitution in terms of the hypothesis was definitely known, though towards the close of the experiments evidence was specially sought as to the relationship between the *romulus* and *polytes* ♀ s.

Broods 37, 39, 47 may first be dealt with:—



Brood 37 arose from a wild *cyrus* ♀ and contained only ♀ s of the *cyrus* form, and therefore the ♂ s in this brood must have been all Pphh; brood 39 was the F₁ from a wild ♀ *romulus*, and contained equal numbers of *cyrus* and mimetic ♀ s, and so was produced by the mating ppHh × Pphh, which yields mimetic ♀ s of the formula ppHh only. The mating to produce brood 47, therefore, was ppHh × Pphh, which should yield equal numbers of *cyrus* and mimetic ♀ s, the experimental result being 11 ♀ *cyrus*, 9 mimetic ♀ s. It may also be pointed out that the male parent of 47 also produced brood 46 when paired with a *polytes* ♀ of 36, and as the brood contained only ♀ s of the mimetic form, the individuals in it must all have been heterozygous for H, males being PpHh and females ppHh.

Broods 38, 41, 50, 58, 59.—



Brood 38 is evidently an example of the mating $ppHh \times Pphh$, producing equal numbers of *cyrus* ♀s and mimetic ♀s. In brood 41 the female parent was again $ppHh$, but the male was presumably $PpHH$, so that in their offspring the three types of individual should have been represented.

A *cyrus* ♀ of 38 was mated with a ♂ 41 and gave brood 50, which contained only mimetic ♀s. The female parent was $pphh$ and the male parent must have been $PpHH$:— $pphh \times PpHH$ gives $ppHh + PpHh$.

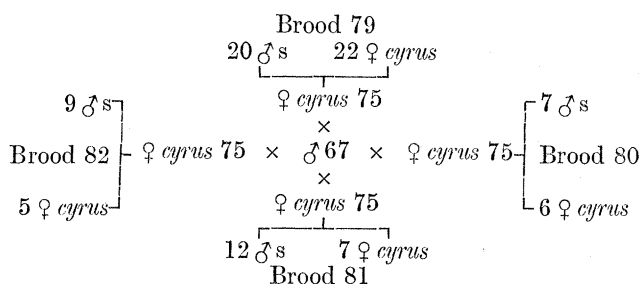
The males in brood 50, therefore, were $PpHh$ and the females $ppHh$; consequently broods 58, 59 arose from the mating $ppHh \times PpHh$:—

$$ppHh \times PpHh = pphh + 2 ppHh + ppHH \text{ and } Pphh + 2 PpHh + PpHH.$$

Therefore, in broods 58, 59, *cyrus* ♀s and mimetic ♀s ought to have appeared in the ratio 1 : 3. The actual results were 1 : 6 and 2 : 10, and there was thus an absence of two *cyrus* ♀s, which need not be considered of great importance in broods of this size.

Another mating between a *romulus* ♀ of 50 and a known ♂ was made, with less favourable results; this is shown in brood 63, which was derived from a *romulus* ♀ 50 ($ppHh$) mated with a ♂ 46, which has already been shown (p. 241) to have been $PpHh$. The experimental results were 6 *cyrus* ♀s, 3 *romulus* ♀s, and 3 *polytes* ♀s, instead of the calculated 1 ♀ *cyrus* to 3 mimetic ♀s.

At the period of brood 50, the disease already mentioned began, and became increasingly fatal to the experiments, so that only a very small proportion of the larvæ in any brood became adult. One final series of matings may be referred to in connection with the relation between the *cyrus* and mimetic females. Brood 67 arose from a mating ♀ *cyrus* 65 \times ♂ 64, and contained equal numbers of *cyrus* and *polytes* ♀s. The ♂s in brood 67, therefore, were either $PpHh$ or $Pphh$. A ♂ of 67 paired four times, on each occasion with *cyrus* ♀s of 75; according to hypothesis, if a ♂ pairs with a *cyrus* ♀ and gives only ♀s of this form, then if paired with other *cyrus* ♀s it must in each case give *cyrus* ♀s alone without any mimetic ♀s.



These broods, therefore, again bear out the hypothesis. With brood 82 the experiments ceased, and it is therefore necessary to proceed to a consideration of the relationship between the *romulus* and *polytes* forms which hitherto have been considered together as the “mimetic forms.”

Relation between the romulus and polytes Females.

In some respects this portion of the problem is the more simple of the two, but at the same time it presents many difficulties when the experimental proof of any hypothesis is required. A general review of all the broods seems to justify certain generalisations, which may be tabulated as follows:—

- i. If a brood contains only ♀s of the *polytes* form, or of the *cyrus* and *polytes* forms together, then any pairings between the ♂s and ♀s of that brood will only yield ♀s of the *cyrus* and *polytes* forms, the *romulus* form having been entirely eliminated. The 22 broods, 15–36, and broods 64, 72, instance this.
- ii. A *romulus* ♀ may produce an F₁ containing only ♀s of the *romulus* form, yet *polytes* ♀s may appear in the F₂ or subsequent generations. Instance, broods 3 and 4.
- iii. When *romulus* and *polytes* ♀s appear in the same brood, *romulus* ♀s may be in preponderance or there may be approximate equality, but there is never an excess of *polytes* ♀s. Exception, brood 12.
- iv. The factors for the production of *romulus* ♀s may be introduced into a strain pure to the *polytes* (or *polytes* and *cyrus*) form by pairing a male of this strain with a *romulus* ♀. Instance, 47, 63.
- v. *Romulus* ♀s may also be produced by pairing a *polytes* ♀ with a male from a *romulus* throwing strain, so that, whatever the difference between these ♀s may be, it is also represented in the male sex. Instances, broods 13, 65.

These facts immediately suggest a simple explanation; if the difference between the *romulus* and *polytes* forms is represented by an additional pair of factors R and r, R being such that it converts a mimetic ♀ to the *romulus* form, then the above generalisations would be realised. The fresh factor R can have no external effect in the case of the ♂, owing to the presence of the inhibitor P, while in the *cyrus* ♀ the

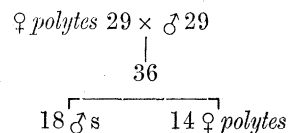
factor it qualifies is absent. The following formulæ then represent the various individuals:—

♂ s.	<i>cyrus</i> ♀ s.	<i>romulus</i> ♀ s.	<i>polytes</i> ♀ s.
PphhRR PphhRr Pphhrr PpHhRR PpHhRr PpHhrr PpHHRR PpHHRr PpHHrr	pphhRR pphhRr pphhrr	ppHhRR ppHhRr ppHHRR ppHHRr	 ppHhrr ppHHrr

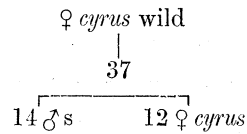
If these formulæ are applied to the experiments in detail they will be found adequate to explain most of the results. There are, however, certain objections. In numerous cases the numbers obtained by experiment do not correspond with the calculated numbers, though the former are not sufficiently large to be really reliable, an argument which, however, cannot be applied to brood 12. Then no instance was observed in which a *cyrus* ♀ carried the factor R; thus, in any brood in which only *cyrus* and *romulus* ♀ s were produced, the *cyrus* ♀ s ought to have been pphhRR or pphhRr, and either of these, if crossed by a ♂ carrying H but free from R (*i.e.* from a “*romulus*-free” strain) should have produced *romulus* ♀ s. Many attempts were made to obtain such a result, particularly in the last 20 broods, but without success. In none of these cases, however, could it be absolutely proved that the parent *cyrus* ♀ ought to have carried the R factor, and so this point must be left open. A further objection is to be found in brood 49, which did not even contain the calculated types of ♀. Brood 49 arose from a *polytes* ♀ paired with a ♂ of 38, which contained 10 *cyrus* ♀ s and 7 *romulus* ♀ s; the ♂ of 38, therefore, ought to have been carrying the factor R, and in his offspring by a *polytes* ♀ there should have been *romulus* ♀ s. The actual result was 12 ♂ s, 6 ♀ *polytes*. It is perhaps worthy of note that there were twice as many ♂ s as ♀ s, and therefore it is just possible that the missing six ♀ s were all of the *romulus* form as demanded by the hypothesis.

Two hypotheses have now been advanced for the explanation of the two problems in *polytes*, and, as an illustration of the combination, broods 36, 37, 39, 46, 47 may be reconsidered.

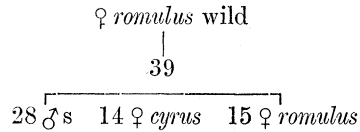
Brood 36.—



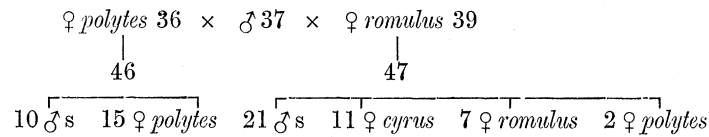
Brood 37.—



Brood 39.—

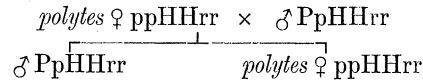


Broods 46 and 47 were derived from the same ♂.

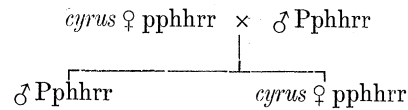


These broods may now be repeated, substituting the formulæ for the various individuals according to expectation.

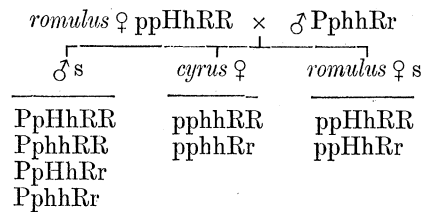
Brood 36.—



Brood 37.—

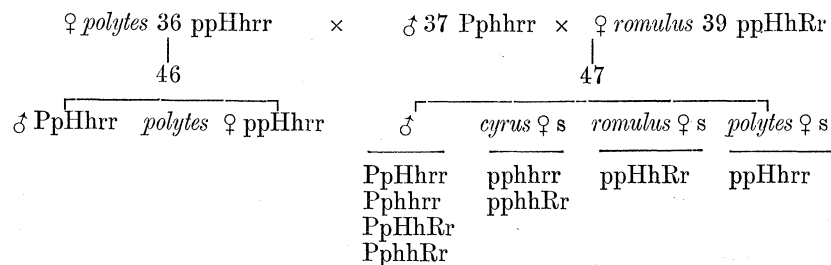


Brood 39.—



The *cyrus* ♀ s should equal the *romulus* ♀ s in number.

Broods 46, 47, then.—



In brood 47 there should be equal numbers of *cyrus* ♀s and mimetic ♀s, while among the latter the *romulus* and *polytes* ♀s ought also to be equal. The first condition is approximately realised, but there were 7 *romulus* ♀s : 2 *polytes* ♀s instead of equality.

The work as a whole seems to show conclusively that the inheritance phenomena in *P. polytes* can be expressed in Mendelian terms; the scheme proposed may have to be modified in accordance with future discoveries, but nevertheless when the difficulties of obtaining reliable numbers in pedigree work with butterflies are considered, it seems that the hypotheses proposed are supported very fairly by the facts produced in the course of the experiments.

CHAPTER III.

General Conclusions and Comparisons.

Although there are a large number of butterflies exhibiting in varying degrees the phenomenon of polymorphism, few have yet been investigated by the method of pedigree breeding. In Oriental regions JACOBSEN's experiments on *Papilio memnon*, Linn., stand alone, while in America *Colias philodoce* seems to be the only species which has yet provided definite results. In Africa the subject is attracting more attention, and the researches of LEIGH,* MILLAR, ROGERS,* CARPENTER,* LAMBORN,* and others on *Papilio dardanus*, *Acræa encedon*, *Leuceronia argia*, *Hypolimnias misippus*, other species of *Hypolimnias* (*Euralia*) and *Pseudacraea* are already producing results of the greatest interest. The cases of sex-limited inheritance, which are being studied in Africa, however, appear to be decidedly complex, so that they cannot yet be expressed in a generalised form, and, until this can be done, comparisons with *polytes* would be too speculative to be profitable.

The case of *C. philodoce*,† though superficially resembling that of *P. polytes*, is in many ways very different; for, though the species has, as a rule, a single form of ♂ (a yellow ♂) and two forms of ♀ (a yellow ♀ and a white ♀), yet occasionally a second ♂ (a white ♂) is found, and this form has not yet been used in the experiments. The results obtained from the other three forms seem to show that white coloration is dominant in the female sex but recessive in the male sex. GERROULD proposes that the ♂s should be represented by XXYY and XXYW, and ♀s by XOYY and XOYW; all the ♂s then are yellow, while of the ♀s XOYY is yellow and XOYW is white; homozygous whites, either ♂ or ♀, are not known, though it would naturally be expected that the white ♂ would be found homozygous for W if it could be studied. As a whole, *C. philodoce* has little in common with *P. polytes*, and further differences may probably be discovered when it has been completely worked out.

* The researches of these observers have for the most part been communicated by Prof. POULTON to the Entomological Society of London, in whose 'Transactions' and 'Proceedings' they may be found.

† GERROULD, 'American Naturalist,' 1911, p. 257.

The case of *P. memnon* is of greater interest, in that it shows a remarkable similarity to that of *P. polytes*. JACOBSEN* carried out his experiments in Java, and the form of *P. memnon* studied has a single form of ♂ and three forms of ♀, of which one, the *laomedon* ♀, somewhat resembles the ♂, while the other two, the *achates* ♀ and the *agenor* ♀, are markedly different; *achates* differs from the ♂ and from the *laomedon* and *agenor* ♀s in that it possesses "tails" to the hind-wings.†

JACOBSEN reared 17 broods on which DE MEIJERE‡ proposed a definite scheme of inheritance. He represented the various individuals as follows:—

♂ s.	♀ s.
LL	LL = <i>laomedon</i> ♀
Ach Ach . . .	Ach Ach = <i>achates</i> „
Ach L	Ach L = „ „
Ach Ag	Ach Ag = „ „
Ag Ag	Ag Ag = <i>agenor</i> „
Ag L	Ag L = „ „

The ♂s are supposed to be unaffected by these factors, the ♀ taking the form shown above. GOLDSCHMIDT§ proposed a modification of this idea, substituting the letters G, G¹, G² for DE MEIJERE'S L, Ag, Ach, and introducing the "sex factors" AA in the ♀ and Aa in the ♂, AA being supposed to inhibit the various ♀ forms. G is "hypostatic" to G¹ and G¹ to G². He therefore used the following formulæ:—

♂ s.	♀ s.
AAGG	AaGG = <i>laomedon</i> ♀
AAG ² G ² . . .	AaG ² G ² = <i>achates</i> „
AAGG ²	AaGG ² = „ „
AAG ¹ G ²	AaG ¹ G ² = „ „
AAG ¹ G ¹	AaG ¹ G ¹ = <i>agenor</i> „
AAGG ¹	AaGG ¹ = „ „

As there are 36 possible combinations among the individuals in the DE MEIJERE'S or GOLDSCHMIDT'S schemes, they are very comprehensive and cover all the possibilities shown by JACOBSEN'S experiments.

A third suggestion is made by BAUR,|| who proposes two sets of factors, A a, B b. When A and B are present in a ♀, it is of the *achates* form; if A alone is present,

* 'Tijdschr. voor Entomologie,' 1909, vol. 53, pp. 125-157.

† It is somewhat curious that the *agenor* form should have been available, as, according to ROTHSCHILD and JORDAN ('Novit. Zool.,' 1895, vol. 2, p. 320), it does not occur in Java.

‡ 'Zeitschrift für Inductive Abstammungslehre,' 1910, vol. 3, Part III, p. 161.

§ 'Zeit. Ind. Abst.,' 1912, vol. 8, Parts I and II, p. 85.

|| 'Einführung in die Experimentelle Vererbungslehre,' pp. 155-9.

the form is that of the *agenor*, while if A is absent, the *laomedon* ♀ is produced. The ♂ is not affected by these factors.

The formulæ for the various individuals, then, are :—

♂ s.		♀ <i>laomedon</i> .		♀ <i>achates</i> .		♀ <i>agenor</i> .
aabb	}		}	aabb		
aaBb				aaBb		
aaBB				aaBB		
AABb	}			AABb		
AABB				AABB		
AaBb				AaBb		
AaBB				AaBB		
AAbb	}					AAbb
Aabb						Aabb

BAUR's scheme also covers all JACOBSEN's results, and on the *memnon* experiments alone it would be difficult to decide between it and that of DE MEIJERE and GOLDSCHMIDT. If, however, they are applied to *polytes*, it will be noticed that BAUR's scheme is in principle almost exactly that proposed for this species in the earlier part of this paper; he leaves out the sex factors and the inhibitor factor which prevented the formation of mimetic ♂s, but his A and B correspond entirely with the H and R factors in *polytes*. BAUR, therefore, would represent *polytes* as being of the *romulus* form when both H and R are present; when H is present alone the *polytes* form is produced, while when H is absent the result is a *cyrus* ♀. BAUR's scheme, therefore, applies equally to *polytes*. GOLDSCHMIDT's scheme, however, is constructed on a different basis, for, except in his sex factors, he avoids the use of the "presence and absence" methods of representation. Thus it arises that certain results possible by BAUR's scheme are impossible by GOLDSCHMIDT's. JACOBSEN, unfortunately, did not happen to make any crosses with *memnon* which would give alternative results according to the correctness of either of the hypotheses. For *polytes*, however, it can be definitely stated that GOLDSCHMIDT's hypothesis is untenable, as is evident from the following examples. In the first place, it would be impossible for a *cyrus* ♀, which corresponds to the *laomedon* ♀ and would have a formula AaGG, to give all three forms of ♀, as occurred in brood 74. Then, if broods 37 and 47 are considered, it will be seen that the ♂ from 37 on GOLDSCHMIDT's scheme would have been AAGG, and such a ♂ could not have given a brood containing all three forms of ♀, which occurred in 47.

The essential features, therefore, of DE MEIJERE's and GOLDSCHMIDT's hypotheses make them untenable in the cases of *P. polytes*, and by analogy it is to be expected that they are also inapplicable to *P. memnon*. At all events, in the absence of further research, some method of representation such as that proposed by BAUR is to be preferred.

The next point to be dealt with concerns the possible effects of selection on such a species as *P. polytes*. Granting that the scheme proposed is correct as a generalisation, and that there are no disturbing forces, it is possible to show mathematically that certain results must follow; of these, the most important is that adverse selection of the *cyrus* ♀ will ultimately cause its disappearance, in spite of the fact that all the males are alike,* and that this will be equally true whether the selection is stringent or not, while finally no stable condition is reached until all the population is homozygous for H. In Ceylon and South India there are two "distasteful" models, each of which is common, and there are two mimetic forms of *polytes* to correspond; in this region, then, selection should be most in favour of the mimetic forms, and the *cyrus* ♀ ought to be in process of disappearance. Actual results, however, show that in no part of the range of *polytes* is the *cyrus* ♀ more common, and it can only be supposed that selection due to mimicry is effective, if it has come into action very recently among a population which consisted in the main of the *cyrus* form. This is improbable and is not supported by any evidence whatever.

Statistics as to the relative abundance of the three ♀s at Peradeniya were obtained by collecting wild larvæ, and, since these were only found singly or in small numbers throughout the whole period of the experiments, it follows that almost every individual was the offspring of a different ♀; it is probable, therefore, that the results obtained are fairly accurate, in spite of the fact that the total number recorded was small. Further, since *polytes* is one of the most migratory of species, statistics obtained in the Peradeniya district apply almost equally to the whole of the island.†

The total number of individuals reared from wild larvæ was 155, among which there were 66 ♂s, 40 ♀ *cyrus*, 24 ♀ *romulus*, and 25 ♀ *polytes*; the numbers of the various ♀s converted into percentages read as ♀ *cyrus* 45 per cent. (44·94...), ♀ *romulus* 27 per cent. (26·96...), ♀ *polytes* 28 per cent. (28·09...), and there were therefore 55 per cent. mimetic ♀s and 45 per cent. *cyrus* ♀s.

This ratio, as was shown by Prof. PUNNETT, is of interest, as it agrees with HARDY'S formula for a population in Mendelian stability; that is, in such a condition that, in the absence of selection, the relative abundance of the three ♀s remains unchanged. Thus, if p = the number of pure dominants, $2q$ = the number of heterozygotes, and r = the number of recessives, then, in the absence of selection, the population is stable if $q^2 = pr$.

In the case of *polytes* only the sum of $2q$ and p (55) is known, and the actual numbers of $2q$ and p are unknown and could only have been discovered by elaborate breeding experiments. Without this knowledge, however, it can easily be seen that

* In a preliminary account of *P. polytes* read before the Entomological Congress at Oxford an exactly opposite view was expressed. Prof. PUNNETT, who kindly communicated the paper, pointed out the fallacy at the time and subsequently enlightened the author as to the correct view.

† In Ceylon the true home of *polytes* appears to be in the "low country" jungles, specially in those of the dry zones and observations tend to show that the species would die out in the hills (1500 ft. above sea level and upwards) without the continual additions by migration from the lower levels.

there are only certain numbers which fulfil the required conditions, as, for instance, when p is 1, $2q$ is 2, and r is 1; or, again, when p is 1, $2q$ is 4, and r is 4. In the latter case the sum of $2q$ and p is 5, and so the ratio $2q + p : r$ is 5 : 4, which may be expressed as 55 : 44. The ratio of $2q + p : r$ obtained from the statistics is 55 : 45, and this coincides in a remarkable way with the calculated 55 : 44 required for a stable population.

In Ceylon, therefore, if the above statistics are reliable, the ratio between the mimetic and non-mimetic ♀s is one which might be expected if it be assumed that there is no selection in favour of either of these forms of ♀; under these conditions the population is stable in composition and may remain so indefinitely.

On the whole question, however, no final conclusions can yet be drawn, for, in the first place, the numbers obtained from the statistics may quite possibly be a coincidence, while in the second the effects of the phenomena discovered in connection with the fertility and mating of the species are quite unknown. Possibly the conclusion which can be drawn with the greatest confidence is that the extraordinary mimicry displayed in the female sex is at present of little importance to the population of the butterfly in Ceylon.

Finally, as regards the polymorphism of *polytes* considered from a more general point of view, it is impossible to draw any definite conclusions. The fact that such dissimilar insects as the three female forms can exist as members of one species suggests that the important characters from the natural selection standpoint are not so largely external as is sometimes supposed. The irregular fertility discovered in the experiments was not investigated sufficiently for its exact nature to be discovered, but it suggests a method by which polymorphic species could be divided into "monomorphic" species, provided the factors for fertility and sterility were coupled with those controlling the external form. If, therefore, forms of equal selective value are not uncommon in nature, as might be deduced from the occurrence of *P. polytes* and other polymorphic species, then the whole question of fertility and sterility is of the greatest importance in the formation of species, and may be worthy of close study in other species.

In concluding this paper the author wishes to express his gratitude to the Balfour Managers and to the Master and Fellows of Gonville and Caius College for enabling him to work in Ceylon. He is also greatly indebted to the authorities at the Royal Botanic Gardens at Peradeniya—Drs. WILLIS and LOCK, Messrs. GREEN, PETCH, and MACMILLAN—for providing him with special facilities for work in the gardens, and to the various correspondents in Ceylon who supplied him with information and material for experiment. Special reference must be made to the assistance rendered by Mr. E. E. GREEN, Government Entomologist, since it was of a nature only to be obtained from one whose knowledge of the entomology of Ceylon is never likely to be rivalled.

Papilio polytes. Pedigree Broods.

Brood No.	Parentage.	♂ s.	cyrus ♀.	romulus ♀.	polytes ♀.
1	♀ cyrus wild	42	36		
2	♀ cyrus 1 × ♂ 1	4	7		
3	♀ romulus wild	17		19	
4	♀ romulus 3 × ♂ 3*	13		7	4
5	♀ romulus 4 × ♂ 4.	4	2	9	
6	♀ romulus wild.	13	5	13	
7	♀ cyrus 6 × ♂ 6	4		4	
8	♀ cyrus 6 × ♂ 3*	9	4	4	
9	♀ romulus 6 × ♂ 3.	11		8	4
10	♀ cyrus 8 × ♂ 8	5		1	
11	♀ romulus 7 × ♂ wild	1		2	1
12	♀ romulus 3 × ♂ wild	58		24	32
13	♀ polytes wild	5	4	4	4
14	♀ romulus 9 × ♂ 9	3	2	2	
15	♀ cyrus 13 × ♂ 12.	9	3		6
16	♀ cyrus 13 × ♂ 12.	2			4
17	♀ polytes 15 × ♂ 15	2	1		3
18	♀ polytes 15 × ♂ 15	8	4		2
19	♀ polytes 15 × ♂ 15	16	7		3
20	♀ polytes 17 × ♂ 18	21	16		16
21	♀ cyrus 18 × ♂ 18.	18	12		
22	♀ polytes 19 × ♂ 19	4	2		4
23	♀ cyrus 19 × ♂ 18.	11	9		6
24	♀ cyrus 19 × ♂ 19.	26	49		
25	♀ polytes 19 × ♂ 19	16	13		6
26	♀ polytes wild × ♂ wild	3			2
27	♀ cyrus 21 × ♂ 21.	9	5		
28	♀ cyrus 21 × ♂ 21.	7	4		
29	♀ polytes 22 × ♂ 22	20			17
30	♀ polytes 22 × ♂ 22				3
31	♀ cyrus 24 × ♂ 24.	18	21		
32	♀ cyrus 24 × ♂ 24.	8	2		
33	♀ polytes 29 × ♂ 29	11			20
34	♀ polytes 29 × ♂ 29†	6			2
35	♀ polytes 29 × ♂ 29	3	1		
36	♀ polytes 29 × ♂ 29†	18			14
37	♀ cyrus wild	14	12		
38	♀ romulus wild.	18	10	7	
39	♀ romulus wild.	28	14	15	
40	♀ romulus wild.	7	4	10	
41	♀ romulus wild.	26	7	26	
42	♀ cyrus wild	2	2	4	
43	♀ cyrus wild × ♂ 37	4	8		
44	♀ cyrus 38 × ♂ 38.	1	3		
45	♀ romulus 39 × ♂ 39	Failed			
46	♀ polytes 36 × ♂ 37‡	10			15
47	♀ romulus 39 × ♂ 37‡	21	11	7	2
48	♀ romulus 41 × ♂ 41	3	1	1	
49	♀ polytes 33 × ♂ 38	12			6
50	♀ cyrus 38 × ♂ 41	7		12	
51	♀ romulus 38 × ♂ 38	6	2	5	

* The ♂ 3 parent of 4 and 8 was the same individual.

† ♂ parent of 36 and 34 the same individual.

‡ ♂ parent of 46 and 47 the same individual.

Papilio polytes. Pedigree Broods—continued.

Brood No.	Parentage.	♂ s.	<i>cyrus</i> ♀.	<i>romulus</i> ♀.	<i>polytes</i> ♀.
52	♀ <i>cyrus</i> 38 × ♂ 38.	3	3		
53*	♀ <i>cyrus</i> 38 × ♂ 37.	5	6	3	
54*	♀ <i>cyrus</i> 43 × ♂ 41.	4	1 ?	7	
55	♀ <i>romulus</i> 40 × ♂ 47.	38		31	
56	♀ <i>polytes</i> 46 × ♂ 47.	14	2	2	1
57	♀ <i>polytes</i> wild × ♂ 47.	5	8		3
58	♀ <i>romulus</i> 50 × ♂ 50.	14	1	6	
59	♀ <i>romulus</i> 50 × ♂ 50.	8	2	10	
60	♀ <i>romulus</i> 50 × ♂ 49.	1		5	2
61	♀ <i>polytes</i> 49 × ♂ 51.	4		1	
62	♀ <i>polytes</i> 49 × ♂ 51.	2	1	1	
63	♀ <i>romulus</i> 50 × ♂ 46.	16	6	3	3
64	♀ <i>cyrus</i> [53] × ♂ 46.	23	15		8
65	♀ <i>polytes</i> 46 × [♂ 54].	24	3	9	4
66	♀ <i>cyrus</i> [53] × ♂ 55.	8	8	3	
67	♀ <i>cyrus</i> 65 × ♂ 64.	36	14		16
68	♀ <i>romulus</i> 65 × ♂ 62.	11	1	6	7
69	♀ <i>cyrus</i> 65 × ♂ 64.	Failed			
70	♀ <i>polytes</i> 65 × ♂ 65.	9	4	8	3
71	♀ <i>romulus</i> 65 × ♂ 64.	41	3	12	8
72	♀ <i>cyrus</i> 64 × ♂ 64.	12	2		3
73	♀ <i>romulus</i> 65 × ♂ 64.	9	3		
74	♀ <i>cyrus</i> 66 × ♂ 66.	6	8	2	2
75	♀ <i>cyrus</i> 66 × ♂ 64.	16	20		
76	♀ <i>cyrus</i> 66 × ♂ 64.	6	6		7
77	♀ <i>polytes</i> 64 × ♂ 64.	6	1		1
78	♀ <i>cyrus</i> 66 × ♂ 64.	3	4		1
79	♀ <i>cyrus</i> 75 × ♂ 67†.	20	22		
80	♀ <i>cyrus</i> 75 × ♂ 67†.	7	6		
81	♀ <i>cyrus</i> 75 × ♂ 67†.	12	7		
82	♀ <i>cyrus</i> 75 × ♂ 67†.	9	5		

* Broods 53 and 54 were accidentally mingled ; their results are valueless.

† The ♂ parent in 79–82 was the same individual.

TABLE of Observed Matings in Pedigree *P. polytes*.

Date.	Individuals.	Result.	Brood No.
1911.			
October 16 . .	♀ <i>cyrus</i> 27 × ♂ 28	Sterile	
" 17 . .	♀ <i>polytes</i> 29 × ♂ 29	Sterile	
" 17 . .	♀ <i>cyrus</i> 28 × ♂ 27	Sterile	
" 17 . .	♀ <i>polytes</i> 29 × ♂ 29	Fertile	33
" 17 . .	♀ <i>polytes</i> 29 × ♂ 29 ¹	Fertile	34
" 17 . .	♀ <i>cyrus</i> 27 × ♂ 28	Sterile	
" 18 . .	♀ <i>cyrus</i> 27 × ♂ 27	Sterile	
" 19 . .	♀ <i>polytes</i> 29 × ♂ 29	Sterile	
" 19 . .	♀ <i>polytes</i> 29 × ♂ 29	Fertile	35
" 19 . .	♀ <i>cyrus</i> 31 × ♂ 27	Fertile	Failed
" 21 . .	♀ <i>polytes</i> 29 × ♂ 29	Sterile	
" 22 . .	♀ <i>polytes</i> 29 × ♂ 29 ¹	Fertile	36
December 6 . .	♀ <i>polytes</i> 33 × ♂ 34 ²	Sterile	
" 8 . .	♀ <i>polytes</i> 36 × ♂ 34 ²	Sterile	
" 8 . .	♀ <i>polytes</i> 36 × ♂ 36	Sterile	
" 12 . .	♀ <i>polytes</i> 33 × ♂ 33	Sterile	
" 12 . .	♀ <i>polytes</i> 33 × ♂ 36	Sterile	
1912.			
January 10 . .	♀ <i>cyrus</i> wild × ♂ 37 ³	Fertile	43
" 10 . .	♀ <i>polytes</i> wild × ♂ 36	Sterile	
" 10 . .	♀ <i>romulus</i> 39 × ♂ 39	Sterile	
" 10 . .	♀ <i>romulus</i> 39 × ♂ 39	Sterile	
" 11 . .	♀ <i>cyrus</i> 38 × ♂ 38	Fertile	44
" 11 . .	♀ <i>cyrus</i> 39 × ♂ 37 ³	Sterile	
" 12 . .	♀ <i>romulus</i> 39 × ♂ 39	Fertile	45
" 15 . .	♀ <i>polytes</i> 36 × ♂ 37 ⁴	Fertile	46
" 16 . .	♀ <i>cyrus</i> 40 × ♂ 37 ⁴	Sterile	
" 17 . .	♀ <i>romulus</i> 39 × ♂ 37 ⁴	Fertile	47
" 18 . .	♀ <i>romulus</i> 41 × ♂ 41	Sterile	
" 18 . .	♀ <i>cyrus</i> wild × ♂ 36	Sterile	
" 18 . .	♀ <i>polytes</i> wild × ♂ 37 ⁴	Sterile	
" 19 . .	♀ <i>romulus</i> 41 × ♂ 37 ⁴	Sterile	
" 20 . .	♀ <i>romulus</i> 41 × ♂ 36	Sterile	
" 24 . .	♀ <i>romulus</i> 41 × ♂ 41	Fertile	48
" 26 . .	♀ <i>polytes</i> 33 × ♂ 38	Fertile	49
" 26 . .	♀ <i>romulus</i> 41 × ♂ 34 ⁵	Sterile	
" 28 . .	♀ <i>cyrus</i> 41 × ♂ 34 ⁵	Sterile	
" 28 . .	♀ <i>cyrus</i> 38 × ♂ 41	Fertile	50
" 29 . .	♀ <i>polytes</i> 33 × ♂ 41	Sterile	
" 31 . .	♀ <i>cyrus</i> 41 × ♂ 41 ⁶	Fertile	Discarded.
February 1 . .	♀ <i>romulus</i> 38 × ♂ 38	Fertile	51
" 2 . .	♀ <i>cyrus</i> 37 × ♂ 34 ⁵	Sterile	
" 2 . .	♀ <i>polytes</i> 36 × ♂ 41 ⁶	Sterile	
" 3 . .	♀ <i>cyrus</i> 38 × ♂ 38	Fertile	52
" 4 . .	♀ <i>polytes</i> 33 × ♂ 35	Sterile	
" 4 . .	♀ <i>cyrus</i> 38 × ♂ 37	Fertile	53
" 9 . .	♀ <i>polytes</i> wild × ♂ 39	Sterile	
" 12 . .	♀ <i>romulus</i> 38 × ♂ 38	Fertile	Discarded.
" 12 . .	♀ <i>romulus</i> 39 × ♂ 39 ⁷	Sterile	
" 13 . .	♀ <i>cyrus</i> 40 × ♂ 40	Fertile	Discarded.
" 14 . .	♀ <i>polytes</i> wild × ♂ 39 ⁷	Sterile	
" 21 . .	♀ <i>cyrus</i> 39 × ♂ 40	Fertile	Discarded.
" 21 . .	♀ <i>cyrus</i> 43 × ♂ 41	Fertile	54

TABLE of Observed Matings in Pedigree *P. polytes*—continued.

Date.	Individuals.	Result.	Brood No.
1912.			
February 26 . .	♀ <i>romulus</i> 40 × ♂ 47	Fertile	55
" 27 . .	♀ <i>polytes</i> 46 × ♂ 47	Fertile	56
March 2 . .	♀ <i>polytes</i> wild × ♂ 47	Fertile	57
" 8 . .	♀ <i>romulus</i> 50 × ♂ 50	Fertile	58
" 8 . .	♀ <i>romulus</i> 50 × ♂ 50	Fertile	59
" 14 . .	♀ <i>romulus</i> 50 × ♂ 49	Fertile	60
" 16 . .	♀ <i>polytes</i> 49 × ♂ 51	Fertile	61
" 18 . .	♀ <i>polytes</i> 49 × ♂ 51	Fertile	62
" 29 . .	♀ <i>romulus</i> 50 × ♂ 46	Fertile	63
" 30 . .	♀ <i>cyrus</i> 53 × ♂ 46	Fertile	64
" 30 . .	♀ <i>polytes</i> 46 × ♂ 54	Fertile	65
April 9 . .	♀ <i>cyrus</i> 53 × ♂ 55	Fertile	66
" 24 . .	♀ <i>romulus</i> 61 × ♂ 62 ^s	Fertile	Discarded.
May 4 . .	♀ <i>polytes</i> 63 × ♂ 64	Sterile	
" 5 . .	♀ <i>cyrus</i> 65 × ♂ 64	Fertile	67
" 5 . .	♀ <i>romulus</i> 65 × ♂ 62 ^s	Fertile	68
" 6 . .	♀ <i>cyrus</i> 65 × ♂ 64	Fertile	69
" 7 . .	♀ <i>polytes</i> 65 × ♂ 65	Fertile	70
" 7 . .	♀ <i>cyrus</i> 63 × ♂ 64	Sterile	
" 8 . .	♀ <i>romulus</i> 65 × ♂ 64	Fertile	71
" 10 . .	♀ <i>cyrus</i> 64 × ♂ 64	Fertile	72
" 10 . .	♀ <i>romulus</i> 65 × ♂ 64	Fertile	73
" 11 . .	♀ <i>cyrus</i> 66 × ♂ 66	Fertile	74
" 12 . .	♀ <i>cyrus</i> 66 × ♂ 64	Fertile	75
" 14 . .	♀ <i>cyrus</i> 66 × ♂ 64	Fertile	76
" 14 . .	♀ <i>polytes</i> 64 × ♂ 64	Fertile	77
" 14 . .	♀ <i>cyrus</i> 66 × ♂ 64	Fertile	78
" 17 . .	♀ <i>romulus</i> 66 × ♂ 64	Fertile	Discarded.
" 17 . .	♀ <i>cyrus</i> 66 × ♂ 64	Escaped	
June 27 . .	♀ <i>cyrus</i> 75 × ♂ 67 ⁹	Fertile	79
" 28 . .	♀ <i>cyrus</i> 75 × ♂ 67 ⁹	Fertile	80
" 29 . .	♀ <i>polytes</i> 67 × ♂ 75	Sterile	
" 29 . .	♀ <i>cyrus</i> 75 × ♂ 67 ⁹	Fertile	81
July 1 . .	♀ <i>cyrus</i> 75 × ♂ 67 ⁹	Fertile	82
" 1 . .	♀ <i>polytes</i> 76 × ♂ 75 ¹⁰	Sterile	
" 3 . .	♀ <i>cyrus</i> 76 × ♂ 76	Sterile	
" 4 . .	♀ <i>cyrus</i> 67 × ♂ 75 ¹⁰	Sterile	

1 }
2 }
3 }
4 }
5 } When a ♂ paired more than once it is marked with a raised number—♂ 75¹⁰—showing
6 } that it is the same individual which appears in more than one mating.
7 }
8 }
9 }
10 }

Note.—Pairings before October 17 were made in the small cages, and it is not known what proportion were sterile. At least 50 more pairings must be added to those recorded above.

Note to p. 231.—It may be mentioned that if a female *polytes* paired early in life, two or three days frequently elapsed before the first eggs were laid. On the other hand an old female, as a rule, began to lay the day after pairing.