ON THE MALES AND AN INTERSEX-LIKE SPECIMEN OF THE PARTHENOGENETIC SAW-FLY PRISTIPHORA PALLIPES, LEP.*

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WHILST conducting biological experiments on parthenogenesis in saw-flies during the year 1923, the writer obtained two males and an intersex-like specimen of the species Pristiphora pallipes, Lep., under somewhat peculiar circumstances. As this species appears almost completely thelytokous—the males being exceedingly rare—and as sexual abnormalities in it have never been observed before, and indeed, have only been recorded eight times previously among the Tenthredinidæ, opportunity is here taken of describing and discussing these special appearances. It will be necessary first to dwell upon the experimental conditions as it is not improbable that they may have had a direct bearing upon the results obtained, but in any circumstances the results are of interest in themselves.

I. Rationale of Experimentation.

Investigation into the mechanism and physiology of sex determination in saw-flies is still in the preliminary stages, and it is from Doncaster's (1906) unfinished work that we owe most of the information available. He found in certain thelytokous species that, whilst there are two equational polar divisions, the egg still retained the diploid number of chromosomes. A natural question then suggests itself: is it possible by chemical and physical means to influence the behaviour of the nuclear material, especially during the critical phase of maturation, in such a way as to induce sex-reversal? In the Tenthredinidæ two methods of affecting the germ-plasm are obvious—firstly, by feeding the larvae on foodstuff which has been specially treated, and secondly, by subjecting the eggs to treatment. Both methods have been tried by the writer, but particular attention has been directed to the latter

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as it seemed the more speedy. In recounting this method it should be noted that saw-flies lay very fluid eggs, which are relatively large and easily seen, and which are deposited either openly on plant tissue or embedded partially or completely; further, maturation occurs during the first three hours after laying. Hence the technical problem was to find a method of treating the eggs during these first three critical hours. Eggs laid in such a way, therefore, can be subjected easily to treatment by chemical, electrical, X-ray, radio-active and other physical agencies. All these agencies have been employed, but the only method which need be discussed here is the chemical. A further point is that no matter how exposed or protected the egg there is a close relationship between it and the plant because, during incubation, the egg swells greatly as the result of absorbing moisture from its nidus. The permeability of the shell and the relationship to the plant suggest two possibilities for affecting the living material of the egg by fluids, viz. (1) by chemically impregnating the plant as the result of placing it as a cutting in a chemical solution, and allowing the chemical to penetrate to the region where eggs are to be deposited, and (2) by immersing the plant, with the eggs upon it, in a chemical solution. The first method is the less artificial, but it is uncertain whether a chemical agent dilute in the plant juices would penetrate the egg-shell in sufficient quantity during the short maturation period; and, further, any possible sex-effect produced could also be attributed to the action of the solution upon the developing embryo. This method was used in many experiments, but was abandoned largely because the varying spring weather caused premature wilting of the leaves and premature death of the caterpillars. The immersion method adopted will be described presently.

The species selected for experiment were Allantus pallipes, Spin., Pristiphora pallipes, Lep., and Pteronidea (Nematus) ribesii, Scop., all three of which are very familiar to me after three seasons' breeding work (1923). Allantus pallipes appears completely thelytokous as no male has ever been found in nature or bred in captivity; Pristiphora pallipes, in England at least, appears almost completely thelytokous; in
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*Pteronidea ribesii* the sex-ratio appears to be about 100 males : 140 females [v. Siebold, 1871 and 1884] and, after pairing, both sexes are produced but, parthenogenetically, the species is almost completely arrhenotokous. Occasionally, however, according to the experience of v. Siebold and the writer, there is a female thrown parthenogenetically. In these three species, which present such a range of parthenogenetic states, there appeared good material possibly susceptible of sex-change by experimental means, *A. pallipes* to be "directed" to the production of males, *P. pallipes* to the increased production of males, and *P. ribesii* to the increased production of one or other sex from sexually produced eggs, or to the production of females from parthenogenetic eggs. The experimental conditions relating to *P. pallipes* are what concern us here.

2. Experiments with *Pristiphora pallipes*.

This species buries its eggs completely in pockets situated on the edge of the leaf or in the main veins of gooseberry, but occasionally an egg may be more or less protruded. As the insects are somewhat small (± 4.5 mm.) and the eggs relatively large, it is not surprising that the number of eggs laid should not total more than twenty to thirty per individual, and the rate of laying, except under very favourable conditions, should not be rapid, six per day being quite a good yield. Therefore, in order to secure as many eggs as possible for treatment within the first three hours of laying, a gross preliminary method of experiment was adopted; the eggs were obtained from a number of females placed with the same plant cutting. The obvious advantages were that tedious watchings for eggs of known age were reduced in number, particularly during days unfavourable for laying, and the number of small but laborious breeding experiments was minimised. Insects having been introduced to twigs of the host plant under the breeding-jar, careful watch was kept to ascertain the commencement of egg-laying. After suitable periods the cuttings and their contained eggs were removed, freed from the adult flies, and immersed in magnesium sulphate solution, 0.2 per cent. made with distilled water, the periods of egg-laying and immersion being noted. The cuttings, on first immersing, were moved about
in the fluid in order to free the leaves from air-bubbles, and to assist the wetting of the leaves and eggs. The eggs, therefore, could be reached by the solution in two ways, firstly via the mouth of the egg-pocket, and secondly, via the impregnated leaf-tissue. After immersion the leaves were washed free of the chemical by moving the cuttings about in tap water, and were then allowed to dry in the open air, the cut ends of the twigs, of course, being placed in small vessels containing tap water. As soon as the leaves were dry the twigs, standing in their water vessels, were placed beneath large glass cylinders.

In three experiments, eggs not more than one hour old, and treated for one hour in the solution yielded 8 females; in five other experiments, eggs not more than one and a half hours old and treated for one hour yielded 62 females, 2 males, and 1 intersex-like specimen, the work being performed from June to August 1923.

These results give rise to the question: have these males and the abnormality been produced as the result of, or in spite of, the conditions of experiment, i.e. are they natural or artificial products? No definite answer can be given—the results are too few in number; but the circumstances must be borne in mind in interpreting the appearance of these specimens.

3. Sex-ratios in *Pristiphora pallipes*.

The history of the matter dates from 30th July 1920 when my colleague Miss E. F. Chawner found a wild larva at Lyndhurst, Hants, from which emerged a female *P. pallipes* on 13th August 1920. This female laid parthenogenetically, but the adults from the eggs did not hatch until the next spring, on 3rd April 1921, when a solitary male appeared, and from 20th June onwards, when females only emerged. This strain has been maintained parthenogenetically in the laboratory, but not until over two and a quarter years had elapsed, and in the sixth parthenogenetic generation, did any except females emerge. Then there appeared the two males and the abnormality here discussed. The pedigrees of these specimens show two lines of descent, one producing females and one male and the other producing females, the second male, and the
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abnormality. The blood relationship of these two latter groups is very thin—they are sixteenth cousins; the male and the intersex-like specimen from the same lot of eggs are either "brothers" or cousins, because it is uncertain whether they came from the eggs of one female or from others of the three used.

The number of adults of both lines totals about 170, about 100 of which are common to both strains. In all some 400 adults have been reared by Miss Chawner and the writer during the six parthenogenetic generations mentioned but, counting the seventh and eighth asexual generations, which the writer has maintained since, the total reaches about 600. (Incidentally it may be mentioned that the ninth parthenogenetic generation is now hibernating.) In addition large numbers of eggs have been taken for various purposes and, further, the factor of breeding mortality must be considered. Hence it is impossible to state precisely what percentage of occasional males is thrown, though the above figures suggest a figure between 1.75 per cent. (3 out of 170 adults) and 0.5 per cent. (3 out of 600 adults).

Through the kindness of Mr Gilbert Garlick, Ontario, Canada, I am able to give the following data which he has collected in Canada:

1. Five broods and part of a sixth, comprising 232 individuals, yielded 5 ♂♂ i.e., 2 per cent. (approx.).
2. Larvae from bushes under cultivation yielded 207 ♀♀.
3. Wild larvae from a "wild" bush in a wood yielded 24 adults, 1 being a male, i.e. 4 per cent.
4. No males appeared before the end of July.

According to Enslin [1912-17] the male is not rare in South Europe, but field work and collections in England have so far yielded nothing but females. It is quite possible that the sex-ratios vary in South Europe, Great Britain, and North America with the climatic conditions.

Knowledge of these sex-ratios in Nature and experiment, of course, is very necessary for an appreciation of what would constitute convincing evidence to prove that sex-change had been induced by artificial means.
Table showing a Comparison between the Various Specimens of Pristiphora pallipes.

<table>
<thead>
<tr>
<th>Specimen</th>
<th>Length</th>
<th>Antennae</th>
<th>Legs</th>
<th>Coxa</th>
<th>Trochanter</th>
<th>Femur</th>
<th>Tibia</th>
<th>Tarsus</th>
</tr>
</thead>
<tbody>
<tr>
<td>♂; Enslin's description.</td>
<td>4·75 mm.</td>
<td>Above black, under yellow-brown; 3rd joint somewhat longer than 4th.</td>
<td>...</td>
<td>Bases black, remainder light brownish yellow-white</td>
<td>Light yellow brown (1 and 2), proximally, on inner side a black patch (1), on outer edge of right leg 2 dark patch pronounced but very faint on left; white with faint yellow-brown tinge distally (3).</td>
<td>Yellow-white (1 and 2), brownish (3); bristles light brown (1 and 2), distal part light brownish (3).</td>
<td>Light brown but edged with very dark brown or black (1 and 2); light brown (2 L); almost white, claws and pulvillus dark (2 L); black (3).</td>
<td></td>
</tr>
<tr>
<td>♂; reared.</td>
<td>4·5 to 5·5 mm.</td>
<td>Above black-brown; under dark brown; 3rd and 4th joints equal, somewhat compressed.</td>
<td>Black; knee-yellow white.</td>
<td>...</td>
<td>Black</td>
<td>Yellow-white</td>
<td>Light brownish yellow (1 and 2); proximal two-thirds as 1 and 2, remainder black; bristles light brown (3).</td>
<td></td>
</tr>
<tr>
<td>♂ (1) reared.</td>
<td>4·4 mm.</td>
<td>General male facies but 3rd joint appears somewhat longer than 4th, though the difference is so minute that it is difficult to judge correctly.</td>
<td>Black, distal border light (1 and 3); black (2). Very light brown (1); light (2 R) brownish (2 L) light with brownish area (3).</td>
<td>...</td>
<td>Black</td>
<td>Very light brown</td>
<td>Brown (1 and 2); black (3).</td>
<td></td>
</tr>
<tr>
<td>♂ (2) reared.</td>
<td>3·8 mm.</td>
<td>General male facies</td>
<td>...</td>
<td>...</td>
<td>...</td>
<td>...</td>
<td>...</td>
<td></td>
</tr>
</tbody>
</table>

The figures (1), (2) and (3) refer to the legs; R = right, L = left.
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The following detailed section is necessary for the following reasons: (1) The rarity of the specimens; (2) the paucity of our knowledge on the comparative anatomy of the male genitalia; (3) the necessity for comparison between each of the sexes and the abnormality; (4) the necessity for classifying the latter specimen. In contrast with many species, *pallipes* unfortunately does not present very striking features of sexual dimorphism, and this renders it somewhat difficult to differentiate the male and female characters of the intersex-like specimen. The species is black and the only externalia, except the slimmer build of the male and the genitalia; which differentiate the sexes are restricted principally to the antennæ and limbs, as the table on page 396 will show.

The foregoing table, therefore, shows that such secondary sexual characters (excluding genitalia) as can be differentiated with certainty give the specimen a more female cast than male.

The general condition may readily be described thus: the practically complete genital ring and its appendages of one sex has been interpolated between the anal segment and the practically complete genital ring and appendages of the other sex. Of the male structures, with the exception of the hypopygium (and possibly the ninth tergite), all are present and almost perfect; of the female all are present but the saw-sheath parts are not co-adapted but are gaping and the saws and their guides lie horizontally instead of sagittally. Hence the elements of the female genitalia are present in slightly greater number and are less modified in shape than the corresponding structures of the male, *i.e.* there is a slight preponderance of femaleness.

Before any conclusion may be arrived at touching the significance of the amounts of the internal genitalia of both sexes which are present in this specimen, it is necessary to state the derivation of the various parts. The ontogeny of certain of the parts of the saw-fly is unknown but, as they practically correspond to those of the honey-bee,* Zander's

* I am indebted to Miss A. Betts, B.Sc., for information concerning the ontogeny of the internal genitalia of the honey-bee.

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*Table illustrating the Characters of the External Genitalia of the Sexes and the Intersex-like Specimen.*

<table>
<thead>
<tr>
<th>Abdominal segment</th>
<th>Female.</th>
<th>Intersex-like specimen.</th>
<th>Male.</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Female features.</td>
<td>Male features.</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>presumably absent owing to presence of ♀ homologue, the triangular area.</td>
</tr>
<tr>
<td>VIII. Tergite.</td>
<td>Plate with spiracle</td>
<td>Common</td>
<td>to both</td>
</tr>
<tr>
<td>Sternite.</td>
<td>Triangular area (Zander, 1890) or hypopygium of sternite VII. (Enslin).</td>
<td>Normal</td>
<td>presumably absent owing to presence of ♀ homologue, the triangular area.</td>
</tr>
<tr>
<td></td>
<td>Appendages: saws with their internal supports, the “bows” (Zander). Sternite VII obsolete or perhaps forms the bows (Enslin).</td>
<td>*Saws normal in shape but exposed and lying flat along the posterior, not sagittal as normally.</td>
<td>presumably absent owing to presence of ♀ homologue, the triangular area.</td>
</tr>
<tr>
<td>IX. Tergite.</td>
<td>Epipygium (quadrate plate).</td>
<td>Epipygium very slightly modified, its posterior margin being almost straight and not convex as in normal ♀.</td>
<td>presumably absent owing to presence of ♀ homologue, the epipygium.</td>
</tr>
<tr>
<td>Sternite.</td>
<td>Saw-sheath (oblong plate); note its anterior sclerites.</td>
<td>*Saw-sheath modified in shape and position; posteriorly practically normal, but anteriorly lacks the sclerites; the two halves not co-adapted but widely parted owing to presence of ♀ genitalia.</td>
<td>*Genital plate not present in ♀ condition but represented by the ♀ homologue the saw-sheath</td>
</tr>
<tr>
<td></td>
<td>Appendages: saw-guides and their internal “bows.”</td>
<td>*Saw-guides normal in shape but exposed and lying flat along posterior and not sagittal as normally.</td>
<td>*Claspers and penis normal except the basal and ventral pieces of the outer clasper which are slightly modified in shape.</td>
</tr>
</tbody>
</table>

* Important features.

† The writer has not been able to identify these in *P. pallipes*. Except where specially noted the nomenclature and disposition of the parts are those of Enslin (1912-17).
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findings (1916) for the latter insect are doubtless true for the former. The drawings (Plate II.) and a table will illustrate.

Summary showing the Sex and Derivation of the Internal Genitalia of the Intersex-like Specimen.

<table>
<thead>
<tr>
<th>Gonads</th>
<th>Externally shaped like rudimentary ovaries but cytologically male.</th>
<th>Mesodermal.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Gonoducts</td>
<td>Male vasa deferentia</td>
<td>Mesodermal.</td>
</tr>
<tr>
<td>Seminal vesicles</td>
<td>Male</td>
<td>Mesodermal; derived from genital strands.</td>
</tr>
<tr>
<td>and accessory mucous glands</td>
<td></td>
<td>Ectodermal.</td>
</tr>
<tr>
<td>Ejaculatory duct</td>
<td>Male</td>
<td>Ectodermal.</td>
</tr>
<tr>
<td>Receptaculum seminis</td>
<td></td>
<td>Ectodermal.</td>
</tr>
</tbody>
</table>

The internal genitalia, therefore, consist of the male parts in their entirety with the addition of the female receptaculum seminis only (Plate II., fig. 3).

At first sight one would be justified in regarding the specimen internally, in both its sexual and secondary sexual characters, as a male to which has been added, upon an interpolated and succeeding segment, a small portion of the female secondary sexual apparatus. The genetic nature of the specimen, however, cannot be settled quite so readily because of the conditions presented by the gonads. Cytologically these appear entirely male (Plate II., fig. 4). The follicles are almost empty but contain traces of a mesh, the framework of which probably formed the cysts of developing gametocytes. A few cells of indeterminate character remain, but a few male nurse cells* and relatively few spermatozoa are present, the latter being found also in the vas deferens. No signs of oöcytes and female nurse cells exist as would be the case in an ovary of the same size. Externally the gonads have the appearance of rudimentary and somewhat misshapen ovaries, each with four or five ovariole-like components instead of the normal eight to ten ovarioles. On the other hand, their external shape does not correspond with that shown by

* Nurse cells in saw-flies have not been described yet; the writer found such two years ago but description is withheld for a cytological paper now in preparation.
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those of the male dissected (Plate II., fig. 2). The shape of
the testes is known from one specimen only and the follicles
are globular and seven in number; but as this male never
paired there is a slight possibility that these gonads were
abnormal and immature. Such immaturity in an adult saw-fly
which lived a week would be very unusual of course. Their
cytological structure was not ascertained as, unfortunately,
mainly due to their small size they were lost during embedding.
The elongated follicles of the abnormality differ from the
elongated follicles of many species. The latter are usually
numerous (circa twenty), disposed radially, and terminate bluntly
anteriorly; those of the abnormality are few and are disposed
and taper away anteriorly like the ovarioles of an ovary. These
points are made because, despite the cytological evidence, they
show some reason for suggesting that the gonads are not those
of a typical male, and may even have developed their condition
because they had been subjected to female influences, i.e. they
are intersexual.

5. Discussion on the Nature of the Abnormality.

We are now in a position to judge the nature of the
specimen and three interpretations are possible—it is either
(1) a gynandromorph which genetically is a male with terato-
logical gonads and possessed somatically of certain substitutive
female colour characters and an additive female segment
interpolated posteriorly; or (2) a gynandromorph, genetically
a male with teratological gonads and somatically a female
with an additive male genital ring interpolated posteriorly; or
(3) an intersex predominantly male. Such gynandromorphism
would be comparable to Weinland’s example mentioned by
Morgan and Bridges (1919, p. 40) of which, however, there
is no note regarding the gonads, while such intersexuality is
comparable to that shown in Goldschmidt’s Lymantrias (1923)
and Harrison’s Bistons (1914 and 1919).

Any theoretical considerations based on the foregoing
must of necessity be speculative, but the following general
suggestions may be advanced tentatively. At the outset
certain difficulties must be recognised. We do not know,
firstly, the chromosome behaviour in a thelytokous species when

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it gives rise to an occasional male; or, secondly, what is the sex-chromosome constitution of *pallipes*, i.e. whether \( \varphi = XX \) and \( \sigma = XO \) or XY;* or, thirdly, what is the influence of the autosomes or cytoplasm on sex; or, fourthly, when and how the blastomeres which go to form the germ tissue are segregated from the soma-forming blastomeres.

On the other hand certain simplifications exist, viz., the species is parthenogenetic and consequently the specimen cannot be resultant upon abnormal crossing (hybridity) or abnormal fertilisation.

Doncaster (1906) has shown that in thelytokous species one egg-nucleus and two, then three, polar nuclei are formed but without reduction in chromosome number; further, polar body conjugation takes place between the second polar body and the second half of the first with a subsequent sinking into the egg and degeneration of the conjugants. Hence in the processes involved, should an egg be subjected to abnormal conditions in Nature or in experiment there are many possibilities for irregular chromosome behaviour. For instance, there might occur non-disjunction of one or two sex-chromosomes or/and the autosomes or the second polar body may return and fertilise the egg-nucleus as in Buchner's starfish eggs treated with carbon dioxide (1911). Let us trace out the possibilities of non-disjunction, assuming that the constitution of the thelytokous types of saw-fly is of the XX order, as in other hymenoptera, and that of the male XO.*

**A. If the Specimen is Genetically a Female, i.e. XX.**

(1) Non-disjunction of both sex chromosomes would give a cell of constitution XXXX... = super-female.

(2) Non-disjunction of one sex chromosome would give cells of constitution XXX... = super-female.

and \( X \) = male.

**B. If the Specimen is Genetically a Male, i.e. X.**

(3) Non-disjunction of the sex chromosome would give cells of constitution XX... = female.

and \( O \) = unsexed or dies.

* As the homogametic sex is the female, XX, in hymenoptera, it can hardly be assumed for a parthenogenetic species that the male is constituted XY, unless it be assumed that Y is a fragment of X, a phenomenon which has not been observed.

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Now the chromosome constitution and sex of both the somatic and germ cells of the individual, as well as the distribution of these cells in the body, depend upon when and how non-disjunction occurs during development, and according to the circumstances of their formation and segregation it is quite possible for somatic and germ cells in the same organism to be of different sex constitution, or for the differently constituted cells to be mixed together in the same tissue. Applying these arguments to our specimen we deduce the following.

In the case (2), if non-disjunction occurred in the first segmentation division a lateral gynandromorph would probably result; if later in segmentation an individual might result containing three types of cells, viz., abnormal super-female (XXX), male (X) together with the normal female cells (XX) in keeping with the genetic nature of the individual. In the case (3) non-disjunction in the first segmentation division would produce a female, but in later segmentation would result in an individual containing two types of cells, viz., normally produced male cells plus the abnormally produced female cells. X-less cells probably perish.

Therefore, whether we start from a female or male egg, non-disjunction during segmentation—and preferably during the later stages—according to the circumstances of the formation and distribution of the blastomeres, would yield many possible abnormalities. From these the following only need be considered as bearing upon the specimen under discussion:

Non-disjunction in a female egg may yield (1) an individual having a somatic mosaic consisting of cells of super-female (XXX), female (XX), and male (X) constitution and gonads of germ cells similarly constituted and mixed together, i.e. either a kind of hermaphrodite or an inter-sex; (2) an individual having a somatic mosaic as the foregoing but with gonads of either pure ♂ or ♀ cells, i.e. a gynandromorph; non-disjunction in a male egg may yield (3) either a hermaphrodite or an inter-sex (cf. 1) somatically and germinally composed of female (XX) and male (X) cells; (4) a gynandromorph (cf. 2) somatically a female and male mosaic but germinally either pure ♂ or ♀.

To what category, then, may the specimen be assigned.
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Recalling that somatically it is mixed and germinally it is male in its cytological character, the specimen would appear to be a gynandromorph of the class (2) or (4). But if its general resemblance to the inter-sexes of Goldschmidt, Harrison, and others be recognised, as well as the external female facies of the gonads, it is also possible that it is an inter-sex of the class (1) or (3) which cytologically has finally reached the male sexual condition. A definite pronouncement can only be made if current experiments repeat this solitary result in greater number and range; also, when our knowledge of the sex-ratios is more complete it will be possible to assert whether the female egg—the normal sex of this species—may be induced by artificial means to produce the male, and whether inter-sexuality marks a stage in this process, or whether inter-sexuality marks a sex-change towards femaleness in the extremely rare male of this species.

6. Is the Specimen a Natural or Artificial Product?

In most cases of insect gynandromorphism and inter-sexuality which have been thoroughly investigated there has always been some cause operating to which the resultant abnormalities could be attributed, e.g. the crossings of mutants as in Morgan's and Bridge's *Drosophila* or crossing between races as in Goldschmidt's Lymantrias, but in the case of a parthenogenetic species other explanations must be sought. This specimen may have arisen naturally through an inherent but unknown cause, or through some environmental factor(s) operating, most probably, during egg-development, as it is extremely unlikely that factors operating during larval or pupal life would give expression in the adult soma. The only natural factors likely to produce chromosome irregularity and consequent adult abnormality are disease and disturbance in the physical or/and chemical relationship between the egg and its nidus in the leaf. Of the former there is no evidence organically or cytologically; of the latter the only unnatural condition of which the writer is aware is that occasionally an egg may be incompletely pocketed in the leaf and have up to about half its length exposed to the air. Many such eggs die but the fate of the survivors remains to be discovered. But the factor most in evidence during experimentation was an artificial one,
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namely, the chemical employed upon the eggs during the first two or three hours after laying and the unique fact of one case of gynandromorphism or intersexuality appearing in a species practically thelytokous, coupled with the simultaneous emergence of two rare males under the same conditions of experiment, makes it probable that the specimen, and possibly the males also, resulted from the artificial factor introduced. Further, if this chemical was the prime cause of the production of the specimen it is quite possible that the condition of the gonads was not intersexual but teratological, the chemical affecting the germ tissue in shape only and not in sex.

7. Sexual Abnormalities in Other Species of Saw-flies.

The total number of Tenthredinid sexual abnormalities which I have been able to trace is small—9, and with the exception of that on Morice's specimen, *Strongylogaster cingulata* made eighteen years ago, and this paper on *Pristiphora pallipes*, the records concerning all of them have been compiled by Dalla Torre and Friese (1898). The following notes, however, have been made from the original papers cited below. It has been thought desirable to make reference to these cases here because, in the light of recent knowledge, they present some diversity of interest despite the smallness of their number. The comments made after the brief descriptions are those of the writer, and though an attempt is made to classify the specimens—which until now have been called gynandromorphs—it is acknowledged that such classification is somewhat arbitrary in view of the deficiencies in our knowledge of the germinal characters of the insects. The main criterion adopted in the scheme is comparison with other insects of similar external appearance whose sexual natures have been definitely established as in the cases of Drosophila gynandromorphs (Morgan and Bridges, 1919) and moth hybrids (Goldschmidt, 1923; Harrison, 1914, 1919; and others). The terms "intersex" and "gynandromorph" are used in the Goldschmidtian sense.

1. *Cimbex griffinii*, Leach.—Shuckard (1836) records a male with the right anterior leg that of a female.

*Comment.*—A gynandromorph almost entirely male.
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2. Strongylogaster cingulata, F., 1793, nec Scop., 1763.—Curtis (1838), under the name Tenthredo cingulata (by a misprint called angulata) describes a specimen which, exteriorly, was male on the left side and female on the right. A coloured figure is given but no detail except the body colour and the gross appearance of the external genitalia.

COMMENT.—A lateral gynandromorph.

3. Strongylogaster cingulata.—Cited by Morice (1907). Male: general size and habit. Female: left antenna, right side of abdomen, left side of genitalia. “Its other sexual characters (as far as they could be recognised) seemed to be distinguished in much the same way—the male and female elements being everywhere separated by the longitudinal axis of the insect, but some of each lying to the right and others to the left of that axis.”

COMMENT.—A “criss-cross” gynandromorph.

4. Tenthredo atra, L.—Cited by Slavíček (1893). Male: right femora, left side of abdominal segments 4, 5, and 6. Female: left femora, right sides of abdominal segments 4, 5, and 6; saw-shield reduced to a scarcely perceptible spur at the extreme exterior of its base and its ventral plates in part irregularly shaped; saw split into two blades of which one is completely visible and irregularly bent and the other projecting in part.

COMMENT.—A gynandromorph, predominantly female, of the “criss-cross” type but with the external genitalia somewhat imperfectly developed.

5. Abia sericea, L.—Cited by Gerstäcker (1872). Characters common to both sexes: antennae, thorax, legs. Male: general external appearance—smaller size, slim build; head with large eyes, narrow vertex, frons with bushy hairs; abdomen: dorsum predominantly male though colour bands of segments 4 to 6 only half the usual breadth, yet those of the left side quite pronounced. Female: abdominal segments 7 and 8, ovipositor; ovaries normal except that the oöcyte region was shorter than usual, receptaculum seminis.

The specimen was found in company with males (as well as numerous females) but the receptaculum seminis was empty of sperms. It is suggested, therefore, that the specimen escaped the sexual attentions of the males by reason of its general male facies.

COMMENT.—The specimen is most probably a gynandromorph, difficult to define briefly, but predominantly female. The oöcyte region, being shorter than normal, is noteworthy and may have some intersexual significance, but the modification is more likely to have been due to a physical reason, namely, the smaller and slimmer masculine build.

6. Macrophia rustica, L.—Cited by Krieger (1892). Male: left side-colour of thorax and legs; right side of abdomen with complete male genitalia (both
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sides) but with ventral part of valves (claspers) somewhat reduced. Female: facies and size; right side of thorax and legs; abdominal segments—the first, on the right side, broad as in the female with a small clear patch at hinder angle, the fifth and sixth with clear patches, those on the left somewhat the smaller; genitalia—on the left side (the more male-coloured side), half of an ovipositor complete in all its parts, but with the saw pointing in a direction different from the saw-guide and sheath (Plate II., fig. 5).

The specimen was found in copula with a normal male *rustica*; a true pairing can hardly have occurred owing to the nature of the external genitalia, “but one similar to that of two male cockchafers which have been observed in copula.”

**COMMENT.**—Going by externals the specimen is just as likely intersex as gynandromorph. In its additive genitalia it resembles the *Pristiphora pallipes* specimen except that half the female apparatus is lacking.

7. *Nematinus umbrinus*, Zadd.—Cited by Konow (1887). Two specimens were caught at the same time. In view of the close relationship of the species to *N. ribesii* and his suggestion as to the cause of their abnormality Konow gives detailed descriptions.

Specimen (1). Male: whole general appearance; genitalia—of the valves (claspers) that on the right side complete, that on the left reduced to a stump. Female: ovipositor, the saw-sheath of which has its two parts feebly developed and gaping.

The dorsum of the eighth abdominal segment resembles more or less that of *ribesii*.

8. Specimen (2). The external characters approximate more to those of *ribesii*; there are no male genitalia, but the eighth abdominal tergum is that of the male, and beneath it lies that of the female which in turn covers complete female saw-shields and projecting saws.

**COMMENT.**—These two cases are extremely interesting in the light of recent work. Konow, from the circumstances of their capture and especially from their external characters (which he detailed most carefully) suggested that they were the offspring of an abnormal pairing between a *ribesii* male and an *umbrinus* female. That is, there occurred in Nature an inter-specific crossing with a result the significance of which was not apprehended till recently. Both specimens show additive genitalia as in the *P. pallipes* specimen and the inter-sexual moths of many experimenters. There is strong probability, therefore, that these specimens are intersexes also.
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These nine specimens, then, may be classified tentatively as follows:—

A. *Five of the Gynandromorphic Type; with no Additive Parts.*

2. Strongylogaster cingulata. Lateral, left male, right female.
3. " " " " "Criss-cross"; external genitalia—left male, right female.
4. Tenthredo atra. . . "Criss-cross"; predominantly female with female genitalia somewhat imperfectly developed.
5. Abia sericea. . . Male and female parts scattered but partly dorso-ventral; externally predominantly female; gonads female.

B. *Four of the Intersexual Type; with Additive External Genitalia.*

6. Macrophya rustica. . . "Criss-cross" mostly; male external genitalia almost perfect; female external genitalia of the left side only developed.
7. Nematinus umbrinus. General male facies; external genitalia of both sexes but neither set quite perfect; eighth abdominal tergum like *N. ribesii*. Possibly intersex from natural cross *umbrinus x ribesii*.
8. Nematinus umbrinus. Characters approximate to those of *ribesii*; external genitalia female but with additive male eighth abdominal tergum. Possibly intersex from natural cross *umbrinus x ribesii*.
9. Pristiphora pallipes. General shape like male; certain external female characters; both sets of external genitalia almost perfect; gonads cytologically male but shaped like rudimentary ovaries. Possibly artificially produced by chemical action on the developing egg.

In conclusion, in addition to acknowledgments already made, I must record the assistance of Mr D. C. Geddes, the Laboratory Assistant, in the preparation of sections, of the Rev. F. D. Morice, M.A., in furnishing information regarding the literature of gynandromorphism in saw-flies, of Dr J. W. Heslop Harrison, my colleague, for the provision of papers, his own and those of other workers, on intersexuality, and of the British Association for the Advancement of Science for a grant in aid.

8. Summary.

1. Attempts have been made to modify the sex in various species of Tenthredinidæ by immersing leaves holding saw-fly eggs in chemical solutions during maturation which occurs during the first three hours after egg-laying.
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2. In *Pristiphora pallipes*, Lep., which in England appears almost completely thelytokous, it is possible that sex-change has occurred as the result of such treatment for, in five experiments, eggs up to one and a half hours old treated for one hour in a 0.2 per cent. solution of magnesium sulphate (in distilled water) yielded 62 females, 2 males, and 1 intersex-like specimen.

3. Definitive interpretation of these appearances cannot be made until more experimental results are obtained, and more is known of the sex-ratio of the species.

The breeding experiments of the writer and Miss E. F. Chawner, in England, involving the rearing of some 600 specimens during eight successive parthenogenetic generations show the male percentage to be between 0.5 per cent. and 1.75 per cent. In Canada Garlick finds it to be 2 per cent. from 232 individuals of five successive generations and part of the sixth; larvae from cultivated bushes yielded 207 ♀♀; wild larvae from a wild bush gave 4 per cent.—1 ♂ : 23 ♀♀. In South Europe Enslin states that the male is not rare.

4. The external characters of these rare English males and the abnormality, and the external genitalia of one male and the abnormality are described in detail.

5. Externally the abnormality shows the slim build of the male, but has certain female colour characters; its external genitalia comprise a male set, complete except for the genital plate, succeeded by a complete female set of which the two halves of the saw-sheath are smaller than normal, modified in shape and wide apart; the saws and saw-guides lie horizontally instead of sagittally; internally there is a spermatheca and paired gonads leading into normal male ducts; each gonad to appearance resembles a small ovary with about five follicles, but cytologically they are almost empty except for a few indeterminate cells, a few nurse-cells, and relatively few spermatozoa.

6. This specimen may be either (a) a gynandromorph which genetically is a male with teratological gonads and possessing somatically certain substitutive female characters and an additive female segment interpolated posteriorly; or (b) a gynandromorph genetically a male with teratological gonads and somatically a female with an additive male genital
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ring interpolated posteriorly; or (c) an intersex predominantly male (cf. moth intersexes of Goldschmidt, Harrison, and others).

7. Non-disjunction in either a male (X) or female (XX) *pallipes* egg during segmentation—and preferably during the later stages—could produce the condition of the abnormality.

8. The prime cause to non-disjunction in this almost completely thelytokous species cannot be abnormal intra- or inter-specific fertilisation, but may be hereditary or pathological—both unlikely—or physical or/and chemical disturbance in the relationship between the egg and its nidus in the leaf. Of the latter a possible natural cause is the occasional imperfect deposition of an egg so that a portion of it is exposed to the outer air, but the more likely explanation is the artificial experimental treatment.

9. The simultaneous appearance of two of the extremely rare English males and a unique abnormality from eggs treated as mentioned under (2) strengthen the possibility that these results were artificially produced. It is quite possible that the gonads of the abnormality were not intersexual but teratological, the chemical affecting the germ-tissue in shape only but not in sex.

10. Eight other sexual abnormalites in saw-flies, from other workers' records, are briefly described in their externals principally; it is tentatively suggested that in the light of recent research they may be classified into two categories, (a) gynandromorphs, (b) intersexes; two of these specimens, *Nematinus umbrinus*, Zadd., taken wild, may be intersexes resultant upon an inter-specific cross *umbrinus* × *ribesii*.

9. References.


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10. Description of Plates.

PLATE I.—EXTERNAL GENITALIA OF FEMALE, MALE, AND INTERSEX-LIKE FORM OF PRISTIPHORA PALLIPS, LEP.

Figs. 1, 2, 3.—Dorsal view of posterior of ♀, ♂, and ♁ respectively.

Fig. 4.—Male genitalia dissected out. Dorsal view.

Figs. 5, 6, 7.—Side view of posterior of ♀, ♂, and ♁ respectively.

Figs. 8, 9, 10.—Ventral view of posterior of ♀, ♂, and ♁ respectively, the male genitalia exposed after the removal of the hypopygium; in fig. 8 note that the saw-sheath is made up of sclerites, the dotted lines marking the hidden or obscure outlines of certain of them; in fig. 9 the base of outer clasper may be either or both ventral and basal piece; it is difficult to distinguish their boundaries.

Fig. 11.—Dissection showing shape and relationship of inner and middle claspers of ♁.

Fig. 12.—Left side: left half of ♁ genitalia dissected out; right side: inner view of penis tip and its hooks. t = tergite, s = sternite.

PLATE II.—PREPARATIONS OF GENITALIA OF MALE AND INTERSEX-LIKE FORM OF PRISTIPHORA PALLIPS, LEP.

Fig. 1.—Posterior segments of the intersex-like specimen after removal from body and clearing in xylol. Note that the saws and their guides have become separated (cf. Plate I, fig. 9) Ventral view.

Fig. 2.—Internal genitalia of male; left side. From dissection.

Fig. 3.—Dissection of internal genitalia of intersex-like specimen.

Fig. 4.—Section of distal portions of three follicles and beginning of vas deferens of gonad of intersex-like specimen; the uppermost follicle contains a few of the indeterminate cells. Note the sperms in the left follicle and in the vas deferens, the cells of which show deeply staining nuclei. Section stained with iron-hæmatoxylin and safranin.

Fig. 5.—External genitalia of MACROPHYA RUSTICA, L., showing complete set of male apparatus asymmetrically placed to the left, and half of the female apparatus on the right of the insect. Ventral view. After Krieger. D = tergite, V = sternite.