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Scope of Study: Gynandromorphs are individuals in which the distinction between male and female is somewhat vague. These sex mosaics are separated from the other mosaics in that the tissue differences are due to differences in the sex chromosome content of the cells of the tissues. This report deals with the mechanisms which bring about these gynandromorphic occurrences. The majority of the work done with sex mosaics has been with the fruit fly, _Drosophila_. Also of concern is the frequency of gynandromorphic incidence for both spontaneous and irradiation induced occurrences. The distribution of sex mosaics in forms of life other than _Drosophila_ is included in this report. Material for this report was compiled from books and journals dealing with gynandromorphs and related subjects.

Findings and Conclusions: Gynandromorphs occur in many forms of life. The method of occurrence differs between the various types of organisms. The most widely distributed method by which sex mosaics arise is by the elimination of a sex chromosome in an early stage of cleavage divisions.

ADVISER'S APPROVAL L. Herbert Bruneau

GYNANDROMORPHS

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GYNANDROMORPHS

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PREFACE

The purpose of this paper is to review the literature on the subject of gynandromorphs. This paper primarily covers the occurrence of gynandromorphs in the fruit fly, *Drosophila*.

The writer wishes to express his appreciation to Dr. L. Herbert Bruneau for his suggestions and ideas.

The writer also wishes to express his appreciation to his wife, June, for the typing of this report.

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CHAPTER I

THE ORIGIN OF GYNANDROMORPHS

Most animals are divided into two relatively distinct catagories, male and female. This is very often not the case in many primitive forms of life, but we will consider the more advanced forms. In the higher forms of animal life, this distinction is due to several factors. These are the genetic make-up of the organism and the hormonally controlled secondary sexual characteristics. In the lower, but not primitive, forms of animal life, sex is controlled by the genetic make-up alone. This is due to a lack of hormones comparable to those present in the higher forms. Occasionally, there occurs in animals, individuals which exhibit both male and female characteristics. When this occurs in higher animals, it may be due to irregularities in the production or distribution of hormones. However, this occurrence in lower animals, such as insects, denotes an upset in the sex-determining chromosome behavior. This results in an animal which is called a sexual mosaic or gynandromorph.

The occurrence of gynandromorphs is important for several reasons. The gynanders afford opportunities for studies to be made on the hereditary mechanisms of sexual determination which made these occurrences possible. Gynandromorphs are also important in studies on interpretation of genic action and the processes involved in differentiation.

The organism most commonly used in the studies of gynandromorphs and from which most of the knowledge of the events responsible for their occurrence is the fruit fly of the genus Drosophila. The majority of this paper will then be concerned with this genus.

Sex determination in Drosophila is of the XX - XY type. In this setup the egg will have an X chromosome and the sperm will have either an X chromosome or a Y chromosome. Upon fertilization, a zygote, which receives an X from the sperm and already has an X, will become a female. The sex chromosomal make-up of the female is therefore XX. The male comes from an egg with the X chromosome and a sperm which has a Y chromosome. The make-up of the male is then XY. This type of sex determination is dependent on the X chromosome and autosome balance. A male is a male because there is only one X chromosome and not because the Y chromosome is present. For the same reason a female is a female since there are two X chromosomes.

Gynandromorphs may be very simple or very complex in the distribution of male and female parts. Catagorizing is made according to the approximate distribution of these parts into (1) bilateral, (2) anterior-posterior, (3) mainly male, (4) mainly female, and (5) irregular. Cases of the more simple distribution would be those which are of the bilateral arrangement. These cases have one side of the body male and the other side female. An example of a more complex distribution in a gynandromorph might be one in which the entire head, the right dorsal portion of the thorax, and the left leg are female. The rest of the body is male.

The occurrence of gynandromorphs puzzled the scientists for a long time. In 1888, Boveri proposed that a spermatozoan, on entering the egg, might be delayed before it reached the region of the egg-nucleus. During this period of delay, the egg-nucleus may have begun division. The chromosomes brought in by the sperm may then unite with only one set of the daughter chromosomes of the egg. With this arrangement, two types of nuclei would be present in the embryo. That portion of the dividing cells which did not receive the sperm-nucleus will then develop as haploid cells. Those coming from the egg-nucleus which did receive the sperm-nucleus will be diploid cells. When this theory is applied to Drosophila, those body parts whose cell nuclei are derived from the haploid nucleus would be male, since it contains only one X chromosome. Those body parts coming from the diploid cell would therefore have two X chromosomes and be female. This, of course, assumes that the sperm carried an X chromosome. Also, if the parents differ in at least one characteristic, the male body parts will exhibit the maternal characteristic and the female parts will show the paternal characteristic, providing the paternal characteristic is dominant.

In 1905, Morgan found several cases which were not in accordance with Boveri's hypothesis. Morgan then suggested a hypothesis based on the fact that more than one spermatozoan may be found to enter the egg. Diploid cells would arise from the combination of one sperm-nucleus and the egg-nucleus. If a second sperm-nucleus should develop, it would give rise to haploid cells. The results of these occurrences would be that the haploid cells would be paternal and produce male parts, and the diploid cells would be maternal and produce female parts. These are the reverse of the results predicted by Boveri's suggestion.

When the two above hypotheses failed to account for many of the occurrences of gynandromorphs in Drosophila, Morgan in 1914 proposed a third alternative. This hypothesis was based on elimination of one X chromosome at some early division of the embryo. This occurs when one of the X chromosomes of one of the daughter halves of the dividing cell fails to reach its pole. This X chromosome is then lost in the mid-plate of the dividing cells. The embryo resulting from this would then contain two types of nuclei. One of these nuclei types would contain only one X chromosome. The other would contain two X chromosomes, assuming that the sperm carried an X chromosome. According to this hypothesis, the gynandromorph would arise due to the loss of an X chromosome without any differences in the autosomal content of the organism.

The evidence in support of the chromosomal elimination hypothesis was concluded from the analysis of many cases of gynandromorphs in Drosophila. One of these cases was that of a yellow-white female crossed with a male which was homozygous recessive for the autosomal genes for rough eyes, spineless body, peach eye-color, kidney eye-shape, and sooty body color. Among the off-spring, a gynandromorph was found which was male on one side of its body and female on the other side. This gynandromorph failed to express on either side the recessive paternal characteristics. Boveri's hypothesis stated the male side should have had yellow body color and a white eye. These were not present in this gynandromorph. Therefore, Boveri's hypothesis of a delay in the union of the sperm-nucleus and the egg-nucleus does not account for this case.

An analysis of this gynandromorph on the basis of the polyspermy hypothesis of Morgan (1905) also meets with problems. According to this hypothesis, the male side should exhibit the recessive traits brought in by the sperm. The absence of these recessive traits rules out the polyspermy hypothesis for this case.

The chromosomal elimination theory predicts that the gynander began as a normal XX female. One of these X chromosomes carries the genes for yellow and for white. The other X chromosome transports the normal allelomorphs of yellow and white, that is for gray and for red. Either of these X chromosomes could possibly have been eliminated. In this particular case it was the chromosome which carried the genes for yellow and for white which failed to reach the daughter cell. The male side of the gynandromorph would then receive the gray-red chromosome and express the corresponding traits. The gynandromorph is correctly predicted by the chromosomal elimination theory.

Further support for the chromosomal elimination theory was drawn from the cross of a yellow-white female mated with a male carrying a recessive autosomal gene for ebony body color. The gynandromorph was of the bilateral type in which one side of the body is male and the other side is female. The body color was gray on both sides of the gynander. Since there is a lack of entire maternal characteristics on the male side, this case cannot be explained on the basis of delayed sperm-nucleus theory. The polyspermy hypothesis also fails to account for this gynandromorph due to the lack of ebony body color on the male side. The chromosomal elimination hypothesis proposed that, if the gynandromorph had lost a maternal yellow-white daughter chromosome, both sides would have red eyes and lack yellow body color. The results again support the chromosomal elimination hypothesis.

Since these two early cases, many gynandromorphs have been reported and analyzed. In the majority of these cases the chromosomal elimination theory is the most plausible explanation. However, there are several cases of gynandromorphs which are best explained on the basis of a binucleated egg being fertilized by two male sperm. Evidence to support these infrequent events has been presented by Morgan and Bridges (1919), Crew and Lamey (1938), and Hollingsworth (1955).

The hypothesis of chromosal elimination at an early cleavage mitosis of a female zygote as the cause of the majority of gynandromorphs in Drosophila has been generally accepted. This hypothesis was further confirmed in work done by Patterson and Stone (1938) on the distribution of male and female parts of spontaneous and x-ray-induced gynandromorphs. The loss of a chromosome at an early cleavage also explains why most gynandromorphs are approximately bilateral, since the left and right sides of the body are determined at the first zygatic cleavage.

As the chromosomal elimination theory became accepted, the question was raised as to which X chromosome was eliminated, the maternal or the paternal. Most of the early ideas stated that the paternal X chromosome was eliminated. These ideas were based on the assumption that this elimination was probably due to a delay in the unraveling of the chromosomes of the sperm. However, after many cases of gynandromorphs have been analyzed, it appears that the maternal X is lost as frequently as the paternal X. The factors which then affect the elimination of the X chromosome must be involved in the chromosome and not in its source. Several of these factors might be a delay in division or slowness of the chromosome in reaching the poles of the spindle.

There also occurs individuals in Drosophila which have patches or spots which are different than the tissue around them. In this respect these mosaic individuals are much like gynandromorphs. The difference between these mosaics and gynandromorphs is found in the method by which these mosaics originate. This is not to say that the mechanism of occurrence is not the same, only that the chromosome eliminated is not an X chromosome. The chromosome eliminated in these mosaics is one of the autosomal compliment of the cell.

In explaining mosaics the impression must not be left that they may occur only by autosomal elimination. These mosaics may also arise by a mechanism of somatic crossing-over and segregation leading to a homozygous condition from a previously heterozygous condition. By this is meant that if the chromatids of a chromosome are heterozygous for several traits, crossing-over may occur in such a way as to link the recessives on the same chromatid. Then if segregation occurs so as to place these recessives in separate daughter cells from the previously linked dominants, these recessives will be able to express themselves. By this method, mosaics may be formed.

As the chromosomal elimination theory was being accepted, Bridges (1925) reported two cases of flies which by the requirements for gynandromorphy and for somatic mosaics would fit into both groups. One of these individuals had a spot which appeared to be only a mosaic. On closer analysis it was seen also to be gynandromorphic. This occurrence was explained on the basis that all the maternal chromosomes of the spot had been eliminated. This meant that the spot was strictly haploid in chromosome number and paternal in parentage. The spot could be classified as a mosaic, since it had lost its maternal autosomal complement. It may also be grouped as a gynandromorph, as the elimination of a maternal X chromosome has occurred.

The fact that the cells of this spot had one, and only one, X chromosome, and this from the father, was shown by the expression in the mosaic spot of several characters. There characters were recessive sex-linked characters which would not have been expressed in the presence of the maternal X chromosome. The cells of the spot were also much smaller, which is to be expected in haploid cells.

The other case was a fly in which the mosaic spot covered the entire dorsal and ventral side of the left thorax. The left wing was only about three-fourths the size of the wing of the other side. This difference in wing size is even greater than would be expected between the male and female characteristics. All three left legs were included in the spot. These legs were only four-fifths as long as the legs of the other side of the body. The shorter legs were also somewhat more slender in proportion. These smaller characteristics agree with the expectation for haploid tissue. When the characteristics of this individual were analyzed, it was found that it was both a gynandromorph and a somatic mosaic.

These two cases provide another method for the origin of gynandromorphs. This method may be expressed as the occurrence of gynandromorphs through the expression of haploid tissue by the elimination of a whole set of chromosomes. This gives rise to both a gynandromorph by the elimination of a sex chromosome and a somatic mosaic by the elimination of autosomes.

Hollingsworth (1955) reported a case of a gynandromorph in Drosophila subobscura which could not adequately be explained by using the existing theories on the origin of gynandromorphs. This case can best be explained by assuming double fertilization by X- and Y-bearing sperm of the egg and second polar body. The zygote formed by the union of the sperm bearing the Y chromosome and one of the nuclei formed the male anterior portion of the insect. The zygote formed in the union of the X-bearing sperm and the other nucleus formed the female posterior portion of the fly. This explanation is very similar to the polyspermy hypothesis previously mentioned, but it is also very different. This difference lies in the fact that the polyspermy theory requires the development of a sperm. On the other hand, the double fertilization theory required that two nuclei within the egg are fertilized by two sperm. This double fertilization theory gives us another explanation for the origin of gynandromorphs.

CHAPTER II

FREQUENCY OF OCCURRENCE OF GYNANDROMORPHS

The frequency of gynandromorphic occurrence is estimated to be about one gynandromorph in every 2,000 to 3,000 normal flies. Morgan (1914) found 32 flies which exhibited gynandromorphism to some extent in 42,409 flies. The frequency of occurrence of gynandromorphs seems to vary, not only between species, but also between different stocks of the same species.

Gardner (1962) reported that Spencer Brown and Aloha Hannah-Alva devised a technique to increase experimentally the frequency of gynandromorphic occurrence. This technique makes use of a ring X chromosome. It has been found that a ring X chromosome is frequently eliminated by natural processes in very mature eggs. When virgin females are aged from eight to seventeen days before mating, the proportion of gynandromorphs which arise is greatly increased. It was found also that if excess yeast is added to the culture, the portion of gynandromorphs produced is increased even more. When the ring X chromosome and the excess yeast in the culture are used together, the frequency of gynandromorphic occurrence approaches 20 per cent. This affords investigators the opportunity to control to some extent the natural process of chromosome elimination and the rate of gynandromorph production.

Patterson (1931) did work in determining whether irradiation of the germ cells of Drosophila melanogaster will increase the rate of production of gynandromorphs. From the reported occurrences of gynandromorphs, it appears that the frequency of occurrence is about one gynander in every 2,200 flies. Since there is a great deal of variation in the reports of the rate of occurrence, very little can be drawn from this figure.

In this experiment two groups of flies were used. These two groups were genetically identical, were collected from the same culture, were grown under the same conditions, and were examined with great care. All of these precautions were taken to reduce the effects of anything except irradiation on the rate of gynandromorph production.

The total number of flies examined from cultures in which one of the parents had been treated was 190,299. There occurred ninety-three gynandromorphs in this sample. This gives a ratio of one gynander in every 2,046 flies.

The total number of control flies was 116,399. Among these flies which received no irradiation, there occurred spontaneously only nineteen gynandromorphs. This gives a ratio of one gynander in every 6,126 flies.

The conclusion which can be drawn from these facts is that irradiation of the germ cells of Drosophila melanogaster distinctly increases the number of gynandromorphs appearing in the offspring.

This experiment was continued to see if there was any difference in the frequencies of elimination in irradiated maternal or paternal germ cells. It was found in the preceeding part of the exercise that the rate of elimination of the X chromosome from untreated germ cells is equally distributed between the maternal and paternal germ cells. However, if the paternal germ cell is exposed to radiation, there is a significant increase in the elimination of the exposed X chromosome. The untreated maternal X shows little or no abnormal tendency to be eliminated.

Results which are quite different are obtained if the egg cells are treated with the radiation. When the offspring of the treated mothers were analyzed, there were forty-nine gynanders, twenty-five were cases of elimination of the treated maternal X chromosome. However, the other twenty-four were caused by the elimination of the untreated paternal X chromosome.

It was also found in this experiment that gynandromorphs could be produced by chromosome breakage due to irradiation rather than by complete elimination. In these breaks, the broken portion is eliminated to produce the male parts of the fly.

> The results obtained in this study strongly support the elimination hypothesis of the production of gynandromorphs. They also show that the male parts of the gynandromorph may sometimes contain, in addition to one X chromosome, a piece of another X chromosome. (Patterson, 1931).

CHAPTER III

COURTSHIP OF GYNANDROMORPHS

In dealing with flies which possess both male and female parts, the subject of sex recognition and courtship becomes interesting, to see how these individuals will react. In the courtship procedure, the behavior of the two sexes is quite different. A male, even when isolated, will make movements with his wings which are called scissoring. In this process the wings are brought out and back. The frequency of this action is greatly increased when the male is in the presence of other flies. This scissoring seems to be an indication that the male will court if given the opportunity.

When a male and a female are put together, the male approaches the female. He will then tap her with his front legs. After this tapping action, the male then moves so as to approach the female head-to-head. The male then extends his proboscis. The movements which have been called the dance then take place. The female sidesteps to and fro. The male in an effort to stay in front of her duplicates this back and forth action. Termination of the dance may or may not end in mating. If the female jumps, turns, or flies away, mating will not take place. However, if the female maintains her position, extends her proboscis, and slightly parts her wings, mating will probably occur. The male then stiffens his wings sideways, circles the female, and mating is undertaken.

Sturtevant (1915) reported the action of several gynandromorphs. One of these had the male features of two sex combs and a smaller right wing. The entire abdomen was female. This fly was courted by males and also courted females, thus performing both parts of the courtship dance. Another of these was a bilateral gynander. This individual was counted by males, but showed no indication of male behavior.

Another report also described the behavior of several gynandromorphs. The most interesting of these was a fly which had a female head, but the gonads were both testes. The behavior of this individual was found to be indifferent. It would not court females, but was courted by males.

In an effort to determine the influence of the gonads on the sexual behavior, several investigations on the type of the gonads will be reviewed. Morgan and Bridges (1919) reported that in all the gynandromorphs examined the gonads were of one type, either male or female. This occurred even though the external markings of the abdomen may be male on one side and female of the other.

In contrast to the above report, Dobzhansky (1931) investigated 171 gynandromorphs in _Drosophila simulans_. Of these, 29 had one ovary and one testis. Support for these findings are furnished by Huetner (1923). He found that the fertilized egg divides eight times forming 256 nuclei. Of these, from five to eleven nuclei will go on to form the gonads. Only by pure chance might the entire group of these germ cells be of only one sex in a gynandromorph. This evidence must then be interpreted to mean that gonadic mosaics are not only possible, but are also fairly common with gynanders. With respect to these findings, the results of Morgan and Bridges previously mentioned are hard to correlate.

Hollingsworth (1955) described the sexual behavior of a fore-and-aft gynandromorph. Previous reference to this particular individual has been made in Chapter One of this paper. The action of this individual seemed to be determined by the genetic composition of the anterior part, the region which contains the brain. In this case the anterior region was male. This fly performed the characteristically male action of scissoring in the presence of other flies.

Smith (1956) reports that in Drosophila subobscura visual stimuli are the most important in influencing courtship behavior. Mating was found not to occur in the dark.

From these observations, it would seem that the sexual behavior of gynandromorphs is probably determined in the main part by the sex of the brain of the fly. However, the effects of the gonads on courtship cannot, at the present time, be completely ruled out as a possible source of influence.

CHAPTER IV

GYNANDROMORPHS IN OTHER FORMS

Many reports of gynandromorphs have been reported for the order Hymenoptera. The majority of these reports pertain to gynanders occurring in bees, but several references have been made to incidences in ants and wasps. Since most of the information is concerning bees, this is the group which will receive the major emphasis.

In bees the queen has a diploid set of chromosomes. This diploid set is reduced to a haploid number in the egg. If fertilization of the egg occurs, a diploid, or female, organism is formed. However, eggs which are not fertilized develop as haploid males or drones. Even though this mechanism for sexual determination is different from that of Drosophila, the chromosomal elimination theory is generally accepted as an explanation of the occurrence of gynandromorphs in the group of Hymenoptera.

One of the first reports of gynandromorphs was made on honey bees. These sex mosaics were hybrid offspring of a queen of a yellow Italian race which was mated to a drone of a darker German race. Analysis of these gynanders was the basis for the hypothesis of sex mosaics occurring as a result of a delay in the sperm and egg nuclei union.

A group which has produced many gynandromorphs is the group of Lepidoptera. This group includes the moths and butterflies. The number of recorded cases is very high. Whether this high frequency of reports is due to a higher rate of occurrence, or to more distinct differences between normal individuals and gynandromorphs is open to question.

The method by which these sex mosaics occur in moths deviates slightly from the method exhibited in Drosophila. This deviation is due to the fact that in moths the male is homozygous for the sex chromosomes, that is XX. The female conversely is heterozygous for the sex chromosomes, XY. In accordance with this fact, the male must be the basis for the elimination of a sex chromosome to form a gynandromorph. This theory of chromosomal omission appears to be the most plausible in the group of Lepidoptera.

Very few cases of gynandromorphs have been recorded for spiders. Due to the fact that only a few have been recorded, an analysis of the origin is not available.

Gynandromorphs are almost totally lacking in the groups of crustaceans and molluscs. This lack of sex mosaics is true also for echinoderms with several exceptions. These exceptions are easily explained by the hypothesis of an X chromosome elimination.

Several cases of gynanders have been reported in the fishes. One of these was a shark in which the left pelvic fin was female, while the right fin possessed a well-developed clasper, which is distinctly male. An ovary and both oviducts were present. The right side possessed a testis and a normal male duct. Very little information is available on the origin of these few cases of gynandromorphs.

Gynandromorphs in the class Amphibia seem to be lacking. Numerous cases of hermaphroditic individuals have been recorded, but no mention of gynandromorphs was made.

Only a few cases of gynanders in reptiles have been cited. One of these was the case of a lizard, which was externally male but possessed internally a well-developed oviduct on each side. This case has been explained on the basis of the chromosomal elimination theory.

The external differences between male and female birds are a great help in discovering and analyzing gynandromorphs. There have been several cases of gynandromorphic occurrences in individuals of this group.

Sex determination is different in birds than that present in Drosophila. In birds the homogametic sex is male and the heterogametic sex is female. In this group the sperm contain an X chromosome. The eggs may or may not contain an X chromosome. Male offspring are then produced when a sperm, which contains an X, fertilizes an egg which also contains an X chromosome. Females arise from the fertilization of an egg which lacks an X chromosome. It would then seem that gynandromorphs might arise from the elimination of an X chromosome from previously male cells. This would then produce a female cell. This method seems very similar to that which exists in the group of moths and butterflies.

Even though the cases of gynandromorphs in birds seem to be explained by the chromosomal elimination theory, difficulty is encountered when the results are correlated with evidence reported on the secondary sexual characteristics. Due to these difficulties it cannot be definitely stated that the elimination theory is valid in the case of gynandromorphs in birds.

Cases of gynandromorphism in man are extremely rare, if they exist at all. In man it is very difficult to classify the cases under the heading of gynandromorphism or the heading of hermaphroditism. If the chromosomal elimination theory holds true for man, gynandromorphs probably occur by the same mechanism which exists in Drosophila. With the information available, even the occurrence of true gynandromorphs is still in doubt.

CHAPTER V

RECENT INVESTIGATIONS OF GYNANDROMORPHS

Several of the ideas previously presented in this paper have been either supplemented or altered by evidence provided in recent investigations. Much of this recent work is very specific with respect to the organisms used. This makes correlation with the somewhat general ideas of this paper difficult. The method by which gynandromorphs occur in Drosophila has not been changed. The method of occurrence in several other forms is open to question in light of new investigations.

Rothenbuhler (1952) reported evidence which seems to support the hypothesis that gynandromorphs in honeybees arise from androgenesis with zygogenesis. This evidence was drawn from analysis of the gynandromorphic offspring of crosses between queens homozygous for the recessive ivory-eye gene and drones hemizygous for the recessive gene for chartreuse eyes. These genes were established to be nonalletic and nonlinked. The sex mosaics which resulted from these crosses were found to have black female eye facets and chartreuse male eye facets. These results support the hypothesis of Morgan (1905) which expresses the idea of the development of not only a zygote from normal syngamy, but also an accessory sperm. This method of occurrence differs from the chromosomal elimination theory. Further work is necessary before a definite answer is available.

Hollander (1956) reported work done on gynandromorphs in mice. The incident rate of sex mosaics in the Bragg albino strain of mice was 0.5 per cent. In this study it was evident that the chromosomal elimination theory was a plausible explanation of the method of occurrence. This investigator found gonadic mosaics were also present in the gynanders studied. These gonadic mosaics cannot be explained by the hypothesis that gynandromorphs occur in vertebrates because of irregular endocrine effects on development. Further experiments must be undertaken to establish the correct solution.

Hutt (1937) described a gynandromorphic occurrence in a bird. This bird showed both male and female characteristics in plumage and skeletal structure. A testis and normal vas deferens was present on the male right side of the bird. On the female left side was an ovary and oviduct. This investigator stated that the most probable origin of this sex mosaic fowl was from the loss of an X chromosome in a zygote which was originally male.

Even though the method of gynandromorphic occurrence is well established in <u>Drosophila</u>, it seems that much more research is needed to impart the same certainty to the methods involved in other forms of life.

CHAPTER V

CONCLUSIONS

This report is a literature survey on the subject of gynandromorphs.

Sex mosaics, or gynandromorphs, are individuals which are composed of both male and female tissue. The arrangement of this tissue is determined at the stage of zygotic cleavage at which the events responsible for the gynander occurred.

Gynandromorphs occur in many forms of life. The group on which the most work has been done and to which the majority of this report is devoted is *Drosophila*, the fruit fly. The method of occurrence in *Drosophila* and several other forms is generally accepted to be by chromosomal elimination. The fact that other methods may exist in other forms is evident in the work done on the honeybee.

Gynandromorphs occur spontaneously in *Drosophila* at the rate of about one in every 2,000 to 3,000 flies. This rate is quite variable. The frequency of occurrence is greatly increased by the treatment of the flies with x-ray radiation.

Sex mosaics occur in forms of life other than *Drosophila*. The literature on these other forms is much less than that on the fruit fly.

In conclusion, gynandromorphs occur by (1) elimination of a sex chromosome during development, (2) from haploid tissue arising from the loss of a whole set of parental chromosomes, and (3) the development of an accessory sperm along with a normal zygote.

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