Contribution towards the Knowledge of the Mosaic of the Silk-worm (Bombyx mori L.).

By

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Introduction.

This paper deals with a study of the mosaic of silk-worm (Bombyx mori L.) among which the mosaic of race character, not combining with gynandromorph are found.

Previous to this investigation, the study of the mosaic insect, in general, has not been extended further than the gonad-dissection, owing to the fact that the investigations had to be made on the adult insect. An attempt however was made to sustantiate Morgan's hypothetical view (Morgan, 1905, 1919) on some relation between the first cleavage plain and the body axis of the mosaic marked body, by examining the chromatin differences.

Material and Method.

Materials used for the microscopical study were given to me by many of my friends. All of them were preserved in a strong alcohol or in 10% formaldehyde solution. As a rule such fixations were not satisfactory, but the formalin fixation has proved to be fairly successful in many cases.

CARNOY'S fluid was also employed for many fixations with success. Sections were made in the thickness of from six to ten micra for the dorsal middle, the ventral, the lateral region, the stomach and the fatty tissue; then stained chiefly with Heidenhein's iron haematoxyline, and sometimes with Delafield's haematoxyline.

In the case of study of the cytoplasmic portions orange and BISMARK brown were used.

Occurrence of Mosaics.

The mosaic of racial character (called character mosaics for convenience) occurs mostly in the FI generation or in its descending generations from the hybrid of different races, exhibiting two racial characters in one and the same individual. The character mosaics appeared in six out of my seven cases from the hybrid of different races and one from an imported Chinese race (Taiki) which is not clear whether it belongs to the hybrid or to the pure breed.

In twenty-two other examples, twenty such specimens were bred from hybridized offsprings, and only two appeared from the pure breeds. Out of twenty nine specimens of mosaic, five individuals were combined with sex mosaic, i. e., gynandromorph.

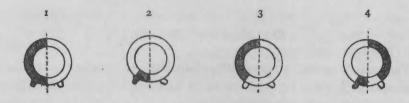
The percentage of the racial mosaic from the hybrid was ninety, and ten from the pure breed; while the percentage of the gynandromorphism was twenty.

Classification of Mosaics.

Dalla Torre and Friese (1898) adopted the system of four group classification in respect of the gynandromorphism of ants. This system, however, was not applied to our mosaics of the silk-worm, because the whole mosaics have different characters on the two sides of the body with the median axis as the dividing line, while there is no mosaic individual of which the demarkation line between the two different characters is dividing the body exactly into the anterior and the postrior half. This fact suggested the existence of some relation between the first cleavage plain to the body axis. Accordingly the author proposes a following system which classifies any mosaics in to four main groups, namely A, B, C and D according to the pattern of one segment regardless whether such patterns extend through the entire series of the body segments or not.

The definition of each group is as follows:-

- A,......Unilateral mosaic; mosaic elements extended from the ventral mesen to the dorsal mesen (Text fig. 1).
- B,Ventral mosaic; mosaic element are limited on the ventral region alone (Text fig. 2).
- C,Semilateral mosaic; mosaic element extends from the lateral side to the dorsal mesen (Text fig. 3).
- D,Diagonal mosaic; mosaic elements on two sides of the mesen, are reversed diagonally (Text fig. 4).



Description of Mosaic.

In order to be familiar with the character mosaic of the silk worm, which are suggestive as to the probable cell liniage in the embryonic development, I mention all the mosaics which have been recorded by the other authors besides my own examples.

Group A.

1) Multilunar and normal mosaic. (Pl. XXIV, fig. 10-17)

This specimen belongs to the Chinese TAIKI, representing abnormally the irregular multilunar character on the right dorsal side of the dody. Abdominal appendages of the right side are slender (fig. 12) and longer than the left ones (fig. 13). Gonads are male; the right testis is smaller and triangularly shaped like the ovary (fig. 17), but sections of them proved no abnormality on germ cell formation.

There were no difference in the head appentages on each side (fig. 14, 15), and also in the attachment of male genital ducts, (fig. 16).

2) Plaine and moricaud mosaic. (Pl. XXIII, fig. 1, 2)

This specimen was bred from a mother of Siokei (Chinese race) which had been back crossed to FI of Siokei (Chinese) and Aojiku. The left half of the body is moricand (Pl. XXIII, fig. 1, 2). Both gonads are female.

3) Moricaud and normal mosaic.

TANAKA's mosaic 1; Jour. Coll. Agric. Tohoku Imp. Univ. Vol. VII, pt. 3, p. 236, pl. VI, fig. 68, 1916.

4) Opaque and oily mosaic.

TANAKA's mosaic 2; Jour. Coll. Agric. Tohoku Imp. Univ. Vol. VII, pt. 3, p. 236, pl. VI, fig. 69, 1916.

5) Right dark and left pale mosaic.

TANAKA's mosaic 4; Jour. Coll. Agric. Tohoku Imp. Univ. Vol. VII, pt. 3, pp. 236—237, 1916.

6) Normal opaque and transparent mosaic.

TANAKA's mosaic 7; Jour, Coll. Agric. Tohoku Imp. Univ. Vol. VII, pt. 3, p. 238, 1916.

7) Normal and moricaud mosaic.

IKEDA's mosaic; Dainippon Sansikaiho, (Report of the Sericultural Association of Japan), No. 197, pp. 4—8, 1908.

8) Normal and moricaud mosaic.

TAKAHASI'S mosaic 1; Dainippon Sansikaiho (Report of the Sericultural Association of Japan), No. 267, p. 23, 1914.

9) Normal and transparent mosaic.

TAKAHASI's mosaic 2; Dainippon Sansikaiho (Report of the Sericultural Association of Japan), No. 267, p. 23, 1914.

10) Normal and transparent mosaic.

TAKAHASI's mosaic 3; Dainippon Sansikaiho (Report of the Sericultural Association of Japan), No. 267, p. 23, 1914.

11) Right normal and left plain gynandromorphous mosaic.

IKEDA's mosaic 1; Dainippon Sansikaiho (Rept. Seric. Assoc. Japan), No. 197, pp. 4—8, 1908.

12) Right multilunar-normal and left multilunar-plain gynandromorphous mosaic.

IKEDA's mosaic 2; Dainippon Sansikaiho (Rept. Seric. Assoc. Japan), No. 197, pp. 4—8, 1908.

13) Right zebra and left normal gynandromorphous mosaic.

TOYAMA's mosaic 1; Bull. Coll. Agric. Tokyo Imp. Univ. Vol. VII, pp. 353-358, pl. VI, 1906.

14) The same mosaic as above.

TOYAMA's mosaic 2; Bull. Coll. Agric. Tokyo Imp. Univ. Vol. VII, pp. 353-358, pl. VI, 1906.

Group B.

Right opaque (☼) and left transparent (♀) mosaic.
ТАКАНАSI'S mosaic 3; Dainippon Sansikaiho (Rept. Seric. Assoc. Japan),
No. 267, p. 23, 1914.

2) Right opaque and left transparent mosaic.

TANAKA's mosaic 8; Jour. Coll. Agric. Tohoku Imp. Univ., Vol. VII, pt. 3, pp. 238, 1916.

Group C.

1) Plain and moricaud mosaic. (Pl. XXIII, fig. 6)

This specimen was bred from the cross of the plain and the moricaud. On the left half of the body, the segments, from the first to the seventh have the plain character, but from the eighth to the eleventh segment presents the moricaud character with the gradual increase of the moricaud pattern; the pattern on the twelveth segment is quite the same as that of the right side.

2) Plain and striped mosaic 1. (Pl. XXIII, fig. 78, 9)

This specimen was bred from the FI offspring of the cross of the plain female and striped male. On the left half of the body the plain character is represented by the same whiteness of a parent, extending to the right side of the third thoracic segment laterally, however two short stripes can be recognized on the fourth to the eleventh segment, which may belong to the moricaud. It is interesting to note that the specimen exhibits abnormal segmentation of the third and fourth abdominal segment (Pl. XXIII, fig. 9) which may have been divided into right and left, possibly produced by pressing of the next segment in the embryonic stage. Characters of the two sides are not different on the ventral surface.

3) Plain and striped mosaic 2. (Pl. XXIII, fig. 74)

This specimen also belongs to the FI offspring of the same cross as above, representing the white character on the left laterodorsal side of the third to the last abdominal segment, and on the other part, the striped character which is seen in the normal worm of the FI generation, is noted.

The specimen has abnormal segments between the sixth and the last segment (Pl. XXIII, fig. 8). The right and the left side have no difference in the character on the ventral surface.

4) Plain and oily mosaic. (Pl. XXIII, fig. 5)

The specimen exhibits some oily patches on the lateral side of each right segment.

5) Mosaic striped with white spots.

TANAKA's mosaic; Jour. Coll. Agric. Tohoku Imp. Univ., Vol. VII, pt. 3, p. 240, fig. 74, pl. VI, 1916.

6) Transparent and normal mosaic.

Tanaka's mosaic; Kaiko no Iden to Hinsiukairyo, pp. 213-214, 1918.

7) Right normal and left multilunar zebra mosaic.

TANAKA's mosaic 10; Jour. Coll. Agric. Tohoku Imp. Univ., Vol. VII, pt. 3, p. 238, 1916.

8) Right opaque and left transparent mosaic.

TANAKA's mosaic 9; Jour. Coll. Agric. Tohoku Imp. Univ., Vol. VII, pt. 3, p. 239, 1916.

9) Right quail and left striped quail mosaic.

TANAKA's mosaic; Kaiko no Iden to Hinsiukairyo, p. 213, pl. VI, fig. 11.

Group D.

1) Stripe and normal mosaic.

TANAKA's mosaic 5; Jour. Coll. Agric. Tohoku Imp. Univ., Vol. VII, pt. 3, p. 237, fig. 72, pl. VI, 1916.

2) Stripe and normal mosaic.

TANAKA's mosaic 3; Jour. Coll. Agric. Tohoku Imp. Univ., Vol. VII, pt. 3, p. 236, fig. 70-71, pl. VI, 1916.

3) Transparent and opaque mosaic.

TANAKA's mosaic 6; Jour. Coll. Agric. Tohoku Imp. Univ., Vol. VII, pt. 3, p. 237, 1916.

4) Right normal and left moricaud mosaic.

This specimen was obtained from the cross of Japanese white (?) and Italian yellow (?) race.

On the left latero-dorsal side of the body the moricaud character appeared, and on the right the normal character is observed, while on the ventral area the right side is characterized by the slightly moricaudal pigment, especially in the third segment to the last, and the left side is white, so that the distribution of two characters on the ventral side appears to be reversed from dorsal side.

Careful observation revealed that the dark spots which may belong to the moricaud are also scattered on the right lateral side of the abdominal prolegs.

This specimen was cut into the sections, which proved to be helpful in obtaining some data on the mosaic phenomena.

Cytological Observation of a Diagonal Mosaic.

The author selected for the cytological studies the most complex type which manifested a diagonal character, viz., group, D No. 4. Sections of the ventral part from the first to the last abdominal segment, and of dorsal part from third to the last segment, and of two testes on two sides have been carefuly studied, paying special attention to the nuclear contents.

Cross section of the 2nd and 3rd abdominal dorsal segment. (Pl. XXV, fig. 20, 21, 22, 23).

The hucleus of the hypodermal cells of these segments contain the chromatin in conspicuous glanules.

The hypodermal nucleus on the right side of the ventral mesen is provided with less number (Pl. XXVI, fig. 26, cn. cnd.) of chromatin masses than that of the left side (Pl. XXVI, fig. 27, cn. cnd.).

Chitinous pigment and pigment glanules of the hypodermis are not seen on the ventral mesen, while on distal (ca. 1.2 mm) parts from the mesen the nuclear contents and the chitinous process are different in conspicuous man-

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ner (Pl. XXVII, fig. 28, 29, 30, 31).

The pigment glanules in cell of the right side are smaller in shape and less in number than those in the cells of the left side (Pl. XXVII, fig. 28, pg.).

Hypodermal pigment glanules began to appear at a distance far from the mesen (about 50 cells interval), and the two kinds of cells, those which produce pigment and the other which do not, exist wall by wall.

The sharply pointed process (7 micra) generally stands on the pigmented hypodermis, and Y-shaped process stands on the pigmentless hypodermis. The processes on the right side are forked markedly than those on the left side.

2. Cross section of the abdominal ventral segment, from the 2nd to the 8th (Pl. XXV, fig. 18, 19, 24).

The pigmentation of the chitinous chracter in the section of the second to the eighth segments has been proven to have some relation with the characters of hypodermal nuclear contents. The nuclei in the right side of the body contain 6 or 7 chromatin masses (Pl. XXVIII, fig. 32), while in the left 4 or 5 large angulous chromatin masses can be detected (Pl. XXVIII, fig. 33). The primary cuticular layer of both sides of the body, is slightly thicker than that of the dorsal side, and there are numerous slender and shorter processes and no pigmentation.

3. Cross section of the whole dorsal segments.

Section of the dorsal segments of the left side differ greatly from those on the right side of the body in the hypodermal and chitinous pigmentation. Nuclei on the left side have about 12 number of chromatin masses (Pl. XXIX, fig. 37, cn. c), and some nuclei in the same side are concidered to have been derived from a normal cell which contains the lesser chromatin number (Pl. XXIX, fig. 38, 39). Pigment granules in the cytoplasm become brownish in colour when stained negatively with the Heidenhein's iron haematoxylin, as if the pigment lobes in the primary cuticula become brownish when treated similarly.

Nuclei on the right side of the body contain no chromatin masses while chromatin granules can be seen in the nucleus except in very rare cases, in which they are substituted by the loosely aggregated masses (Pl. XXIX, fig. 36). In the latter case sometimes the cytoplasm exhibits minutes granules. Chitinous pigment can not be detected on the right side of the body except in the area where the black character had been intermingled.

4. Chromosomes in the germ cell.

The author tried to detect the difference of chromosomes in the germ cell in both testes. He however is not in position at this time to propose any particular difference in regard to twenty-eight (in haploid) chromosomes of both testes (Pl. XXX, fig. 44, 45) although a difference on ripening of germ cells in two gonads are noted.

In the right testicular tubes, numerous spermatocysts which are filled with the mature spermatozoa occuy spaciously the distal part from the Verson's cell, and the other part was occupied by the cells of the second spermatocyte in the mitotic stage. In the left testes, however, the spermatocysts that contain the cells of early first spermatocyte, spaciously occupy the middle region of each testicular tubes.

5. Capsular coat.

The nucleus in the capsular coat on both testes contains ordinarily one to four large chromatin masses (Pl. XXX, fig. 40, 42, 45, tc.). The manner of aggregation of masses on the left testes differs from that on the right testis. In the former the mass is aggregated compactly while in latter loosely.

Developmental Consideration on the Mosaic Body.

On the cause of the mosaic development, two hypotheses may be acceptable, viz., (1) somatic mutation or segmentation of factors, and (2) the chromatic unequal division of blastomeres either in the first cleavage or in the later cleavage of preembryonic stage.

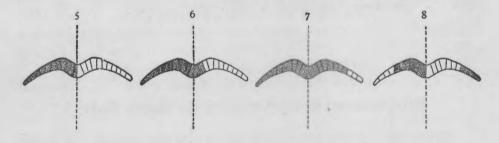
Prof. Y. TANAKA (1916) adopted the first explanation which conveniently can be applied for our mosaic examples produced from hybridization, and will be described in next chapter.

If we take the second hypothesis, the following explanation may be made on the occurence of four groups of mosaic.

The blastmeres which carry the "Anlage" of pigment productive factor in the first cleavage of fertilized egg nucleus, have peripherous motion, divide several times on the pathway through the yolk glanules, which perhaps impede the straight movement on their way. Consequently the boundary between the different characteristic blastomeres does not alway take the straight line; in other words, it does not always correspond with the first cleavage

plain. However according to the law of probability, the axis of blastoderm may sometime arises at the same point of the plain of first cleavage or, very near to the point, and sometimes afar from there. From the foregoing consideration the all cases of mosaic occurence may be explained as follows:

- I) Unilateral mosaic; when the invagination occurs at almost the same line of boundary between the different characteristic blastomeres or very closely to the point where the boundary is folded into the groove of invagination; the body character will be seperated by the ventral mesen and dorsal mesen. (Text fig. 5, 6).
- 2) Ventral mosaic; when one chracteristic blastomere occupies the one side of the primitive groove except in its distal region, and the other part is wholly characterized by the opposite one.
- 3) Semilateral mosaic; when the body axis arises from the area of one characteristic blastomeres and the other character occupies only the peripheral portion of the one side (Text fig. 7) of the embryo; the mosaic has latero-dorsally different characters.
- 4) Diagonal mosaic; this may be produced from crossing movement of two characteristic blastomeres from one side to the other being divided into two groups on both sides of the primitive groove (Text fig. 8). The locomotion on the same principle as above may occur toward antero-posteriorly.



Genetical Consideration on one Mosaic Example.

The author encountered a case that two semilateral mosaics were produced by crossing the striped male to the albino female (Pl. XXIII, fig. 7, p). One specimen shows the heterozygous character as in the FI offspring, but neutral whitish pattern is found on the left side of the third to the last abdominal segment laterodorsally (Pl. XXIII, fig. 7, 2).

The other specimen shows the pure striped character as it was seen on the parent male, on the right side of the body from the first to the last abdominal segment, and pure white character on the left side of abdomen and whole thorax (Pl. XXX, fig. 7, 3).

If we express the striping factor with SS and its absence with ss the former specimen will be a representative of SSss on the right side as in the normal FI worms. On the other hand the neutral whitish part of left side will be a septorial chimera like character of SSss.

The other specimen has a body in which somatic segmentation of factors occurred, viz., SSSS, on the left side and ssss, on the right.

Besides the abnormality noted above each mosaic worm has abnormal segmentation on dorsal side, one on each third and fourth segment (Pl. XXIII, fig. 9), and the other has lost the left half of the eighth segment (Pl. XXIII, fig. 8).

Summary.

- r. Several types of the mosaics occur in the silk worm, in which characters of the two sexes do not appear in one and the same individual.
- 2. The appearance of the mosaic was chiefly observed in the crossed offsprings and rarely in those from the pure breed.
- 3. Mosaics are classified into the following four fundamental types; namely bilateral, ventral, semilateral, and diagonal.
- 4. Cytological studies of one mosaic specimen prove that each characteristic part on the hypodermal nucleus contained some characteristic chromatin masses differing in number and in its manner of agregation. Pigment granules also differ in their size in each characteristic cell.
- 5. Chromatin masses in the capsular coat of both testes were different in their manner of agregation which corresponds with the chromatin masses of the outer hypodermis.
- 6. Difference of chromosomes in both testes were not detected but the difference of maturation of the germ cell in both testes had apparently been recognized, corresponding to their racial external characters.
- 7. In my mosaic specimens the coincidence exists between the ectodermal and the methodermal characters.
- 8. It may be one of the causes of the occurrence of mosaic that the "Anlage" of the factor which will characterize chromatin contents in the nucleus of the later embryo, is carried unequally into the first two cleavage nuclei. From the law of probability, it may be accepted that the body axis of the embryo of Bombyx mori L. will sometimes arise on the plain of the first cleavage or near to it.
- 9. Somatic segregation of factor or chimera like phenomena may be a cause of mosaic phenomena.

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Explanation of Plates.

Plate XXIII.

- Fig. 1. Dorsal view of the plain and moricaud mosaic.
 - , 2. Ventral view of do
- ., 3. Dorsal view of the complex mosaic.
 - 4. Ventral view of do.
- " 5. Right side of the plain and oily.
 - 6. Dorsal view of the plain and moricaud mosaic.
- " 7. Dorsal view of the plain and striped mosaics, P—Parents, FI—FI generation, I—normal, 2 & 3—mosaic.
- " 8. Abnormally segmented part of the 3rd to 5th abdominal segments of No. 3 in Fig. 7, and 10th to 12th segment of No. 2 in Fig. 7.
- , 9. Abnormally segmented part of the 6th to 8th segment of fig. 7 mosaic.

Plate XXIV.

External characters and both testes of multilunar and normal mosaic.

- Fig. 10. Dorsal aspect.
- " II. Ventral aspect.

- Fig. 12. Side view of the right 1st proleg.
- " 13. Side view of the left 1st proleg (Mark -- indicate caudad).
- " 14. Upper view of the head capsule.
- " 15. Under view of mouth parts.
- " 16. Ventral view of the 11th to 13th segment to show the attachment of the male genital ducts, x.
- " 17. Under aspect of both testes.
 - R.....Right, L.....Left testis, Tr.....Trachea, Br.....Blood vessel.

Plate XXV.

- Fig. 18. Dorsal view of plain and moricaud mosaic that sectioned.
- " 19. Enlarged figure of the 2nd and 3rd abdominal dorsal segment of do.
- , 20. Ventral view of the do.
- " 21. Enlarged figure of the 2nd and 3rd abdominal ventral segment of do.
- " 22. Right side view of the 3rd segment of do.
- " 23. Left side view of the 3rd segment of do.
- , 24. Ventral view of the 10th to the 13th segment.
- " 25. Surface view of the dorsal chitin at the part of the dorsal closure cutting into 50 micra square, the left half of the figure represents the pigmented portion and the right the non-pigmented portion. (×1600)

Plate XXVI.

- Fig. 26. Cross section of the 5th ventral segment on the right side near to the body axis. (×1600) (In figure 26 to 37, the right and left are reversed from the preparation.)
- " 27. Cross section of the 5th ventral segment on the left side near to the body axis. (×1600)

Plate XXVII.

- Fig. 28. Cross section of the 5th ventral segment on the right side afar (ca 1.2 mm) from the body axis. (×1600)
- " 29. Two kinds of side view of a forked process on the above segment. (× 1600)
- " 30. Cross section of the 5th ventral segment afar (ca 1.2 mm) from the body axis. (×1600)
- " 31. Two kinds of side view of a forked process on the above segment. (×1600)

Plate XXVIII.

- Fig. 32. Cross section of 6th ventral segment on the right side near the proleg. (×1600)
 - " 33. Cross section of 6th ventral segment on the left side near the proleg. (× 1600)

Plate XXIX.

- Fig. 34. Cross section of 6th dorsal segment on the right side. (×1600)
- " 35. Hypodermal cell which include chromatin masses in the nucleus and pigment granules in the cytoplasm, on dorsal right side. (×1600)
- " 36. Nucleus that contains a full number of chromatin masses, on dorsal right side. (×1600)
- " 37. Cross section of dorsal 6th segment on the left side. (×1600)

- Hypodermal cell that contains the pigment granules. (x1600)
- " 39. Hypodermal cell containing a full number of chromatin masses in its nucleus, being in early stage of pigment production. (x 1600)

Plate XXX.

- Fig. 40. Cross section of the wall of the right testis. (x 1600)
 - " 41. Types of chromatin mass in nuclei of the capsular coat on the right testis. (×1600) a-d, nuclei of one chromatin mass.
 - e-h, nuclei of two chromatin masses.
 - i-j, nuclei of two or three chromatin masses.
 - k-l, nuclei of three chromatin masses.
 - m-n, nuclei of four chromatin masses.
 - 42. Cross section of the wall of the left testis. (×1600)
 - 43. Four types of chromatin mass in nuclei of the capsular coat on the left testis. (× 1600) a', nucleus of one chromatin mass.
 - b'-d', nuclei of two chromatin masses.
 - e'-f', nuclei of two chromatin masses, being in division.
 - g'-h', nuclei of three chromatin masses.
 - i'-n', nuclei of four chromatin masses.
 - " 44. Polar view of metaphase of the first spermatocyte in the right testis. (×1600)
 - 45. Polar view of metaphase of the first spermatocyte in the left testis. (×1600)

Abbreviations.

- Basement membrane. bm, Chromatin mass.
- cm.
- Cell in mitotic stage. cmt,
- Chitinous minor layer.
- ct1, Primary cuticula.
- Cell wall. CW.
- Hypodermis. Hp.
- Linin net work. ln.
- Pore canal. Pc.
- Pl. Pigment lobe.
- Tc, Testicular tube coat.
- Trachea, tv,

- Chromatin granule.
- Chromatin mass to be divided. cmd.
- clma. Chitinous major laver.
- ct. Cell of tracheal wall.
- Secondary cuticula. cts,
- Ftb. Forked process.
- Lumen between cytoplasmic walls. lm,
- Nuclear wall. nw,
- Pigment granule. Pg,
- tb, Process of surface chitin.
- Tracheal membrane. tm.
- Vacuole. VC,

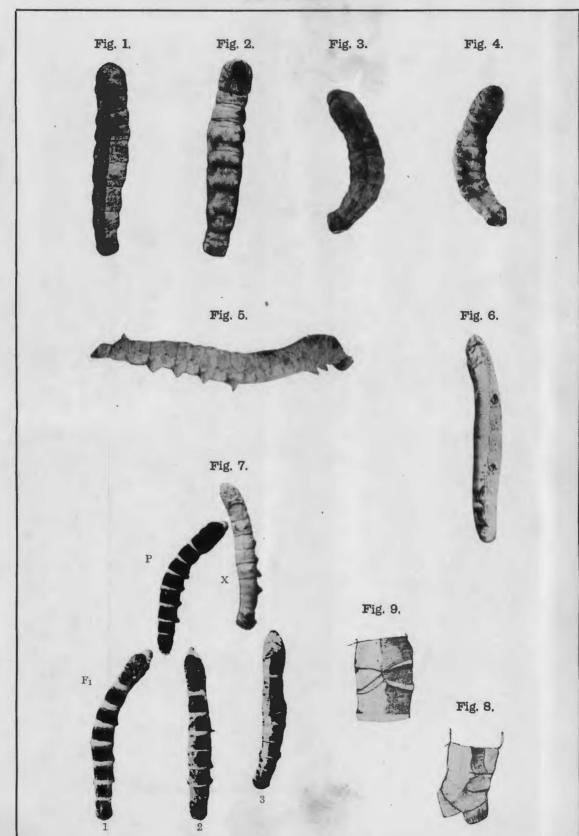


Fig. 10. Fig. 11. Fig. 14. Fig. 15. Fig. 16. Fig. 12. Fig. 13. Fig. 17.

