28.

Asymmetrical Lepidoptera: Description of two new Examples of Somatic Mosaics.

By
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Among the insects some individuals may sometimes be met with which differ in some way from the normal ones by being asymmetrical. Especially among Lepidoptera with their large characteristically marked wings such abnormal individuals easily attract attention.

Some of these individuals are of a purely pathological origin, for instance such in which one wing has been unable to expand entirely during the development of the imago. Moreover individuals are not rarely met with in which one wing is fully developed, but is much smaller than the others. Thus my collection includes a specimen of *Odontosia carmelita* Esp. the left hind wing of which is of normal appearance, but in linear measurement only half as large as the right one.

However, of greater interest are such asymmetrical individuals in which all the wings are normally developed, but the two halves of which differ, the plane of division falling more or less exactly in the symmetry plane of the specimen.

1. Halved Gynandromorphs.

A special group of this kind of individuals is formed by the so-called gynandromorphs, in which one half of

the insect is male, while the other half is female. When the male and the female of a species are fairly alike, such individuals will, of course, easily escape observation, whereas they are at once noticed within species in which the two sexes differ considerably in appearance (*Euchloë cardamines, Orgyia antiqua,* etc.).

The first case of gynandromorphy was described in 1761 by Schäffer, who figured a specimen of *Lymantria dispar* L. bred in 1756, the left side of which was female and the right side male.

Later on such halved gynandromorphs have been observed in large numbers and within many different species of Lepidoptera. Hagen (1861, pp. 259—286) gives a summary of the cases of gynandromorphy in insects recorded in the literature up to 1860, mentioning 99 species of Lepidoptera. Of several later papers mention may be made of that by Sjöstedt (1928), who enumerates a very large number of cases distributed over a total of 326 different species of Lepidoptera. At present altogether several thousands of gynandromorphic individuals are known. Gynandromorphy seems to be especially frequent in *Smerinthus populi* L., *Euchloë cardamines* L., and within the genus *Lycaena*. In the last two cases this is due to such gynandromorphs being especially readily noticed, whereas as regards *Smerinthus populi* it must be due to this species having a special tendency to form gynandromorphic individuals.

Thus, even though the phenomenon is particularly well known, gynandromorphic individuals are not commonly met with. Sjöstedt (l. c. p. 5) mentions, for instance, that no such find is known from Sweden. As to Denmark, some few cases are recorded and, among others, a gynandromorphic specimen of *Porthesia similis* Fuessl. is mentioned (Flora & Fauna 1920, p. 44); this species is not included in Sjöstedt's list.

2. Somatic Mosaics.

Another equally interesting group of asymmetrical Lepidoptera, which, however, is of much rarer occurrence than the gynandromorphs, comprises such individuals as are, likewise, divided more or less exactly through the symmetry plane, but still the sexes of both halves are the same, whereas otherwise they may exhibit a highly different appearance; in most cases one half has the appearance of the typical form while the other represents one of the well-known aberrations of the species.

The first recorded case of this nature seems to be a specimen of *Acronycta leporina* L. with left side typical and right side ab. *bradyporina* Tr. (Proceed. Ent. Soc. Lond. 1872, p. X).

Cockayne (1915, p. 83) named these individuals heterocroics, but later on, in accordance with Morgan, who demonstrated the occurrence of such specimens in *Drosophila,* he altered the name to somatic mosaics.

Based upon the literature Cockayne (1922, pp. 106—111) gives a list of all the specimens of this kind known to him. The list comprises 65 individuals distributed over 35 species. However, not all of these are true cases of somatic mosaics. Later on Cockayne (1922a, pp. 200—201 and 1924, pp. 17—20) has further supplemented the list by 13 cases.

Edelsten (Entom. Rec. 22, 1910, p. 149) figures two *Senta maritima* Tausch which may be somatic mosaics but possibly are only pathological individuals. Warnecke (1924, pp. 53—54) mentions two specimens of *Chrysophanus phlaeas* L., one with the left pair of wings glittering white and the right pair normal, the other with the left pair of wings normal and the right pair yellowish-white. Both these specimens may be somatic mosaics. He also records a male of *Chrysophanus hippothoë* L. the left side of which is normal while the

right side is ab. *confluens* Gerh. If the form *confluens* is a hereditarily fixed form and not an abnormity due to external influences, this is a somatic mosaic.

Asymmetry seems to have been observed especially frequently in *Dilina tiliae* L. Cockayne (1922, p. 106, and 1924, p. 19) mentions a true somatic mosaic in a female of this species, in which the right side has the normal green colour, while the left side has the brownish-red colour of ab. *brunnea* Bartel — a form whose hereditary characters are recessive to the typical form — and in addition eight females and two males one side of which is typical, the other deviating. Those specimens in which the markings of the deviating side have been reduced to a central spot, ab. *centripuncta* Clark, a character which is likewise recessive to the typical form, must be somatic mosaics, while the assymmetry of the others is possibly due to injury. Oudemans (1907, pp. 144—145) figures two asymmetric specimens which cannot, either, be regarded as undoubted somatic mosaics, and Warnecke (1926, p. 65), also, mentions a case in *Dilina tiliae.*

Warnecke (1926, Fig. 6) also figures a *Jaspidea celsia* L. whose left forewing has a transverse band, while the right one has only a marginal spot.

Kühn (1932, p. 335) states that within a few broods of *Ephestia kuehniella* Zell. some specimens have emerged in which almost half of the body including the extremities attached to it had different scaling.

Rothschild (Ent. Rec. 45, 1933, p. 155) demonstrates a somatic mosaic of *Colias croceus* Fourcr. ♀ with one pair of wings typical, the other pair ab. *helice* Hb.

Very probably several other cases of somatic mosaism have been published; it is, however, a fact that the number of such specimens is much smaller than the number of gynandromorphs. The cases mentioned above amount to c. 90, c. 50 of which may be regarded

as absolutely undoubted cases of somatic mosaism, whereas there are several thousands of known gynandromorphs.

It is difficult to give the precise proportion between the sexes within the somatic mosaics, for the sex is not always stated. The undoubted cases, in which the sex is known, comprise 27 females and 12 males, that is to say that c. 70 per cent are females and only 30 per cent are males.

3. Description of two new Somatic Mosaics.

Malacosoma neustria L. Fig. 1.

Male. Right half of the normal reddish brown form with the exception of a sector of the fore wing and a minor area of the hairs of the abdomen, the colour of which is a light ochre. The left half is yellow without any mixture of brown (ab. *ochracea* Tutt). Furthermore, the left pair of wings is somewhat larger than the right. In the specimen itself the boundary line between the brown and the yellow half can be distinctly seen — though less distinctly in the reproduction —; it coincides precisely with the symmetry plane of the insect.

The specimen is preserved in Mr. Erling Pedersen's collection and was bred by him from a pupa taken at Sønderby on Møen $^{27}/_{7}$ 1932. Both the typical form and ab. *ochracea* are of common occurrence in the locality.

Acidalia immutata L. Figs. 2a and 2b.

Male. The right pair of wings has the white ground colour of the typical form; their upper side differs from a normal *immutata* only in having a very narrow radially placed stripe of blackish brown scales on the hind wing. The under side of the right pair of wings likewise has the predominant colour of the typical form, but narrow stripes of blackish brown scales are found on the apical part of the fore wing behind the costa.

The tornus of the hind wing is strewn with scattered dark scales as far as the middle of the wing. The left pair of wings is melanic, and both the upper and the under sides are closely, but not uniformly covered with dark scales. The abdomen is not sharply divided along the symmetry plane, but exhibits narrow belts of dark scales, more sparsely on the right than on the left side. The abdomen of the normal *immutata* is entirely white.

The specimen was caught in Horreby Lyng, Falster, by Mr. Forum Petersen $^{17}/_{7}$ 1939 on an excursion in which I myself took part, and I was thus able to observe the specimen immidiately after the capture. The typical form of *immutata* is of common occurrence in the locality, whereas the melanic form has not been observed there. Altogether only one Danish specimen is known, which was taken $^{16}/_{7}$ 1941, likewise by Mr. Forum Petersen. These two specimens of *immutata* have been briefly described and figured (Wolff 1942, pp. 203—204). Both of them are preserved in Mr. Forum Petersen's collection.

4. **Somatic Mosaism associated with Gynandromorphism.**

In addition to the aforementioned gynandromorphs and somatic mosaics some individuals are known in which both phenomena occur at the same time, thus for instance an *Aglia tau* L. one side of which is a normally coloured male, while the other is an ab. *ferenigra* female, or specimens of *Argynnis paphia* L. with one side *paphia* ♂ and the other ab. *valesina* ♀. However, the two examples mentioned here are actually representatives of two different groups, the first one comprising such cases in which the aberrant form may just as well appear in the male as in the female, whereas the other comprises such in which the aberrant form is genetically sex-limited.

Cockayne (1915, pp. 83—86, and 1922, p. 111) mentions the occurrence of such individuals belonging to the first group within 22 species of Lepidoptera, but does not give the precise figure of individuals known; for instance as to *Aglia tau* L. it is only stated that "several of these are known" and as to *Smerinthus populi* L. that "many *A. populi* gynandromorphs show great difference in ground colour on the two sides, which is not a sexual one". If "several" is regarded as at least three, and "many" as at least five, the list includes at least 44 of this group.

Of the other group mention is made (l. c. pp. 93—95) of 33 individuals (of these 23 are *paphia* ♂-*valesina* ♀) distributed over seven species. Warnecke (1924, pp. 45—46) records two more *paphia-valesina,* the number of this group being thus increased to 35, that of the two groups together to about 80, which figure is of about the same order of magnitude as the number of known unisexual somatic mosaics (c. 90 cases, of which at least 50 are undoubted).

5. Incompleteness in halved Gynandromorphs and Somatic Mosaics.

The individuals dealt with here, gynandromorphs and somatic mosaics, are not, generally, accurately halved, one half often exhibiting well delimited minor areas of the appearance of the other half.

As regards the gynandromorphs this is perhaps most distinctly visible in Sjöstedt's figure (l. c. Plate 1) of *Morpho rhetenor* Cram., in which the brown female side has a sector in both the fore wing and the hind wing of the shining blue colour of the male. Of the specimens of somatic mosaics described above *Malacosoma neustria* has a sector in the normally coloured fore wing and on the abdomen a smaller area of the colour of

the aberrant side, while in *Acidalia immutata* minor black areas are found on the white wings.

It would seem to be a specially common feature that precisely a sector in the wing of one side has been transformed.

Thus Kühn (1932, p. 333) figures (Abb. 17) a fore wing of *Ephestia kuehniella,* in which part of the wing behind the costa is dark.

Fig. 3 shows a male of *Lymantria monacha* L., in which a narrow area behind the costa on the upper side of the right fore wing presents the white markings of the normal form, while the whole remaining part of the specimen is ab. *eremita* Ochs. This specimen, which is preserved in my collection, was taken by me at Snogebæk on Bornholm $^{25}/_{7}$ 1936.

6. Explanations of Gynandromorphism and Somatic Mosaism.

Among the different hypotheses which may be propounded in explanation of the development of the abovementioned individuals mention may be made of a curious interpretation of a gynandromorphic *Dendrolimus pini* put foreward by Scopuli in 1777, according to which this specimen was supposed to have arisen by fusion of two pupæ within the same cocoon. This hypothesis might, of course, just as well be applied to the different halved somatic mosaics.

That the phenomenon is not quite so simple, but, on the contrary, is very complicated, and that an intimate knowledge of the genetics within the species in question is required, has been shown by later studies, principally the fundamental investigations on the fly *Drosophila melanogaster* made by Morgan (Morgan & Bridges 1919).

Since, as far as is known to me, the inheritance of the aforementioned aberrant characters in *Malacosoma*

neustria and *Acidalia immutata* has not yet been elucidated and accordingly no definite interpretation of these individuals can be given, I shall merely mention below — in all essentials on the basis of Cockayne's papers (l. c.) — some of the processes during the development of the organism which may be supposed to give rise to the occurrence of individuals like those described above. From this it will appear that no generally valid explanation can be given, but that each case must be analysed separately.

a. Elimination of a sex chromosome. In Lepidoptera the female is heterozygous for sex and in the body cells has two sets of autosomes + one sex (x) chromosome. The male is homozygous for sex and in the body cells has two sets of autosomes + two x chromosomes. There will therefore be two kinds of egg cells, half of them with a set of autosomes + one x chromosome, the other half with autosomes, while there is only one kind of spermatozoa, all having a set of autosomes + one x chromosome. This is the case in Lepidoptera, some Trichoptera, and a few fishes, whereas, conversely, as far as is known so far, in all other animal organisms (including *Drosophila*) it is the female which is homozygous for sex and the male which is heterozygous for sex (Winge 1937, p. 182). Hence in Lepidoptera, by fertilisation of an egg cell with an x chromosome, an individual with two x chromosomes will arise, that is to say a male, whereas by fertilisation of an egg cell which lacks the x chromosome, an individual with only one x chromosome will arise, that is to say a female.

If, now, an individual is destined to be a male (with 2 x chromosomes in the fertilised egg cell), and an elimination of an x chromosome takes place during the first nuclear division so that one daughter cell receives 2 x chromosomes but the other only one x chromosome, the egg will develop into an individual the two sides

of which have different sex, that is to say, a halved gynandromorph.

If, in addition, the two original x chromosomes contain mutant genes, the recessive genes of the remaining x chromosome will give phenotypical manifestations, the corresponding dominating normal genes of the eliminated chromosome having disappeared (Winge 1937, p. 295).

In this way, then, the occurrence of gynandromorphs and "combined" somatic mosaics, but not of unisexual somatic mosaics, may be explained.

b. Elimination of an autosome. Corresponding to the elimination of a sex chromosome which produced a gynandromorph, it might be supposed that the elimination of an autosomal chromosome might produce an unisexual somatic mosaic (Morgan p. 26). This cannot, of course, explain the cases in which the particular gene or genes are carried by the x chromosome (sex-linked inheritance), and several such cases are known.

c. Fertilisation of a binucleate ovum. Within *Drosophila* as well as within Lepidoptera cases have been demonstrated in which both the two nuclei arising from the reduction division in the female happen to remain in the egg and may there be fertilised each by its spermatozoon, and thus only a single individual arises out of these two nuclei.

If such a binucleate egg be fertilised by two spermatozoa with different predispositions, one for the aberration, the other for the typical form, a somatic mosaic may arise.

d. Somatic mutation. A mutation in a somatic cell generally occurs in only one chromosome of a pair; thus, its immediate result will not be seen except when the mutation is dominant. If a dominant mutation occurs in one of the daughter cells formed at the first division of the fertilised egg, the result may be a somatic mo-

saic. However, by far the greater number of predispositions for colour in the Lepidoptera are recessive.

Should a recessive somatic mutation occur in the x chromosome of a female, it will show at once in those parts of the body whose cells contain the changed gene because the female has only one x chromosome. If a recessive mutation occurs in the x chromosome of a male, its effect would not appear in the soma because the male has two x chromosomes, and the normal allelomorph in the other will conceal it (Morgan p. 31). It will be seen that only somatic mosaic females can arise in this way. As mentioned above, the predominant number are, indeed, females.

A true somatic mosaic male with recessive predispositions must either have arisen by elimination of an autosome, by fertilisation of a binucleate ovum, or from another unknown cause.

e. Migration of cells. Normally an individual develops from the ovum by numerous divisions of the two daughter cells which approximately give rise each to its half of the animal. It may happen, however, that cells formed by one daughter cell mixes with the cells of the other. In this way it may be explained that in gynandromorphs as well as in somatic mosaics one half of the insect may exhibit minor areas of the same appearance as the other half. The earlier the migration of the cells takes place, the more extensive will the admixture be.

It is possible, also, that some of these differences in the appearance of the two halves must be explained as somatic mutations which occurred during the division processes later in the development.

I am indebted to Mr. Erling Pedersen, Bogø, and Mr. Forum Petersen, Copenhagen, for permission to examine and describe the specimens of *Malacosoma neustria* and *Acidalia immutata* dealt with here. I further

wish to thank Professor Dr. C. M. Steenberg and Mr. Aksel Nielsen for the photograph of Fig. 2. Finally I ask Dr. H. Lemche to accept my thanks for the photograph of Fig. 1 and for advice and guidance in several of the hereditary questions dealt with above.

Explanation of Plate.

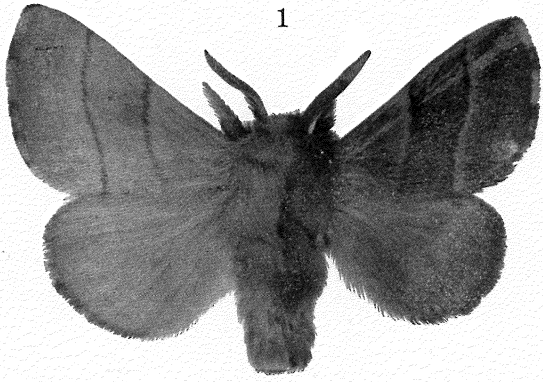
Fig. 1: *Malacosoma neustria* L. ♂. Somatic Mosaic. Right side typical, left side ab. *ochracea* Tutt. × c. 2.
(H. Lemche photo.)

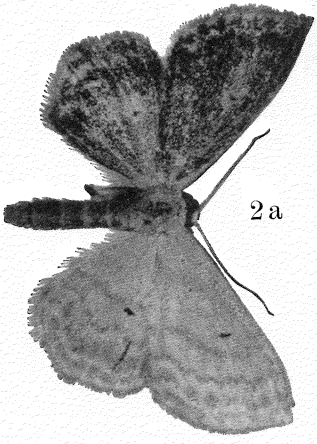
Fig. 2a: *Acidalia immutata* L. ♂. Somatic Mosaic. Right side typical, left side melanic. × c. $2^1/_2$.
(A. Nielsen photo.)

Fig. 2b: Same specimen as above. Underside. × c. $2^1/_2$.
(A. Nielsen photo.).

Fig. 3: *Lymantria monacha* L. ab. *eremita* Ochs. ♂. Right forewing with narrow area behind costa showing type colour. × 2.
(Aut. photo.)

1





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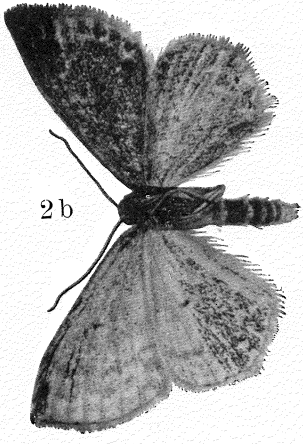

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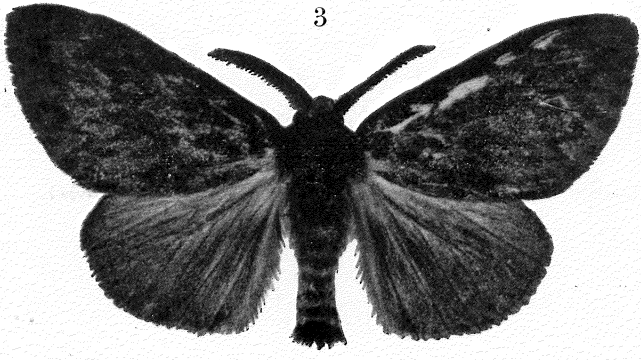

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Dansk Oversigt.

Følgende grupper af asymmetriske sommerfugle er af særlig interesse.

a. Halverede gynandromorfer, d. v. s. sådanne individer, hvis ene halvdel er en normal ♂, medens den anden halvdel er en normal ♀. Selvom sådanne individer er sjældent forekommende, kendes dog adskillige tusinde tilfælde fordelt på 3—400 forskellige arter.

b. Halverede somatiske mosaikexemplarer, hvis to halvdele er af samme køn, men hvis ene halvdel har artens normale udseende, medens den anden repræsenterer en af artens aberrationer.

Sådanne individer er langt sjældnere forekommende end gynandromorferne, idet der i literaturen er omtalt knapt 100 tilfælde. Ikke alle disse er dog sikre, idet der let sker forvexling med gynandromorfer eller patologiske asymmetriske individer, men ihvertfald ca. 50 er ægte somatiske mosaikexemplarer. Den overvejende del er hunner (ca. 70 %).

c. Exemplarer, der foruden at være halverede gynandromorfer, tillige er somatiske mosaikexemplarer. Hyppigheden af sådanne tilfælde synes at være af samme størrelsesorden som af enkønnede, halverede mosaikexemplarer.

To nye tilfælde af somatiske mosaikexemplarer beskrives og afbildes: *Malacosoma neustria* ♂ fig. 1 (højre side typisk og venstre ab. *ochracea*) og *Acidalia immutata* ♂ fig. 2a og 2b (højre side typisk og venstre melanistisk).

Asymmetrien er almindeligvis ikke fuldstændig, idet hos gynandromorfer den ene side ofte er isprængt skarpt afgrænsede partier med det andet køns farve og tegning, og de somatiske mosaikexemplarer på den typiske side kan have partier af aberrationen. I begge tilfælde viser dette sig ofte særlig tydeligt på en sektor i for- eller bagvingen.

En ♂ af *Lymantria monacha,* hvis højre forvinge på overside har en smal stribe af den typiske forms farve, medens resten af dyret er ab. *eremita,* afbildes.

Forskellige hypotheser — i det væsentlige fremsat af Morgan — til forklaring af disse formers opståen omtales. Nogen almengyldig forklaring kan ikke gives, idet hvert tilfælde må analyseres for sig ud fra kendskab til den pågældende forms arvelighedsforhold.

En gynandromorf (med eller uden somatiske ændringer) må antages almindeligvis at opstå ved tab af et kønskromosom i den til ♂ anlagte, befrugtede ægcelle. Et enkønnet somatisk mosaikexemplar kan tænkes at opstå enten ved tab af et autosom, ved befrugtning af et dobbeltkerneæg af to forskellige sædceller, eller ved somatisk mutation. En recessiv somatisk mutation vil dog ikke kunne give sig synligt udslag hos en ♂.

Under kløvningerne kan celler fra den ene dattercelle blande sig med cellerne fra den anden dattercelle, hvorved der kan opstå isolerede partier på dyrets ene halvdel med den anden halvdels udseende. Sådanne kan også tænkes opstået ved somatiske mutationer.