XVI. *Mr. Merrifield's Experiments in Temperature-Variation as bearing on Theories of Heredity.* By Frederick A. Dixey, M.A., M.D., F.E.S., Fellow of Wadham College, Oxford.

[Read March 14th, 1894.]

The results of Mr. Merrifield's experiments on the variations produced in butterflies by the exposure of the pupa to different conditions of temperature, are in themselves of great interest. But the interest becomes enhanced when it is recognized that many of the new features which make their appearance under these conditions are identical with those occurring normally in other species more or less closely allied to the subjects of experiment; that in not a few instances the disturbance of natural temperature-conditions appears to have caused reversion to an earlier stage in the phylogenetic history of the species; and further, that the ancestral features thus revived seem to vary with the nature of the disturbance.

Examples of these phenomena, from a previous series of experiments, were given in Trans. Ent. Soc. Lond. 1893, p. 55, and were commented on by me (*Ibid.* p. 69). The latest results obtained by Mr. Merrifield, besides confirming many of the former, furnish further instances of the same nature, as follows:—

I. Vanessa atalanta.

A. *Warmed.*

(1) The occurrence of red scales in the dark ground-colour between the middle of the scarlet band and the large white costal spot c. This is an approach to the condition in *V. huntera* and *V. myrinna*, and more remotely to that in *Grapta* and *Argynnis*. A corresponding feature is seen in *V. io*, which in this respect is more ancestral than *V. atalanta*.

(2) The tendency towards the formation of a scattered ring of red scales round the spots β and γ of Series D.

This again recalls a common condition in *V. myrinna* and *V. huntera*.

(3) The appearance of a new red spot on the underside of the forewing, just below the stem of the median nervure before bifurcation. This represents a pale patch of various shades in *V. callirrhoe*, *V. myrinna*, *V. huntera*, *V. cardui*, etc.

(4) The appearance of another red spot on the underside of the forewing, just below the first median nervule. This represents a patch visible on both surfaces of *V. callirrhoe*, and fully developed in all the species nearly allied to *V. cardui*.

(5) The tendency towards resolution of the inner margin of the red band, as in *V. callirrhoe*.

(6) The suffusion of the dark ground colour with golden brown, also as in *V. callirrhoe*.

Of these, Nos. (1) (2) and (3) are points now observed for the first time; while (4) (5) and (6) are confirmations of previous results. (See a former paper by the author in Trans. Ent. Soc. Lond. 1893, p. 70.)

B. *Cooled.*

(1) Much substitution of lavender or metallic blue-green scales for black. This points to the ancestral condition seen in the females and parts of the males in many species of *Argynnis*, *e.g.*, *A. paphia*, var. *valesina*, *A. sagana* ♀, *A. niphe* ♂ and ♀, and *A. diana* ♀.

(2) The presence of minute patches of bluish scales near the margin of the dark ground-colour in the hindwing, indicating the blue centres of the almost completely merged Series III.—an ancient feature of *Vanessa* and *Grapta*.

(3) The marked increase of marginal blue, especially about the anal angle of the hindwing. This appears to represent the condition seen in *Argynnis niphe*, and ultimately to point back to the primitive Argynnid colouring of *A. valesina* and *A. diana* ♀.

These are all confirmations of former results.

II. Vanessa io.

In this species, warming tends to revive, in the forewing, a series of dark spots (II), occurring normally in

Araschnia levana. Cooling tends in the first place to separate certain constituents of the ocellus, and when carried to a high extent has the remarkable effect of causing an unmistakable resolution of the ocellus in the forewing, the appearance finally produced being that of the ordinary *Vanessa* character in a comparatively unmodified form. It is interesting to see how completely these cooled specimens bear out the views which I ventured to express, some years ago, on the origin and constitution of this ocellus (Trans. Ent. Soc. Lond., 1890, pp. 99, 100, pl. i., fig. 12). The ocellus of the hindwing is also affected in the same direction.

III. Vanessa polychloros.

Cooling tends to produce several features which appear to be ancestral. The chief of these are (1) the pupilling with black of the spots of Series D in the forewing; (2) the occasional indication of Series III. in the hindwing; and (3) the tendency towards the formation of a new dark spot between II. 8 and III. 8. These points approximate towards the condition in *Grapta.*

IV. Grapta c-album.

In both broods cooling tends to induce or increase a darkness of ground-colour; this being undoubtedly an ancestral character.*

In all cases of this kind the obvious question occurs—are we to consider these phenomena as true instances of reversion, or is it merely that like causes have produced *de novo* a like effect in descendant and ancestor? The latter explanation may account for some of the facts, but, I think, not for all. It may perhaps give the reason for a general diffusion of bluish scales, or for a change of the ground-colour from black to brown, but it is scarcely adequate to explain the special formation of a definite pattern, as of Series III. with its blue centres in *V. atalanta,* or the reduction of the ocellus in *V. io* to the primitive *Vanessa* condition. Without raising the vexed question of sexual selection, we may yet affirm that

* The observations on the three last species are new; those on *V. atalanta,* as has been seen, are partly new and partly old. On the whole subject of the ancestral markings in *Argynnis* and *Vanessa,* see the author's paper in Trans. Ent. Soc. Lond., 1890.

among the features induced or revived by altered temperature-conditions, there is at least a residuum which must have owed its first origin to causes other than the direct action of temperature on the organism. Nor, again, are these to be considered as cases of "arrested development"; for the stages reproduced are stages in the phylogeny of the species, not in the ontogeny of the individual.

If, then, these revived features are really ancestral, how is their revival to be accounted for? The whole subject of reversion abounds with difficulty. An explanation commonly offered is that the characters last developed in the history of a species, or of an individual, are less stable than those that have a longer history behind them, and that have become firmly established under the operation of a long-continued process of heredity. Any disturbance—such as an exceptional condition of temperature—of the normal course of growth, may therefore be expected to act in the first place on the newer and less stable features, interfering with their usual line of development, and shaking back the species as it were to an earlier and more firmly-founded stage of its development—just as in an earthquake the freshly-built wing of a house, where the mortar was not yet dry, might fall and leave the older portions standing. Such an explanation, however, is in itself at best but partial, for it gives no real reason why the newer features should be less stable than the old; and indeed it comes to little more than restating the difficulty in another form.

The two attempts to find a more definite explanation of reversion which may be said at present to hold the field, are those which pass respectively under the names of Darwin and Weismann. If the Darwinian assumption of centripetal "gemmules" be granted, the commonest case of reversion, that namely which results from hybridization, especially between recently-established species, is capable of explanation under the hypothesis of pangenesis. But it may be questioned whether pangenesis as stated by Darwin is capable of accounting for such cases as the present, inasmuch as in them the condition of full maturity is almost reached before the introduction of the modifying disturbance. Although the ovum from which the individual has originated may under the Darwinian hypothesis have contained numerous gemmules of an

ancestral type, which though usually dormant might under certain circumstances become active in the ontogenetic process, it would yet seem a legitimate conclusion from the hypothesis, that the introduction of any cause analogous to hybridization in its action on the developing organism must belong to a far earlier stage in the ontogeny than the beginning of the pupal condition; it must belong, in fact, to the stage of fertilization of the ovum. There are, however, a few facts on record, such as the assumption of ancestral characters by an old hen (Darwin, "Animals and Plants under Domestication," 1868, vol. ii., p. 54), and the appearance of an earlier vertebrate condition in limbs of Amphibia reproduced after amputation (*Ibid.*, ii., p. 15), which seem in some respects analogous to the present instances, as being apparently cases in which a disturbance of normal conditions at a comparatively late ontogenetic stage has in some way led to reversion in the course of the individual growth. These cases are regarded by Darwin as not incompatible with pangenesis, though not fully explained by it.

If, on the other hand, we postulate with Weismann the existence of "ids" and "determinants," endowed with the nature and properties that he supposes, the instances that we are considering become more explicable. For according to this theory every feature in the structure of the individual organism is the result of a "struggle of the ids" in ontogeny, the final character of each histological unit being fixed at the moment of the liberation of its proper determinants by the disintegration of the "ids." The competition between the carriers of heredity, many of which must under the theory be ancestral in character, so far from being confined to the ovum, is being waged throughout the entire ontogeny, and is renewed at every successive stage of development. This being the case, it is to be expected that any external influence, such as temperature, on coming into force at any given stage, should be able to exert an effect upon the struggle proceeding at that particular time between determinants which are just beginning to play their parts in the ontogeny, and should in consequence be able to modify *pro tanto* the resulting adult organism. It would be, moreover, natural to expect the different determinants to be affected by different temperatures, nor would it be surprising to find that temperature-conditions, which are

ex hypothesi diverse from those normal to the species, should favour one or other set of ancestral determinants at the expense of those more proper to the species. This would explain why the effect of heat differs from that of cold, though both lead to reversion.

There is, however, one fact which shows that the above explanation is not entirely adequate—the fact, namely, of the hereditary transmissibility of certain temperature modifications, as determined in the case of *Polyommatus phlæas* by Weismann himself ("The Germ-Plasm," 1893, p. 399). This phenomenon admits of a ready explanation under the theory of pangenesis; the point that pangenesis fails to explain is the reversionary character of the original change, unless, indeed, we suppose a "struggle of gemmules," analogous to the "struggle of determinants," and continued, like the latter, throughout the ontogeny; in which struggle certain conditions favour the ancestral rather than the modern gemmules. But just as the theory of pangenesis seems to require some such addition as that suggested, so also, under the rival hypothesis, it seems necessary to supplement the explanation above given with another supposition already propounded by Weismann, namely, that the temperature-conditions are capable, in some cases, of actually altering the constitution of unexhausted determinants wherever they occur, even in the germ plasm of the ovum itself.

I am myself inclined to think that, granting Weismann's general theory of heredity, the more special cases of reversion are to be chiefly explained, as above, by the critical influence of the temperature-conditions on the struggle of the determinants, rather than by an intrinsic effect on the determinants themselves. The latter may account for such cases as a general lightening or darkening of the ground-colour, as in Weismann's *P. phlæas*, which strictly speaking are not really but only accidentally reversionary; it will not, however, account in my opinion for the special ancestral marks shown by Mr. Merrifield's *V. atalanta* and *V. io*.

The point is capable of verification. If it be true that there is a selective influence which is exerted upon the actual struggle of the determinants, that influence would find a different expression in the adult according to the particular stage in the ontogeny at which the influence was applied, as it would affect those determinants only

between which at that time the struggle was being waged.* If, on the other hand, there is no such influence, but the effect is entirely a direct one and modifies the individual determinant, then all the as yet unexhausted determinants that are capable of reacting to this particular disturbance would be affected in some degree; though no doubt, as Weismann supposes, to a greater extent if they had reached the point of disintegration than otherwise.

Again, it seems to me to be of great importance to ascertain if possible which of these modifications are transmissible to descendants. If all the modifications, including those which I have supposed to be produced in the first way, can be shown to be hereditarily transmissible, this would amount to a demonstration that the second explanation is adequate; and the first may then be abandoned as unnecessary. Should only some be inheritable, the presumption would be in favour of the co-existence of both modes of action; moreover, the greater the number of non-transmissible variations that can be produced, the more will the case be strengthened against pangenesis, and in favour of the "centrifugal" theory.

I am anxious to see, if possible, the results of breeding experiments on specimens like these for yet another reason. It seems to me that by comparative experiments, with and without artificial selection, on such variations as may be transmissible, a measure might be obtained of the relative importance of selection and the mere action of external influences in the transformation of a species. I think, too, that no better group for such experiments as these of Mr. Merrifield's could be selected than the Vanessas. For, in the first place, it is only among poikilothermic animals that the *direct* effects of temperature can be fully studied; then among these the Lepidoptera are pre-eminent for the extremely delicate register of variation afforded by their wings; and, lastly,

---

* The fact that in *V. polychloros* forcing invariably tends to produce a certain effect, whether preceded by warming or cooling; while refrigeration brings about another definite effect, whether followed or not by forcing, seems so far favourable to this hypothesis. See above, p. 432.

among the Lepidoptera the Vanessas belong to an assemblage the phylogeny of which may claim to be at any rate partially known.* It is hardly necessary to point out how much service may be rendered to researches of this kind by the careful working out of the true internal affinities of Lepidopterous groups. In proportion as their phylogeny is placed on a secure basis, we shall be able to pronounce with confidence on the real character, whether reversionary or not, of these remarkable variations; and shall accordingly be able to estimate at its proper value the evidence they bring towards the solution of the great problem of Heredity.

---

* See the author's paper already referred to, in Trans. Ent. Soc. Lond., 1890, p. 89.