PSYCHE.

A NEW HYPOTHESIS OF SEASONAL-DIMORPHISM IN LEPIDOPTERA. — II.

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(2) *New Hypothesis of Seasonal-Dimorphism.*

I know of only one experiment upon the effect of *excessive* heat upon Lepidoptera, and that was performed upon the pupae of *Vanessa antiopa*, by Fischer ('95) who, it will be remembered, subjected them, when fresh, for 3 hours and then daily for 2-3 hours to a temperature of 40°–42° C. keeping them at all other times at 35°–38° C. The butterflies which issued resembled those which would have resulted from exposure to cold of 0°–1° C.

It has occurred to me that in this remarkable fact we may have a clue to at least a partial explanation of the action of cold upon seasonally-dimorphic Lepidoptera. It is well known from the researches of Dutrochet, Rossbach, and Plateau that if organisms be subjected to gradually increasing heat the metabolic processes as evinced by increased excretion in protoplasm, and more rapid rate of development, become more and more active; until suddenly all movements cease and heat rigor sets in. This is not death however for if the organism be now cooled down, recovery takes place, and the life processes return with normal vigor. According to Plateau* the temperature of heat rigor in various insects varies between 38°–43° C. It is highly probable then that the high temperature of 40°-42° C. produced *heat rigor* in the pupae, and therefore the metabolic processes were checked, exactly as they would have been by the benumbing influence of cold. If this be true it becomes probable that the peculiar color-aberrations caused by cold are only an expression of the *decreased metabolism* in the pupae. It will be remembered that heat of 35° C. produces an aberration in *V. antiopa* which is just the reverse of that caused by cold. In this case the peculiar coloration could be explained as one of the results of the increased metabolism in the pupae.

Now it may well be that it is an advantage to a pupa which is destined to withstand the winter's cold to *inherit* a tendency toward a low metabolism, for resistance to the cold would naturally require the possession of low metabolic processes; hence those pupae which already possessed low metabolism would

* Plateau, '72; Bulletin d l'Academie royale des sciences de Belgique, xxxiv, pp. 315-317.

be in better condition to withstand the effects of the cold. Natural selection would then operate to weed out all pupae having high metabolic processes, for they would be more likely to freeze; whereas those individuals in which the metabolism was low would be preserved. Also this inherited tendency in the overwintering pupae to possess low metabolic activity might become so strongly fixed that it would be found difficult to alter it by the mere subjection of the pupae to a high temperature, such as 32°–35° C. Moreover it would doubtless be of advantage to the insects if they had the power to resist the influence of such warmth, for there are often hot periods of weather in the autumn through which the over-wintering pupae must pass; but their development must not be hastened thereby, for if the butterflies emerged they or their progeny would probably perish of the cold.

Professor Weismann's former (1875, '82) idea that in the seasonally-dimorphic butterflies of the temperate zone the phylogenetically older form issues from the wintered chrysalids, and represents the form which existed during the glacial epoch, is to my mind improbable. His hypothesis may be true as far as the European *Vanessa levana-prorsa* is concerned, because, as is well known, the butterflies of Europe are more closely related to those of Siberia, than to those of Africa or India. (See Bath ('95)).* The cause of this lies in the well known fact that there has been, according to Geikie, no land connection between Europe and Africa since the close of the glacial epoch. Moreover the deserts of Sahara, and Arabia, and the snow clad peaks of the Himalayas form an insuperable barrier beyond which tropical forms could not pass to enter the northern regions. In America, however, the case is very different, for almost 50% of all the known species of Lepidoptera of the world come from South America,* and there can be but little doubt that the ancestors of most of the North American butterflies came from South America. The ancestors of the North American forms have gradually crept in from South America after the glacial epoch, and as their range extended further and further north, they were obliged to become adapted to the cold, or perish. This adaptation would mean the acquisition of a low metabolism in the *over-wintering* pupae. In this connection it is interesting to notice that Merrifield ('93) has shown that in England those pupae of *Pyrameis atalanta* which form in the autumn all perish of the cold. This insect usually hibernates as an imago, and is not seasonally-dimorphic. Indeed, the seasonally-dimorphic butterflies, of the temperate zone, according to Scudder (Butterflies of New England, 1889, p. 1384) probably all *winter*

* Bath, W. H. 1895; Entomologist Vol. 28, p. 247.

* Schatz ('92) finds that there are in South America 272 genera of butterflies comprising 4560 species, and that 231 of these genera are proper to South America alone. In North America, on the other hand, there are according to Edwards only 66 genera and 612 species.

over as pupae. Dr. Scudder has also observed, that in a few cases of seasonal-dimorphism we find differences between the earlier and later appearing members of the spring brood, the later members showing an *approach toward the summer form.*

It is highly probable that the vast majority of Lepidoptera which existed in North America before the glacial epoch, simply retreated southward upon the approach of the ice. For to have them remain we are obliged to assume that not only they, but their food plants, also, became acclimated to the cold. Many of those which did remain, and succeeded in defying the cold would probably for the most part become so thoroughly acclimated to it that they would finally *prefer* a cold climate, and when the ice retreated they would probably follow it northward leaving a few representatives stranded, as it were, upon the tops of the highest mountains; as has been shown by Grote and, also, Scudder ('89 p. 588) to have been the case with *Oeneis semidea* of Mount Washington.

In the case of *Papilio ajax*, which was experimented upon by Edwards, I have reason to believe that it could not have existed in North America during the ice period. For its nearest allies are all in Mexico, and South America, none of them being found in the colder parts of North America. Moreover its food plant, the papaw (*Asimina triloba*, Dunal.) belongs to the characteristically tropical family Anonaceae, and cannot live in a cold climate. This leads me to suggest that walshii or telemonides are not primitive forms as would be the case were Weismann's 1875 hypothesis true. I also predict that if the overwintering pupae of *Papilio ajax* be subjected to a constant heat of from 30°-35° C. they will be transformed into the summer form marcellus.

Conclusions: In lepidoptera of the temperate regions it is an advantage for the summer pupae to possess *high* metabolic processes, for under these circumstances their development is rapid. On the other hand it is an advantage for the overwintering pupae to posses *low* metabolic process, for under these circumstances they would be the better able to withstand the influence of warm periods of weather in the autumn; for if the butterflies emerged at this time they or their progeny would probably perish of the cold. Moreover in order that the pupae may withstand the influence of the winter's cold it is essential that they possess a low metabolism. Natural selection would then operate to cause all summer pupae to *inherit* a high metabolism, while all overwintering pupae would be forced to *inherit* a low metabolism. Pupae which possess a constitutional tendency toward high metabolism give rise to the summer form of imago, while those pupae which possess a constitutional tendency toward low metabolism give rise to the overwintered form of butterfly. The summer and winter forms of imago are only expressions of this difference in constitution of the summer and winter pupae.

It is well known through the re-

searches of Barker,* Brandes,† Butler,‡ and others that tropical butterflies exhibit seasonal dimorphism. It has occurred to me that this may *possibly* be due to the direct influence of the varying humidity upon the pupae. Pupae reared in a dry atmosphere may give rise to the dry season form, while those reared in a humid atmosphere may give rise to the wet season form. I am assured by Mr. E. A. C. Olive of Cooktown, Queensland, Australia that the development of pupae in that region is more rapid in the wet season than in the dry.

I freely admit that Weismann's "adaptive" seasonal-dimorphism *may* exist, but I believe that the explanation given in this paper is more probable. I hope that some of the many able entomologists who are carrying out researches upon seasonal-dimorphism will test its truth or falsity by experiment.

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* Barker, C. W.; Notes on Seasonal-Dimorphism of Rhopalocera in Natal. Trans. Ent. Soc. Lond. 1895, pp. 413–428.

† Brandes, G.; Der Saison-Dimorphismus bei einheimischen und exotischen Schmetterlingen. Zeit. Naturw. Leipzig, 66. Bd., pp. 277–300, Fig. T. 2. 1894.

‡ Butler, A. G.; Notes on Seasonal-Dimorphism in Certain African Butterflies. Trans. Ent. Soc. Lond. 1895, pp. 519–522.