PSYCHE.

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

BY ALFRED GOLDSBOROUGH MAYER, CAMBRIDGE, MASS.

(1). Previous Researches.

In 1830 it was discovered that the two European butterflies Vanessa prorsa and Vanessa levana were in reality only different broods of one and the same species of insect. The chrysalids of the last summer's brood winter over and give rise to butterflies of the light colored, or levana, type. Then follow several summer generations all of the prorsa type, having wings of a dark brown color. The chrysalids from the last prorsa generation winter over and produce levanas the next spring. There is, however, in addition to the forms levana and prorsa, an intermediate form, porima, which is very rarely met with in nature; and, indeed, it was on account of the extreme rarity of this intermediate form that the older naturalists failed to recognize that levana and prorsa were only different forms of the same butterfly.

Dorfmeister (64) showed that if chrysalids which were naturally destined to produce the prorsa form be subjected to cold, they will give butterflies which are not prorsa but porima, and that if the cold is as intense as 0°C, the butterflies which issue are hardly distinguishable from typical levanas. Later in 1875 Weismann repeated these experiments with the same result. He also tried the reverse experiment. That is, he took chrysalids of the last summer's brood of butterflies and subjected them to the heat of a green house, varying from 15°-31°C. The chrysalids however remained over winter and produced levanas the next spring just as they normally would had they been exposed to the winter's cold. Weismann was deceived by this experiment, and lead into the false conclusion that it was impossible for heat to cause chrysalids destined to produce levanas to give rise to anything but levana. In 1895, however, he published a paper in which he acknowledges that heat can cause the chrysalids which are naturally destined to produce levana to give rise to butterflies of the porima, or even of the prorsa type. His final conclusions (95 p. 644) are as follows: levana and prorsa follow each other in a regular cycle, levana appears in April, prorsa in June. By the influence of cold chrysalids destined to give rise to the prorsa form can be changed into levana.
This change is not accomplished however without resistance, for the chrysalids show a strong tendency to produce prorsas, as is seen by the production of many porimas among the butterflies whose chrysalids have been subjected to the cold. On the other hand the third, or autumnal, generation of chrysalids shows a strong tendency to over-winter and produce butterflies of the levana type next spring. Heat of 27°-30°C., can, however, counteract this tendency and cause some of these chrysalids to give rise to porimas, or even to prorsas.

In (1875-'82) Weismann was lead into the conclusion that levana represents the more primitive or ancestral form of the butterfly which existed in Europe at the time of the glacial epoch. As the mean temperature at that time was much lower than at present, and the summer was short, the butterfly was probably single brooded, and consisted of only the form levana. The form prorsa, however, gradually made its appearance after the glacial epoch when the climate became milder, and the butterfly began to produce summer generations. The form prorsa, according to this hypothesis, is phylogenetically newer than levana, and the application of cold simply causes it to revert to its ancestral type. The levana form, on the other hand, could not possibly be made to revert into prorsa because prorsa is phylogenetically younger than levana.

In 1895, however, Weismann finds that he is mistaken in this for, it will be remembered, he succeeded in forcing chrysalids which were naturally destined to produce levana to give rise to prorsa by subjecting them to a high temperature. He is therefore obliged to modify his former (1875-'82) conclusions, and finally decides that there are two kinds of seasonal-dimorphism; one of which he calls "direct seasonal-dimorphism," and the other "adaptive seasonal-dimorphism." By "direct" seasonal-dimorphism Weismann means the direct effect of the temperature stimulus upon the pupae at the time when the colors are produced. This direct influence may induce chemical changes, etc., which determine the coloration of the wings. An excellent example of direct seasonal-dimorphism is afforded by Chrysopeplus phileas where heat causes the pupae of any brood to give rise to dark colored butterflies; while cold induces them to give light golden red forms.

In "adaptive" seasonal-dimorphism, on the other hand, we have the additional factor that one or both of the dimorphic forms possesses a peculiar advantage correlated with the season in which it occurs. Under these circumstances there has arisen, through the agency of natural selection, a tendency to produce different forms in the different seasons. For example we find inherent in the pupae of Vanessa levana-prorsa, two separate, and distinct, tendencies; the one to produce levana, and the other prorsa. The tendency to produce levana is strong in the over-wintering pupae, while the tendency to produce prorsa is strong in the summer pupae. These tendencies can however
be altered by temperatures which are the reverse of the normal ones to which the pupae would be subjected in nature. Cold is only the initiatory stimulus for the levana tendency, and heat for the prorsa tendency. An example of adaptive seasonal-dimorphism may be afforded by *Vanessa levana-prorsa* where the summer form prorsa may gain some advantage by its general resemblance to *Limenitis sibylla* and *camilla*; while it is possible that the overwintered form, levana, may gain some advantage from its resemblance to the dead leaves of the spring woods.

We shall now describe a few more experiments the bearing of which will become apparent when we discuss the results of the researches.

In 1875, '77, '80, Edwards performed some interesting temperature experiments upon *Papilio ajax*. There are four generations of *Papilio ajax* in West Virginia, three being summer generations, and one which winters over in the chrysalis state, and may produce two distinct forms of butterflies, walshii and telemonides. The summer generations are all alike and belong to the form marcellus. The eggs laid by the spring forms usually change into pupae from which the summer form, marcellus, emerges; some of these pupae, however, winter over and produce walshii or telemonides the following spring.

Edwards subjected the pupae reared from eggs laid by captive females of walshii or telemonides, to the cold of an ice house for periods varying from 11 days to 2 months. These pupae would normally have produced only marcellus, but owing to the influence of the cold, the majority of them gave rise to butterflies colored like telemonides. A few, however, defied the cold and remained marcellus, and still fewer were converted into the coloration of walshii. Edwards also tried the reverse experiment, that is he subjected the overwintering chrysalids to the heat of a greenhouse, but they gave rise to telemonides and walshii just as they normally would had they been exposed to the winter's cold.

But by far the most remarkable experiments upon the effects of temperature which have been performed thus far, are those of Fischer ('95) upon *Vanessa antiope*. When the pupae of this form are placed upon ice at 0-1° C. the butterfly is greatly modified. The ground color is a darker velvet brown than in the normal antiope, and the blue spots are greatly enlarged, and changed into an intense violet-blue. Fischer describes this form in the "Gubener entomologischer Zeitschrift as *V. antiope* artemis. A temperature of 35° C., however, produces a form which is exactly the opposite of that produced by cold. Fischer describes it in the "Gubener entomologischer Zeitschrift, July 1894" as *V. antiope*, aberratio sphione. The ground color is lighter than the normal, and the blue spots much reduced in size. But the most astonishing result obtained by Fischer came from experiments with abnormally high temperatures. He subjected fresh
pupae for about three hours, and then daily for 2–3 hours to a temperature of 40°–42° C, keeping them during the remainder of the time at 35°–38° C. The results were very striking and similar to those obtained from pupae kept on ice at from 0°–1° C; indeed among these specimens he obtained a typical aberratio artemis. The blue spots were much enlarged and the ground color much darkened.

NOTES ON NEW ENGLAND ACRIDIDAE.—III. OEDIPODINAE.—III.

BY ALBERT P. MORSE, WELLESLEY, MASS.

11. Arphia Stal.

Arphia Stal 1873. Recensio orthopterorum, i, 113.


Figs. 16, 16a.


Tomonotus xanthopterus. Thomas, 105.

Arphia xanthoptera. Saussure, 67; Fermaid, 39; Morse, 105; Beutenmüller, 297.

This species is perhaps the Locusta sulphurea of which Harris speaks as occurring in September.

Antenna: ♂, 10–11; ♀, 9–11.5. H. fem.: ♂, 14.5–17.3; ♀, 17–18.5.

Teg.: ♂, 22.5–27; ♀, 26.5–30.

Body: ♂, 21–25; ♀, 28–32. Total length: ♂, 30–34; ♀, 34.5–40 mm.

While most likely to be confused with its congener if any, this locust should be readily distinguished even by the tyro by the characters indicated in the Key, which are not merely specific in value but pertain to different series in the genus. While the two species overlap slightly in season sulphurea has mostly disappeared at the time xanthoptera begins to be common.

This species varies much in color, some specimens being almost black, others bright reddish or yellowish brown. The wings of younger examples are noticeably paler in color but the general tint of a large series is quite uniform. Sometimes the veins, and rarely the venules of the whole disk, are somewhat suffused with brownish. In about one-fifth of the specimens examined the subfrontal shoot extends one-half of the distance to the base of the wing. I have yet to see an orange winged example from New England, but in a series collected for me at Clay City, Ill., by S. W. Denton, about one-half of the specimens have the disk of the wing of a deep reddish orange. It is possible that this is a distinct race or even species but the structural differences are extremely slight.

Xanthoptera is equally common with its congener of the spring-time and is found in the same situations, viz., amid