XIII.

ANTIGENY, OR SEXUAL DIMORPHISM IN BUTTERFLIES.

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In his work on Selection in relation to sex, Darwin discusses the difference of coloring which frequently distinguishes the sexes of butterflies, and concludes that "the male, as a general rule, is the most beautiful, and departs most from the usual type of coloring of the group to which the species belongs." (op. cit. i. 390.) Of the first proposition there can be no doubt; but, in the second, two distinct elements appear to be confounded: the separation of these is the object of the present communication.

Sexual dimorphism, or antigeny,* as exhibited in butterflies, is of two kinds, — colorational and structural. Colorational antigeny again may be divided into two classes: the first including those cases in which it is partial; the second, those in which it is complete.

As one example of partial antigeny, we may take *Cyaniris pseudargiolus* (Boisd.-LeC.). In the south, a portion of the females of the spring brood have the upper surface of the wings uniformly brown; another portion have the greater part blue, like the male; in the north, all the females are blue. In *Jasoniades Turnus* (Linn.), the males, and in the north all the females, are yellow above, heavily banded with black; in the south, a large proportion of the females have lost the yellow ground, and become wholly black; while others retain the universal ground-tint of the male. The dark female of *Atrytone Zabulon* (Boisd.-LeC.) was for a long while considered a species distinct from the normal female, in which the tawny colors of the male are shared by its mate.

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* This term, signifying opposition or diversity of the sexes, is proposed to avoid circumlocution; for there are so many forms of sexual dimorphism requiring specific names, that a compound term for the general phenomenon becomes inconvenient.

These are all cases of melanism, and may be taken as examples of a class; in the first two, perhaps in all, it is only toward the southern part of the insect's range that the melanism appears, and is in accordance with the general rule that melanic antigeny is more common at the south, while its opposite, albinism, is more frequent toward the north.

Albinism, for instance, is a common feature in the northern genus *Eurymus*. In our common *E. Philodice* (God.) and *E. Eurytheme* (Boisd.), many females may be found in which the bright yellow or orange of the upper surface is replaced by a sordid greenish-white; and if we go farther north, or to higher altitudes, we shall find other species, in which the albinism has become complete, affecting all the females.

It is a curious circumstance that, while albinic antigeny finds its most complete expression in high temperate regions, and melanic antigeny prevails toward the tropics, the albinic females of a partially antigenic species never appear in the spring brood, but increase in numbers throughout the hot season; while, at least in the case of the blue butterfly mentioned, the melanic females emerge in early spring, are confined to this brood, and are replaced in warmer weather by the gynandromorphic females; thus, spring apparition appears to be correlated with southern distribution, and summer apparition with northern distribution: these two phenomena appear, in either case, to be directly antagonistic.

Although both albinism and melanism may become complete, partial antigeny, wherever it exists, is confined to the phenomena of melanism and albinism, and does not extend to the more varied forms of complete colorational antigeny, to which reference will now be made.

In the male of *Xanthidia Nicippe* (Cram.), the black bordering band of the wings is sharply defined, and extends across the entire outer margin; in the female, the band is blurred, and stops abruptly before it reaches the lower angle of the front wings, or has half traversed the hind wings. In *Hedone Brettus* (Boisd.-LeC.), the female is very dark-brown, almost black, with two little yellow spots in the middle of the front wings; while the male differs totally, being tawny with indented brown borders and an oblique black dash in the middle of the front wings: at first glance, no one could suppose them identical. In *Semnopsyche Diana* (Cram.), the male is a rich dark-brown with a very broad fulvous margin upon all the wings, marked on the front wings by one or two rows of black spots. The female, on the

other hand, is a rich purple-black, with no trace of fulvous, but with the space where it belongs occupied on the fore wings by three rows of white spots and dashes, and on the hind wings by two belts of blue, broken into spots, one of the belts narrow, the other exceedingly broad. In *Erora læta* (Edw.), the male is wholly brown, with a border of deep blue on a portion of the hind wings; while in the female, the blue has extended so as to cover almost all the hind wings, and even the base of the fore wings. But it is in the Coppers (*Villicantes*) that this phenomenon is most common. Here the females are usually of a fulvous color heavily spotted with black, and particularly noticeable for their conspicuous broad dark border, and a row of spots crossing the wing beyond the middle; while the males are either of some dark-brown shade with a purplish gloss, or of a fiery hue, almost always without any border or spots.

Now in all these cases of colorational antigeny, it is the female, and never the male, which first departs from the normal type of coloring of the group to which the species belongs. Occasionally the feminine peculiarity has been transmitted to the male, and, by this means, a new type of coloration established in the group; but I recall no case where the male alone departs from the general type of coloring peculiar to the group. This is precisely the opposite conclusion to that which Darwin reached. He gives several examples on the authority of Bates, which certainly favor his conclusion, but may, at the same time, be explained from the opposite point of view. He gives other examples from the European blue butterflies, which not only do not support, but even oppose, his general statement.

Take the case of *Semn. Diana*, than which we could hardly find a stronger, since the group (*Dryades*) to which it belongs is remarkably uniform, exhibiting in all its numerous members the same characteristic play of fulvous and black markings. The male of *S. Diana* is indeed very unlike most other fritillaries, but it retains, nevertheless, abundant traces of the same style of ornamentation, and has precisely the same colors, while the female departs widely from the characteristic features of ornamentation, and, in addition, loses every trace of fulvous, so that no one at first glance would recognize it as a member of the group. Take again *Eurymus Philodice* and its allies. In some species, indeed, there are only pale females; but in others all, or most of the females, are yellow or orange, like the males; and any one who knows how yellow and orange tints prevail throughout the group of *Fugacia* will acknowledge that the color of the males is normal. So too with the Blues (*Adolescentes*), which Darwin him-

self quotes: in almost all of them, both males and females are of some shade of blue; in comparatively few, the males are blue and the females brown; in exceedingly few, both sexes are brown; and the very fact that they are familiarly known as "Blues" is a popular recognition of the prevailing color. In the group of Skippers to which *H. Brettus* belongs (*Astyci*), the prevailing colors, at least in the temperate zones, are certainly tawny and black, or brown; the latter, marginal. This is the case with the male of *H. Brettus*, while the female diverges from the type in becoming wholly brown. In *Jasoniades Turnus*, where we sometimes have a black female, it is more difficult to decide what should be considered the normal color, owing to diversity of view upon the relationship of many of the Swallow-tails; but, to judge only from those agreed by all to be most nearly allied to it, there can be no question whatever that the striped character prevails.

It will also be noticed, in this last case and others given, that wherever partial antigeny or dimorphism is confined to one sex, it is always to the female: there seems to be no exception to this rule. In these instances, on my hypothesis, half of the females depart from the type; on Darwin's, half of the females, and all of the males. But if, on Darwin's theory, sometimes one-half, and sometimes three-quarters of a species has diverged from the type, why does it never happen that only one-fourth of the species diverges? This seems to be a very pertinent and damaging inquiry.

The instances given by Darwin, which strongly sustain his view, are drawn from specimens of the South American genus *Epicalia*, found in the rich cabinet of Mr. Bates. The facts, as stated by him, are these: There are twelve species of the genus discussed by him;* of these, nine have gaudy males and plain females; one has plain male and plain female; and two have gaudy males and gaudy females. The plain females, he adds, "resemble each other in their general type of coloration, and likewise resemble both sexes in several allied genera, found in various parts of the world." To examine this case fairly would need a large collection of exotic butterflies. If we confine ourselves to *Epicalia*, we evidently cannot say whether the gaudy or the plain coloring be normal: there would be less variation from the standard on the supposition that the gaudy were the normal type, and in this case it is the female which has departed from the type; but the difference is not enough to form an objection. It is only when we look outside of *Epicalia* that judgment seems to lean toward Darwin's

* Kirby, in his last general catalogue, gives fifteen.

side; but, from the unfortunate want of material, I cannot fairly discuss this point.

Take, however, another case, which appears to be equally complicated, — our native Coppers (*Villicantes*). We have one species in which both sexes are fiery red marked with black; another where both are fulvous marked with black; others where both sexes are brown; and several where the male is brown, marked with fulvous, and the female fulvous, marked with brown; others where the male is wholly brown, and the female fulvous, spotted with brown; and again others with fiery male, and brown female. We have nearly every possible variation, but the prevalent feature is a dark male, often with more or less metallic reflections, which sometimes increase so as to give the insect a fiery copper hue; and a fulvous, spotted, and margined female. I do not see how we can possibly discover, with any certainty, from within the limits of the group of Coppers, what should be considered the normal type. Nor are we much better off in an examination outside the group: there the prevailing tint is either brown or blue; and I am inclined to think that brown, tending strongly to copper, should be considered the normal type; in which case the males are normal, and the species generally antigenic.

But sexual dimorphism is not confined to color or pattern; there is also structural, as well as colorational, antigeny. This term embraces all those minor features which, in these and other animals, have been classed as accessory or secondary sexual peculiarities. Structural antigeny is always complete, and, in direct opposition to the features we have been discussing, is wholly confined to the males.

In butterflies, structural antigeny is mostly confined to the wings and the legs; occasionally it appears in the antennæ. Sometimes it affects the contour of the wings. One of the most conspicuous cases among our own butterflies is in *Strymon Titus* (Fabr.), where the fore wings of the male have a pointed tip, and the hind wings have the inner angle sharply defined; while in the female both the tip of the fore wings and the inner angle of the hind wings are broadly rounded.

Or it may affect the direction of the veins of the wings. Usually the difference between the sexes is slight, and concerns the point of origin of one or two of the upper branches of the subcostal vein of the fore wings; but occasionally it is very marked, as in many hair-streaks, such as *Thecla Edwardsii* Saund., where the branches of the subcostal vein near the end of the cell are thrown far out of place to accommodate a patch of peculiar crowded scales; this patch itself,

moreover, is a feature of the males alone, and occurs in many hair-streaks where the position of the veins is not altered.

One of the most curious patches of this kind is found in the males of some species of *Eurymus*, although wholly absent from others intimately allied to them. It is a little patch of lustreless scales, which occurs at that part of the base of the hind wings which is always covered by the front wings, so that it is quite concealed from sight. Patches of a different nature also mark the male sex; thus, next the middle of the lower median vein of the hind wing of *Danaida Plexippus* (Linn.), and in some of its allies, we have a heavy thickening of the membrane, conspicuous from its covering of black scales.

In very many males of the larger Skippers (*Hesperides*), the front edge of the fore wing is abnormally expanded, and folded compactly upon the upper face of the wing, so snugly that often it can only be discovered with the lens; moreover the scales within this have turned to white silken floss, which, when the fold is raised, contrast conspicuously with the ordinarily dark surface of this part of the wing. In certain Swallow-tails (*Equites*) also, the inner border of the hind wings is folded back in a similar, though looser, manner; but is so much larger that, when opened, it often exposes a white downy surface as large as the abdomen.

Then again there is much variety of male adornment in special modifications of hairs or scales upon the wings. The patch of the hair-streaks already mentioned is one instance of this; another example is found among the *Dryades*, in a row of long, fulvous, partially erect hairs along the upper edge of the cell of the hind wings; this is accompanied by a curious apparent thickening of the veins in the middle of the fore wing, due altogether to the presence of a multitude of small and densely clustered black scales, crowded against the veins at this point. A faint oblique patch of minute and crowded lustreless scales, accompanied by long silky hairs, is often seen crossing the wings of some of the Satyrids; but this feature finds fullest expression in the *Astyci*, or smaller Skippers, where a large proportion of males have a patch or oblique dash of peculiar scales covering veins and membrane indiscriminately, but usually, and in our native butterflies always, occupying the middle of the front wing, and crossing the median veins obliquely near their base. This dash is variously formed, but the scales which compose it are much larger than the ordinary scales, are black, and frequently partially erect. They may also differ in various parts of the patch itself, and alter its character abruptly; for instance, some comparatively huge and brilliant scales may occupy the

middle line, and be buttressed by a multitude of minute, crowded, lustreless scales; or there may be at one point a sort of whirlpool of large party-colored scales, imbricated, in the most regular fashion, like the normal scales, and, beyond them again, a multitude of the minute, crowded, lustreless scales. These peculiarities, however, must be studied with a glass; the naked eye may indeed discern that the patch differs in different insects, but the general effect in all alike is a variously formed velvety patch or oblique streak of black.

It may be remarked, in passing, that wherever antigeny, colorational or structural, manifests itself in the wings of butterflies, the differences between the sexes almost invariably occur upon the upper surface, and generally upon the front wing only; it occasionally happens that there is a slight difference in the general tone of color on the under surface of both sexes, corresponding to what appears above, as in *Semnopsyche Diana;* but it rarely affects the markings of the wings. The differences upon the upper surface, however, and especially upon the fore wings, are, as we have seen, often conspicuous and very curious. One can scarcely doubt that this is in direct relation with the general absence of all ornamentation from the lower surface of both wings, and usually also from the upper surface of the hind wings, of moths.

Sexual dimorphism in the legs shows itself in the proportional length of the different pairs in the two sexes, in the special development of certain joints, in the appendages, and in the clothing. It appears remarkably in the appendages of the two higher families of butterflies, *Nymphales* and *Rurales*, and especially in the latter family, where the terminal appendages of the fore legs are nearly or quite lost in the males, and are as conspicuous as on the other legs in the female. I have not discovered that the differences in the length of the leg-joints follow any general law, although there are few of our butterflies whose sexes do not vary in this particular; this form of antigeny is also most conspicuous in the *Rurales*. The males of certain *Villicantes* (*Chrysophanus*, *Epidemia*, *Heodes*, *Feniseca*) also present another curious feature in a tumid swelling of the basal joint of the middle and hind tarsi. Finally, the fore legs of the males of *Nymphales* are frequently furnished with a spreading brush of hairs; or, in other butterflies, the thighs and shanks of the middle and hind legs are supplied with curious pencils or fringes of stiff hair, which appear to have the same significance as similar adornments in higher animals.

Darwin supposes that these various male appurtenances, which occur throughout the animal kingdom, have all arisen by natural selection, — that one of rival males being selected as a mate whose outward

charms are greatest. He certainly brings powerful argument and a strong array of facts to support this hypothesis; but what then shall be said of the following illustration of structural antigeny; viz., the presence in many males, but in no females whatever, of scales of the most exquisite beauty and delicacy, scattered among the more common sort, and invisible to the naked eye? Even with the help of the microscope, they can often only be discovered by ruffling the wing, and forcibly extracting them from their concealment; and, so far as we can see, they give to the wing no peculiar character by which it may be distinguished from other wings.

These peculiar scales, or androconia, as they may be called in reference to their masculine nature, were first noticed by Bernard Deschamps more than forty years ago,* but have never been properly studied throughout the butterflies. Deschamps called them plumules, from their feathery tips; but the term is utterly inappropriate to most of them; and their form is so varied that only some word expressing their masculine character should be accepted, since this is their single common peculiarity.

These androconia are very capricious in their occurrence; a number of allied genera may possess them, while a single genus, as closely allied, may be quite destitute. This is true throughout the butterflies, and yet there are large groups in which they are altogether wanting, and others in which their absence is extremely rare. In the highest butterflies, they are long, slender, and invariably feathered at the tip. In one small group (the *Heliconii*), they are toothed as well as feathered. With the exception of the *Heliconii*, they may generally be distinguished from ordinary scales by the absence of any dentation at the tip. In the *Voracia*, they are fringed, and, with a single known exception, their extreme base is expanded into a sort of bulb; elsewhere, even in the other Pierids, they are not fringed, but have a smooth rounded edge. In the *Adolescentes* they assume a battledore or fan shape, with a smooth edge, and are generally beaded, and more heavily striate than the scales. The same is true, but with more variations, in the *Villicantes* and *Ephori*, where they have been considered wanting. In the *Equites*, where also they have been supposed to be wanting, they differ but little from the scales, but are much smaller and more coarsely striate. In the *Urbicolæ*, where no one has hitherto recognized them, they present the greatest variety in the same individ-

* Récherches microscopiques sur l'organisation des ailes des Lépidoptères, Ann. Sc. Nat. [2] III. 111–37 (1835).

ual; in one group (*Hesperides*) there are hair-like androconia, and others which are exceedingly large and spindle-shaped. In the *Astyci*, besides hair-like and gigantic androconia, there are usually some which are spoon-shaped, with long handles.

As a general rule, these androconia are present in the patches to which we have alluded as forming one phase of the antigenic characters of the male; but often, as in the *Adolescentes* and *Voracia*, they are scattered indiscriminately or in rows over the upper surface of the wings; and there are many patches, like those at the base of the hind wings of some *Fugacia*, and next the median vein of the same wing in *Dan. Plexippus*, where androconia are not found. They do, however, sometimes occur in patches on the hind wings, as in the fold next the inner margin of the *Equites;* but, with the exception of the discal spot of the *Ephori*, they seem to be present in all patches found on the front wings; occasionally forming the principal part of such patches, as in the *Callidryades*, and again taking no part in the display. Take, for example, the *Dryades*, where so many small black scales are crowded against certain veins as to give them a thickened appearance; the androconia are also present in great numbers, but entirely concealed; only by removing the scales can even the tassels of their long and slender blades be seen. Perhaps even more curious than this is the arrangement by which all the androconia of the *Equites* and *Hesperides* are tightly enclosed in a fold of the membrane; it is not impossible that this fold can be opened at will by the insect, and it would then become conspicuous, and probably an attraction to the butterfly's mate; but what possible advantage can there be in partially or wholly concealed androconia, scattered separately over the wing? In some *Adolescentes*, they are exceedingly scarce, numbering not more than one to a hundred scales, and the exposed surface of this one not one-tenth that of the scales about it. One might search an hour with a microscope over an unruffled wing and overlook it; indeed, it is as the merest speck of dust in a dust heap. Does the sight of these creatures surpass our power of vision with the microscope? The theory of sexual selection proposed by Darwin appears to fail here, just where it should aid us most.