CHAPTER XII.

LINEAR SERIES—*continued.* COLOUR-MARKINGS.

OCELLAR MARKINGS[1], ESPECIALLY THOSE OF LEPIDOPTERA.

UPON the bodies of animals belonging to many classes are markings which consist of a central patch of colour surrounded by a variable number of concentric rings of different colours. Such markings are known as ocelli or eye-spots from their resemblance to the pupil and iris of vertebrates. Eye-spots are perhaps best known in Lepidoptera, but similar markings are not unfrequent in other groups and especially on the feathers of Birds and in Fishes.

In one of the best known chapters in the *Descent of Man*[2] the nature and mode of evolution of these markings is the subject of a full discussion, the case of eye-spots on feathers being chiefly taken in illustration. As is well known, Darwin by the comparative method, comparing the eye-spots found in different species, on the different feathers of the same bird, or on different parts of the same feather, found that it was possible to construct a complete progression from a plain spot to a fully-formed ocellus. Though no one examining such a series can possibly doubt that the simple spot and the fully-formed ocellus are really of the same nature and that the one represents a modification of the other, there remains nevertheless the difficulty that members of a series of parts cannot be assumed to represent conditions through which the other members of the same series have passed, and it is of course clear that the conditions found in some forms do not necessarily correspond with phylogenetic phases of other forms. In the present instance however Darwin is not specially urging this view, but brings forward the comparative evidence chiefly in illustration of the possibility that such structures may exist in an imperfect state and so may be conceived of as having had a gradual origin.

[1] The evidence concerning eyespots of Lepidoptera is taken here because eyespots when repeated in series, though borne on appendicular parts, are nevertheless arranged chiefly with reference to the chief axis of symmetry of the body. In some few forms, *e.g. Taygetis*, there is a conspicuous Minor Symmetry within the limits of a single wing (the posterior), but this is not often the case.

[2] *Descent of Man*, 1871, II. pp. 132—153.

Though doubtless the eye-spots of Birds are in their nature not different from those of Lepidoptera yet their manifestations in the latter are usually in some respects simpler than they are in Birds. From the abundance of material also the Variation of eye-spots is most easily studied in Lepidoptera and it is to them that the present evidence chiefly relates.

In preface to the evidence a few remarks are needed to direct attention to certain features in the mode of normal occurrence of eye-spots and in the manner of their Variation.

On a survey of the facts it is at once seen that eye-spots are extraordinarily variable both in number and size, some of the best formed being occasionally absent, and large and perfect ocelli being sometimes added in situations having normally no trace of such marks. With this fact Darwin was well acquainted and he refers to observations in illustration of it. In speaking of *Cyllo leda* he concludes that from the great variability of the eye-spots "in cases like these, the development of a perfect ocellus does not require a long course of variation and selection;" and again, that bearing in mind "the extraordinary variability of the ocelli in many Lepidoptera, the formation of these beautiful ornaments can hardly be a highly complex process, and probably depends on some slight and graduated change in the nature of the tissues." The facts to be given and the circumstances attendant on the variation of ocelli tend to support this conclusion.

Considered from the point of view of Meristic Variation the chief feature in the manner of occurrence of eye-spots in Lepidoptera is the frequency with which they are repeated. A single spot may be repeated in homologous places in both pairs of wings; in other cases there is a series along the margins of one or both wings. Besides the repetitions thus occurring it is especially worthy of notice that ocelli are very commonly repeated on *both* surfaces of the wing (Satyridæ, &c.), the centres of the upper and lower ocelli coinciding. It need scarcely be remarked that this effect is not produced by transparency of the wing-membranes and scales, but is an actual repetition, the scales of both surfaces being so coloured as to form an eye-spot on each side, the two having their centres coincident. In some cases, *e.g. Saturnia carpini* (the Emperor Moth), the rings and centres of the upper and lower ocelli have nearly the same colouring, but in the majority *e.g. Pararge megæra* (The Wall), *Erebia blandina*, &c., the upper and lower spots, though coincident, have quite different colours. In considering the Variation of the spots these facts as to the repetition of the spots should be remembered, for, as has been often insisted on in other cases of repetitions, we are concerned with the evolution of the *series* and not of one member only. Here therefore regard must be had to the degree of correspondence between the variations of the eye-spots in the fore and hind wings, on the upper and lower surfaces of the same wing, in the several eye-spots along the margin of the same wing, or in all of these, as the case may be. The evidence will shew that there is sometimes a close correspondence between the variations of eye-spots in these several positions.

But though these are the matters with which we have now the more direct concern it will be convenient to speak at the same time more generally of eye-spots. It should be remembered first that there are eye-spots of various complexity. In the simplest all the bands are circular, having one centre; the ocellus is then as a rule complete in one cell of the wing, though sometimes the outer zones of colour overspread parts of the adjacent cells. In some cases the spot is double, having two centres, the bands being disposed round them in an hour-glass shape. As to the visible structure of eye-spots it can be seen with the microscope that the colour of the eye-spot lies in the colours of the scales. The scales are arranged in parallel rows running (with little crossing or anastomosing) as nearly as possible at right angles to the nearest nervures, being disposed in regard to them much as the circular threads of a cobweb are in regard to the radial threads. Across these rows of scales run the colour-zones, in no way limited or guided by them. On the other hand it can be seen that the patterns are almost wholly made up by the colours of single scales, each having its own colour, particoloured scales being exceptional. The effect thus seen is very like that of a mosaic picture made of similar pieces, or of a design worked in cross-stitch on canvas, all the stitches being in rows and each stitch having its own colour.

As regards the position of eye-spots it should be noticed that the simpler sort, *e.g.* those of *Morpho* or of Satyridæ, *are usually placed in such a position that each of their centres is on the line of one of the creases or fold-marks of the wing*, and it sometimes happens that these creases seem to begin from the centre of an ocellus. From the fact that the creases for the most part run evenly between two nervures, bisecting a cell, it commonly results that the centre of the eye-spot is exactly halfway between two nervures. The large spots on the hind wings of some Pieridæ, *e.g.* *Parnassius apollo*, are an exception to this rule.

In that cell of the hind wing which lies between the submedian and first median nervures in many ocellated forms (Satyridæ, *Morpho*, &c.) there are *two* creases, and it is especially interesting to notice that in this cell there are commonly two ocelli, one on each crease; but if there is only one ocellus its centre does *not* correspond with the middle of the cell but is nearer to the first median nervure, being placed exactly on the anterior of the two creases. In spite of the excessive variability of ocelli, in for instance Satyridæ, it appears that they are not formed in situations other than these, being so far as I have seen always on one of the creases [1].

[1] These remarks refer to simple ocelli with one or more definite centres.

On looking at such a series of repeated ocelli as those on the hind wing of *Pararge megæra*, from this fact that the ocelli are on these creases or folds the question naturally arises whether the wing may not have been, in its development, folded along these creases so as to bring the ocelli into contact with each other like the fold-edges of a fan. If this were the case it might be supposed that the repetition of the ocelli was due to the action of some one cause on all the folded edges together. As a matter of fact, however, so far at least as can be judged from the condition of the wings in the pupal state before scales or pigments are excreted, there is no such folding, but each wing is laid smoothly out, and the increase in extent of the wings of the imago is attained, not by a process of unfolding, but by a stretching of the elastic wing-membranes on inflation from the tracheæ. On the whole it does not seem likely that the repetition of similar eye-spots on the Lepidopteran wing arises in any way more immediately mechanical than that by which other repeated patterns are elsewhere formed on animals.

The Variation of eye-spots as already stated may be very great, and examples are to be given both of the total absence of large eye-spots present in the normal, and of the presence of perfect eye-spots in abnormal places. Besides these extreme cases there is immense Variation in the degree to which eye-spots are developed, and such variability is nearly always to be seen in any species possessing simple ringed ocelli. In the manner of Variation of ocelli the following things are noteworthy.

(1) The *whole* of an eye-spot, centre and various concentric bands together, may be wanting; conversely a *whole* new eye-spot having the centre and all the bands pertaining to the normal eye-spot of the species may suddenly appear upon a crease normally bearing no eye-spot. Eye-spots therefore *may* come or disappear in their entirety.

(2) If a number of specimens of some much ocellated species are taken and compared, examples will be found in which some of the normal ocelli are absent altogether. But besides these there may generally be found specimens having an ocellus in a reduced and imperfect condition. Speaking generally such reduction commonly occurs by diminution of the diameter of the whole spot; but if any of its component parts are wanting the *centre* is the first to disappear, then the next innermost band, and so on. In Fig. 76 is shewn a series of specimens illustrating this fact in the case of *Hipparchia tithonus.* The eye-spot in its least form is represented by a plain black patch. In the more complete condition a white centre appears. A similar case in *Morpho* is shewn in Fig. 81. Here on the right side a certain eye-spot is absent altogether, while on the left side it is present in a reduced state; the white centre and the innermost broad black band are absent, and the actual centre is of the yellow-red colour which in the normal eye-spot of the species is the third colour from the centre. The spots

on the upper surface of the hind wings of the Wall (*P. megæra*) are an excellent illustration of these principles of Variation.

The principle here stated, though generally followed, is not absolutely universal, and in other instances it occasionally happens that even when of very minute size an eye-spot still retains all its bands; but the statement that the order of disappearance is from the centre outwards and not the reverse is substantially true. Some have expressed a belief that ocelli arise by the breaking up of bands of colour, but this view finds no support in the facts of Variation so far as the simple ocelli of such forms as *Morpho* and the Satyridæ are concerned; for in its rudimentary condition a circular eye-spot is in them a circular eye-spot still.

The fact just stated, that in the reduction of a circular ocellus its central parts are the first to disappear, recalls phenomena seen in many cases of disturbance propagated from a centre through a homogeneous medium. A whole eye-spot may come, or it may go (as seen in cases of *Morpho*), leaving the field of the cell plain and without a speck. The suggestion is strong that the whole series of rings may have been formed by some one central disturbance, somewhat as a series of concentric waves may be formed by the splash of a stone thrown into a pool. It is especially interesting to remember that the formation even of a number of concentric rings of different colours from an animal pigment by the even diffusion of one reagent from a centre occurs actually in Gmelin's test for bile-pigments. Bile is spread on a white plate and a drop of nitric acid yellow with nitrous acid is dropped on it. As the acid diffuses itself distinct rings of yellow, red, violet, blue and green are formed concentrically round it by the progressive oxidation of the bile-pigment.

If the experiment is made by letting a drop of the acid fall on a piece of blotting-paper wetted with bile, a fairly permanent imitation of an ocellar mark can be made. It will be noticed that as in the natural eye-spot, so here, the outermost zone appears first and the central colour last. As also is usually the case in the ocellus, when all the zones are formed, the centre may greatly increase in diameter without any increase in the breadths of the circular zones, which merely get larger in diameter, remaining of the same breadth.

There is of course no reason whatever for supposing that ocelli are actually formed by the oxidation or other simple chemical change of the pigments of the field, but this example is merely given as an illustration of the possibility that a series of discontinuous chemical effects may be produced in concentric zones by a single central disturbance. Indeed, that the formation of an ocellus cannot be in reality of such simplicity is shewn by the fact that the scales of the centres of ocelli generally exhibit interference-colours (usually white or blue) and are then wholly or partially without pigment, while in not a few cases the centres of ocelli are deficient in, or destitute of, scales. It must also be remembered that occasionally the colour of one of the outer zones is repeated in an inner zone, which would scarcely be expected on the analogy of the oxidation of bile-pigments.

(3) As in the case of Teeth at the ends of series, disappearance of a member of a close series of eye-spots commonly occurs by the

loss of the spot standing at one of the *ends* of the series. This is easily seen in *P. megæra*, &c. Likewise as was found in Teeth, disappearance of such a terminal eye-spot is associated with reduction in the size of the other members of the series, and especially of those nearest to the place of the absent member. If as in *Satyrus hyperanthus* and many others, the series is broken into groups, then as in the case of heterodont dentitions containing gaps, a new member may be added on to the end of either group.

(4) The condition of the ocelli may vary similarly and simultaneously in both anterior and posterior wings. In a series of *Saturnia carpini* for example I notice that the size of the ocelli varies greatly, those of a particular female specimen in the Cambridge University Museum being nearly a quarter larger than those of the specimen having the smallest ocelli; but the size of the ocelli in the hind wings of each individual varies with that of the ocelli in the fore wings not less closely than the size of the right ocelli does with that of the left.

(5) This correlation between the wings of the two pairs is seen also in the presence or absence of ocelli as exhibited for instance in *H. tithonus* (Fig. 76). It is of course often very irregular, but for our purpose it is even of consequence that such correlation may occur sometimes.

(6) As mentioned, ocelli are often coincident on the upper and lower surfaces. When this is so, the degree of development of the spots on the one surface is generally an accurate measure of the degree to which they are developed on the other surface. But in species having spots developed thus coincidently on the two surfaces it can be found that, in varying, an ocellus always first appears in its least condition *either* on one surface *or* on the other, and not indefinitely sometimes on one and sometimes on the other. In *P. megæra*, for example, ocelli of both pairs of wings can be seen on the under surface when not formed on the upper and conversely. Nevertheless there is always a close correlation between the degrees of development on the two surfaces.

(7) Lastly, attention is called to the circumstance that in two cases of great variation in ocellar markings there was a variation in the neuration. In the first case, *P. megæra*, No. 458, the second median nervure was absent from both fore and hind wings. In the fore wing upon the line where it should be there was an eye-spot: in the hind wing the eye-spots of the two cells which should be separated by the second median were partially coalescent. In the other case, *S. carpini*, No. 459, the large ocellus was *absent* from each wing, and it is stated that a nervure was also absent, but of this case no proper description has appeared, and it is uncertain which nervure was absent. When however these facts are considered in connexion with the circumstance that ocelli stand on the creases of the wings it seems likely that in some way unknown the positions and perhaps even the existence of the eye-spots may

be determined by the manner of stretching of the wing-membranes. It must still be remembered that in the great majority of cases of ocellar variation there is no change in the neuration.

As to the *function* of ocellar markings nothing is known, and I am not aware that any suggestion has been made which calls for serious notice.

EVIDENCE AS TO VARIATION OF OCELLI IN LEPIDOPTERA.

General variability of ocelli.

The following are chosen to illustrate the general variability of ocelli in Satyridæ. Any of the common forms, such as *C. davus*, *P. megæra*, &c. shew similar variations. Generally speaking the condition is bilaterally symmetrical, but somewhat asymmetrical examples are not rare.

*443. **Hipparchia tithonus:** from some 80 specimens taken in one

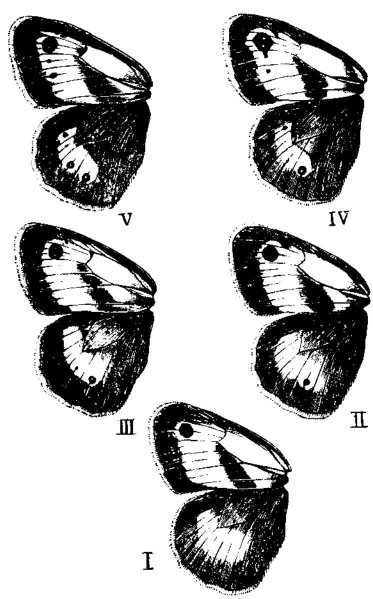

FIG. 76. *Hipparchia tithonus* ♂, cases illustrating Variation in number of ocelli. I. In f. w. the upper half of the large ocellus has a pupil, the lower has none: in h. w. no ocellus. II. Both halves of large ocellus of f. w. have pupils, and the h. w. has one ocellus. III. Pupils of large ocellus of f. w. are larger: h. w. has two ocelli. IV. F. w. has a new ocellus and the large double ocellus is half-joined to a second new ocellus. H. w. has two ocelli, one being placed otherwise than in III. V. F. w. has two ocelli without pupils as well as the large double one. H. w. has three ocelli. The wings of the other side corresponded nearly though not accurately. II. is the most frequent form.

(This figure was drawn with especial care from the specimens by Mr Edwin Wilson.)

ditch in the Cambridgeshire Fens on the same day the individuals shewn in Fig. 76 were selected. These cases especially illustrate the statements numbered (2) and (5), viz. the order of appearance of the colours and the similar Variation of the two pairs of wings.

*444. **Satyrus hyperanthus:** four specimens (Fig. 77) shewing

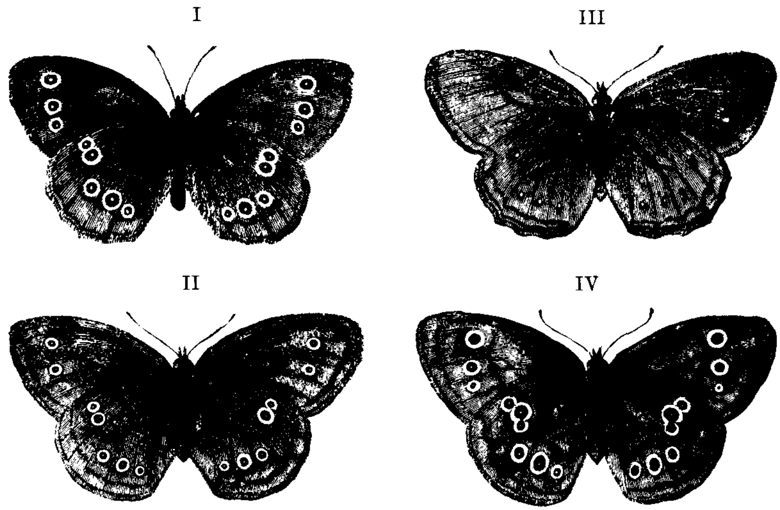

FIG. 77. *Satyrus hyperanthus.* Various conditions of ocelli. II. is the most frequent form.

(From NEWMAN'S *British Butterflies.*)

different conditions of ocelli in this species from NEWMAN'S *British Butterflies.* A form without ocelli is mentioned by PORRITT, *Ent.*, XVI., 1883, p. 188.

On one day I have myself taken all the forms shewn in Fig. 77 (except III.) and others in Monk's Wood, so that here no question of seasonal or local difference is necessarily involved.

445. **Chionobas.** The North-American species of this genus [in general appearance somewhat resembling the British *Hipparchia semele*, the Grayling] are of a brown colour having eye-spots on some or all of the wings. According to STRECKER the number of eye-spots varies extremely, and the following instances are given. The species *norma* may have two spots on fore wings and none on hind wings; two on f. w. and one on h. w.; one on f. w. and one on h. w.; one on f. w. and none on h. w.; three on f. w. and two on h. w. Of the species *uhleri* one of the types has three on f. w. and four on h. w., the other has four on f. w. and five on h. w., the subapical being very small; other examples have only one on f. w. and two or three on h. w. The species *chryxus* may have one on f. w. and none on h. w.; or two on f. w. and one on h. w. STRECKER, *Cat. Macrolepid.*, p. 155.

446. **Arge pherusa**: a butterfly resembling the British *Arge galathea*, the Marbled White, has a variety *plesaura*, in which the eye-spots of hind wing are wanting.

Specimen figured in which the left hind wing is a third smaller than the right and lacks the eye-spots. FAILLA-TEDALDI, *Nat. Sicil.*, I. p. 208, Pl. XI. fig. 8.

* MORPHO.

A number of species of this genus, for example, *M. achilles, menelaus, octavia, montezuma,* &c. are marked upon the under surface of both pairs of wings with large ocelli having four principal zones in addition to the white central spot. Of the zones the outermost is silvery, the next dark brown, the next either red or some shade of yellow. Within this is a band of very variable width having a deep chocolate colour. When very broad, as in *M. montezuma* or *M. achilles,* the inner parts of this band are irregularly sprinkled with red scales. The centre is white or bluish-white, some of the scales in its periphery being nearly always distinctly blue. The centre is commonly not circular but is produced (especially in larger ocelli) in a direction at right angles to the crease on which it stands. Fig. 78, I, taken from a normal specimen of *M. achilles,* shews the usual positions of the eye-spots in all the species whose variations are described below. The ocelli on the fore wing are 3, on the hind wing 4. In speaking of them the letters *a, b, c, d, e, f, g* are used as shewn in the figure. Between *a* and *b* there is a cell normally bearing no ocellus, and between *d* and *e* there are two such cells. The spot *g* as described on p. 90, stands at the anterior side of its cell and not in the middle of it, and a second spot g_1 may appear behind it in the same cell.

The following examples are taken from the series in the collec-

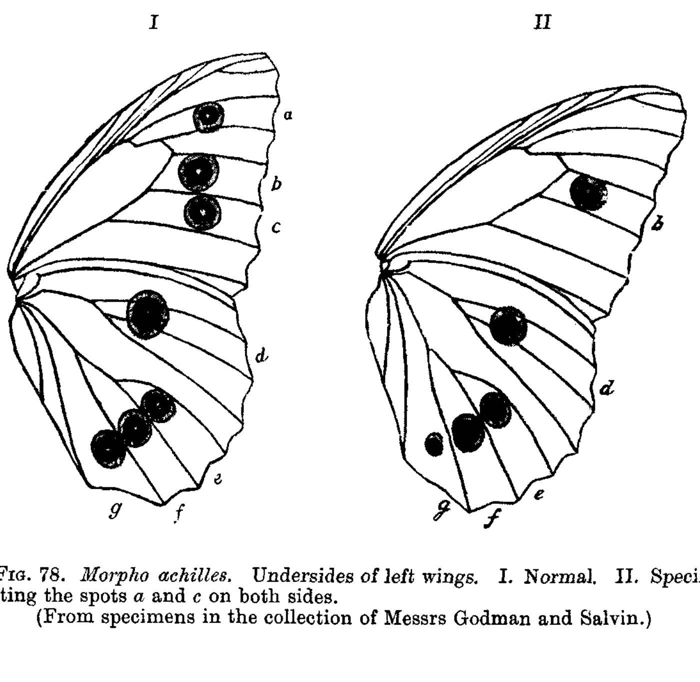

FIG. 78. *Morpho achilles.* Undersides of left wings. I. Normal. II. Specimen wanting the spots *a* and *c* on both sides.
(From specimens in the collection of Messrs Godman and Salvin.)

tion of Mr F. D. Godman and Mr O. Salvin, to whom I am much indebted for permission to examine the specimens[1].

447. **Morpho achilles** ♂. Specimen having the spots *a* and *c* entirely absent (Fig. 78, II) and the spot *g* very small. This specimen occurred together with two normals from Pará. Ten other normal males seen, and also a specimen in Camb. Univ. Mus. having no *c*, the spot *a* being also greatly reduced.

448. **M. montezuma** ♂: 15 specimens *have all the spots from a to g* of fair size. One specimen has a spot in the place a_1, as shewn

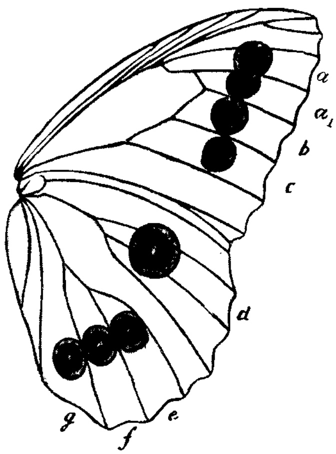

FIG. 79. *Morpho montezuma*. Abnormal specimen having an ocellus on both sides in the position a_1 (where an ocellus normally exists in *M. sulkowskii*). (From a specimen in the collection of Messrs Godman and Salvin.)

in Fig. 79. One specimen has a very *faint* a^1 and g_1; *another has* a^1 as a small ocellus, and g_1 indicated as a bulging of the spot *g*.

In Camb. Univ. Mus. are 4 normal males and one specimen having both a^1 and g_1 marked somewhat as shewn in the case of the abnormal *M. octavia* (Fig. 80).

449. **M. octavia.** Mr Salvin tells me that this form has a very restricted distribution and is probably only a local form of *M. montezuma*. In addition to 12 normal males the following were seen, all being male. *Specimen having* g_1 *as a spot of moderate* size; another having g_1 very small. In another a^1 and g_1 were both present as shewn in Fig. 80. Besides these is one having *g* very small. All are from the Pacific slope of Guatemala. The specimen figured is from El Reposo in this district, one of the normals being from the same place.

[1] In each of the figures the faint lines round the ocelli should be shewn as in Fig. 81; they are omitted for simplicity.

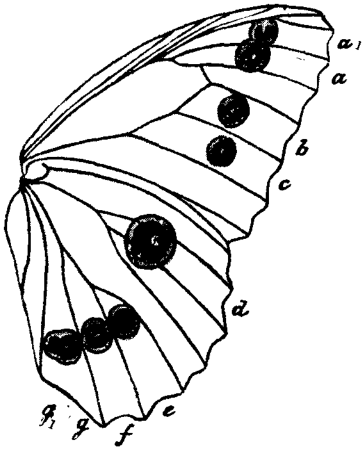

FIG. 80. *Morpho octavia*: abnormal specimen having ocelli on both sides in the positions a^1 and g_1 (where ocelli normally are in *M. sulkowskii*).
(From a specimen in the collection of Messrs Godman and Salvin.)

*450. **M. menelaus** ♂: ten normals, and two having no *a*; one having left *a* absent and right *a* very faint, *c* and *g* both absent. In addition to these, the specimen shewn in Fig. 81, having no *c*

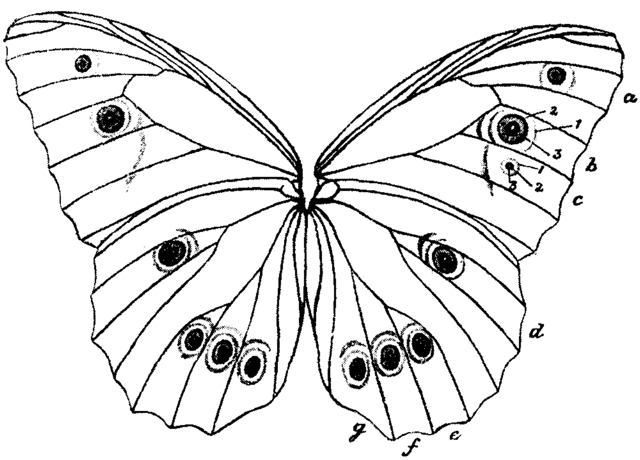

FIG. 81. *Morpho menelaus*: abnormal specimen having no ocellus *c* in rt. f. w. In left f. w. there is a small ocellus *c*, *but it wants the two innermost colours of a normal ocellus.* Compared with a normal ocellus, as that at *b* of the same wing, the abnormal has only the zones 1, 2 and 3, the latter colour forming the centre.

Fig. 78, I. may be taken as approximately shewing the normal for this species also.

(From a specimen in the collection of Messrs Godman and Salvin.)

on right side, while on the left the same spot is reduced as shewn in the figure, the centre being of the colour normally constituting the third band.

In connexion with the above cases it should be mentioned that in another species, *Morpho sulkowskii*, one of the more transparent species, the spots a^1, a_1, and g_1 are all *normally* present. The spot c is however sometimes absent in this species. In *M. psyche* the spot c is normally absent, though present in one specimen examined.

Complex ocelli.

Besides the simpler ocelli there are other forms of ocelli of more complex structure, having two or more centres around which the coloured zones are disposed without an accurate symmetry. Such ocelli may be seen in *Vanessa io* or in *Junonia,* and it is noticeable that they are no less variable than the simpler forms. The following examples may be given.

Vanessa io. Looking at the eye-spot on the fore wing of the Peacock-butterfly one can readily see that it is not a structure of the same nature as the other ocelli that have been already considered. The eye-spot of the hind wing does not materially differ from other eye-spots, being essentially a black spot surrounded by a pale band and containing an irregular and incomplete centre of blue. The eye of the fore wing on the contrary is not actually made up of concentric markings but is quite exceptional, being formed of a combination of patches of different colours. But whether the eye of the fore wing is a true ocellus or not it is nevertheless certain that its formation may vary with that of the eye of the hind wing, as the following examples testify.

451. Specimen, British; reared from a larva in captivity, having all the eye-spots deficient (Fig. 82). On the fore wings the series of white spots along the margin (on the creases) are present. The three which lie within the field of the normal eye-spot are *longer* than usual. The costal black mark is extended so as to cover the greater part of the

FIG. 82. *Vanessa io*, the Peacock butterfly, having all the four eye-spots deficient (No. 451). (From Newman.)

situation of the eye-spot. On the hind wings the eye-spots are entirely obliterated and their place is taken by an ill-defined patch of pale colour. NEWMAN, *Ent.*, 1872, p. 105, Fig.

452. Similar specimen described by GOOSSENS, *Bull. Ent. Soc. France*, S. 5, v. p. cxlix.

453. Similar specimen in Lord WALSINGHAM'S collection in Brit. Mus. Here the blue and black of the eye-spots of the hind wing are altogether absent. The black internal border of the spot is broader than usual, and the place of the spot is lightish in colour. In the spot of the fore wing the blue is deficient, the yellow is largely absent, but the white spots are emphasized.

*454. Specimen in which the eye-spots on the hind wings are obliterated, as in the foregoing: those of the fore wings are also similarly modified, but the white spots of the marginal series are enlarged to a much greater extent. Also another specimen in which the eye-spots were partially deficient. These two specimens were from one brood reared in Germany: of this brood none were typical, and several resembled the specimens described. SOUTH, R., *Ent.*, 1889, XXII. p. 218, Pl.

455. Specimen figured in which the eye-spots are symmetrically absent from both posterior wings. In this case both the greyish yellow bordering of the eye-spots and the blue marks generally contained within them are entirely absent. The ground-colour of the hind wings is greyish brown, and upon this two black marks are placed in the situation of the normal eye-spot and a series of small black lines occurs round the margins of the hind wings. The eye-spots of the anterior wings are modified in a peculiar manner which is not easily described. MOSLEY, S. L., *Varieties of Brit. Lepid.*, Pt. III. Pl. 2, Fig. 3.

456. **Junonia clelia**, Cram. In this species there are normally two ocelli in each fore wing and a similar pair in each hind wing (TRIMEN, *S. Afr. Butterflies*, I. p. 214). In a series of nine specimens in the Cambridge University Museum very great variations in the size of the ocelli appear. The *posterior* ocellus of each wing is more constant in size than the *anterior*. One specimen wants altogether the anterior ocellus of the hind wings, which in most specimens has a diameter of about 2·5 mm. In several the anterior ocellus of the fore wings is hardly visible.

457. **Junonia cœnia**: the degree to which the two eye-spots of each wing are developed varies greatly. In a Californian specimen in Godman and Salvin's collection the spots are all very large, while in a Granada specimen they are almost entirely obliterated. Of four specimens in the same collection from the United States of Colombia (but not from the same locality), one has scarcely a trace of the anterior eye-spot of the fore wing, the second eye being very faint. In the hind wing the anterior eye-spot is very faint and the posterior is absent.

The two following cases are important from the fact that in each of them there is said to have been abnormality in neuration.

*458. **Pararge megæra** ♂ (the Wall Butterfly): specimen in which the second nervure of the median vein is wanting *in each of the four wings*. In the anterior wings the place which should be crossed by this nervure is occupied by an extra ocellus (Fig. 83), which is nearly as large as the normal large ocellus of the wing. The normal ocellus itself is incompletely doubled. In the hind wings, the two ocelli (2nd and 3rd), which in the normal insect are separated by the missing nervure, are elongated towards each other, so that their black borders touch and the usual central white dots join into a line, one-twelfth of an inch long. On the under

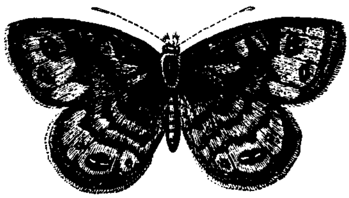

FIG. 83. *Pararge megæra*, the Wall; case described in No. 458. [This copy is rather too light, and the banding on the hind wing is too distinct.] (From WEBB.)

side, the anterior wings have respectively six and five ocelli and the hind wings five and six. The arrangement of the dark colour on the upper surface of the anterior wing differs somewhat in the direction of the pattern of the female. WEBB, S., *Entomologist*, 1889, XXII. p. 289, Fig.

*459. **Saturnia carpini** ♂; variety without eye-spots. (Fig. 84.) This specimen was bred from a larva found with many others

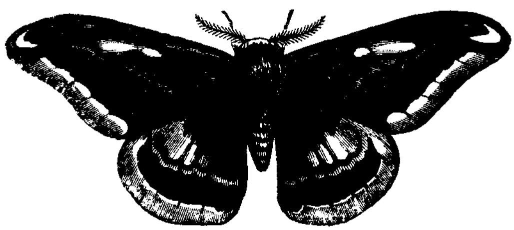

FIG. 84. *Saturnia carpini* lacking the ocellar marks in each wing (No. 459). (From BOND.)

feeding upon sallow in Sawston Fen, Cambridgeshire. "In the colour and markings of the specimen there was perhaps nothing worth notice excepting the absence of the ocellus in each wing and also of one of the veins in each of the anterior wings."

About 50 larvæ were collected at the same time on one large sallow. One of them, a female, was destitute of scales[1], but the remainder of the specimens reared were remarkably fine. BOND, F., *Entomologist*, X., 1877, p. 1, *fig.* [This is the specimen mentioned by HUMPHREYS, *Brit. Moths*, p. 20. It is unfortunate that no further description is given, and the figure is not sufficiently clear to enable one to see which nervure was absent. On the fore wings a narrow, elongated patch of light colour was in the place of each ocellus, and on the hind wings there was a somewhat wider

[1] Partial deficiency of scales, occurring evenly over all the four wings, is not very rare in *S. carpini*. I have myself reared two such specimens.

and irregularly shaped patch of pale colour. If this specimen, which was in the collection of the late Mr F. Bond, is still in existence it is greatly to be wished that a proper description of it should be published.]

460. **Saturnia carpini** ♂: wings yellowish-grey throughout, with the usual markings, *save that on the fore wings there is no ocellus*, and on the hind wings is only a small black eye, without a border, having a yellowish-grey central spot. OCHSENHEIMER, F., *Schmet. von Europa*, 1816, IV. p. 191.

From this evidence it is clear that the range of Variation of ocellar markings in Lepidoptera is very great. It is especially to be noticed that this variability affects no one family, or the species of one geographical region, or one kind of ocellus exclusively, though doubtless it is more marked in some than in others; but it seems rather to be a property belonging to ocelli in general. From the fact that they can bodily come and go, it seems clear that, as was suggested above, each ocellus is as regards its origin *one* structure made up of parts in correlation with each other.

RAIIDÆ.

The great variability of ocellar markings is probably not peculiar to Lepidoptera, but I have no evidence sufficient to produce regarding the variability of ocellar markings in other forms. I may however instance the case of the Raiidæ, many of which have been found marked with a large ocellar mark on the dorsal surface of each pectoral fin. At different times such a mark has been thought to characterize a certain species, but I believe it is now generally admitted that it may appear as a variation in several species. The best figure of this ocellar mark is that given by DONOVAN (*Brit. Fishes*, 1808, V. Pl. CIII.) in a Ray described under
461. the Linnean name *Raia miraletus*. On each "wing" was a large spot, having a dark purple centre, surrounded by a zone of silvery green enclosed by a broad dark boundary composed of five equidistant, contiguous spots of blackish purple. Donovan suspected that the fish might be a variety of the Homelyn (**R. maculata**), and it has been generally believed by other authors to have been so. Donovan states that a similar eye-spot was seen by him in various degrees of definition in several young Skates.

462. **R. clavata,** the Thornback, also sometimes has a large white spot surrounded with black on the "wings." DAY, *Brit. Fishes*, II. p. 344.

Raia circularis, the Cuckoo Ray, has *normally* on each "wing" a large black blotch banded with yellow and surrounded by yellow spots. This structure may be absent as a variation. DAY, *Brit. Fishes*, II. p. 349.

SIMULTANEITY OF COLOUR-VARIATION IN PARTS REPEATED IN LINEAR SERIES.

Reference was made (Introduction, Section V.) to that relation subsisting between the several members of a linear series of segments or other repeated parts, by virtue of which they may resemble each other in respect of colour or pattern of colours. From the fact that the several members do in such cases often bear the same colours or patterns it is clear that they must at some time or other have undergone similar Variation. In order to measure the possible rapidity of the process of evolution by which such parts may have reached their present condition it is important to ascertain the extent to which their several variations may be simultaneous.

Variations in colour are of course Substantive variations and a full consideration of their nature cannot be taken here. For the present we are only concerned with the consequences of the fact that the parts are repeated in series. As was pointed out in the Introduction the problem of the resemblance between the colours of such segments is only a special case of the same problem of Symmetry which is again presented in bilateral or other Repetition.

Simultaneous colour-variation taking place abruptly in a large number of organs, such as hairs, feathers, &c. is a very common occurrence, and the part that repetition of structures plays in producing the total effect is apt to be overlooked. In comparing two varieties of some whole-coloured animal, a bay horse with a chestnut for example, it must be remembered that the difference is really made up of a simultaneous variation in the pigment of each particular hair. Similarly if a caterpillar normally green appears in a uniformly brown variety we may conceive the total change as brought about by variation occurring simultaneously in the skin of the several segments, or in some smaller units. But whatever unit be taken, whether segment, or hairs, or cells, that all or any particular groups of such units should vary together and in the same direction is not a matter of necessity. That such simultaneity is not universal and that segments may vary independently of each other is a matter of common observation, and indeed is sufficiently proved by the occurrence of differentiation between segments. Nevertheless the evidence goes to shew that between parts repeated in series there may be a relationship of the kind spoken of, though its causes, nature and limitations are unknown. In the case of actual segmentation this relationship may appear either in the simultaneous variation of the colour-patterns of the segments, or of some one colour or patch borne by each, or by the appearance of some unusual mark or patch on several of them at once.

In some cases it happens that certain of the segments may vary together, the rest remaining unchanged, and, as seen in

Chiton marmoreus, (*q.v.*), the segments thus undergoing the same variation are not always even adjacent to each other.

The whole question is a very large one and it is not possible here to do more than refer briefly to a few cases illustrating some of its different aspects. Fuller treatment will be attempted in connexion with the evidence of Substantive Variation.

463. *As examples of a form whose segments in their colour-variations* manifest a very close agreement with each other, the Hirudinea may be taken. Figures of numerous varieties of medicinal Leeches are given by ÉBRARD, *Nouvelle monogr. des Sangsues*, 1857, and other cases are represented by MOQUIN-TANDON, *Monogr. de la famille des Hirudinées*, 1827 (see especially Pl. v. fig. 1). As these figures testify, there is a wide diversity both in the ground-colour and in the size, colour and manner of distribution of the lines and spots with which it is decorated, but so far as may be judged from the figures and descriptions the same decorations are repeated on the various segments. It cannot be doubted that a close scrutiny of the specimens would shew points of difference even between adjacent segments but substantially the patterns are the same for the segments of an individual. The patterns of the varieties may thus, like patterns of ribbon, be each represented by a drawing of a short piece of the body in the way adopted by the writers named.

As regards the larvæ of Lepidoptera a good deal of information bearing on this subject exists, and some of these results, especially those relating to Sphingidæ, are of interest[1].

*464. In the larvæ of many species of Sphingidæ there is a more or less regular dimorphism in colour. Notable examples of this are *Acherontia atropos*, *Chærocampa elpenor*, *C. porcellus* and *Macroglossa stellatarum*, in each of which the larva is known both in a light green and in a dark form[2]. The dark form is the commonest in *C. porcellus* but in *A. atropos* it is much rarer than the green form. Judging from the figures, the ground-colour of the segments generally varies as a

[1] The facts which follow are chiefly taken from WILSON, *Larvæ of Lepidoptera*, 1880; WEISMANN, *Studies in Theory of Descent*, Eng. Trans., 1882; POULTON, *Trans. Ent. Soc.*, 1884, 1885, 1886, 1887; BUCKLER, *Larvæ of Brit. Butterf. and Moths*, Vol. III. Ray Soc., 1887.

[2] That this dimorphism is 'phytophagic' is not very likely, but the possibility should be remembered. It seems to be established that in many of the species the colour-varieties are definite and largely discontinuous. Of *M. stellatarum* WEISMANN (p. 250) bred 140 from one batch of eggs, and of these 49 were of the green form and 63 of the brown form, only 28 being transitional. The discontinuous character of the variation was illustrated by one most remarkable specimen. In it the body was *particoloured*, being partly of the green and partly of the brown form. The head, prothorax, all the abdominal segments behind the 2nd, and the *right* side of the remainder were brown, but the left side of the meso- and meta-thorax, of the 1st abdominal, and part of the left side of the 2nd abdominal were green [according to the figure 9 on Pl. III., with which the description in the text, p. 249, differs slightly]. In *A. atropos* I know no account of any intermediate form. In most of the species the dimorphic or polymorphic character appears in the later periods of larval life and especially after the last moult; but in *C. porcellus*, according to both WEISMANN (p. 188) and BUCKLER (p. 117) though the larvæ are of both kinds in the penultimate state all or nearly all after the last moult turn to the dark form.

whole, shewing only slight differences in tint in different parts of the body. To this there are certain exceptions, of which *A. atropos* is especially remarkable. In the brown variety of this species the abdominal segments have a dark ground-colour composed of shades of brown, while the three thoracic segments in it are *white* "like linen" (see WILSON, Pl. VI.; BUCKLER, Pl. XXI.; POULTON, 1886, p. 149; HAMMOND, *Zool.*, 6282; BALDING, *Ent. Mo. Mag.* XXII. p. 279; GIRARD, *Bull. Soc. ent. Fr.*, 1865, S. 4, v. p. xlix. &c.).

In *M. stellatarum* though the ground-colour of the head and of all the segments varies greatly it appears that the head and prothorax vary in colour simultaneously with each other and are of one colour, while the other two thoracic segments and the abdominal segments also vary together but usually differ from the head and pro-thorax (see WEISMANN, Pl. III.).

In illustration of the degree to which simultaneity of Variation is possible over considerable areas of the body the varieties in markings are perhaps more important than those in ground-colour. Of such changes simultaneously occurring in several segments there are many examples.

465. In all the varieties of ground-colour in *M. stellatarum* the pattern of the markings remains the same though of differing intensities (WEISMANN, p. 248), but in the brown variety of *A. atropos* the pattern is quite peculiar and cannot even be recognized as a representation of the markings seen in the green form. Even the oblique stripes are absent (POULTON, 1886, p. 149; see also authors quoted above). But *as in the ground-colour so in the markings, the abdominal segments* have one new pattern while the thoracic segments have another.

*466. The figures of larvæ of *Deiphila euphorbiæ* given by BUCKLER and by WEISMANN are especially interesting in this connexion, shewing that in the complex variations of this polymorphic form the particular pattern of the individual is carried out with little difference in each segment behind the prothorax. Some of these changes are extensive, but to be at all appreciated the figures must be referred to. In one case all the triangles at the posterior part of each segment were red instead of green as usual, and this change was found in many specimens from one locality (see WEISMANN, p. 206, Pl. V.). This identical *variation was known to and figured by* HÜBNER (WEISMANN). In one specimen from the same place as the last the second row of marks which should occur just below the sub-dorsal mark of each segment was absent throughout the whole line, and the ring-spots of the upper or sub-dorsal row had, as a variation, a red centre or nucleus, well marked in the posterior spots but fading away anteriorly. The occurrence of *these considerable changes is still more noteworthy if, as* WEISMANN states, the members of each batch are much alike. He remarks also that the variability is great in some localities but little in others.

467. The larva of *Deilephila hippophaës* has a sub-dorsal row of red markings upon a variable number of segments from the 7th abdominal to the 3rd or even 2nd abdominal, increasing in size and distinctness from behind forwards. The size of these markings differs greatly in different specimens, varying from a mere dot to a distinct red spot with a black ring. As the figures shew, there is a considerable cor-

respondence between the segments in the extent to which the spots are developed, though in each case they fade away in the anterior segments (see WEISMANN's figs. 59 and 60).

468. Another interesting example of considerable uniformity in the colour-variation of a series of segments is to be seen in *Saturnia carpini*. In this species besides change in the tint of the green ground-colour [two chief tints being found, one dark and one light] there is immense difference in the amount of black pigment deposited, most marked in the last two stages of the larvæ. Good figures and descriptions of these are given by WEISMANN (Pl. VIII.). Though no two segments are alike and though there are differences perceptible even between the two sides of most segments, yet the general scheme of colour of each individual is carried out with fair constancy over the several segments. As I have myself seen, the lightest and darkest may both be reared from one batch of eggs and in the same breeding-cage or sleeve.

469. The colour of the tubercles of *S. carpini* also varies greatly. They may be light yellow, dark yellow, pink, violet, or white, but the yellow and pink forms are the commonest. As I have myself observed, there is generally a close agreement between the different tubercles of each larva in point of colour. In a few specimens I have seen the tubercles of the anterior and posterior segments pinkish, while the remainder were yellow, but this diversity is exceptional. The importance of this case is increased by the fact that POULTON (1887, p. 311) has found that the offspring of a pair whose tubercles had been pink shewed a high proportion of larvæ with pink tubercles. The two parents were from a lot of 80 larvæ found together, of which only 3 had pink tubercles: but of their 88 offspring 64 had pink tubercles.

470. The case of the occurrence of red spots on the larvæ of *Smerinthus ocellatus* and *S. populi*[1] may be quoted as an instance of great irregularity in the degree to which the segments agree in their colour-variations. This well-known case is also of great interest as an example of a parallel variation occurring in different species. The larvæ of both species are most commonly without any red spots, but not rarely a number of red spots are present. In extreme cases each of the spiracles is surrounded with red, and there is in addition a row of red spots in the sub-dorsal region of all segments from the 1st thoracic to 7th abdominal, and also a red spot on each clasper. The number of spots, number of rows, the size and tint and distinctness of the spots is exceedingly variable. In point of time the spots of the 3rd abdominal segment appear first and those of the 2nd thoracic next (POULTON, 1887, p. 285, &c.). Though in much spotted specimens the spots may remain till the larva is full-fed, in some cases a few spots appear at an early stage and are afterwards lost. Among the individuals of the same brood there may be great diversity, some having spots and others being without them (POULTON, 1887, p. 287). In several cases a spot present on one side of a segment has been found absent on the other side. As Poulton observes, it is especially

[1] I have not referred to the case of *S. tiliæ*, as it is possibly of a different nature.

remarkable that though there are no spiracular openings on the meso- and meta-thoracic segments, yet in cases of extremely spotted larvæ there are red spots at the level of and continuing the spiracular series of spots upon these segments also (*S. ocellatus*, BUCKLER, Pl. xx. fig. 1 *a*; POULTON, 1887, Pl. x. fig. 1. *S. populi*, POULTON, 1887, p. 286). As an indication of an element of definiteness in this variation may be mentioned the fact that in fully spotted larvæ of *S. populi* the sub-dorsal spot on the 7th abdominal seems to be always the smallest in that row (POULTON, 1887, p. 285; WILSON, Pl. v. fig. 2 *a*; FLEMYNG, *Ent.*, 1880, p. 243, &c.).

In our present consideration the fact that these very large variations sometimes occur simultaneously over a large range of segments and are sometimes restricted to particular segments is of considerable importance.

We may note that WEISMANN (p. 360) is prepared to believe that these spots represent a new variation arising similarly and independently in the different species of *Smerinthus*. As however is usual in cases of considerable Variation an attempt has been made to lessen the value of these indications of the magnitude of Variation by suggesting that they may be of the nature of "reversion" (POULTON, 1884, p. 28). Apart however from a general reluctance to recognize the possibility of the occurrence of large variations there seem to be no special grounds for the suggestion here. It is nevertheless true that in the case of the *Smerinthus* larvæ a complete disproof of the hypothesis of "reversion" is wanting. This is only to be obtained in cases (like that of *D. euphorbiæ*), in which a great number of complex and mutually exclusive variations exist side by side. In the absence of such complete refutation the hypothesis of reversion may still find favour.

*471. **Chitonidæ.** The following facts observed in certain Chitons are given in illustration of the existence of a similar possibility of simultaneous Variation between parts which are repeated in series but whose repetition is not of the kind commonly included in the term Metameric. Unfortunately the material at hand is very limited and I do not know what might be the result of further examination, but the facts seen suggest that the subject is worth investigating.

The dorsal plates of Chitons are eight in number. Though the colours and markings in different species are complex and various yet in many species all the plates are alike or nearly so. The question then arises do all the plates change colour together, or do they change one by one, or otherwise? From the few observations made it seems that in this respect the species differ, but variation uniformly occurring in all the plates seems to be rare. This may perhaps be due to the constitution of such specimens as separate species, but I saw little likelihood of this. On the other hand in several cases the same variation was present in more than one segment, and in particular there was strong evidence that in some species the segments 2, 4 and 7 shew a noticeable agreement with each other in colour-variation. The specimens are all in the MacAndrew Collection in the Cambridge University Museum, and I have as usual simply followed the labelling of the specimens.

C. arbustum, Australia. 10 specimens, of which the plates in 6 are nearly uniform. In one there is a white band in the centre of each plate; in 2 the plates are irregularly coloured; in one the plates 1 and 6 agree in being broadly marked with white.

Chiton hennahi, Peru. 4 specimens. 3 are uniformly dark brown; but in the other specimen there is *a strong white mark on the centre of plates* 2—7, and a faint one on plates 1 and 8.

C. elegans, Chili. 2 specimens. In one, complicated markings are repeated on each plate nearly uniformly; in the other specimen *a much simpler pattern recurs on each segment.*

On the other hand, *C. pellis-serpentis*, New Zealand, 8 specimens: great diversity of markings and no uniformity among plates in 4 specimens, but in one specimen plates 2—5 were black and the rest light-coloured. Similar want of uniformity among the plates in 2 specimens of *C. incanus*, New Zealand.

The evidence of agreement between segments 2, 4 and 7 in the following cases is very striking.

C. (*Tonicia*) *marmoreus*, "Hebrides, &c." 18 specimens, all of a light brown colour marked with dark red.

In 4 specimens the plates are uniformly marked or nearly so.

In 6 specimens plates 2, 4 and 7 are much darker than the others, being for the most part of a uniform dark red.

In 5 specimens plates 2, 4, 7 *and* 8 are darker than the rest.

In 1 specimen plates 2, 4, 5 and 7 are darker than the rest.

In 2 specimens the central parts of most of the plates have dark markings, but no segment is specially distinguished.

Of 18 specimens therefore 12 have plates 2, 4 and 7 darker than the rest.

Among 3 specimens of the same species from Gr. Manan (N. America) 2 are nearly uniform throughout, but in one plates 2, 4, 7 and 8 are much darker than the rest.

C. (*Tonicia*) *lineatus*, 2 specimens. In one the markings on all the plates are nearly similar, and the white wavy streaks characterizing the species are almost similarly distributed on the sides of all the plates. In the other specimen these lines are absent on the plates 2, 4 and 7, which are much darker than the rest; but the lines, though less extensive than in the first specimen, are present on plates 1, 3, 5, 6 and 8.

The preceding evidence may suffice to indicate the nature of this important question of the degree to which the colour-variations of parts repeated in Linear Series may be similar and simultaneous, a question which, as must be evident, is of the highest consequence in estimating the magnitude of the steps by which Evolution may proceed. To the consideration of this matter it will be necessary to return when the evidence of Substantive Variation is considered.

Meanwhile it will not be forgotten that though we have only spoken of this question in reference to colour and to Linear Series, the same question arises also with regard to other variations and in reference to all parts which are in any way repeated and resemble each other, whether such repetition is strictly serial or not. In a survey of any group of animals cases will be seen in which organs in one region are repetitions of organs in another region though not necessarily in serial homology with them in any sense in which the term is commonly used. Many such cases were spoken of by Darwin in the chapter on "Correlated Variability[1]" and are now famous. The simultaneous colour-variations of the mane and tail of horses[2], the correspondence between the large quills of the wings and those of the tail of pigeons[3] and other birds are among the most familiar of such cases.

When with such facts in mind we turn to some species which differs from an ally in the presence of some characteristic development or condition common to a number of its parts, in making any estimate of the steps by which it may have been evolved it must be remembered that it is at least possible that the common feature characterizing these several parts may have been assumed by all simultaneously. To take a single instance of this kind, the species of the genus *Hippocampus*, the Sea-horses, have the shields produced into more or less prominent tubercles or spines. The back of the head is also drawn out into a prominent knob. In an allied genus from Australia, *Phyllopteryx*, many of these spines are provided with ragged looking tags of coloured skin, like the seaweed which the fishes frequent[4], giving the animal a most fantastic appearance and no doubt contributing greatly to its concealment [probably from its prey]. If in this case it were necessary to suppose that the variations by which this form has departed from the ordinary *Hippocampi* had occurred separately, and that each spine had separately developed its tag of skin, the number of variations and selections to be postulated would be enormous; but probably no such supposition is needed. We are, as I think, entitled to expect that if we had before us the line of ancestors of *Phyllopteryx*, we should see that many and perhaps all of the spines which are thus modified in different parts of the body had simultaneously broken out, as we may say, into tags of skin, just as the feathers of the Moor-hen (*Gallinula chloropus*)[5] may collectively take on the "hairy" form, or as, to take the case

[1] *Animals and Plants under Domestication*, ed. 1885, II. chap. XXV.

[2] As Darwin mentions, simultaneity in the variations of the hair may be manifested in size and texture as well as in colour. A bay horse was lately exhibited at the Westminster Aquarium standing 16½ hands, having the hair of both mane and tail of prodigious length. The longest hairs of the mane measured 14 ft. and those of the tail 13 ft. It did not appear that the hair of the fetlocks or body was unusual in character, but these were kept closely clipped and nothing could be affirmed on this point.

[3] By the courtesy of Professor L. VAILLANT I was enabled to examine a number of specimens of the singular breeds of Gold-fish from China in the Paris Museum of Natural History. Some of these are characterized by the great length both of the appendicular fins and of the caudal fin also. Measurement shewed that there was a substantial correspondence between the lengths of these parts, those with long appendicular fins having also very long tails. The correlation between these parts is not however universal in Gold-fishes, and in many of the ordinary "Telescope" Gold-fish the tail may be longer than that of a common Gold-fish of the same size, though the length of the appendicular fins be not exceptional (v. *infra*).

[4] GÜNTHER, *Study of Fishes*, 1880, p. 682, fig. 309.

[5] See Introduction, p. 55.

of Radial Series, the petals of a flower may all together take on the laciniated condition[1].

Further study will indeed probably lead to the recognition of a principle which may be thus expressed: that *parts which in any one body are alike*, which have, that is to say, undergone similar Variation in the past, *may undergo similar variations simultaneously*; a principle which, if true at all, is true without regard to the morphological position of the parts in question.

[1] For cases see MASTERS, *Vegetable Teratology*, 1869, p. 67.