

- II. *Further notes upon the markings and attitudes of lepidopterous larvæ, together with a complete account of the life-history of Sphinx ligustri and Selenia illunaria (larvæ).* By EDWARD B. POULTON, M.A., F.G.S., F.Z.S., of Jesus and Keble Colleges, Oxford.

[Read September 3rd, 1884.]

PLATE VII.

IN the following paper I have described the segments of larvæ as follows:—Head, 1st, 2nd, and 3rd thoracic segments (or prothorax, mesothorax, and metathorax), followed by the abdominal segments numbered one to nine. It seemed better to adopt this more accurate method of description than to number the segments from the head backwards after the ordinary manner (which was used in my last paper in this Society's 'Transactions,' 1884, pp. 27—60).

1. THE ONTOGENY OF SPHINX LIGUSTRI.—I was enabled to obtain ova through the kindness of Mr. Meldola and Mr. William White (who informed me that Messrs. W. and J. Davis. of Dartford, had fertile ova for sale). This was very fortunate, as I was anxious to work out the ontogeny, and fertile ova of *Sphinx ligustri* have always been difficult to obtain.

*Ovum.*—The ova were laid July 8th (1884): they are oval, but without much difference between the two sexes (about 1.75 mm. long and 1.5 mm. wide). They are slightly flattened from above downwards; the colour is a bright yellowish green, evidently harmonizing better with the under than the upper sides of the leaves of its food-plants, and especially so with regard to privet. Twenty of the eggs sent to me were fixed to privet-leaves, and of these seventeen were attached to the under side and only three to the upper. Of course these were laid in confinement, and it is very likely that all the ova are fixed to the under side in a state of nature. There is also a probably more important



reason why this should be the case, for the ova are thus protected to a large extent from rain and sun, besides being sheltered from observation. After a few days a depression appears on the upper surface, and the colour becomes less delicate and transparent. Soon afterwards the ovum is opaque, yellowish, and mottled with bright green. The young larvæ emerged July 16th—18th, their development being thus very rapid.

*Stage I.*—The following statements depend upon the observation of about fifty larvæ fed in separate divisions upon privet, lilac, and ash. It may be regarded as certain that these young larvæ generally eat part of the egg-shell after emergence. I did not see this actually taking place, but I watched it in the case of *Smerinthus ocellatus*, and a comparison of what was left of the shells in both cases showed that *S. ligustri* has the same habit. The amount eaten was very variable, but was never more than three-quarters of the whole, and often there was an aperture barely large enough for emergence. In such cases the larvæ cannot have eaten the shell after hatching.

The larva just after emergence was 5.25 mm. long when extended in walking, and the horn was 3 mm. long. Sometimes, however, the horn was very nearly as long as the body. The colour of the body is a pale, transparent, very slightly greenish yellow, the head being much greener than the body (see fig. 1,  $\times$  4, Plate VII). The horn is black, but the upper half of its length is transparent and greenish, because the green internal fluid shines through the dark exterior. It certainly cannot be called "green," as Kleemann states. The horn tapers very slightly and is straight, except that the upper part is bent downwards in a gentle curve. The blunt tip is bifid, and each process ends in a fine and fairly long bristle, so that the structure is prong-like when viewed from above. The body is thinly clothed with long fine black hairs. These are arranged in four rows, two dorsal (one on each side of the middle line), and two lateral (a little above the spiracles). Each of these four rows is made up of two hairs on each segment, from the 1st to the 7th abdominal (both inclusive). Posterior to the latter the hairs are more abundant, but still thin, and without definite arrangement. Upon the thoracic segments the hairs are arranged so as to continue the four lines described above, but they are less numerous (at any rate



in the case of the two upper rows, where there is only one hair to each row on each segment). The head is thinly covered with similar hairs.

In addition to these long hairs there must be a comparatively thick coating of much smaller ones. I was able to prove their existence at a later date by the use of the compound microscope, or even by a powerful hand lens; but I was away from home and without a sufficiency of appliances when the larvæ were in the first stage. There can be no doubt of their presence, and they cover the horn as well as the body. The two bristles forming the terminal prong are also hairs. The mandibles are green with the cutting edges black: the ocelli are black and distinct. The spiracles are hard to make out, and the dorsal vessel is visible but not distinct. The head is rounded and of a generalised larval shape and not *Sphinx*-like. The horn is flexible and movable. It soon becomes straight, and may be held at an angle or parallel with the back. The young larvæ spin webs for foot-hold, and readily suspend themselves by threads. This fact has already been observed by Kleemann, and it is very interesting, as the habit is so entirely abandoned later, although it appears again before pupation. The disappearance of this habit probably follows from the great size and weight of the larva, which render this method of attachment and suspension comparatively useless. It is of especial use when the larva clings to the flat under side of the leaf at any point except (that usually selected) the projecting midrib. Later the larva gains security by the extreme power of its claspers. A similar change of habit is better seen in the larva of *Dicranura vinula*, because here the presence of the web exactly corresponds to foot-hold upon the leaf. It is to be noted, however, that this larva does not lose the habit to the same extent as *S. ligustri* (or *S. ocellatus*), and that when young it clings to the smooth upper surface of the leaf. The protective resemblance is to the under side of the leaf, and the larvæ are especially hard to distinguish when seated on the midrib, and in this position they seem nearly always to rest. The dorsal vessel becomes very distinct after the larvæ have fed for a short time, and the tracheal system is visible. The larva becomes greener, and the first trace of marking appears with the formation of a white circular patch round the base of



each long hair in the four rows. The patches are especially distinct on the dorsal rows, and the larva therefore shows four spots on the back of each abdominal segment in front of the 8th, and two spots on the back of each thoracic segment. Weismann describes and figures similar spots on the thoracic segments of a larva of *Smerinthus populi* in the first stage. These white patches are the first readily seen shagreen dots. Then minute white spots appear all over the body, which are the white areas round the bases of the smaller hairs. Then by a linear arrangement of the white spots (in which both large and small take part) the essential markings are established (see fig. 2,  $\times 3$ , Plate VII.). The subdorsal becomes distinct before the oblique stripes, and the latter are rather faint during the whole of this stage. The white subdorsal is perfectly normal, extending the whole length of the body and bending gently upwards anteriorly in the 1st thoracic segment, and posteriorly into the base of the horn (being continuous with the 7th oblique stripe). The subdorsal may be seen to be formed of white dots, which are also present over the whole surface, but are not conspicuous. So also with regard to the oblique stripes, but here there is an interesting relation to the larger spots. The anterior dorsal pair on each segment always form part of the stripes, but the latter, converging posteriorly, fall within the hinder pair. So also the anterior spots only of the lateral rows on each segment fall into the oblique lines. The long hairs can still be seen on the spots while the latter are contributing to the oblique lines. There is a very minute and faint "8th stripe" in front of the 1st oblique stripe on the 1st abdominal segment. It does not extend downwards far enough to meet the subdorsal. The effect of the series of large dorsal dots on the thoracic segments (two on each) is to produce the appearance of a very indistinct line above and parallel with the anterior part of the subdorsal. This line is also contributed to by the smaller dots. As the small anterior oblique stripe does not reach the subdorsal, but stops at about the level of the hinder end of this indistinct line, there is an appearance of continuity between the anterior stripe and the line. This, however, does not really take place, as the former stripe is prolonged for a very slight distance below the posterior end of the horizontal line. These markings are very



persistent in after stages, and they are therefore described in detail. This stage lasts about six or seven days in most instances. At the close of the stage (before changing the skin) the larvæ are about 12 mm. long when extended in walking. (Fig. 2,  $\times$  3, Plate VII., shows a larva at this period of growth). The larva is about 10.5 mm. long when rather retracted at rest, the horn 4 mm. long.

*Stage II.*—The markings of this stage almost exactly resemble those of the last (see fig. 3,  $\times$  2, Plate VII.), and the origin of the lines and stripes from linear series of shagreen dots is equally obvious. The large spots and long hairs have now disappeared, except those that enter into the 8th stripe and indistinct line above the subdorsal on the thoracic segments. This line is whiter than the other markings, which are yellowish white (see fig. 8,  $\times$  3). Minute hairs still terminate the shagreen dots, whether arranged in lines or covering the surface of the body. This fact is true of the dots whenever they appear in any stage. The margins of the claspers, tips of true feet, and spiracles have a pinkish tinge. The horn is pink immediately after the change of skin, but it soon darkens, and possesses a brownish-red ground colour covered with dark tubercles (shagreen dots) pointing upwards and terminated by minute hairs. The apical pair is arranged so as to cause a bifid termination, but this is not nearly so distinct as in the last stage. On each side of the base the ground colour of the horn is free from tubercles, and hence appears as a brownish red continuation of the 7th oblique stripe. The horn is movable, and is sometimes depressed, so as to become parallel with the line of the back, while at other times it is elevated to the usual position of an angle of  $45^{\circ}$ . The same thing occurs in the first stage. The larva still rests, as a rule, on the midrib of the under side of a leaf. The head is shagreened, and shows indications of its ultimate appearance in the occurrence of a marginal line (white) round the face. In this stage the oblique stripes are very distinct, and the subdorsal indistinct, except anteriorly. The length of a full-grown larva comfortably stretched at rest is about 18 mm. After ecdysis the skin is, I believe, always eaten, except the head and horn, which seem to be invariably rejected. This stage lasted about nine days in most cases.



*Stage III.*—After the second ecdysis the larvæ very much resemble the previous stage. The chief difference is in the subdorsal, which has disappeared except anteriorly, and is indistinct even where it is retained. The horizontal stripe above the subdorsal is distinct, and so are the prominent white spots on the thoracic segments (one pair on each). This line has the same relation to the 8th stripe, but the continuity is only apparent, for careful observation shows that the latter extends below the posterior extremity of the former. This is also true of previous stages. At this time, and in the second stage, the larva bears the closest resemblance to a *Smerinthus* larva in every respect, except the dark colour of the horn and the shape of the head. In this stage the larva habitually rests (still upon the mid-rib) in the *Sphinx* attitude, which is also assumed, though exceptionally, in the second stage, and is even seen in the first. There is still a trace of the bifid termination to the horn (see fig. 10,  $\times 50$ , Plate VII.). Shortly after ecdysis the colours darken in certain parts: the pink horn becomes dark brown with black tubercles, as before, the effect being nearly black, except at the sides of the base. A black cloud appears on the side of the head and extends downwards behind the yellow line at the margin of the face. There is much variability in this respect, some larvæ having no trace of black on the head. The spiracles are ochreous, as in the adult, but more faintly. The true legs become red, and a dark purplish margin appears round the claspers. The anal flap has a white margin. The ground colour is yellowish green above, darker green below, and this latter extends upwards in front of the oblique stripes as a dark shading for one-third of their length. (The depth of colour is very variable). The shagreen dots are yellowish white, those forming the stripes being much larger and whiter than the others. At first the component dots of the stripes are distinctly separate, but later they enlarge and fuse, producing the appearance of a white band, upon which is a single row of tubercles, each emitting a minute hair. These tubercles are the original shagreen dots, and each is placed in the centre of a white area, which has spread from the base of the former into the ground colour. The areas form the white stripe, and they can be readily distinguished, as each is situated upon one of the secondary rings into which each



segment is divided. The secondary annulation began in the first stage, and is present throughout larval life. There are eight of these annuli on each of the segments that bear the oblique stripes, except the 8th abdominal. Where this latter segment is crossed by the upper part of the 7th stripe entering the base of the horn the annulation is not present, and the adjacent areas are not separated by furrows (between the annuli on other segments), and therefore fuse at an early date. The 7th stripe is also much whiter and more conspicuous than the others. As the larva advances in this stage the subdorsal and the stripe above it become indistinct, but the 8th stripe becomes more prominent, and is especially well seen as a V when the larva is looked at from above. The head is shagreened, as in previous stages.

But the most interesting fact about this stage is the appearance of the purple borders to the white stripes. These were never present at ecdysis, and in some instances they did not appear at all in this stage (in the case of very light varieties). So also the time at which they made their appearance varied greatly, and the extent to which they were developed. The stripes are linear and very narrow: they first appear as a brownish rather than purple edge to the central part of the 1st and 7th stripes. Then they appear in front of the others nearly at the same time, and without any definite order. It seemed that the 1st stripe gained a border rather before the 7th. The purple edge is not a modification of the white stripe, but is distinctly due to a darkening of the ground colour. So far from the shagreen dots having any relation to the border, they are either absent from it or very small (which is also true of the ground colour anterior to the whole length of the stripe). There is nothing spot-like in the first appearance of the border; it is always very narrow and linear. Its first appearance confirms the view that I expressed last year (*Trans. Ent. Soc. Lond.*, pt. I., 1884), *i. e.*, that the border is a modification of the ground colour in front of the white stripe, and is not due to the drawing out of patches of colour that appear in this position: in fact that the border is linear primarily and not secondarily. Kleemann states that the larvæ acquire the purple borders in the fourth stage, and Weismann says that he has observed the same thing. Nearly all my larvæ acquired the borders in the third stage, as



above. At the conclusion of this stage the larva is about 25 mm. long, when stretched comfortably at rest. This stage only lasted about six days. A larva at the end of this stage, comfortably extended at rest, is shown at fig. 4,  $\times 2$ .

*Stage IV.*—The larva at the beginning of this stage is exactly similar to one in the last, except for the greater size of the purple borders. The subdorsal and line above it are present at first, but subsequently disappear, while the 8th stripe remains. The pair of distinct dots are at first visible on each thoracic segment, but they afterwards cease to be recognisable, together with the line of which they form part. The 7th stripe is continuous, and so also are the central parts of the others where the purple border is present. The latter varies in amount, and I have seen it almost absent, except on the 1st and 7th stripes. Immediately after ecdysis the dots of the stripes are separate (fig. 9,  $\times 4$ ). The stripes are pure white where they are bordered with purple, but yellowish above this part, while the purple gives place to dark green. The purple and pure white change to the other colours before reaching the posterior limits of the segment they are crossing, while in the fifth stage the change takes place in the next segment posteriorly. The white stripes are continued inferiorly and anteriorly into a very distinct row of white tubercles on the next segment anteriorly (as in the adult). The ground colour of the part of the surface on which the oblique stripes run (except the inferior continuations just mentioned) is a much brighter and yellower green than the rest of the body. The upper yellowish part of the oblique stripes is formed of distinct and separate yellow tubercles. This is the stage of the *Sphinx* attitude, and the head is held higher and further back than at any other time. As the larva approaches the end of the stage it becomes very adult-looking, this effect being especially produced by the shagreen dots becoming less conspicuous. There is great variation in the darkness of the larvæ, the dark forms having black sides to the head, while the purple borders deepen anteriorly and inferiorly into very nearly black. The lightest larvæ have hardly any black on the head, and the purple only deepens to brownish. There is every shade of difference between these extremes. A full-grown larva in this stage is about 33 mm. long in the *Sphinx* attitude, but much longer when extended



(see fig. 5, rather over natural size). This stage lasts about six days.

*Stage V.*—At the beginning of this stage the larva is about 33 mm. long when at rest in a rather contracted state after the effort of ecdysis. This is the last stage, and the larva is, of course, well known. Nevertheless, there are some extremely interesting facts about it, especially concerning the change from a shagreened to a very smooth larva. Immediately after ecdysis the body is shagreened all over with minute dots, which still terminate in hairs (see fig. 6, Plate VII., natural size). I formerly suggested (in the paper already referred to) that the row of white dots continued anteriorly and inferiorly from the white stripes were the remnants of the shagreen dots. This is now certain, for they have been traced through the ontogeny, and further, even in this stage, each one of them terminates in a minute hair, which is retained to the end. The shagreening very quickly disappears, but it can be detected with a powerful lens, and always remains visible (though very minute) upon the under surface of the body. Although the horn is so smooth and shining in this stage, traces of the tubercles can still be made out. The 8th stripe is always present after ecdysis, but it quickly disappears. The deep black of the horn and sides of the head are replaced by dark green after ecdysis, but the latter darkens in a few hours. The shagreening seems to disappear by a change of colour into that of the surrounding ground colour, and a gradual disappearance of the raised eminence which forms each dot. There is the same variability in darkness as shown by the different degrees of depth attained by the lower part of the purple border. When this becomes very dark some patches appear on the other (inferior) side of the white stripe. I described this variety last year from a single instance found in the field, but it was quite common among the larvæ reared during the past summer. The larvæ turned brown in many cases on August 21st, this stage having lasted about nine days. Thus the whole larval life lasts about five weeks. There were many exceptions to the periods given for each stage (which were, as far as possible, average instances).

*Summary.*—There are many interesting points about this life-history. Such are the well-developed subdorsal in the early stages (for the probable existence of which



Weismann argued, although it had not been observed by Kleemann), the 8th stripe and horizontal stripe above the subdorsal (anteriorly), the relation of the large shagreen dots to the markings in the first stage, and their long persistence on the thoracic segments, the appearance of the purple stripes in the course of the third stage, the change from a shagreened to a smooth larva in the fifth stage, and the immense size of the horn in the first stage, its bifid tip, and the fact that it is movable. The great resemblance to a *Smerinthus* larva is also very interesting, the only essential differences being the loss of shagreen in the last stage and the acquisition of purple borders in the third, and the shape of the head. It is probable that the ontogeny is in some respects more primitive than that of *Smerinthus* larvæ. It is certainly more advanced in the later stages, as is proved by the purple borders, the change to a smooth skin, and the relatively early and complete disappearance of the subdorsal. Nevertheless, in the first stage the subdorsal predominates over the oblique lines to a greater extent than in *Smerinthus*, and the horn is far larger, more distinctly bifid and it is movable. It is very probable that all these are primitive characters. It is certain that relative size is primitive, for the horn is universally largest in the earliest stages. In this respect *S. ligustri* is probably the most primitive *Sphinx* larva known. It is therefore likely that the other characters are also primitive, and that additional knowledge concerning the horn of the ancestral *Sphinx* larva is afforded in the early stages of this ontogeny. I shall presently give reasons for the belief that the bifid termination is a primitive feature, derived from a comparison of the larvæ in which it has been observed. It will further be rendered probable that the power of movement is also primitive.

2. FURTHER NOTES UPON THE ONTOGENY OF *SMERINTHUS* *OCCELLATUS*. — As I was rearing a number of these larvæ from the egg for the purpose of experimenting upon phytophagic coloration, there was a good opportunity for noting any additional facts in their ontogeny (which is systematically given by Dr. Weismann).

*Stage I.*—I have seen the young larva eating its egg-shell after emergence, but it is never completely eaten, and sometimes only enough for escape. Sometimes a



larva eats part of another empty shell lying close to the one from which it has just emerged. In one case I saw a newly-hatched larva attack a thread of the gauze to which the eggs were attached, but it soon left this and ate its shell. The process of gnawing through the shell can be watched with a lens. Very slow progress is made as long as the larva is completely within, and is biting at the concave surface of the shell. When a small hole has been made one mandible is thrust outside, and the shell is very quickly eaten away from the edge of the aperture, until the larva can emerge. The young larva is of a beautiful yellowish-green colour upon the body, while the horn is red. (The length is 5.5 mm. when extended in walking; the horn 2 mm. long, and thus much shorter than that of *S. ligustri*). The horn is bifid, like that of *S. ligustri* (but to a less extent), and terminates in two bristles, while the rest of its surface and that of the body is densely covered with short whitish hairs. There were never any indications that the horn could be moved. The head is thinly covered with similar hairs. The larva spins a web in the same manner as *S. ligustri*. (It should be mentioned that these webs are very slight, and only detected by careful watching. This may explain the failure of other observers in finding them). The ocelli are black and very distinct on the light green head. The oblique stripes and subdorsal can be just made out with difficulty in a newly-hatched larva, but there is no darkening of the ground colour in front of the stripes, although this appears at the end of the stage. The usual attitude on the leaf was as in *S. ligustri*, and with the same protective significance. At the end of the stage the regular markings are very distinct. Even at this time the subdorsal is more distinct anteriorly than in the rest of its extent. I was very much astonished to find a very small proportion of the larvæ with the head of the typical *Smerinthus* shape, while the others possessed the more generalised round shape. I could at first hardly believe the accuracy of the observation, but it was subsequently confirmed, and there can be no doubt that this is an instance of the passage backwards of a character in the ontogeny actually taking place before us. The shagreen dots are very numerous, and each hair springs from the summit of a dot. The markings are caused by the dots becoming arranged in a linear series, without the ground



colour being as yet affected. The annulation of the segments is very distinct and continues throughout. The 8th stripe is present. The markings are yellowish. Weismann has stated that there are no markings on the newly-hatched larvæ. This is certainly the general effect of the larvæ, but a lens and a good light will prove that the markings are really present.

*Stage II.*—In this stage the markings are whiter. On the summit of the head are two prominent light red tubercles; these are only enlarged shagreen dots, and each has a hair upon it. The apical tubercles are the topmost of the two rows that form a marginal line round the head as seen from the front. The horn is red and bifid. It is covered with hair-bearing tubercles, which persist upon it and upon the body throughout the whole of larval life. The gradual spreading of a white area from the base of a tubercle in the oblique stripes is well seen in this stage. At the beginning the stripes are only rows of separate tubercles, except where the 7th stripe enters the 8th abdominal segment. In this case the ground colour is white from the first (and here there is no annulation to keep the dots apart). Although the tubercles enlarge in this stage they do not coalesce, except in the 7th stripe, and here they ultimately coalesce where the stripe crosses the 7th as well as the 8th abdominal segment. The markings are exactly on the plan of the adult, except that the subdorsal is faintly continued posteriorly between the oblique stripes (and even this is sometimes present in the adult). The best way of seeing the hairs of this larva is to hold it up to the light and examine some surface (*e.g.*, the back) in profile with a lens. It is then seen to be densely covered with very short hairs, each projecting from the summit of a shagreen dot.

*Stage III.*—Almost exactly similar to the last. The subdorsal has disappeared, except anteriorly. The horn is bifid in many cases, and is red above, faintly so below, white at the sides. There is much variability in the amount of red on the horn. The red tubercles on the head are rather less defined in shape, and the colour often spreads on to the smaller tubercles near the two large ones (see fig. 12,  $\times 3$ , Plate VII.). The 8th stripe is barely indicated by a linear arrangement of tubercles. There is a linear arrangement of dots on each side of the dorsal vessel, which is very conspicuous when the



larvæ are seen from above. The darkening of the ground colour in front of the oblique stripes takes place from above downwards: in *Sphinx ligustri* it was in the reverse direction (but the purple appeared in front of the middle of a stripe). The *Sphinx* attitude of this larva is somewhat geometriform, the last two and sometimes three pairs of claspers being used, the others retracted very completely. This is also true of the other stages. On examining the hairs upon the shagreen dots with a compound microscope (using a lens of about fifty diameters) it is seen that nearly all of them are forked at the tip. The fork generally consists of two prongs, but occasionally of three or even four, and sometimes the hairs end simply. With higher powers (200 diameters) it is seen, in optical section, that the base of the hair penetrates the apex of the shagreen tubercle (see fig. 11,  $\times 188$ , Plate VII.). The hairs on the red tubercles (on the summit of the head) seemed to be rudimentary, and were not forked in any larvæ that I examined. The ends of the hairs often appeared as if they were cut off short, while the sides were produced into slight horns: this is evidently a form of two-pronged fork. These appearances are found on the hairs of the whole surface. I do not yet know how far these facts about the hairs are true of all the other stages.

*Stage IV.*—The markings are similar to those described in the last stage. The darkened ground colour in front of the stripes has no dots on it, or only very small ones. So also with the dark dorsal line, which has a row of dots on each side of it, producing altogether a very midrib-like appearance. Thus in a larva uniformly dotted with white tubercles, the linear arrangement of the tubercles produces white stripes, while their linear disappearance produces dark lines. The red tubercles are still present, and their colour tinges a few small ones near to them. Towards the close of the stage their colour becomes less conspicuous, and often inclines towards orange. It is now noticed for the first time that the first spiracle is concealed beneath a fold of the contracted prothorax in the protective attitude. The horn is still red and white. The hairs, which are so minute over the general surface, are at all times much longer upon the anal flap and last pair of claspers. At the close of the stage the horn becomes light blue, but



its tip is sometimes green. Before ecdysis the light red tubercles on the head of the last stage can be seen through the skin of the fourth.

*Stage V.*—A faint pink tinge is very common upon the white stripes of this species, and it is especially noticeable in this stage, although it also occurs in the fourth. It occurs on the tubercles and ground colour, and is chiefly developed on the 7th stripe, although it is often present on the others, and even on the remnant of the subdorsal. The two tubercles on the head are now blunt, but still large: their summits are red at the beginning of the stage, the bases yellow (see fig. 13,  $\times 2$ , Plate VII.). Very soon the red is entirely replaced by yellow (see fig. 14,  $\times 2$ , Plate VII.). The head is not generally a bright blue, like the tail, but is greenish at first, becoming greenish blue later (sometimes it is bright blue). My larvæ did not, as a rule, nibble off each other's horns, but a few were treated in this way. I found seven larvæ on one small tree of *Salix Babylonica*, and nearly all of them had lost more or less of the horn. This injury may take place quite early in the life-history, and I think that it is often extremely hurtful or even fatal, as a considerable amount of fluid is lost. The midrib-like appearance often occurs in this stage also, produced by the dark dorsal line with a row of white tubercles on each side.

*Conclusions.*—I formerly suggested that the red spots which sometimes appear in *Smerinthus* larvæ are due to reversion to a more brightly coloured condition. It is possible that the pink tinge to the white stripes is to be explained in the same manner. But the brightly-coloured and prominent tubercles on the head can only be interpreted as of historic significance, indicating that the shape and colour of this larva have become subdued for protective purposes. The tubercles are important both in shape and colour in the second and third stage; the colour becomes faint at the close of the fourth, and in the last stage their shape has altered, becoming inconspicuous, while the bright colour which now only appears on the tips of the tubercles, disappears soon after the beginning of this period. Thus we have a character that strongly supports the interpretation of the bright spots as due to reversion. The difference seems to be that the history of the disappearance of the head tubercles can be traced in every ontogeny, while the



spots have ceased to form any part in the average ontogeny. Nevertheless, when they are present, their variability is so excessive that the various steps towards the disappearance of the system can be made out with a fair degree of probability. It is also likely that the history of the rise in both cases has been similar to that of the decline. Certainly this is true of the head tubercles. They are enlarged and brightly-coloured shagreen dots; the topmost of each row that forms a yellow margin to the face. This is proved by the hair that still remains on their summits. As they disappear each red tubercle again becomes yellow and similar to the others, except for its greater size. So also the simplest form of the system of red spots is seen in those larvæ with a very small patch on each side of the spiracles (except the 1st), and perhaps a small patch on each of the four anterior pairs of claspers. Then we have larvæ with these rows formed of large and conspicuous patches, and with another series of patches above the spiracular row. The spiracles are in all larvæ surrounded by a reddish line, and the simplest form of the system seems to consist in a slight peripheral spreading of this colour. These coloured patches consist of modified ground colour, although shagreen dots may be found upon them. The apparently uniform occurrence of the patches in the later stages is certainly an argument against my explanation, and is in favour of that offered by Weismann. Mr. William White's observations upon this subject render it probable that the spots often appear at a much earlier date than that at which they were noticed by Weismann. The uniformity of this ontogeny is very remarkable. There is practically no difference between the first and last stages, except the more obvious hairs and complete subdorsal of the former and the triangular head of the latter. Two of these distinctions occasionally fail, as has been shown. This uniformity may point to very long-continued protection by the existing form of markings. Traces of other conditions are seen in the hairs, head-tubercles, and reddish spots. It will probably be very instructive to examine the hairs of the young larva with fairly high powers. At present I have only used the hand-lens (except in more advanced stages). It will be interesting to ascertain the form of the forked ends of the hairs in the early stages (if, indeed, they are forked at such times).



Since writing the above I have examined the larvæ in the first stage under high powers, and I find that both *S. ocellatus* and *S. populi* are covered with minute hairs with highly forked ends, while there are more thinly scattered longer hairs some of which are not forked at all, while others terminate in a comparatively small and simple fork. These longer hairs are arranged upon the back in the same way as the long hairs of the first stage of *S. ligustri*, and in *S. ocellatus* there are similar dorsal rows of white spots, which form part of the oblique stripes, as in *S. ligustri*, except that the spots of the posterior pair are included in the stripes of the former, while they fall outside them in the latter. These facts bring the young stages of *Smerinthus* and *Sphinx* very near together. There is also a specially prominent row of the longer hairs upon the prothorax, just behind the head, of the young *Smerinthus* larvæ, and these leave their effects, much later in the ontogeny, as a row of conspicuous shagreen dots in this situation.

Mr. Meldola describes from Mr. Roland Trimen, in the Appendix to his translation of Weismann's book ('Studies in the Theory of Descent,' part ii., p. 527), a very remarkable larva of a Smerinthine hawk-moth, *Lophostethus Dumolini*, which seems to throw some light upon the appearance of *Smerinthus* larvæ, when the forked bristles remained of appreciable size throughout the ontogeny. This larva bears on all segments (except the head and prothorax) black spines, springing from *tubercular bases*. The longest spines form *two dorsal rows* from the metathorax to the 7th abdominal segment. Some of these spines are beset with prickles for the upper three-fourths of their length, and the caudal horn is also *covered with prickles*. There are also lateral rows of spines. The young larvæ have longer spines with long prickles on them, and the caudal horn and the spines on the meso- and metathorax are *distinctly forked*. I expect that it will be proved that the caudal horn does not correspond to a spine, but that the prickles upon it represent dwarfed spines. This is certainly so in *Smerinthus*, where traces of the long and short hairs with their forked extremities are found upon the horn in the first stage. The points of special resemblance have been italicised in the above description.



3. NOTES UPON THE ADULT LARVA OF *SMERINTHUS POPULI*.—The anterior spiracle is hidden when the larva is at rest, as in *S. ocellatus*, and it is also less conspicuous when exposed. There is hardly any ground colour in the oblique stripes, except the 1st and 7th, and only a fair amount in the upper part of the 7th (extending anteriorly through the 7th abdominal segment). There is just a trace of the subdorsal anteriorly, but it is barely visible, and only consists of dots. The 7th stripe is continued anteriorly and inferiorly on to the 6th abdominal segment by a line of dots. So also similar lines of dots are seen upon the 3rd, 4th, and 5th abdominal segments, but they are not as continuous with the oblique stripes behind them as in the former instance. In all cases they are less oblique than the normal stripes, and they have the appearance of a subspiracular line which has been diverted upon each segment into approximate parallelism with the oblique lines. There is the usual annulation of the segments. I could not feel sure about the existence of apical tubercles on the head during previous stages. There is no 8th stripe. The shagreen dots terminate in the usual (simple) hairs. These observations were made upon two larvæ in the last stage found upon two species of *Salix*. Both larvæ were yellowish green.

4. NOTES UPON AN ADULT LARVA OF *SMERINTHUS TILIÆ*.—The ontogeny of this species is described by Weismann, but it was important for me to examine the larva, especially concerning the question of the origin and structure of shagreen dots. An adult larva was found at Oxford, August 13th, 1884. There was no trace of an 8th stripe or of the subdorsal. The shagreen dots are not nearly so rough as those of *S. ocellatus* or *populi*, and yet they terminate in hairs in nearly all cases. The hairs are short and bristle-like, with simple ends. The curious and brightly-coloured plate above the anus is simply composed of large coalesced tubercles still retaining their hairs. The horn is covered with hair-bearing tubercles. The yellow stripes have rather dark anterior margins formed by a deepening of the ground colour. There are two blunt apical tubercles on the head, of a rather darker orange than the band round the face, which has now spread into the ground colour, although the scattered hairs upon it show its origin in



shagreen dots. The annulation of the segments is very regular and distinct, and the shagreen dots are arranged in rings, one to each annulation (this is always the case in shagreened larvæ). The prothorax has three or four such rings, but they are rather confused; the mesothorax has five, the metathorax six, the 1st abdominal seven, and the succeeding six segments eight rings each. Posterior to these there are no rings or annuli, with the exception of three rings upon some irregular folds behind the caudal horn, which represent (I believe) the 9th abdominal segment.

5. NOTES UPON THE ADULT LARVA OF *MACROGLOSSA STELLATARUM*.—This ontogeny has been given very fully by Weismann. I received a large number of larvæ in the last stage from Malvern during the past summer. The bifid termination of the horn could be traced in several individuals, even at this late stage. It is probably very distinct at earlier periods. The spiracle upon the prothorax is red, while the eight others are black and far more distinct. There is a black line round the former, which can only be seen by careful searching. I have not before noticed an instance of different coloration among the spiracles. The segments are distinctly annulated, except the 8th abdominal, and the number of rings seems to be as in the larvæ described (eight upon most of the segments). In a rather contracted attitude the segments taper rapidly from the 1st abdominal to the small head. When startled the head and thoracic segments are sharply retracted into the 1st and 2nd abdominal, which become swollen. (This is especially true of the former segment.) When the larva is stretched the tapering is not so distinct, and extends further back. Thus we have a behaviour identical with that of *Chærocampa elpenor* without the modification of marking which have appeared in the latter. Weismann and Meldola give instances of such terrifying attitudes without the co-operation of terrifying markings, but it is probable that the object of *M. stellatarum* is simply that of a rapid withdrawal from danger, and perhaps a partial protection of the head. It is thus likely that the first stage in the evolution of the terrifying attitude (such as that of *C. elpenor*, &c.), is a case of protection in one of its simplest forms. The habit becoming fixed and producing further structural modifications as the



withdrawal of the anterior part of the body became more complete, the attitude acquired an entirely new significance when the sudden swelling of the segments became a source of terror to enemies. After this the course taken must have been that described by Weismann. I do not think that *M. stellatarum* has yet reached the point at which terror is caused by its attitude. The white shagreen dots are terminated by minute and simple hairs, and the relation of the larval markings to the shagreen dots is exactly similar to that described in *S. ocellatus*, &c. Anteriorly the subdorsal consists of a linear series of enlarged dots only; posteriorly the effect of the dots is heightened by a whitening of the ground colour. These two conditions gradually shade into each other. Above the line there are no dots upon the shading of darkened ground colour. The subspiracular line has no doubt a similar history, but it does not show the whole origin in its different parts as is the case with the subdorsal. The shagreen dots upon the horn are black.

6. THE ORIGIN OF SHAGREEN DOTS IN SPHINGIDÆ.—This is rendered apparent by an examination of a larva of *S. ligustri* or *S. ocellatus* in the first stage. In both species the dots are terminated by hairs which are of considerable length; they are hairy larvæ with tubercles at the base of the hairs. In later stages the tubercles are alone apparent to the naked eye, but the use of a lens at once shows that a rudimentary hair is present upon the summit of each, and this remains true throughout the ontogeny. This explanation holds good for all shagreened *Sphinx* larvæ yet examined from this point of view (the genera *Smerinthus*, *Sphinx*, and *Macroglossa*), and there can be no doubt about the validity of this interpretation of the shagreen dots of *Sphingidæ*. Shagreen dots are the persistent tubercles at the bases of hairs which have become so shortened as to escape notice.

Weismann mentions the presence of small warts, each emitting a single bristle, upon the larva of *Deilephila euphorbiæ* in the first stage (page 202 of the English translation of his Essay on the markings of Caterpillars, &c.). Although these warts must be the origin of the shagreen dots in this species, Weismann does not take such a view, for he describes the independent origin of



the shagreened appearance in the third stage (page 203). So also, on page 246, he describes the larva of *Macroglossa stellatarum* in the first stage as "set with small single bristles," and he figures tubercles at the base of the bristles (plate iii., fig. 1); but he describes the shagreening as appearing for the first time in the fourth stage (page 247). Inasmuch as I have proved that the shagreen dots of the adult *Macroglossa* larva terminate in minute hairs, there can be no doubt of the real origin of the dots in the first stage, where the hairs are more apparent.

7. THE ORIGIN OF THE OBLIQUE AND OTHER LINES IN SPHINGIDÆ.—Last year I suggested that these stripes were primarily due to the linear arrangement and large size of some of the shagreen dots, and that secondarily the ground colour became affected. This suggestion followed from an examination of a larva of *S. ocellatus*, in which the colours had undergone the changes which precede pupation. It was then seen that all the white had faded from the ground colour of the oblique stripes, but that the latter could still be distinctly traced by the disposition of large shagreen dots. The paragraph upon this subject concluded with the words, "It is very probable that the origin of the white markings from the shagreen dots can be proved in the ontogeny." It seems to me that this suggested origin is now abundantly proved in the ontogenies described in the present paper. In *Sphinx ligustri* it is very marked in all stages except the last, and it occurs even in this (in the anterior inferior extremities of the stripes). In the other stages, directly after ecdysis, the oblique stripes consist of dots only without any change in the ground colour (see fig. 9,  $\times$  4, &c., Plate VII.). Later, in some of the stages, the bases of the dots spread into the ground colour, so that the latter is affected peripherally from the base of each dot. As this process continues the areas meet, and a continuous stripe results. Thus the history is repeated in most of the stages in the ontogeny. Some markings may remain in the condition of a row of dots only, even in the adult larva. This is the case with nearly all the markings of *S. populi*, or of the lines which border the dorsal vessel of *S. ocellatus*, &c. Or the same marking may show both conditions transitional into each other, as in the subdorsal of *M. stellatarum*,



&c. There is one fact about the formation of the oblique stripes that strongly confirms this opinion. It has already been pointed out that the 7th stripe is always the first to have its ground colour altered to the tint of the dots, and the first part of the stripe to undergo this change is that which crosses the 8th abdominal segment and enters the base of the horn. Now this is the only segment crossed by the oblique stripes which is not annulated. All segments anterior to the 8th abdominal are divided into rings (generally eight in number), and upon these shagreen dots are arranged in regular rows, one upon each ring. It follows that the rows of dots are separated by the deep furrows that intervene between the rings, and the enlarged dots that form the oblique stripes are therefore similarly separated. Hence these dots are rendered distinct, and the constitution of the stripe is quite apparent, when fusion would have taken place (producing quite different appearances), if the segments were not annulated. But the 8th abdominal segment is not annulated, and here therefore the spreading area round the base of each dot has not to cross a furrow in order to coalesce with that of the next dot. Consequently fusion takes place at an early date, and this stripe is generally much larger and more distinct than the others, being the oldest continuous stripe in the individual ontogeny, and doubtless in the phylogeny also. Some appearances led me to suspect that the stretching of the larval skin during growth in each stage was one factor in causing the dots to spread and fuse. It was at all times obvious that the dots were most entirely separate immediately after ecdysis. Again, the rapid disappearance of the small dots upon the back, at the beginning of the fifth stage of *S. ligustri*, seems to be chiefly due to this process.

The importance of the shagreen dots in this respect is seen in the fact that most of the larval markings of all the English species of *Smerinthus*, of *Macroglossa*, and of *Sphinx ligustri*, are due to their arrangement, size, and fusion (in many cases). The same thing is probably true of many other *Sphingidæ*, but they have not hitherto been examined from this point of view.

Since writing the above I find that Weismann attributes importance to the shagreen dots in relation to markings in *Deilephila euphorbiæ* and *D. hippophaës*, suggesting



the origin of certain marks by the gradual crowding and coalescence of the dots in the former species, and the special coloration and fusion of two dots upon a variable number of segments in the case of *D. hippophaës* (see pp. 204 and 221 of the English translation of the Essay on the markings of Caterpillars).

8. THE ORIGIN OF THE COLOURED BORDERS TO THE OBLIQUE AND OTHER LINES IN SPHINGIDÆ.—These borders seem to be always formed of modified ground colour. Dots are either absent from the borders, or, when present, very small. It seems probable that the first trace of a border arose in the diminishing in size of the dots. This alone makes a relatively dark stripe, for the colour of the larva elsewhere is due to the ground colour modified by the closely-set light-coloured dots. After this the effect must have been increased by a special darkening of the ground colour, and in some instances (e.g., *Sphinx ligustri*) by a change of colour altogether. The dark superior border to the subdorsal of *M. stellatarum* has a similar history. This theory of the origin of the dark borders is borne out by the ontogeny of those species which I have been able to observe.

9. SOME CHARACTERS OF THE HORN IN THE PRIMITIVE SPHINX LARVA.—It has been seen that the horn of *S. ligustri* is distinctly bifid in the first stage (see figs. 1 and 2, Plate VII.), and less markedly so later (see fig. 3). The same was true of *S. ocellatus*, and this character persists through a considerable part of the ontogeny. (This summer, 1885, I have found that the horn of the young larva of *S. populi* is also forked). The same structure is described by Weismann in the first and second stages of *Anceryx pinastri*. The fork is so marked in this species that I have no doubt that it really exists in more advanced stages, but requires a lens for its detection. Weismann also figures, in his Essay on the markings of Caterpillars (plate v., fig. 38), the margined larva of *Deilephila euphorbiæ* shortly after emergence from the egg, with the horn terminated by two diverging bristles. Mr. Meldola also, in an editorial appendix to his translation of Weismann's essay, quotes from Mr. Roland Trimen the fact that the caudal horn of the young larva of *Lophostethus Dumolini* is forked at the



extremity (page 528). Finally, in certain individuals of *M. stellatarum*, I found distinct traces of the fork in the last stage. Comparing these observations, the structure appears to be most persistent in the larva (*M. stellatarum*) with a primitive form of marking, longitudinal stripes; and especially prominent in early stages of another larva with the same marking (*A. pinastri*). I have no doubt that it is largely developed in the first stage of *M. stellatarum* also. It further occurs in the earlier stages of the larvæ with the more advanced oblique stripes at the time when the primitive markings (afterwards lost or much diminished) are well developed upon them. This is especially well seen in *S. ligustri*, where the fork is very distinct in the first stage, when the subdorsal is also the most prominent marking, while the fork ceases to be recognisable about the time when the last traces of the subdorsal disappear (after the third ecdysis). We are thus led to the conclusion that the forking of the horn is a primitive character, of historic value only in the ontogeny, and remaining longest in forms that have other primitive features persistent. The horn was also covered with hairs (in common with the rest of the body), each of which projected from a tubercle. The terminal prong consisted of two enlarged diverging tubercles terminated by large hairs or bristles. In the difficult question of assigning a function to this structure the bifid termination must be taken into consideration. So also the immense size of the primitive horn must be remembered, shown by its greater relative predominance in the earlier stages of the ontogeny, especially in the case of *S. ligustri*. Finally, great importance must be attached to the fact that the horn is movable in the two first stages of *S. ligustri*, and entirely under the control of the animal's will. These facts seem to indicate that the horn was primarily a defensive structure. Further, Mr. Meldola, in the above-mentioned Appendix (page 527), states that the caudal horn of *Chærocampa Lycetus* is freely movable, and he suggests that the horn may be "a remnant of a flagellate organ having a similar function to the head-tentacles of the *Papilio*-larvæ, or to the caudal appendages of *Dicranura*." A curious point was incidentally discovered in examining the larvæ under a compound microscope. The caudal horn exhibits distinct movements synchronous with the contractions of the dorsal



vessel. This was often seen in *S. ligustri* and *S. ocellatus*, by the use of a lens magnifying fifty diameters. The movement always took place, and was a source of considerable difficulty when I tried to obtain an outline drawing of the horn by means of the camera lucida. It seems that this movement (which is in the vertical plane) is less in amount before ecdysis.

10. INSTANCES OF THE PROBABLE PASSING BACKWARDS OF CHARACTERS IN THE ONTOGENY.—In the above-described ontogenies there were certain cases in which we seem to witness the actual passage of characters backwards into an earlier stage than that in which it had previously appeared for the first time. Thus in *S. ocellatus* a very small proportion of the larvæ in the first stage possessed the specialised head of the genus, the others having a rounded head. The gradual acquisition of this character by the first stage is to be expected, for this period has already acquired everything else that is distinctive of the second or even later stages. Again, in *S. ligustri* the purple borders to the oblique stripes appear, as a rule, in the third stage, but the time at which they appear and the extent to which they develop are very variable, and sometimes they are not present at all. The instances in which the borders did not appear until the fourth stage were, however, rare in my experience, but they seem to have been universal in the case of other observers. Here, then, is a character which has nearly, but not quite, established itself in the third stage. So also with the forked termination of the caudal horn in *S. ocellatus* and *S. ligustri*. This character is fading out of the advanced stages of these two ontogenies. In the first stages it is always present, but later the structure is very irregular in the degree to which it is developed, and it is only present in a certain proportion of the larvæ, that proportion becoming smaller as the stages advance.

11. THE IMPORTANCE OF MAINTAINING THE CONTINUITY OF SERIAL MARKINGS.—I have already pointed out (last year) that a slight suggestion may produce the effect of a continued series when the marking has been repeated sufficiently often. If the series be of protective value such suggested continuity may be of great importance to the species. Conversely a very decided break in an



otherwise complete series must tend to attract attention. Such a break is rendered necessary by very deep-seated anatomical facts in any series of markings that arise round the spiracles, because of the absence of these latter upon the meso- and metathorax. The series could be rendered continuous in either of the following ways:—(1) by concealing the spiracle on the prothorax (which is the real difficulty, for the series is complete, and ends at the 1st abdominal without it); (2) by acquiring a different mark round this spiracle so as to prevent it from forming part of the series; or (3) by continuing the marks upon the meso- and metathorax regardless of the absence of spiracles. This latter is seen in the extreme forms of the spotted varieties of *S. populi*. The second is seen in *M. stellatarum*, where the anterior spiracle is red (and far less conspicuous); the others black. The very interesting cases of *S. ocellatus* and *populi* are instances of the first method. In the protective attitude the anterior spiracle is completely concealed by approximated folds of skin. In *S. populi* also it is less conspicuous at all times. This is very interesting, because the spiracles are brightly coloured (in both species), and that upon the prothorax would be far more conspicuous than the others in the *Sphinx* attitude. In *S. ligustri* the spiracles are far less conspicuous, and the interruption does not attract attention. There are probably many other instances of the different methods by which a series of spiracular markings may be rendered continuous. In many *Noctua* larvæ the first and last spiracles are much larger than the others, but this is probably due to physiological needs, and the series is not rendered conspicuous by size or colour.

12. PHYTOPHAGIC COLORATION.—(1) *S. ocellatus*.—During the past summer I bred a number of larvæ from the egg, and I certainly found some considerable difference produced by the different food-plants. Thus apple and crab caused whitish-green larvæ; while *Salix cinerea*, and especially *S. rubra*, produced adult larvæ tending towards the yellowish form. *S. viminalis* did not produce nearly such white larvæ as the apple, but, contrary to my expectation and experience, the larvæ were almost intermediate. Thirty larvæ were experimented upon, in five batches, fed respectively upon the food-plants mentioned above. All the larvæ, except two or



three, arrived at maturity. At the same time the effect produced was not so great as I expected in the case of the yellowish forms, which were hardly more than intermediate varieties. But there can be no doubt that some effect was produced, and the subject must be considered settled to that extent. The ova were bought from Mr. Davis, of Dartford, and the numbers selected were too great for accident to have caused the results (which were uniform in each of the five lots). At the same time my experience in the field this year has been different from that of previous years (recorded in my last paper), in that I have come across many instances of larvæ upon food-plants which tended towards the variety other than that found. The most noteworthy instance was that of a bright yellowish variety upon apple, and of two opposite varieties on a tree of *Salix ferruginea* (?).

Hence the question is more complicated than it formerly appeared to be. It seems that the only way in which the results of the breeding experiments and experience in the field can be correlated is by supposing that phytophagic effects are hereditary and gradually accumulate until the influence of a food-plant during a single larval life may not be sufficient to overcome the inherited tendencies following from the effects of another kind of food upon many generations of larvæ. Thus in my breeding experiments there was a much greater tendency towards the whitish rather than the yellowish variety. I was unable to ascertain if this was due to the food of the parents, as Mr. Davis informed me that his larvæ had been kept together (having been found upon various species of food-plants). As a matter of fact, however, there was already evidence before me (last year) that the solution of the difficulty is not so simple as it appeared to be. I read Mr. Meldola's notes upon this subject (in Weismann's 'Studies in the Theory of Descent,' part ii.), and assumed that his instances pointed in the same direction as my own observations. On reading them a second time I found that I had made a mistake (reversing in my mind the effects of the two food-plants), and that the instances are in exact opposition to what I should have expected. He quotes instances of numerous yellow-green larvæ being found upon *S. viminalis* and white-green upon *S. triandra*. Now these results are the very reverse of protective, for *S. viminalis* has leaves with very white under sides, and



those of *S. triandra* are green underneath, as in *S. rubra*. My own observations being very strongly in favour of the protective value of the coloration in this species, and Mr. Meldola apparently believing the same thing, I had fallen into the error of supposing that his instances agreed with my own. Furthermore, all the larvæ I had found upon *S. viminalis* had been white-green, and those upon willows (*S. rubra*) with green under sides, like *S. triandra*, had been yellow-green; so that my observations were the exact reverse of those quoted by Mr. Meldola. But even without observations upon the particular species (*S. viminalis*) I should have doubted whether the instances alluded to were entirely normal, and expressed the real phytophagic tendency of the two plants. Such doubts would follow from the general conclusions arrived at concerning the effect of leaves, with certain colours and surfaces. The same opposition in experience is also indicated by Mr. Meldola when he speaks of six larvæ being found upon a species of willow, four of them being bright green and two bluish green. Nevertheless, my experiments rather supported Mr. Meldola's instances than my own view, for the *S. viminalis* larvæ were not nearly so whitish as those fed upon apple. I am hoping to experiment upon the effect of this food-plant and of *S. triandra*, on a large scale during the present summer (1885).

(2) *S. ligustri*.—Mr. Meldola quotes two instances of phytophagic coloration in this larva. In one case the larvæ feeding on laurustinus were darker than those upon privet; in the other instance ash produced a more greyish green than either lilac or privet. I have noticed the same thing with regard to larvæ found upon ash, but I should say that these larvæ resembled the lilac forms, and differed from the privet. Mr. W. Davis's expression "greyish green," quoted by Mr. Meldola, applies extremely well to the larvæ which I have found upon lilac. It is now many years since I have observed this difference (at Reading, Oxford, and this year at Great Malvern) between the adult larvæ found upon privet and lilac. The difference is very hard to define, but very real. The green ground colour and the purple stripes are duller in the lilac larvæ, and the difference is independent of the lightness or darkness of the larvæ, for light and dark individuals occur in both varieties. This year I reared twenty-four larvæ from the egg, in two separate



lots, fed respectively upon lilac and privet. I also fed a detachment upon ash, but the larvæ did not thrive. In the fifth stage the difference appears, and is quite obvious, although much less so than that of *S. ocellatus*. An attempt has been made to show the effects of this experiment in fig. 7A (lilac) and B (privet), natural size (Plate VII.). This phytophagic effect is also protective, for the under sides of privet leaves are of a yellower brighter green than in the case of lilac, and the total effect of the two bushes is in the same direction, especially when looked at from a little distance. The difference is made by texture rather than colour. The protective nature of the two colours is also very apparent when the larvæ are found upon the bushes.

(3) *S. populi*.—There are very great differences in the ground colour of these larvæ, quite equal to those of *S. ocellatus*, but it is not known whether there is any relation with the food-plant. The two chief varieties are similar to those of *S. ocellatus*, a bright yellowish green and a very white bluish green. I feel sure that many years ago I found the latter variety with a blue horn, and so resembling *S. ocellatus* that they could not be distinguished for certain (until pupation). *S. populi* is occasionally found upon various species of *Salix*, and this year I have come across one upon *S. Babylonica* and one upon a tree evidently allied to *S. cinerea*. Both larvæ were light yellowish varieties, and this would be the tendency of the food-plants in the case of *S. ocellatus*. On the other hand, the larvæ bred from the same batch of eggs may vary greatly, even if fed upon the same plant. During the past summer Mr. A. Sidgwick proved this, poplar being the food used. It is very likely that further work upon this larva may throw light upon the case of *S. ocellatus*. It will be especially interesting to note the relation of the red spots (which are more common and more developed in this species than in *S. ocellatus*) to the ground colour. I believe that in this species the spots have no relation to any particular shade of ground colour. I certainly remember yellowish larvæ with the spots, and in my paper in the 'Transactions' of this Society (Part I., April, 1884, Plate I., fig. 2) an extremely pale larva is figured with the spots developed to a very remarkable extent (I am indebted to the kindness of Mr. G. C. Bignell for the loan of the drawing which was figured). These facts would favour



the suggestion that there is no significance in the red spots occurring only upon the yellowish variety of *S. ocellatus*.

A more detailed account of the experiments upon *S. ocellatus* and *S. ligustri*, together with a consideration of the difficulties attending the interpretation of many facts by a theory of "phytophagic" coloration, and an account of the structural basis of colour in larvæ and its dependence upon the food-plant, will be found in my paper, "On the essential nature of the colouring of phytophagous larvæ," &c., Proc. Roy. Soc., vol. xxxviii., No. 237, pp. 269—315.

13. THE ONTOGENY OF THE LARVA OF *SELENIA ILLUNARIA*.—The eggs were laid (April 4th and 5th, 1884) by a captured female of the spring brood, and were kindly sent to me a few days later by Mr. W. Holland, of Reading. They are oval, 1 mm. in their longer, and .75 mm. in their shorter diameter, and a little flattened from above downwards. The eggs were all red-brown in colour when they reached me, but subsequent observations upon the later brood showed that they are first light yellow, and that they darken to red-brown in two or at most three days after being laid. Just before hatching the eggs again change colour, becoming very dark grey, almost black. This darkening is generally complete in one day, but it takes place more rapidly in the ova which hatch latest. The larvæ emerge in from one to three days after the last darkening is complete. The larvæ first appeared May 2nd, and all had emerged by May 11th, but a large proportion of the ova (23 out of 57) were hatched on the first two days of this period, while the rest of the eggs gradually hatched on the remaining days.

The chief object in working out this ontogeny was to test further the theory I suggested last year (after work on the *Ephyridæ*) that young Geometer larvæ assume attitudes conducing towards protection during rest upon the surface of leaves, which will, of course, be very different to the well-known positions taken up in later life, when the larvæ cling to branches of the food-plant.

*Stage I.*—The young larvæ (fig. 15,  $\times 6$ , Plate VII.), when first hatched, are about 2.75 mm. long when extended, and are rather stout. They have the habit (very common among Geometer larvæ) of moving the



anterior part of the body rhythmically to and fro for a considerable time, while holding by their claspers. When disturbed they sometimes fall with a thread, but generally quite passively, bending the body into a (ventrally concave) U, and remaining in that position for a long time. In this attitude the head and three thoracic segments are bent backwards, and the true legs folded upwards towards the head, while the anterior pair of claspers are bent backwards towards the last pair. This attitude is sometimes imperfectly assumed, but, if the larva be further disturbed, all the details are carried out in full. The favourite attitude of rest is that shown in fig. 15, Plate VII., the back being curved so that the head is only slightly raised above the supporting surface. In this position the rhythmic lateral movements often result from gentle disturbance, and also occur spontaneously. The body of the larva is nearly cylindrical, the head being much the widest part, and, after this, the region of the posterior claspers; the intermediate part being nearly uniform, but becoming slightly wider towards the extremities. The ground colour is black, as seen from above, but in many specimens the two anterior thoracic segments, and those behind the 5th abdominal, are lighter in colour, the hind part of the hind claspers and anal flap being lightest. The sides and ventral surface are brown, of which the shade varies in depth in different individuals. There are four white intersegmental bands across the back, in the central part of the body, separating the segments from the 1st to the 5th abdominal inclusive. These bands are made up of irregularly-shaped white spots, which produce the effect of a continuous stripe upon a superficial examination. The first band is the most distinct, but they are all very prominent, because of their strong contrast with the ground colour. Only the first band is continued ventrally (much less broad), while the others cease at the spiracular level, where they are broadest. The head is not of the common Geometer shape, with a deeply-notched crown, nor does it present any of the other irregularities so often met with in this group. It is rounded and lobed by a mesial line, which divides below enclosing a white or greyish triangular mark (the clypeus) above the labrum, which is also light-coloured. The rest of the head is black. The whole of the body is thinly clothed with fine long hairs. There



is a small tubercle with a few prominent hairs on each side of and above the anus. The spiracles cannot be distinguished with the naked eye. After twenty-four hours' feeding the larvæ are about 4 mm. long, and they are not quite so stout proportionately. When disturbed they now let themselves down with a thread. In the bent-up (U-like) attitude a slight lateral bend of the head is sometimes seen. This is an interesting fact, as it exhibits a tendency towards the greater asymmetry afterwards more commonly observed. A light line now appears on the sides of the three thoracic segments, and the white markings of the four bands at the same level appear to continue this line backwards as an interrupted spiracular line. There are traces of a fifth band between the 5th and 6th abdominal segments. The anterior band is, as before, far more distinct than the others. The light ground colour which appeared anteriorly and posteriorly in some specimens has now generally darkened. This seems to take place directly after feeding for the first time. In two days the length is 5 mm., and the larva is very uniformly cylindrical. There is no change in the markings or habits. A little later the ground colour of the larvæ becomes less black, though still remaining dark. In six days the larvæ are about 7 mm. long, and in nine days most of them (eight out of twelve) changed their skins for the first time.

*Stage II.*—(See fig. 16,  $\times 2$ , Plate VII.). I was not able to observe whether the skins were eaten, but this is probably the case, as no traces of the cast skins could be found. In this and succeeding stages the same lateral movements occur, although they are less often seen after the second stage. The larvæ are stout and about 8 mm. long at the beginning of this stage. During rest the head (which is unchanged in colour and shape, except for a little flattening) and two anterior thoracic segments are bent backwards, and the bend pointed and made apparently angular by the 3rd pair of true legs, which are held out straight. Thus this position is assumed *before* the appearance of the ridge bearing the 3rd pair of true legs in later stages, which makes the same attitude so much more irregular and effective. The irregular spiral attitude is also often seen in this stage, and when this is the case the head and two anterior thoracic segments are bent on one side as well as



backwards. There is not much tendency towards falling after disturbance, but a thread is always ready if the larva should be roughly shaken from its hold. The larva is still hairy, but the hairs are less prominent. There is the same pair of small tubercles posteriorly, and they remain throughout larval life. The markings are very similar to those of the last stage. The anterior white band is by far the most distinct, and consists of two chief rather yellowish patches with smaller dots. It is continued underneath, but is interrupted at the sides. The two succeeding bands are comparatively inconspicuous, and are formed of small dots. The fourth is not sharply defined and bright, but is much broader than any of the others, being continued on to the 5th abdominal segment as a light greyish cloud. This cloud is continued (becoming narrower) on to the ventral surface. There is a light line on the sides of the first three thoracic segments, and traces of the same line further backwards at the junction of the lighter ventral and darker dorsal ground colours. There is also a very faint white line in the position of the subdorsal, extending from the 2nd abdominal segment to the posterior end of the body. The dorsal ground colour is very dark brown, becoming dull black behind the 5th abdominal segment. The colour is darker in front of and behind the first white band and anterior to the last band. The depth of the ground colour varies in different individuals. The ventral ground colour is lighter brown. The darkening in front of the posterior white band is continued on to the sides, but not ventrally. The protective resemblance (in colour and attitude) is evidently to the excrement of birds. The size is rather small for this, but it is probable that both the colours and the habit have been handed backwards from more advanced stages. It is, however, very likely that the resemblance is of use in this stage, although the small size must be the chief protection, at any rate, from some enemies. Towards the close of the stage there are some changes which anticipate the appearances which follow the next ecdysis. Thus the 4th and 5th abdominal segments become rather swollen, and the light cloudy colour extends and produces a somewhat mottled appearance on this part of the larva.

*Stage III.*—(See fig. 17, natural size, Plate VII.). This stage began sixteen days after hatching in the case



of nearly all the larvæ observed. Only at this point in the ontogeny are there considerable changes in the larvæ, for the first two stages were very similar to each other, and the last two are practically the same as the third. The length is about 11 mm. when the second ecdysis is taking place, and the larva is fairly stout on entering the third stage. It is very difficult to accurately measure the larvæ in this and (to a less extent) in succeeding stages, because the body is so rarely extended. The important structural characters of the larva from this time forward concern the head, the 3rd pair of thoracic legs, and the 4th and 5th abdominal segments. The head is much flattened, and appears merely as a continuation of the body, the constriction between it and the 1st thoracic segment becoming quite inconspicuous. The 3rd pair of thoracic legs are placed upon the summit of a very large and prominent transversely-directed ventral ridge. The importance of this structure is to render conspicuous the dorsal bend of the body at the 3rd thoracic segment in the protective attitude assumed during rest. At such a time the head and 1st and 2nd thoracic segments are bent backwards so far as to be almost parallel with the anterior abdominal segments, while the 3rd pair of legs are held straight out from their ridge on the convexity of the abrupt bend in the 3rd thoracic segment; but the extremities of the legs are generally curved inwards so as to nearly meet. The effect is greatly increased by lateral swellings on the 2nd thoracic segment, and by the 1st and 2nd pair of legs being bent up towards the head, and thus becoming invisible except on a close inspection. The colours, as will be seen, greatly aid the effect of this extremely irregular and unlarva-like attitude. The protection is by resemblance to a brown and crumpled leaf-fragment, or to the excrement of birds, according to the colour; and at this stage the larva is generally at rest upon the leaves. The 1st, 2nd, and 3rd abdominal segments are extremely round and cylindrical, and it is difficult to detect the furrows between them. The 4th and 5th abdominal segments are much swollen, and each has two small dark dorsal tubercles terminated by a single hair. These two segments are held in a slight curve with the concavity below. Other similar, but much smaller, tubercles are sparingly scattered over the body of the larva. There are also the two posteriorly-directed



anal tubercles. The lateral margins of the anal flap are invisible, except upon careful observation. A few scattered hairs are still present, and are rather more abundant anteriorly and posteriorly. The ground colour varies from red-brown to dull yellow; in all cases mottled with lighter tints. The anterior white ring of earlier stages is present as two short transverse pale yellow lines, one on each side of the dorsal middle line in the anterior part of the 2nd abdominal segment. An inconspicuous lightish cloud sometimes extends backwards from these marks for a short distance. The transverse markings are sometimes covered by the reflected posterior part of the 1st abdominal segment in the protective attitude. There are no traces of the next two bands, but the light colours on the side of the swollen 4th and 5th abdominal segments are the remains of the fourth band, which became diffuse and cloudy in the second stage. The 4th abdominal segment is not covered with the light cloud to such an extent as the 5th. There is a tendency towards a longitudinal arrangement of the lighter markings, especially in the more cylindrical parts of the larva. The under side of the head and 1st and 2nd thoracic segments is much lighter, and of a dull yellow colour. This of course becomes the upper side in the protective attitude (see fig. 17, Plate VII.). The spiracles are *very* indistinct at all stages. The segments behind the fifth abdominal are darker in colour, generally showing a combination of very dark grey and rich brown. The ventral surface of the first four abdominal segments is rich brown with creamy mottlings longitudinally arranged, the colours being continued on to the under side of the transverse ridge bearing the 3rd pair of true legs. The upper surface of this ridge is very dark. In many larvæ the brown is replaced by greyish tints. The protective attitude of Stage III. is remarkable for its excessive irregularity in the vertical plane. Occasionally there is a deviation to one side, especially in the bend at the 3rd thoracic segment; but this is exceptional, and the efficiency of the attitude is not, as a rule, due to a spiral or bilaterally asymmetrical position, as in the case of the *Ephyridæ*. Nevertheless, the larva at rest is wholly unlike a Geometer in the usual position of resemblance to a twig, although this attitude is assumed during later stages. During the maintenance of the



former attitude the larva nearly always clings to the leaf on which it is feeding, and does not return to the twig in the intervals of rest (as during the succeeding stages). The great feature of the attitude is the remarkable bend in the 3rd thoracic segment, and the intensely exaggerated effect produced by the 3rd pair of thoracic legs projecting from their prominent ridge. There is also a bend (in the opposite direction, dorsally concave) in the 2nd abdominal segment, and another (ventrally concave) between the 4th and 5th, pointed by the pair of dorsal tubercles on each of these segments. The larva is supported by a thread of silk in the protective attitude. When the thread is cut in two the larva falls into another position, showing that there is considerable tension on the thread. In this second position it remains steady for some time, but eventually the first attitude is again assumed, usually after the appearance of the lateral movements. When a larva is disturbed it is most remarkably passive, thus carrying out its resemblance to immovable objects; but if the disturbance be increased the lateral movements begin.

*Fourth and Fifth Stages.* — The colours and markings of the last two stages are quite similar to those of the third in nearly all cases (see fig. 18, natural size, Plate VII.; end of fifth stage). Occasionally the white band on the 2nd abdominal segment seems to be absent, and sometimes it is concealed beneath the reflected hinder part of the 1st abdominal segment. The attitude is, however, quite different from that assumed in the third stage, and is of the type most usual among Geometers, protection being gained by resemblance to a twig. The head and first two thoracic segments are bent back, as in the third stage, but not to an equal extent, and the 3rd pair of thoracic legs are held as before, and the supporting thread often passes between them. The bend is, as before, rendered more effective by the swollen sides of the 2nd thoracic segment. The rest of the body is held straight, especially the cylindrical 1st, 2nd, and 3rd abdominal segments. The resemblance to a twig, with a projection on one side of the extremity, is very striking. The projection is formed by the head and first two thoracic segments, for by position, shape, and colouring the line of the body is continued into the ridge on the 3rd thoracic segment and the 3rd pair of thoracic legs, which appear as the real termination of the object.



When the larva is not at rest the ridge bearing the 3rd pair of thoracic legs is bent upwards, so as to be nearly parallel with the head and two anterior thoracic segments, presenting a remarkable appearance. The colouring of the whole, the swollen 4th and 5th abdominal segments with their tubercles, and the manner in which the claspers are applied to the branch,—all assist in forming a very perfect imitation of a twig. Just before spinning up the larva becomes very stout and short. The fourth stage began twenty-three days after hatching in the case of most of the larvæ, but press of work prevented me from ascertaining the length of this stage and the one succeeding it. The duration of the stages is, however, extremely variable. Thus out of seventeen larvæ hatched in the same twenty-four hours, one was changing the first skin, several the second, while many had already entered the third stage. Four larvæ (out of the seventeen) spun slight cocoons just thirty days after hatching. In these instances the whole period was shorter than usual, and hence each of the stages mentioned above (as far as possible average) was also abbreviated. The larvæ of this and other batches pupated after variable periods all greater than thirty days, but most of them less than forty. In some few instances, however, the two last stages (especially) were immensely prolonged, so that larvæ which hatched about May 5th had not spun up at the end of July. Although these last larvæ died before pupation there can be little doubt that in this greatly prolonged larval period, in a few cases, and in the extreme irregularity altogether, there are indications of an older monogoneutic condition. This is all the more interesting in a species which exhibits seasonal dimorphism to such a marked degree as *S. illunaria* (in the perfect state). This dimorphism must, of course, have arisen gradually, long after a digoneutic condition had been established; and the very exceptional degree which is shown by the former implies immense antiquity for the latter. Furthermore, the species has been polygoneutic in the present year (1884), but the indications of the ancient monogoneutic condition are less remarkable in relation to polygoneutism than to such extreme and exceptional seasonal dimorphism, for well-marked instances of the former relationship have been already adduced. It must also be remembered that the dimorphism of this



species includes a very great difference in size between the imagines of the two broods, as well as a most decided divergence in colour.

The dates of the various events of the life-history during the present year (1884) have been as follows:—The ova were laid April 14th and 15th; the larvæ hatched from May 2nd to the 11th; the first larvæ spun up June 1st, the others at various subsequent dates all through June and into July. I conducted experiments with artificially induced cold upon most of the pupæ, but the imagines emerged a few days after the withdrawal of the ice in all cases. A few pupæ were not exposed to cold, and these had pupated towards the beginning of July, emerging in about twelve days. The eggs of the next brood were laid on July 4th, and a few days afterwards, by a moth which had been exposed to ice in the pupal state for thirteen days. (The male which fertilised the eggs had been similarly exposed for nine days). The tendency of this cold would, of course, be towards diminishing the number of broods in the year, and, as it did not have this effect, it may be left out of consideration, except as keeping back all subsequent events by a period about equal to that passed in the cold. The eggs hatched in the middle of July, and the larvæ spun up from the 20th of August to the middle of September. One, however, only spun up on October 29th. The perfect insects emerged in from two to three weeks, but a considerable proportion have not emerged and constitute the winter brood. Eggs for a third brood were laid September 15th and the following days, turning brown in two or three days, as on previous occasions. The larvæ began to hatch on October 4th. These larvæ are not adult at the present date (December 18th). They have been partially kept back by the difficulty of obtaining food at this time of the year, but there is great doubt as to whether they could have lived at all in the open air, unless, indeed, these larvæ hibernate. Thus there have been three broods of larvæ this year, and some individuals of the first brood showed tendencies towards a winter pupation (but died as larvæ); many individuals of the second brood are passing the winter as pupæ, and it seems likely that the third brood will hibernate as larvæ.

*Summary.*—There are a few especially interesting features in this ontogeny. The two first stages are



extremely unlike the remaining three in ground colour, markings, and shape. The two former are very dark, almost black, with white bands at intervals round the central part of the body, while the larva is cylindrical. The three last stages are very similar to one another, but much more complicated than the first two, and the break very sudden. The chief traces of continuity are seen in the permanence of the anterior white band in a modified form, and in the changes that take place towards the end of the second stage. These latter, however, are probably due in a great measure to the actual existence of the third stage beneath the tightening skin of the second. The last three stages bring out the importance of attitude in a very interesting way. With a similar colouring and structure the appearance of a larva in the third stage at rest is extremely different from one in the fourth or fifth stage, and the difference is correlated with a position upon leaves or branches respectively. It is very likely that some such difference will be found in the ontogeny of all *Geometer* larvæ which are protected in the advanced stages by resembling twigs. The rhythmical lateral movements are very hard to explain. The habit seems to be extremely ancient, as it is so widespread and so frequently manifested. At present I can only suggest a possible use in the unvarying and mechanical characters of the movements which are certainly very unlike those generally seen in organic forms.

14. THE UTILISATION OF THE CHANGES IN COLOUR BEFORE PUPATION FOR PROTECTIVE PURPOSES. — In a paper read before this Society last year (November 7th, 1883), I suggested that the darkening of certain larvæ before pupation is probably of protective value. I was not then aware that this suggestion had been previously made by Mr. Meldola (see his paper in *Proc. Zool. Soc.*, 1873, p. 155, and the Appendix to his translation of Weismann's book quoted above, p. 525). Mr. Meldola instances the darkening of *Sphinx ligustri*, and this was the very larva which prompted me to make an identical suggestion, quite independently, although many years afterwards. In my last paper I gave instances of green larvæ protected by their resemblance to leaves, which became brown when they wandered over the bare ground before burying, and other larvæ which darkened less, still retaining green as their predominating colour, and



which found suitable places for pupation in damper and greener situations. I did not then know any instance of protection by a change of colour in the reverse direction. I am now able to supply such an instance. During the present summer (1884) I bred a number of the larvæ of *Ennomos angularia*. The adult larva is dark brown in colour, and in this respect, as well as by its attitude, is extremely well protected by resemblance to the dark twigs of its food-plant (elm). The pupal period is very short, and passed in the hottest part of summer, and the cocoon is very loosely constructed of leaves, between which the larva and subsequently the pupa are generally visible. In this case the brown colour of the larva is discharged before pupation, and it becomes green (see fig. 19, natural size, Plate VII.), and is therefore well protected in its new surroundings. The pupa is also green, but is dimorphic, one form being light bluish green covered with white dots, and the other dark brownish green sprinkled with black dots (see figs. 20 and 21, natural size, Plate VII.). Both forms are well protected in the cocoon, and it is probable that the dimorphism is of *direct* value (see my paper quoted above for other instances of the direct value of dimorphism). In *S. illunaria* the larva only becomes green over a small part of its surface, and the pupa is of the ordinary shining reddish brown colour, but the cocoon is fairly complete, so that the contents are hidden. I may also add to the instances adduced last year the case of *M. stellatarum* feeding on *Galium verum* in dry situations exposed to the sun, which darkens very completely all over before pupation, and which wanders over the earth before making a slight cocoon, within which it may be sometimes visible. Again, there is the unusual darkening of the larva of *D. vinula*, which makes its cocoon on the bark; while other larvæ (*S. populi* and *ocellatus*), with the same food, darken very slightly, but pupate in the earth, which is covered with green vegetation beneath such trees (growing in moist places). Of course there will remain a great many larvæ which do not gain protection in this way, for example, all those which form complete cocoons at once or bury without wandering and exposing themselves in new surroundings with which their colours do not harmonise. I only urge that certain larvæ gain protection by making use (through natural selection) of the



changes of colour before pupation, and this theory is, I think, much supported by the unusual change of colour in the larva of *E. angularia*.

15. ON A CURIOUS HABIT OBSERVED IN SOME LARVÆ BEFORE PUPATION.— This summer (1884) I have been told by my sister of a curious habit that she has noticed in the full-fed larvæ of *M. stellatarum*. When these have ceased to feed, but before the colour has darkened, they cover themselves all over with a brown fluid from their mouths. My sister describes the process as occupying considerable time, being conducted with the greatest care. The mouth is even brought into contact with the dorsal surface of the 1st thoracic segment, so that this is moistened together with all other parts of the larva. The same observer considers that several layers of fluid are poured out over the larva, and she believes that the changes of colour before pupation are produced in this way, stating that the moistened part of the surface is quite different in colour from that which has been hitherto untouched. This interesting observation seemed to render intelligible a fact which must have been noticed by every breeder of caterpillars, *i. e.*, that adult larvæ which are thoroughly wet all over the body are often seen in the breeding-cages. I had also noticed that such larvæ had ceased to feed before this took place, and that soon afterwards they changed colour and wandered about to find a spot suitable for pupation. With this interpretation I watched carefully, and in a few days I saw the adult larva of *S. populi* carefully and very systematically covering itself with fluid. I then recognised the moistened surface as quite similar to that which I had often seen before, when I did not know of the method by which the moisture was applied. Since then I have seen the same thing in *M. stellatarum*, although in this case the fluid (if any) seemed to dry at once, and was hardly ever visible. The movements of the head are exactly those indicated by the term "licking." It seems likely that this habit is really very common, perhaps universal, among larvæ, but I do not feel any certainty as to its use. I do not see how it can affect the change of colour, for this must be due to comparatively deep-seated processes, whereas the fluid is superficial. Further, the larva of *S. populi* does not change in colour to any extent, and only on the back,



while the fluid was applied to the ventral surface as well as to all other parts. At the same time it is very likely that the moistened part may, while wet, appear different in colour from the dry part. The change of skin at pupation does not essentially differ from an ordinary ecdysis, and it is therefore difficult to understand why the skin should receive such elaborate preparation for the former event only. It is to be hoped that further observation may decide upon the frequency of the occurrence and lead to some suggestion as to its use.

16. AN ANATOMICAL REASON FOR THE SPECIAL PROTECTION OF LARVÆ.—Larvæ differ from most other organisms in their liability to death from slight injuries. The reason for this is to be chiefly found in the anatomical construction of a larva, which may be described as a soft-walled cylindrical tube which owes its firmness, and, indeed, the maintenance of its shape, to the fact that it contains fluid under considerable pressure. The pressure is exerted by the muscular parieties of the body. The advantage of this construction is as obvious as its danger: the larva possesses a motive force which can be applied to any movable part of the surface through the medium of the fluid. Indeed, it does not seem possible that the emission of a process of the body-wall could be effected with any great power under any other system of construction, at any rate, in soft-bodied animals. And it is necessary that larvæ should thrust out various projections with great force. Thus the claspers must retain the larva (often of considerable weight) upon the food-plant during high winds; and the force with which they hold is seen in the fact that larvæ may be often injured by roughly and rapidly detaching them. Again, many larvæ possess flagella or shorter projections, which must be swiftly emitted for the purpose of driving away ichneumon flies, &c. Then there are fluid secretions, which must be ejected with considerable force, and glands producing a disagreeable odour, which are bodily everted at a moment's notice (larvæ of certain phytophagous Hymenoptera). This motive force is also known in very different organisms: the eye-bearing "tentacles" of the snail are thrust out by such means. The retraction of all processes which are emitted in this way must be by invagination, and this is most readily performed by means of an axial muscle attached to the



interior surface of the apex. The retractor muscle of the snail's tentacle is well known to have this arrangement, and I have found striated muscle fibres similarly attached to the eversible glands of hymenopterous larvæ. The most striking of all the instances of this kind of protrusion is, I think, afforded by the well-known flagella of the larva of *D. vinula*. The pink flagella are very long and narrow, and are protruded with great rapidity. At the base of each flagellum there is a small transparent area extending round the whole circumference, and through this, as through a window, the processes of invagination and evagination can be readily watched. When the invaginating flagellum has shortened to half its length, the tip has, of course, been drawn inwards as far as the transparent base, and a pink line is seen in the axis of the latter, rapidly lengthening inwards until the whole axis is pink. As invagination becomes complete the pink axis disappears inwards as the transparent part is itself invaginated. The same phenomena are also seen in evagination in the reverse order. The protrusion and withdrawal of claspers seems to be essentially due to the same process. The whole shape of the larva also depends on the fact that it contains fluid under considerable pressure, as can be readily seen in a dying larva, in which the muscles have lost their tone. Under these circumstances the larva entirely collapses, and the only traces of movement are seen in its thoracic legs, which depend upon their own muscles, and are not moved by the fluid (although the elevations upon which they are placed owe their firmness to this cause).

It is hardly necessary to point out that this construction is extremely dangerous, for a very slight wound entails great loss of blood, while a moderate injury must prove fatal. The larvæ of *S. ocellatus* (and many others) nibble off each other's horns, and the wounded larvæ (although they do not seem to be aware of the injury) lose a great deal of blood, and, although they may recover, are generally stunted; and often, I am sure, the loss of blood proves fatal. If the wound be at all extensive the fat-body and viscera protrude, owing to the pressure on the side distal to the wound (that on the proximal side having been relieved by escape of blood). It is, I believe, in consequence of these facts that the various means of protection in larvæ



are almost always of a passive kind. When active (flagella) they seem to be directed against the attacks of ichneumons, which produce fatal results in quite another way. Nearly all the means of defence against other enemies are such as tend to prevent the larva from being seen or touched, rarely such as to be of any avail when actually attacked. There may be various changes in the mode of defence, but the object is always the same,—to leave the larva untouched, a touch being practically fatal. If the disguise of a twig-like Geometer be seen through, in some cases the larva may drop to the ground; but, if followed, there is no further defence. The larva of *C. elpenor* is protected by resemblance to the brown or green (according to its colour) parts of its food-plant. When it is discovered and attacked it assumes the terrifying attitude, but, if this fail to terrify, it possesses no other means of protection. So also the unpleasant taste or smell are powerless for those foes which attack the larvæ notwithstanding such protection, and the “warning colours” of distasteful larvæ have been acquired to prevent experimental or inadvertent “tasting” on the part of enemies (which would, of course, be fatal owing to the larval construction). And of all the various modes of protection, by far the commonest is that of resemblance to surrounding objects, a means for rendering the larva practically invisible. It seems probable that the extremely perfect and very various means of defence are related to the unusual delicacy which results from larval organisation.

---

---

#### EXPLANATION OF PLATE VII.

---

FIG. 1,  $\times 4$  diam.—The larva of *Sphinx ligustri* just after hatching, extended in walking. There are no markings, the colour is yellowish, the head greenish. There are two rows of hairs on the back, two hairs in each row upon most of the segments. There is another row of hairs upon each side slightly above the spiracles (with the same arrangement of hairs). The hairs are scattered thinly and irregularly upon the head and posterior to the 7th abdominal segment. The caudal horn is seen to be immensely long, and distinctly bifid at the tip. Its colour is black, but the upper half is greenish, because the black surface is rather trans-



parent, and allows the green fluid within to shine through. The termination consists of two tubercles, from each of which a single bristle projects.

FIG. 2,  $\times 3$  diam.—A larva of *S. ligustri* at the close of the first stage, extended in walking. The horn is somewhat longer in this individual, and is now held straight, sometimes at the angle shown, and sometimes parallel with the back. The larva is now bright green, and shows the (white) markings of the stage,—a subdorsal and the system of oblique stripes. These markings are formed by the linear arrangement of minute white shagreen dots that cover the body (not shown), and of larger dots at the bases of some of the long hairs. The two kinds of dots are essentially similar, for the smaller ones also terminate in minute hairs (seen with a lens). Before these markings were established there was a stage when the dots at the bases of the larger hairs became conspicuous, especially in the case of the dorsal rows, so that most of the segments showed four large white spots when looked at from above. On the thoracic segments there were only two such spots. These spots can still be seen in the figure, some of them taking part in the stripes, while some are outside the latter. The subdorsal is more distinct than the stripes, and is entirely made up of the smaller dots. A very faint and small "8th stripe" is seen upon the 1st abdominal segment above the subdorsal. There is a horizontal line upon the thoracic segments parallel with and above the subdorsal. It is chiefly formed by the single pair of large dots upon each segment, and on a superficial examination it looks like the anterior continuation of the 8th stripe. This, however, is not really the case, as the latter is prolonged slightly below its posterior termination.

FIG. 3,  $\times 2$  diam.—A larva of *S. ligustri* at the close of the second stage, comfortably extended at rest. The larva much resembles that shown in fig. 2. The movable horn is brownish red, covered with black tubercles (shagreen dots), which are absent at the sides of the base, and thus cause the appearance of a reddish patch where the 7th stripe enters the base of the horn. The tip is still bifid, but less markedly so. The fork is due to two pronounced tubercles with the hairs upon them. The origin of the larval markings from the arrangement of shagreen dots is very obvious. The dots terminate in minute hairs at this time and in future stages. The long hairs have now disappeared, and so also have the large spots, except those that enter into the "8th stripe" and the line above the subdorsal. The latter is now less distinct, except anteriorly, while the oblique stripes are very clear. There is a pink tinge upon the thoracic legs, claspers, and spiracles. The shagreened head is surrounded by a marginal white line.



FIG. 4,  $\times 2$  diam.—A larva of the same species at the close of the third stage, comfortably extended at rest. The markings are very similar to the last. The subdorsal is now indistinct anteriorly and absent elsewhere. The large white spots are still present upon the anterior segments, and contribute to their markings. There is still a trace of the bifid termination of the horn in some individuals, but this feature requires higher magnification for its detection than has been employed in this figure. The side of the head is now often darkened by a black cloud, which spreads from above downwards, behind the (yellow) marginal line. There is great variability in this character, and it is often absent, as in the individual figured. The spiracles are faintly ochreous, the thoracic legs red, and the claspers dark purplish. The ground colour is often dark green below, which extends upwards as a border to the lower third of the white stripes in the darker individuals. During growth in this stage the shagreen dots of the oblique stripes become enlarged, fuse, and form continuous lines. The annulation of the segments keeps the dots separate for some time (as each dot in a stripe is on a separate annulus, and there is a deep furrow between adjacent annuli). In the 8th abdominal segment there is no annulation, and here therefore the dots coalesce much earlier than elsewhere, and the stripe is more distinct than the others. The anal flap is bordered with white. The purple borders to the oblique stripes appear in this stage. They are never present at the beginning, and there is extreme irregularity in the time at which they appear and the extent to which they are developed. Sometimes they are not present at all in this stage. The borders are linear, and they are first seen in front of the middle of the 1st and last stripe, afterwards upon the intermediate ones. The shagreen dots are absent from the purple borders, or, if present, are very small, the borders being modified from the ground colour. At this stage the *Sphinx* attitude is often assumed during rest; in previous stages it was also seen, but far less commonly. In the present stage, and in the second, there is the greatest resemblance between this larva and that of *Smerinthus ocellatus*. The purple borders of the individual figured are rather more developed than usual.

FIG. 5.—Slightly over the natural size. Larva of *S. ligustri* at the close of the fourth stage, at rest in the *Sphinx* attitude, which is more marked in this stage than in any other. The larva at first exactly resembles the appearance in the last stage, but the purple borders are broader. The remnant of the subdorsal and line above it, with the large dots, are at first present, but disappear later. The "8th stripe" remains. The stripes are white where they are bordered with purple, yellowish above this, while the purple is replaced superiorly by dark green. The ground colour



round the oblique stripes is much yellower and brighter than elsewhere. The larva is shagreened all over, but the stripes become continuous at an earlier period than in the third stage. The purple borders are darker anteriorly and inferiorly, becoming black in the darker individuals (there is great variability).

FIG. 6, natural size.—Larva of the same species at the beginning of the fifth (and last) stage immediately after ecdysis. The larva in this stage is well known. For a few hours after ecdysis the horn and sides of the head are greenish, gradually becoming black. The shagreen dots (terminating in hairs) are also present, but very minute, and the "8th stripe" is visible. Very soon these characters cease to be recognisable, although the scattered white points which form the anterior inferior extremities of the stripes remain to the end, and are true shagreen dots, for each of them has a minute hair upon it. There are also very small but distinct dots on the ventral aspect of the body. Traces of shagreening can even be detected at first upon the caudal horn, which later becomes very smooth and polished.

FIG. 7, A and B, natural size.—Two abdominal segments from the central part of the body of a full-grown larva of *S. ligustri*, viewed from the left side, showing phytophagic differences. The larva from which (A) was drawn had been fed upon lilac for its whole life, while (B) had been fed upon privet. Both are dark varieties, but it is seen that (A) has a darker duller ground colour, and the purple border is not bright, as in (B). It is very difficult to bring out the differences between the larvæ in a figure. Too many annuli are represented on the segments: there should be eight upon each.

FIG. 8,  $\times 3$  diam.—The head and anterior segments of the larva of *S. ligustri* at the close of the second stage, viewed from above. The figure shows the subdorsal, distinct in front, faint behind, between the 1st and 2nd oblique stripes. These markings are formed of yellow shagreen dots. The "8th stripe" and line above the subdorsal are formed of white dots, among which the larger spots are conspicuous. The annulation of the segments is shown, and it is seen that the dots composing the markings are separated by the furrows between the annuli.

FIG. 9,  $\times 4$  diam.—The 1st and 2nd abdominal segments of the larva of *S. ligustri*, rather strongly contracted, just after the third ecdysis (fourth stage). The segments are looked at from above. At this early period in the stage the arrangement of the shagreening is well seen, and the relation of the dots covering the body generally to those forming the markings. It is seen that there is a ring of dots upon every annulus in the segment, and that a single dot in each ring becomes much enlarged and very white.



when the level of the oblique stripe is reached. By this enlargement of a single dot at the appropriate level in each annulus the oblique stripes and other white markings arise. The 8th stripes are seen together as a V, and their constitution is shown to be similar to that of the other stripes. The purple borders are very small at the beginning of the stage, but the figure shows that this marking has nothing to do with the dots (which are absent from it), but arises as a darkening of the ground colour. The annulation of the segments is very distinct.

FIG. 10,  $\times 50$  diam.—The extremity of a well-formed horn of a larva of *S. ligustri* in the third stage, viewed from above. The horn is covered with black tubercles (shagreen dots) terminated by minute hairs, which are always directed upwards. The bifid tip is formed of two rather larger tubercles with longer hairs. This feature is, of course, much more pronounced in earlier stages.

FIG. 11,  $\times 188$  diam.—A single tubercle (dot), seen in optical section, from the side of the horn of the larva of *Smerinthus ocellatus* at the end of the third stage. The hair upon the apex is forked. The great majority are of this kind, but sometimes three or even four prongs are found in this species; and some hairs terminate simply. The penetration of the base of the hair into the apex of the tubercle can be just made out, as shown in the figure. The hairs are transparent and colourless.

FIG. 12,  $\times 3$  diam.—The head of the larva of *S. ocellatus* in the third stage, as seen from the front. The larva was an extremely yellow variety, even at this period. (It was a larva found upon *Salix rubra* in the summer of 1884). The head is covered with yellow shagreen dots (with hairs). These are arranged round the margin as a yellow line in which they have coalesced, but are still recognisable. The two dots at the apex of the head and the summit of the marginal lines are bright red in colour, and greatly enlarged (although they still retain the hairs). At this time they form a very conspicuous feature.

FIG. 13,  $\times 2$  diam. — The head of a whitish-green larva of *S. ocellatus* at the beginning of the fifth stage, viewed from the front. The red tubercles, which were so distinct in the last figure (12), were also prominent in the second stage, and continued into the fourth. At the close of this latter stage, however, the colour becomes yellowish or orange. In this figure (13) it is shown that the tubercles still retain the red colour upon their rounded summits, but their relative size is much less, and their shape is not conspicuous.

FIG. 14,  $\times 2$  diam.—The head of a yellowish-green larva of *S. ocellatus*, advanced in fifth stage (about 50 mm. long) when looked at from the front. In this figure the red has entirely



disappeared from the tubercles, which are now only distinguished from the others by their greater size. In these three figures there is traced the gradual disappearance of a structure which must have been very conspicuous, from its colour and position, when it reached its culmination in the fifth stage. Its present significance appears to be historic. This seems to support the argument that the *Smerinthus* larva was brightly coloured, but has undergone alterations for protective purposes. The brightly-coloured spots that often appear on the body of *Smerinthus* larvæ are explained as due to reversion by this theory.

FIG. 15,  $\times 6$  diam.—The larva of *Selenia illunaria* just after emergence from the egg, seen from the left side. The figure represents the habitual attitude of rest at this stage. The body is almost black, thinly covered with hairs (not shown), and encircled by four white interrupted bands.

FIG. 16,  $\times 2$  diam.—The larva of *S. illunaria* towards the beginning of the second stage, seen from above. The ground colour is not so dark, the anterior band is distinct, the others much less so; the posterior band has become broad, and has spread backwards over the 5th abdominal segment as a light greyish cloud. The ground colour is still dark brown, becoming dull black posteriorly, but there is much variability. The protection at this stage is due to a resemblance to the excrement of birds, which is much assisted by the irregular (sometimes) asymmetrical attitude.

FIG. 17, natural size.—The larva of *S. illunaria* in the third stage, seen from the right side, at rest in the protective attitude. The appearance is now much altered. The anterior band is visible as two transverse pale yellow marks on the dorsal surface of the anterior part of the 2nd abdominal segment. The last band is also present as a light cloud upon the sides of the 4th and 5th abdominal segments, which are swollen, and each of them has two tubercles on the back. The ground colour consists of various shades of brown, or sometimes of dull yellow. The last pair of thoracic legs are placed on a prominent transverse ridge projecting from the ventral surface of the 3rd thoracic segment. By holding the ridge and the legs, as shown in the figure, the bend in the 3rd thoracic segment is made to appear exceedingly angular. The head is very flattened, and continues the line of the two anterior thoracic segments, and, like them, it is lighter on the under surface. The 1st and 2nd pairs of thoracic legs are bent upwards, and are thus inconspicuous. There are also other bends in the body of the larva, as shown in the figure. The very irregular attitude is assumed upon the surface of the leaves of the food-plant, for the larva does not at this time retire to rest upon the twigs. Hence



the protection is not by resemblance to a twig, but to an irregular fragment upon a leaf, such as the excrement of a bird or a brown piece of leaf.

FIG. 18, natural size.—The full-grown larva of *S. illunaria*, seen from the left side, at rest upon a twig. There is no essential difference between the colouring of this stage (fifth) and that of the third (fig. 17), and the intervening fourth stage is, of course, similar. Nevertheless, the appearance is very different, and this is entirely due to the attitude. The bend in the 3rd thoracic segment is still very prominent, but it is not so great as in the third stage. The effect is still to prolong the line of the body into the ridge on the ventral aspect of the 3rd thoracic segment and the 3rd pair of thoracic legs. The rest of the body is held straight, and the resemblance is to a lateral twig of the branch upon which the larva is resting. The effect of the anterior bend is very peculiar and unlarva-like. The white marks upon the 2nd abdominal segment are nearly always present. The thread which supports the larva in the protective attitude often passes between the 3rd pair of thoracic legs (see figure). The attitude and appearance in the fourth stage is similar to that just described and shown in fig. 18. The ground colour is very variable.

FIG. 19, natural size.—The larva of *Ennomos angularia* before pupation, seen from the right side. The colours have undergone change, and the larva was taken out of its cocoon to be figured. The adult larva was dark coloured and twig-like, but the colours have entirely changed to greenish tints. Thus the larva is inconspicuous against the surrounding leaves, which are fastened together to form its cocoon. This is important, for the loose construction of the latter renders the larva easily visible.

FIG. 20, natural size.—The pupa of *E. angularia*, seen from the left side. The pupa was nearly ready for the emergence of the imago, for the darkened eyes can be seen through the covering. In this form the pupa is bluish green, covered with white points.

FIG. 21, natural size.—The pupa of *E. angularia*, seen from above. The figure shows the other form of this dimorphic pupa. It is of a brownish-green colour, sprinkled with black dots. Both these forms are well protected in the cocoon, and it is probable that the species is directly benefitted by the dimorphism.





Poulton, Edward Bagnall. 1885. "II. Further notes upon the markings and attitudes of lepidopterous larvæ, together with a complete account of the life-history of *Sphinx ligustri* and *Selenia illunaria* (larvæ)." *Transactions of the Entomological Society of London* 33, 281–329.

<https://doi.org/10.1111/j.1365-2311.1885.tb00887.x>.

**View This Item Online:** <https://www.biodiversitylibrary.org/item/48719>

**DOI:** <https://doi.org/10.1111/j.1365-2311.1885.tb00887.x>

**Permalink:** <https://www.biodiversitylibrary.org/partpdf/19020>

#### **Holding Institution**

Smithsonian Libraries and Archives

#### **Sponsored by**

Smithsonian

#### **Copyright & Reuse**

Copyright Status: Public domain. The BHL considers that this work is no longer under copyright protection.

This document was created from content at the **Biodiversity Heritage Library**, the world's largest open access digital library for biodiversity literature and archives. Visit BHL at <https://www.biodiversitylibrary.org>.