

XIII. *On the Arrangement of the Cutaneous Muscles of the Larva of Pygæra bucephala.*

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LYONET'S celebrated memoir on the larva of *Cossus ligniperda*, and Straus-Dürckheim's still more beautiful work on *Melolontha vulgaris*, are the most perfect, and indeed the only monographs we have at all complete, on the general anatomy of any insects.

The very complicated arrangement of the cutaneous muscles in the caterpillar of *Cossus* inspired me with the wish to see how far the muscles of other larvæ would agree with, or differ from, this type.

With this view I dissected with great care some larvæ of *Tipula oleracea* and of *Ctenophora bimaculata*; but on comparing two or three specimens together, I found to my astonishment very considerable variations. It then occurred to me to compare several specimens together, in order to ascertain the nature and amount of these variations. The larvæ, however, of the different species of *Tipulidæ* so much resemble one another, that I could not feel certain that these supposed variations were not rather specific differences.

In order to remove this element of doubt, I selected the larvæ of *Pygæra bucephala*, which were obtainable in any numbers, and could not be confused with those of any other species. Moreover, as some of these caterpillars live on oak- and some on beech-leaves, I was curious to observe whether this difference in the food induced any alterations in the muscles. It did not, however, appear to have any such effect.

The full-grown caterpillars are about two inches long, and of a brown colour with dark longitudinal bars.

I have divided my paper into three sections:—

First, a description of the cutaneous muscles of the larva of *Pygæra*.

Secondly, a description of the variations observed in these muscles; and

Thirdly, a comparison, as complete as possible, of these muscles in *Pygæra* with the corresponding muscles of other larvæ.

In examining closely Lyonet's drawings, I have always found them inconveniently small: moreover he has represented alternately the two sides of the insect, so as to reverse the directions of many of the muscles; and as he has also figured the same muscle in different plates, it is difficult to ascertain the exact number of muscles in each segment.

In my drawings I have always represented the left side of the insect, and have never introduced the same muscle into two plates.

I propose to commence my description of the muscles at the third abdominal segment, and then, passing forward on the one hand and backward on the other, to point out the differences which exist in the muscles of the anterior and posterior segments.

No. 1 is a broad and strong muscle which is inserted into the skin near the front of the segment on one side of the dorsal vessel, and passes straight back to be inserted into the fore part of the following segment (fourth abdominal). This muscle is identical with that marked A by Lyonet.

No. 2 (B of Lyonet) is in fact treble, and consists of three muscles joined end to end; posteriorly it is inserted at the ventral side of the preceding, and passes forward parallel to it; but instead of being attached at the fore part of the third abdominal segment, it unites with the corresponding muscles of the two preceding muscles, and is inserted into the fore part of the first abdominal segment.

No. 3 is absent from this segment.

No. 4 (D of Lyonet) lies under No. 1, and is inserted in front, immediately under and behind it; posteriorly, however, it does not pass quite so far back, but is inserted at the line of separation of the third and fourth abdominal segments. It is not wholly straight in its direction, but inclines a little downward in front.

No. 5 (G of Lyonet) lies under the preceding, and is in some respects opposite to it; that is to say, the anterior insertion is on the dorsal side, and the posterior on the ventral, but on the same transverse lines.

These first five muscles must tend to contract the skin of the back.

No. 6 (E of Lyonet). This muscle lies at the ventral side of 2, and just at the dorsal side of the great lateral trachea. Its attachments are hidden by the transverse muscle 35, which will presently be described, and are on the same transverse lines as those of No. 1.

No. 7 (H of Lyonet). This muscle rises on the ventral side of No. 6 and on the same transverse line as the posterior insertions of Nos. 4 and 5, and passing forward and upward under Nos. 6 and 8, is attached on the dorsal side and near the anterior end of No. 6; this muscle and the next following bear the same relation to No. 6 that Nos. 4 and 5 do to No. 1.

No. 8 (F of Lyonet) rises posteriorly between 5 and 6, and passing forward and downward between 6 and 7, is inserted at the ventral side of the anterior end of 6.

No. 9 (I of Lyonet). This muscle is a little more than half as long as 5 and parallel to it, lying on the dorsal side of the posterior half.

Nos. 10 and 11 (L of Lyonet) are attached between the posterior insertions of 1 and 6, one on each side of the posterior end of 8, and pass straight forward for two-thirds of the length of the segment.

Nos. 12 to 15 (Q of Lyonet) rise almost on the same transverse line and underneath 4, and pass forward and downward, so as to cross under 9 and 5, for one-third of the length of the segment.

I have thus described all the longitudinal muscles in the upper half of the segment, and shall now pass to those in the lower half.

No. 16 (*d* of Lyonet) rises on the same transverse line as 4 and 5, and consequently on the line of division between the third and fourth abdominal segment, on the ventral side of the great lateral trachea, and passes straight forward to the front of the third abdominal segment.

Nos. 17 and 18 (*c* and *b* of Lyonet) are parallel, similar to, and on the ventral side of 16.

Nos. 19 and 20 (*ff* and *e* of Lyonet) arise under the posterior ends of 16 and 17, and are inserted in front under the anterior ends of 17 and 18. They are therefore not quite parallel to the axis of the body, but pass a little downward in their course forward, and are moreover nearer together in front. They appear to correspond to the two muscles marked *ff* and *e* by Lyonet; these two, however, are not parallel to and at the side of one another, but the latter overlaps the former in front.

No. 21 (*a* of Lyonet) is parallel to 16, 17 and 18, but is altogether rather further back, so that its attachments in some respect alternate with those of 16, 17 and 18, though they are not nearly midway.

No. 22 (*i* of Lyonet) lies under the preceding muscle, but inclines to the median line behind. It is generally bifid in front.

No. 23 (*f* of Lyonet) rises on the dorsal side of 24 and runs parallel with it, to be inserted under the fore end of 16.

No. 24 (part of *g* of Lyonet) rises just in front of the ganglion and on the same transverse line as 21, and passing forward and upward joins 23, and is inserted with it under the fore end of 17.

No. 25 (part of *g* of Lyonet) rises near the middle line of the body, and passing diagonally forward and upward joins 24, and is inserted with it under the fore end of 17.

No. 26 (*h* of Lyonet) rises on the same transverse line as 25 and 17, close to the dorsal side of the posterior end of 23, and under 25, and passes forward and upward parallel to that muscle, to be inserted under its anterior attachment.

No. 27 (part of *k* of Lyonet) is wanting in this segment.

No. 28 (part of *k* of Lyonet) rises on the ventral side of the hind end of 19, and passing forward and downward towards the ganglion is attached to a ridge, which commences near the middle line of the posterior end of the segment and is continued forward, at the same time curving upward. It is broadest in front, where also it is often divided into several heads.

Nos. 29 and 30 (*p* of Lyonet). These two muscles lie on the ventral side of, and parallel to, the preceding. These three muscles vary considerably in form and relative size.

No. 31 (part of  $\zeta$  of Lyonet) rises under the posterior end of 18, and passing forward and upward at about one-third of the segment at an angle of  $50^\circ$ , is very much hidden by the fold of skin forming the boundary of the two segments.

No. 32 (part of  $\zeta$  of Lyonet) lies parallel to, and on the dorsal side of, the preceding.

Nos. 33 and 34 (part of  $\zeta$  of Lyonet) lie parallel to, and on the dorsal side of, the preceding.

I have now completed the description of the longitudinal muscles and come therefore to that of the transverse series.

The first two of this series pass over or rather inside the great lateral trachea and the muscle 6; the other transverse muscles lie between the longitudinal series and the skin.

No. 35 (part of  $\theta$  of Lyonet), arising in part opposite and on the dorsal side of 16 of this segment, and partly opposite the hind part of the corresponding muscle of the preceding

segment, passes upward, with a slight inclination backward, dividing at the same time into two heads, which are inserted on the ventral side of 2, and nearly opposite the anterior attachment of 1.

No. 36 (part of  $\theta$  of Lyonet) is parallel to the preceding and has similar attachments, but lies rather further back.

No. 37 (part of  $\alpha$  of Lyonet) rises under the fore end of 16, and running forward and upward is inserted under the middle part of 35.

No. 38 (part of  $\alpha$  of Lyonet) bears the same relation to 36 that 37 does to 35.

No. 39 (part of  $l$  of Lyonet) is attached under the fore end of 19, and passes backward and upward to be inserted into the trachea close to the spiracle.

Nos. 40 and 41 ( $m$  of Lyonet). These two muscles rise anteriorly under 20, and pass diagonally backward and upward for about one-third of the length of the segment.

No. 42 ( $n$  of Lyonet) is parallel to and on the ventral side of the preceding.

Nos. 43 and 44 rise on the dorsal side of 28 and pass backward and upward along the posterior margin of 42, opposite to about the middle of which they are inserted.

No. 45 (part of  $l$  of Lyonet) may perhaps be regarded as a continuation of 39. It is inserted into the posterior and lower side of the trachea, close to the spiracle, and passes backward and upward to be inserted close to the upper end of 49.

Nos. 46, 47 and 48 ( $\beta$  of Lyonet). These three transverse muscles lie on the outer side of the following, and are therefore covered by it in the drawing: 46 and 47 are usually joined together at the upper end. With the two following they are concerned in the movements of the proleg.

No. 49 ( $\gamma$  of Lyonet) is attached below the proleg, and passing upward to the inner side of the preceding, is inserted just above it.

No. 50 also is attached at its lower extremity to the proleg, and, passing upward and backward, is inserted under the great lateral trachea.

No. 51 ( $\delta$  of Lyonet) ought almost to be considered as two muscles, since, though it rises singly close to the anterior end of 34, it divides almost immediately. Both branches pass upward, inclining at the same time, and especially the posterior branch, backward, to be attached under 6.

No. 52 ( $\epsilon$  of Lyonet) is a short transverse muscle which lies altogether on the outer side of the anterior branch of 51.

No. 53 ( $r$  of Lyonet) rises at the lower end of 48, and passing straight down, at the same time expanding in width, enters the proleg.

Under this muscle lie four other small ones, which also are attached to the proleg by their lower ends.

No. 54 (perhaps part of  $t$  of Lyonet) is a transverse muscle which lies on the outside of 31 and 32, and partly of 28 also. This muscle and the following are often difficult to find, from their being covered by the skin-fold.

No. 55 (perhaps part of  $t$  of Lyonet) is in this segment generally completely double, and lies parallel to and just behind the preceding.

No. 56 is a series of about eight transverse muscular fascicles which lie on the outside of 28, 29 and 30, and are much hidden in a fold which is bounded by the ridge already

mentioned in connexion with those muscles. The fascicles of which this series is composed vary considerably in number and form in different specimens.

No. 57 (perhaps part of *x* of Lyonet) rises near the middle of the upper side of 56, and passes straight back to the posterior end of the segment.

No. 58 (perhaps part of *x* of Lyonet) rises close to 57, and passes backward and downward to the posterior end of the segment.

Besides these muscles, there are two small ones (86 and 87) which lie under and parallel to 53, and another (88) which runs under and transverse to 46, 47, 48 and 53.

*Anterior Segments.*—The first two abdominal segments are very similar to one another, and may therefore conveniently be considered together. The chief differences which exist between them and the third abdominal segment depend on the absence of prolegs.

It has been already mentioned that the muscle 2, belonging to the second abdominal segment, is quite free from the skin, being attached by its ends to the corresponding muscle of the preceding and succeeding segments. The other superior longitudinal muscles very closely resemble those of the third abdominal segment. In the first abdominal segment there are the two following variations:—First, Nos. 10 and 11 are either united together in front, or at least closely approach one another,—a tendency which is more developed in the two posterior thoracic segments, where they have completely coalesced; and secondly, No. 6 sends off a branch from the upper side of its anterior end.

Nos. 10 and 11 reach to the fore end of the first abdominal segment, and converge in front or sometimes unite.

In the ventral longitudinal series, No. 18 of the first abdominal segment is considerably swollen anteriorly, so as to overlap 21, which in this segment is inserted as nearly as possible on the same transverse line as 16, 17 and 18, and under the latter.

No. 22 of the same segment is single in front.

No. 27 was absent in the third abdominal segment; in the first two it rises on the dorsal side of 28 and passes forward parallel to that muscle.

Nos. 29 and 30 are small in the second abdominal segment, having the same attachment posteriorly, but not passing so far forward. In the first abdominal segment it is difficult to distinguish them from 31 and 32.

In the first abdominal segment, the four small muscles marked 29, 30, 57 and 58 appear to correspond with those so named in other segments; but it is difficult to determine which is which.

No. 35 is completely simple in the first abdominal segment, where also 36 is wanting. In this segment also there are only three muscles to represent 40, 41, 42, 43 and 44, though it is difficult to say which of the five have disappeared.

In both these segments 46 is inserted under or rather outside of 49 above, and in front of it below; the dorsal end of 49 is inserted just above 46, and above 51 below; and 48 is in general quite single.

Nos. 47, 48, 50, 52, 53 and 56 are completely absent in both segments.

*Third Thoracic Segment.*—The muscles in this segment differ so much from those that have been previously described, that in many cases I feel very doubtful whether I have used the right numbers to represent them. A careful examination of the thorax in

different species would throw much light upon this question, but I have not at present the materials necessary for the investigation.

Nos. 2 and 3 are entirely absent.

No. 4 passes straight forward, but does not reach the front of the segment.

No. 5 is completely double. One branch rises at the side of 1, and passes diagonally forward and upward to be inserted under it. The other rises under the lower side of 1, and passes forward parallel with the other branch, to be inserted under its upper part.

No. 6 rises on the same transverse line and a little on the ventral side of 1, and passes back near the hind end of the segment, inclining at the same time downward.

No. 7 lies under or sometimes at the ventral side of, and more or less parallel to, the preceding.

No. 8 is double, and instead of passing straight forward as in the abdominal segments, inclines to the ventral side in front. Both branches rise at about the middle line of the front of the segment, and diverge gradually. The one is inserted under the hinder end of 1, and the other under and at the side of the lower branch of 5.

No. 9 rises under the posterior ends of No. 5', and passes forward and upward, almost to the middle line of the back and for three-fourths of the length of the segment.

Nos. 10 and 11 have coalesced in this segment.

No. 16 is almost entirely covered by 17.

No. 18, instead of being parallel to 16 and 17, as in the abdominal muscles, rises under the posterior end of 17, and passing forward and downward, crosses the middle line of the segment between the two nervous chords, which are here at some distance from one another, and is attached to the fore margin of the segment on the ventral side of No. 21.

Nos. 19 and 20 lie under 17 and 21.

No. 21 rises on the fore margin of the segment and at the ventral side of 17, and passes back, under 18, to the same transverse line as 16 and 17.

No. 22 rises on the posterior margin of the segment under 16, and passing forward and downward, is attached to the skin under the fore end of 21.

No. 23 rises under the posterior end of 21, and passes forward and upward to the fore end of 17, where it is inserted.

Nos. 24 and 25 are attached in front as usual, but instead of extending the whole length of the segment to which they belong, are attached to the middle line of the ventral side, and are not above half the usual length.

No. 26 rises close to the ventral chord not very far from the posterior end of the segment, and passes forward and upward to be attached under the fore end of 20.

No. 27 is entirely absent.

No. 28 rises on the dorsal side of 30 and under 20, and passes forward parallel to 30 and under 26 to the middle ventral line.

No. 30 rises under 23, and passes downward and forward to the posterior end of 26.

Nos. 29, 31, 32 and 33 are altogether absent.

No. 34 is almost as in the first abdominal segment, but lies under instead of over 54 and 55.

No. 35 is as in the abdominal segment.

No. 36 is absent, as in the first abdominal segment.

Nos. 37 and 38 in the thoracic segments pass more forward, so that they are situated at the hinder end of a segment rather than at the front.

No. 39 is absent, as there are no spiracles in the two posterior thoracic segments.

No. 40 is double behind. No. 41 is parallel to 40, but not more than half as long.

No. 42 rises at the lower side of the fore end of 41, and passes upward and backward about as far as 40.

Nos. 43, 44 and 45 are absent.

No. 46 rises under 17, just behind 38, and passes straight upward, and divides at the same time into two diverging branches, both of which are attached to the skin under 7.

Nos. 47 and 48 are not present.

No. 49 much resembles 46, in front of which it is situated. It is however more deeply forked and is shorter, its lower end not passing so far down. It also passes inside 67, while 46 lies outside that muscle.

No. 50 rises under the posterior end of 7 by a double head, and passes forward and downward to be inserted under the middle of 16.

No. 51. This muscle rises immediately behind the upper end of the hinder branch of 46 and passes straight down, diverging however a little from 46, to be attached under the upper side of 16.

No. 52 is small; it rises at the lower end of 50 and passes to the hinder side of the lower end of 51.

No. 53 is absent.

No. 54 rises just behind the lower end of 51 and passes upward, going at the same time under 51, and being attached under the middle of 46.

No. 55 rises close to the lower end of the preceding, and passes upward and backward about as far as the posterior end of 7.

No. 56 differs very materially from the series of muscles so marked in the abdominal segments. It is here double. The two fascicles rise just in front of and rather above 57, and passing downward and forward, at the same time diverging from one another, are inserted opposite the posterior end of the muscles 23, 24 and 25, belonging to the opposite side.

Nos. 57 and 58 are represented by three small muscles which rise under 25 at a little distance apart and pass forward, converging at the same time, and are inserted into the legs. They frequently coalesce so as to form only one muscle.

We have now completed the muscles in the third thoracic segment which appear to represent those of the abdomen. There remain yet fifteen to be described.

Nos. 59 and 60 rise under the fore end of 1, and pass upward and backward to the dorsal line, where they are attached close to the anterior end of 9.

No. 61 rises at the lower side of 60 and passes back parallel to that muscle, but twice as far, and at the same time dividing into two, so that its lower branch is attached close to the fore end of 12.

No. 62 rises close to the posterior end of 60 and passes forward and downward to the fore end of 4. In some specimens I could not find this muscle.

No. 63 rises partly under the fore end of 7 and partly between 7 and 1, and passes backward and downward to the upper end of 49.

No. 64 rises under 7, and just on the lower side of 63, and runs parallel to that muscle. It does not however pass so far back. It is generally completely double.

No. 65, again, rises just below 64, and passes back parallel to it, but is about twice as long, and reaches to the upper end of 42.

No. 66 rises under the posterior end of 17, and passes forward and upward to the posterior end of 64.

No. 67 rises on the lower side of 42 and passes upward to the fore end of 66.

No. 68 rises under the lower end of 49 and passes forward and upward to the anterior end of 8.

No. 69 rises at the fore end of 68 and passes to the lower end of 50.

No. 70 rises at the hinder end of 68 and passes to the hinder end of 40.

No. 71 rises at the lower end of 70 and passes to the upper end of 54.

No. 72 rises at the hinder end of 63 and passes to the lower end of 50.

No. 73 rises under the middle of 17 and passes downward and forward to be inserted close to 24.

No. 74 rises at the upper end of 73 and diverges from it toward the upper side of the lower end of 56.

No. 75 is behind, and almost parallel to, the preceding.

No. 76, rising under the fore end of 8, passes backward and downward to be inserted under the middle of 17.

No. 77 rises at the posterior end of 76, under 17, and passes straight back to the hind end of the segment.

No. 78 also rises at the hind end of 76 and passes downward and backward. It is a short and small muscle, consisting generally of four distinct fascicles.

*First and Second Thoracic Segments.*—The muscles of the thoracic segments differ from one another, as might be expected, much more than do those of the abdomen. It is unnecessary here to mention the muscles which agree with those of the third thoracic segment, and I will therefore confine myself to pointing out the differences, using the third thoracic segment as the standard of comparison.

*Second Thoracic Segment*, however, does not differ very much from the third, and this agreement is even more striking in the small muscles than in the large ones.

Nos. 4 and 7 are thinner and weaker.

The single muscle representing 10 and 11, which are again distinct in the first thoracic segment, is here expanded in front, and usually double.

Nos. 16, 19 and 20 are represented by only two muscles.

No. 18 is double at the posterior end.

No. 22 rises at the upper end of 16, and passes backward and upward to the posterior end of 6.

No. 52 runs from the lower ends of 50 and 72 to those of 54 and 55.

Nos. 57 and 58 in most of my specimens had united together, and were smaller than in the third thoracic segment; but this is not, I presume, always the case.



Nos. 59 and 60 have united together.

No. 61 overlaps 60 at the fore end.

No. 63 is generally, if not always, double.

*First Thoracic Segment.*—In the posterior part of this segment several muscles are wanting, and in the anterior they differ widely from the usual type, being principally modified so as to effect rotations of the head.

The most striking alteration is the presence of the muscle marked 82 (C+ of Lyonet), which is attached in front to the posterior border of the head, and passing through the present segment is attached by four heads along the middle dorsal line of the second thoracic segment; nor did it vary in any of the specimens examined by me. There does not seem to be any muscle comparable to it in the other segments. There are yet three other muscles which seem to be peculiar to this segment. No. 80 rises close to the fore end of 82, and passing over 19, 20 and 26, is attached by two heads near the middle ventral line, close to 56. No. 81 rises with the preceding and follows nearly the same course, but passes under 19, 20 and 26. No. 83 rises from the fore side of the spiracle and passes forward to the upper end of 46.

No. 1 is in this segment divided into two or three separate muscles, which are attached side by side behind, and fixed to the fore part of the segment, or rather into the membrane connecting the head with the thorax.

No. 4 is attached in front, close to 1.

No. 5 is double; in some cases however it is united in front. The one fascicle rises under or at the side of 1, the other rather further down, and both are inserted on the ventral side of 4.

No. 7 lies at the lower side of 6 and parallel to it.

No. 8 perhaps is wrongly identified, since it here lies under 10 and 11, rising close to the fore end of the latter and passing back to the hind end of the former. No. 9 is much broader than usual.

Nos. 10 and 11 are both present, and offer no peculiarity, except that 11 is expanded and sometimes double in front.

Nos. 12, 13 and 14 are absent.

No. 15 is a straight muscle, longer than, and lying at the side of, 9.

No. 16 is completely double; in front it lies at the upper side of 17, and under it behind.

No. 18 rises under the hinder end of 21, and passes forward with a slight inclination downward to be inserted at the lower side of the fore end of the same muscle.

Nos. 19, 20 and 26 are parallel to one another; they rise under 17 and 21, and pass forward and upward to be inserted at the anterior end of the segment, not far above 16.

No. 22 rises under the fore end of 16 and passes backward and upward to the hind end of 6.

Nos. 23, 28, 29 and 34 seem to be absent.

No. 31 is perhaps wrongly identified. It rises under 16 and passes upward and forward in front of the spiracle.

Nos. 37 and 38 appear to be absent.

No. 40 is longer than in the second thoracic. In one specimen it was single behind, and inserted between 51 and 66.

Nos. 46 and 49 are both quite single, and much larger than in the segments following.

No. 50 is wanting.

No. 51 rises at the posterior end of 40, and passes downward to be inserted under 17. This muscle may perhaps be rather the representative of 54.

No. 52 rises close to the lower end of 49 and passes downward and backward.

Nos. 54 and 55 are absent.

Nos. 59 and 60. There are three or four separate fascicles which apparently represent these two muscles. They lie in front of 9, and are parallel to the direction of the segment.

No. 61 is almost or sometimes completely double. It rises at the fore end of 82, and the two branches diverge slightly, both being inserted under 59 and 60.

No. 62 consists of three or four small oblique fascicles which rise along the front of the segment under the three preceding muscles and pass backward and upward.

Nos. 63 and 64 are absent.

No. 65 rises close to the lower end of 49 and passes upward and forward. It is very doubtful whether this muscle is homologous with that marked 65 in the other segments.

No. 66 is much less conspicuous than in the other thoracic segments.

No. 67 rises under the upper end of 49 and passes to the hinder end of 41.

Nos. 68 and 69 rise in front as usual, but pass back parallel with one another to the upper end of 51.

Nos. 70 and 71 are parallel with 65.

Nos. 72, 73, 74 and 75 are absent.

No. 79 lies under 77 as usual, and in this segment is hidden by it.

No. 80 rises close to the anterior end of 19 and passes downward, at the same time with a slight inclination backward, to the middle line of the segment, close to 56. At its lower end it is double.

No. 81 resembles 80, but is smaller; it lies also rather in front, and passes on the outer instead of on the inner side of 19, 20 and 26.

No. 82 has been already described.

No. 83 is devoted to the spiracle, from which it passes forward and upward to the upper end of 46.

Nos. 84 and 85 rise at the lower end and a little in front of 49, and diverging from one another, pass backward and downward; 85 is inserted near the posterior end of 57 and 58, and 84 on the ventral side of them, near their fore end.

*Posterior Abdominal Segments.*—Having thus described the thoracic segments, I now return to the abdomen. The fourth, fifth and sixth abdominal segments do not materially differ from the third. The muscles, however, become narrower and thus occupy less space.

No. 26 is double behind, thus indicating the more complete separation which is to take place in the following segment.

No. 28 is absent. In the fifth and sixth segments there is also a muscle which rises

just above the upper end of 46, and passing downward is inserted just below the lower end of 53.

No. 52 is absent.

No. 55 is single in the sixth segment.

Nos. 16 and 17 approach nearer to one another, and separate a little from 18.

Nos. 47 and 48 are absent.

No. 49 in the fifth and sixth segments is completely double, and stronger than in the fourth segment, which indicates that the prolegs of these segments act in a somewhat different manner.

The gastric muscle  $\zeta$  rises, as in the larva of *Cossus*, on the upper side of 21.

*Seventh Abdominal Segment.*—Owing no doubt principally to the absence of prolegs, this segment differs much from those that immediately precede it. Thus 47, 48 and 56 are entirely absent. 49 and 50 also, though present and well-developed, are much shorter than usual.

On the other hand, in the specimens I examined there were two new muscles lying under 10 and 11, and inserted below them in front. 10 and 11 approach one another in front, and sometimes even unite together.

No. 25 has completely united with 24, and 26 lies on the lower side of these two muscles.

To represent 31, 32, 57 and 58, there are four small variable muscles which seem to be of little importance.

No. 46 also is very thin and weak, so that it is probably of little functional utility, and only present to fulfil the general law of arrangement of the muscles.

No. 51 is single and small. It rises at the lower end of 49 and passes to the front of 34, as in the anterior abdominal segments.

No. 52 is absent.

No. 53 is parallel and similar to 54, though a little shorter; these two muscles are very unlike in front, but become gradually more and more alike.

No. 56. As there are no prolegs to this segment, the series of muscles marked 56 is absent.

Nos. 57 and 58 are represented by two small muscles parallel and similar to 31 and 32.

*Eighth Abdominal Segment.*—In this segment the muscles have become much narrower and weaker, and 31, 32, 33, 34, 50, 53 and 56 are absent.

Nos. 12 and 13 have almost coalesced, so as to form one small muscle, and the same has taken place with 14 and 15.

No. 4 has entirely disappeared, while 3, on the other hand, is double; as also happens in the larva of *Cossus*.

Nos. 7, 8, 10 and 11 have become parallel, and seem to form one series.

In the *Ninth Abdominal Segment* the diminution of the muscles in size and number has proceeded still further; 3, however, is double, as in the preceding segment, and 4 makes its appearance again.

Indeed the number of missing muscles is much greater than of those which are present. These are, Nos. 1, 2, 3, 4, 5, 6, 7, 16, 17, 18, 21, 37, 38, 50 and 51.

The first six of them resemble the same muscles in the preceding segment.

No. 7 rises at the posterior end of 16, and passes forward and upward nearly to the upper end of 37.

Nos. 16 and 17 have coalesced.

Nos. 50 and 51 are even larger than usual, and pass quite back to the posterior end of the segment. 51 is double in front and attached under 16.

Besides these muscles, there are attached to the upright wall of the end of the body, and in a series along the lower middle line of the segment, a number of muscular fascicles which are distributed to the rectum and posterior parts of the alimentary canal; in the same place also are situated the muscles which move the posterior prolegs; I have not, however, examined these muscles with care enough to enable me to describe them satisfactorily.

*Comparison of the Muscles in different Specimens.*—Any one who has carefully examined Lyonet's drawings of the cutaneous muscles in the larva of *Cossus ligniperda*, or still better, has made himself acquainted with the organs themselves, must have been struck with amazement at their number and complicated arrangement.

The muscles in most animals are penetrated by the arteries and capillaries, and are supplied by them with blood; but this not being the case in insects, it is perhaps necessary that their muscles should be divided into numerous fascicles, in order that the blood may have free access to them. Whether for this or some other reason, they are in the shape of thin ribands, the thickness of which varies very much in different muscles and in different parts of the same muscle, but is in the largest about  $\frac{1}{200}$ th of an inch.

The largest muscular fibres in man, which are not penetrated by blood-vessels, are, I am informed by Professor Huxley,  $\frac{1}{400}$ th of an inch in diameter. We can, however, derive no argument from this comparison without knowing the permeability of the muscle and the power of penetration possessed by the blood. It is also worthy of notice, that the wing-muscles of insects are separated into very small fascicles, as if, from the violent and rapid action of these muscles, their particles were more quickly deteriorated, and required therefore more frequently to be removed and replaced by others. The muscles of insects, however, are not only very much divided, but are also very complicated in their arrangement.

Lyonet describes 1647 in the larva of *Cossus*, without counting those which belong to the head and to the internal organs; and truly observes, that this great number "ne pourra qu'étonner ceux qui savent qu'on ne fait ordinairement monter tous les muscles de l'homme qu'à 529, et qu'il y en a même qui le fixent à beaucoup moins." It might be objected, that certain fascicles in insect larvæ, as for instance 16, 17, 18, 19 and 20, ought to be considered as parts of muscles rather than as whole muscles, and that the total number therefore must be very much diminished.

If, however, this were a well-founded objection, we should expect to find these fascicles varying in relative size and number; and as, except in certain instances, they do not do so, we must, I think, admit that Lyonet was right in his mode of estimating their number.

Some few, however, of the smaller muscles do vary; and to determine the number and amount of these variations was my chief object in undertaking the present paper.

No naturalist had previously undertaken this task, though Lyonet has mentioned here and there certain variations observed by him.

It would have taken a great deal of time, and seemed to me scarcely worth while, to make this comparison in all the segments of the body; and I have therefore confined myself to the third, fourth, fifth and sixth, thus including a thoracic somite, two abdominal without prolegs, and one with these appendages.

These four segments I compared carefully in nine different specimens, five of which were fed upon Oak and four upon Beech. But in order to determine a few minor points, I dissected perhaps as many more specimens in a cursory manner, which however confirm me in the opinion that the larger muscles scarcely vary at all. Indeed the only mutation observed in them at all worthy of notice was that in one case the muscles of the third abdominal segment, 16, 17 and 18, were not attached to the skin in front, but were continuous with the corresponding muscles of the preceding segment.

The differences which do exist are not exactly those which I expected to find; whilst some things which I rather thought might vary, remain on the contrary always the same.

Let us take for example Nos. 4 and 5. In the first abdominal segment 4 passes on the inner side of 5; the contrary, however, might apparently have been the case, without alteration of the places of insertion, or of the mode of action of the two muscles; and I thought it probable, therefore, that 5 might sometimes lie on the inner side of 4. But although six segments in at least fifteen specimens were examined, making in all ninety instances, the arrangement was invariably the same in every instance.

This remark is applicable to several other muscles, for instance 6 and 8, 7 and 8, and 23 and 18 in the third abdominal segment; and, indeed, I never observed a case in which a muscle varied in this respect in its relation to another.

The muscles 4 and 5, however, offer a different arrangement in the thorax to that which is so constant in the abdomen. Here, if they are rightly identified, which perhaps may be doubted, though I believe that I am correct, 5 is completely double and lies on the inner side of 4.

This altered arrangement appears to be necessitated by the altered position of the fore end of 4, and by the presence of 60 and 61.

Again, 8, which in the following segments lies on the inner side of 11, in the first thoracic segment has shifted its position and passes on the outer side.

A careful examination of the Plates will show a few more instances of this fact, which, however, are not very frequent.

The relative sizes of the different muscles appeared to vary very little in different specimens, except indeed in those muscles which might be termed the variable muscles.

Such were especially 12, 13, 14 and 15; 28, 29 and 30; 56; 59 and 60; and in a lesser degree, 31, 32, 33 and 34; 57 and 58; 11; 23 and 24 in the third thoracic segment, 8 in the third thoracic segment, and 40, 41 and 42.

If we suppose, as seems probable, that muscles composing the series 12, 13, 14 and 15 usually act together, and that the same is the case with the other three series, 28, 29, 30;

31, 32, 33, 34; and 40, 41 and 42; then the variations observed in these muscles will be of very little importance to the animal.

There are, indeed, other muscles and series of muscles which might *a priori* have been considered equally unimportant, and have therefore been expected to show similar variations. Our knowledge, however, of the mechanism of the muscles, and of the functions they subserve, is so small, that we must be very cautious in forming an opinion on the relative importance of different muscles.

It may perhaps prove that the variability of particular muscles is rather an indication of a different arrangement hereafter to be discovered in certain neighbouring groups. We must, however, suspend our judgment upon these facts until we are better acquainted with the myology of other insect larvæ.

I expected to find, in specimens in which the variable muscles were divided into more fascicles than usual, that this tendency to the division of muscles would pervade the whole animal, or at least the whole segment; this, however, did not appear to be at all the case. It seemed also probable that the variable muscle would either be symmetrical, or at least would tend to be so, in the two opposite sides of the same animal; but in the instances in which both sides were examined, this rule was not found to hold good.

*Differences in the Third Abdominal Segment.*—In the fourth specimen, No. 1 sends off a small branch on the dorsal side at the front end.

No. 5, in the sixth specimen, is partly overlapped by 4 in front.

*The series 12 to 15* consists normally of four small muscles situated in the hinder part of the segment, and passing forward with a slight inclination downward. However, in the third specimen which I examined, the fore end of 15 was turned under 14. No. 12 was double in front, and 13 was almost entirely double, being only joined together in front. In the fourth specimen 13 and 14 were completely double, and 12 and 15 were divided for the anterior portion. The two branches of No. 15 were unequal, the dorsal one being the longer, and inserted under the anterior end of 14. In the fifth specimen, 12, 13, 14 and 15 were double in front. In the sixth and eighth specimens, on the contrary, 12 and 13 were united together; and in the latter are shorter than, in the former the same length as, 14 and 15.

No. 7 is usually single, but in one specimen it was divided into two, for about the posterior one-third.

No. 20, in the sixth specimen, a little overlapped 19 in front.

No. 22 is usually double for about its anterior half; sometimes, however, it is more deeply cleft, and at others it is almost undivided. Sometimes again it is trifid, and in this case the three divisions may differ in size and in degree of division.

No. 25 varies a good deal in width in different specimens.

Nos. 28, 29 and 30 also vary a good deal. Sometimes all three are of about the same width. Sometimes 28 is much the largest, and is bifid, trifid, or even quadrifid. At others 28 is smaller than 29, and the latter is more or less bifid or trifid. Sometimes both these muscles are bifid, and in one instance 30 was completely double.

Nos. 31, 32, 33 and 34. Sometimes 31, sometimes 32, sometimes 34, is double; sometimes both 31 and 34 are double. Sometimes, on the contrary, 33 and 34 have coalesced.

No. 35 in one specimen was divided into three at the upper end.

No. 37 is sometimes a good deal expanded at its upper end, and sometimes divided into two.

No. 38 in the same way is more or less divided at the upper end.

No. 51 is more or less divided, the two main branches of which it consists being sometimes united for a large proportion of their course, and sometimes, on the other hand, almost entirely separate.

No. 52, which is usually single, was, on the contrary, in one specimen double.

No. 56. This series of muscles varies extremely. There are usually from 7 to 11 fascicles, but they were not alike in any two specimens I examined.

No. 57 was double in the second specimen, and

No. 58 in the fifth.

*Second Abdominal Segment.*—The cases of variation in this muscle are almost the same as those already described.

No. 1 in the fourth specimen was completely double.

No. 10 in the second specimen was double for the anterior half. In the fourth specimen 10 and 11 were very small and united in front. In the ninth specimen 11 was double in front.

Nos. 12, 13, 14, 15, 27, 28, 29, 30, 31, 32, 33 and 34 offered various differences of the same nature as those already mentioned; besides which, in the fourth specimen, 14 was much longer than 13 or 15.

No. 26 was completely double in the second specimen.

No. 38 was completely double in the fifth specimen; in which also

Nos. 40 and 41 were united by their lower ends.

No. 54 in the eighth specimen was completely double.

*First Abdominal Segment.*—Nos. 12, 13, 14, 15, 27, 28, 29, 30, 31, 32, 33 and 34 differ as much as usual.

Nos. 10 and 11 are sometimes united in front, sometimes they only converge and do not join.

No. 18 in some specimens does not cover the fore end of 21.

No. 37 in the fifth specimen is double.

*Third Thoracic Segment.*—Nos. 12, 13, 14 and 15 differ as in the above-mentioned segments; 29, 30 and 31, on the contrary, are much more regular.

No. 8 in the fifth specimen was completely double; in the sixth it was double for the greater length, but united in front.

No. 20, in the ninth specimen, was double in front.

Nos. 23 and 24 differed considerably in different specimens. The arrangement figured is, however, perhaps the most usual.

No. 62. This small muscle was in two cases entirely absent.

No. 68 was double in two specimens.

Nos. 59 and 60 are sometimes united; in the fourth specimen they were separate on one side, and had joined on the other. In the ninth specimen the posterior end of 59,

instead of lying at the side of 60, was inserted under, that is to say, at the outer side of it. In two specimens there was a small muscle lying at the dorsal side of 59.

No. 61 is sometimes simple behind, sometimes divided.

I now proceed to compare the muscles of *Pygæra* with those of *Cossus ligniperda*, as described by Lyonet, and of one or two other insects which I have more or less completely dissected.

The following Table shows the letters and numbers used for the corresponding muscles in the abdomen:—

1 = A	16 = <i>d</i>	31 = } <i>t</i>	46 = } <i>γ</i>
2 = B	17 = <i>b</i>	32 = } <i>t</i>	47 = } <i>γ</i>
3 = C	18 = <i>c</i>	33 = } <i>ζ</i>	48 = } <i>β</i>
4 = D	19 = <i>ff</i>	34 = } <i>ζ</i>	49 = } <i>β</i>
5 = G	20 = <i>e</i>	35 = } <i>θ</i>	50 = } <i>β</i>
6 = E	21 = <i>a</i>	36 = } <i>θ</i>	51 = <i>δ</i>
7 = H	22 = <i>i</i>	37 = } <i>α</i>	52 = <i>e</i>
8 = F	23 = <i>f</i>	38 = } <i>α</i>	53 = <i>u</i> { in the first figures
9 = I	24 = } <i>g</i>	39 = <i>l</i> (part)	and <i>r</i> in the last.
10 = } L	25 = } <i>g</i>	40 = <i>m</i>	54 = } <i>y</i>
11 = } L	26 = <i>h</i>	41 = } <i>q</i>	55 = } <i>y</i>
12 = } Q	27 = <i>k</i>	42 = } <i>q</i>	56 absent
13 = } Q	28 = <i>p</i>	43 = } <i>n</i>	57 = } <i>x</i>
14 = } Q	29 } absent	44 = } <i>n</i>	58 = } <i>x</i>
15 = } Q	30 } absent	45 = <i>l</i> (part)	

Thus, with very few exceptions, every muscle of the third abdominal segment in *Pygæra* can be referred to its homologue in *Cossus*.

There are, however, some few differences: B in *Cossus* is only as long as the segment, as is also the case in the larva of *Pontia rapi*; while 2, the corresponding muscle in *Pygæra*, has united with the same muscle of the two preceding segments,—the three together forming only one muscle as long as the first three abdominal segments.

Again, G shows traces of subdivision, and is covered in part by F, while 5 is single, and lies on the dorsal side of 8. I also is treble, while 9 is single. L is treble, while 10 and 11 only form two muscles; on the other hand, Q is only treble, while the series from 12 to 15 is quadruple.

*e* crosses over *ff*, so as to cover it behind instead of lying at the side of it. *k* does not seem to be present in the third abdominal or any of the posterior segments of *Pygæra*, and only makes its appearance in the second abdominal segment.

There seem to be three fascicles, marked *ζ*, to correspond to 33 and 34; and 35 and 36, which are marked *θ*, are represented by several fascicles.

*First and Second Abdominal Segments.*—In these segments there are no further differences of importance. 35 and 36, however, which in *Pygæra* are reduced to a single muscle, continue in *Cossus* compound as before.

Nos. 46, 47, 48, 49 and 50 appear all to be represented by *β*.

*ff* and *e* resemble 19 and 20 more than in the posterior segments.

In the thoracic segments it is much more difficult to compare the muscles of *Cossus* and *Pygæra*; indeed, after devoting a good deal of time and thought to it, I have been obliged



to give up this task, and do not think that it can be effectually accomplished until we know the arrangement which exists in some of the intermediate genera.

Some, however, of the more remarkable peculiarities of the thoracic segments in *Pygæra* are equally present in *Cossus*. Thus, the altered position of 1, 8, 8', 18, 22 and 82 resemble those of D, C and E, *c* and *e* and C+. The remarkable muscles, however, marked 76 and 77, do not appear to have any close representative in *Cossus*.

This comparison, however, is made far more difficult by the arrangement of Lyonet's figures, and by the fact that the same letters are certainly not always used for the corresponding muscles in different segments.

In the first abdominal segment of the larva of *Pontia rapi* the larger muscles were arranged nearly as in *Pygæra*, except that 2 was attached to the skin at the posterior end of the segment, as in the larva of *Cossus*. In the larva of *Disphragis cæruleocephala* the muscles 1 and 2 on the one hand, and 16, 17 and 18 on the other, were represented by numerous separate fascicles, amounting to at least ten in each instance.

This separation of the fibres composing a muscle into separate fascicles is carried to a much greater extent in the larvæ of Coleoptera, or at least in *Dyticus* and the wood-feeding Lamellicorns, which alone I have examined. In these two groups each of the larger muscles is represented by at least twenty separate fascicles, which makes it far more difficult to distinguish the arrangement of the muscles.

The reserves of fat in the larvæ of these Lamellicorns are stored up in large vesicles, as much as .01 of an inch in diameter, and which, being connected together into thin membranes, like a mesentery, have a beautiful bead-like appearance to the naked eye.

The muscular system of the larva of *Tipula oleracea* and of *Ctenophora bimaculata*\* offers us many interesting points of difference. Being unprovided with legs, these little creatures move by resting one part of their body against some solid object, and then pushing the anterior part forwards. To enable them to do this with facility, an immense number of muscles are attached to the inner side of the skin. The total number, indeed, falls a little, though very little, short of that in *Cossus*; yet the real complexity is greater, since the average number of muscles in each of the body-segments is rather over seventy in *Tipula*, while in *Cossus* it is about sixty. This surely shows greater complexity than the larger total, which is merely made up by the irrelative repetition of a lesser number of muscles in a greater number of segments.

The joints of the back in the larva of *Cossus*, like those of *Pygæra*, allow much less play than those of the ventral side, and we find the muscles entirely in accordance with this structure. On the contrary, in the larva of *Tipula* and of *Ctenophora bimaculata*, the back can be bent almost, if not quite, as much as the belly; and if this were not already known, it might be deduced from the arrangement of the muscles.

Lyonet remarks (p. 154, *l. c.*) that his "*a*," which corresponds to my 21, "est remarquable, en ce que, pendant que les autres muscles droits se terminent aux divisions de leurs anneaux, son extrémité postérieure passe au 4, 5, 6, 7, 8, et 9 anneaux cette division, et s'insère assez avant dans l'anneau qui suit; ce qui vraisemblablement a été ainsi

\* Mr. Walker was kind enough to name for me specimens bred from larvæ resembling, and found with, those which I dissected.

ménagé pour faciliter l'ondoyement que fait le corps de la chenille quand elle marche, et qui en rend le mouvement progressif plus aisé que s'il étoit vermiculaire."

It is hardly necessary to say, that there is no similar muscle on the dorsal side in *Cossus* or in *Pygæra*. In *Tipula*, on the contrary, there is a dorsal muscle to which these remarks would well apply.

The great flexibility of the back shows itself, however, in many other ways. In *Tipula* there lie upon each side of the muscle 6, which is here represented by four distinct fascicles, five muscles, corresponding to 16, 17 and 18 on the ventral side; those on the other side being apparently a great development of 2, which becomes almost as important as 16, 17 and 18 together. Moreover, 1 and 21, instead of having their anterior terminations a little behind those of 16, 17 and 18, completely alternate with them; and, again, there are other muscles whose posterior insertions are close to those of 1 and 21, while they pass as far forwards as 2 on the one hand, and 16, 17 and 18 on the other. These arrangements must make the body much more supple.

Once more, there are strong oblique muscles both at the back and at the ventral side, which must give the animal great powers of twisting itself forward with a corkscrew-like motion.

I hope, however, at some future time to be able to lay before the Society a complete account of the muscles of these larvæ, which I have dissected and figured with great care, and shall content myself at present with mentioning one other remarkable peculiarity.

The muscles of the first four body-segments are alike, and very different from those of the posterior somites; we must suppose, therefore, either that the thorax of insects has in reality four segments, or that the muscles of the first abdominal or last cephalic segment have become developed like those of the thorax; in fact, that the first segment of the abdomen, or the last of the head, has detached itself from its usual position and joined itself to the thorax.

The latter hypothesis seems to me more probable, and it is also supported by the position of the anterior ganglia, which are contained in the second segment (first body-segment), and that of the labium, which also rises in this segment, although its upper surface has partially coalesced with the under side of the head. I am reminded, however, by Prof. Huxley that neither of these conditions is conclusive. The anterior abdominal ganglia not unfrequently move forwards into the thorax, so that the cephalic ganglia may perhaps in this case be moved back; and the labium, not being homologous with a pair of coalesced appendages, but simply a protrusion of the sternal surface, may perhaps in this case have carried out with it a portion of the sternum of the first thoracic segment, in addition to that belonging to the second maxillary segment, of which it normally consists.

Dr. Ratzeburg was under the impression that the last segment of the head put on a thoracic character in the larvæ of certain Hymenoptera. Mr. Westwood, however, has thrown great doubt upon this supposition, if indeed he has not disproved it altogether\*.

\* See the Trans. Ent. Soc. vol. ii. p. 125, and Todd's Cyclopædia, article Insecta, p. 871.

## DESCRIPTION OF THE PLATES.

## TAB. XXXIV. AND XXXV.

In Tab. XXXIV. the insect is supposed to have been cut open down the side, the internal organs to have been removed, and then the skin to have been flattened. The muscles of one side only are represented.

In the first figure of Tab. XXXV. the muscles figured in the former plate are supposed to have been cut away, so as to expose many others which would at first have been partly concealed.

In the second figure of Tab. XXXV. the remainder of the cutaneous muscles are represented.

Of course the muscles represented in the last two figures would have partly appeared between those figured in Tab. XXXIV., but I thought it would cause confusion if they were inserted more than once.

All three figures refer to the three thoracic and first four abdominal segments, and are magnified about 8 times.



Lubbock, John. 1858. "On the Arrangement of the Cutaneous Muscles of the Larava of *Pygæra bucephala*." *Transactions of the Linnean Society of London* 22, 173–191. <https://doi.org/10.1111/j.1096-3642.1856.tb00091.x>.

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