A functional study of the skeleton, musculature and limbs of the larval thorax of *Triaenodes bicolor* (Curtis) and species of the genus *Limnephilus* (Trichoptera).

by

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Contents

Introduction 1

Taxonomy 4

Anatomy of the thorax of Limnephilus 17

Thoracic musculature of Limnephilus 29

Abdominal musculature of Limnephilus 57

Remarks on muscles and homologies of muscles 61

Remarks on thoracic muscles 63

Remarks on abdominal muscles 72

Remarks on skeletal morphology of the thorax of Limnephilus 74

The anatomy and musculature of the legs of Limnephilus 94

(i) skeleton 94

(ii) trochanteral annulus 99

(iii) muscles 101

The use of the legs in limnephilids 106

(i) case building 106

(ii) feeding 108

(iii) locomotion 111

(iv) other 116

Analysis of leg movements 118

(i) swing of pleural sclerite 118

(ii) rotation of the leg on the coxa 119

(iii) walking movements 121
Analysis of leg movements (contd.)

(iv) flexion and extension of the legs

(a) the pivot joints

(b) the trochantero-femoral joint

(c) the hinge joint (referred to the general discussion)

(d) extension of the distal parts of the leg

Introduction to Triaenodes bicolor

The thoracic skeleton of Triaenodes

The thoracic muscles of Triaenodes

Remarks on the musculature of the thorax of Triaenodes

Comparison of the thoracic muscles of Limnephilus and Triaenodes

Morphology of the legs of Triaenodes

Intrinsic muscles of the legs of Triaenodes

Comparison between the legs and leg muscles of Limnephilus and Triaenodes

(i) leg lengths

(ii) exoskeleton of the legs

(iii) muscles of the legs

Comparison of the leg muscles in Limnephilus and Triaenodes with those of other insects

The use of the legs by Triaenodes

(i) case building

(ii) feeding
The use of the legs by *Triaenodes* (contd.)

(iii) locomotion 216

(iv) other observations relating to swimming 227

(v) miscellaneous leg movements 228

Further analysis of leg movements and actions in *Triaenodes* 230

Analysis of the swimming process in *Triaenodes* 236

The traction of a swimming larva and the drag it has to overcome 242

General discussion

(i) morphology of the thorax 245

(ii) morphology of the leg joints 247

(a) hinge joints 248

(b) pivot joints 250

(iii) morphology of joints and their muscles 251

(iv) correlations of the muscular and skeletal systems 254

(a) relation between length and leverage of a muscle 254

(b) relation between length of a muscle and its displacement 260

(c) position of a muscle and its action 261

(v) physiology of the muscles 262

(a) the extrinsic and intrinsic muscles of the legs 264
<table>
<thead>
<tr>
<th>Section</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>physiology of the muscles (contd.)</td>
<td></td>
</tr>
<tr>
<td>(b) the pulling power of limnephilid legs</td>
<td>267</td>
</tr>
<tr>
<td>(c) the abdominal musculature</td>
<td>272</td>
</tr>
<tr>
<td>1. rhythmic movements and the nerve cord</td>
<td>273</td>
</tr>
<tr>
<td>2. the length-tension relationship</td>
<td>275</td>
</tr>
<tr>
<td>3. the absolute muscle force</td>
<td>277</td>
</tr>
<tr>
<td>4. twitch contractions</td>
<td>278</td>
</tr>
<tr>
<td>5. tetanic contractions</td>
<td>279</td>
</tr>
<tr>
<td>6. comparison with non-striated muscles</td>
<td>280</td>
</tr>
</tbody>
</table>

Summary                                                   | 282  |

Acknowledgments                                            | 292  |

List of abbreviations                                      | 293  |

References                                                 | 298  |

Appendix 1                                                 | 315  |

Appendix 2                                                 | 317  |
INTRODUCTION

In this thesis an attempt is made to compare the thoracic skeletal and muscular systems of the larvae of two species of Trichoptera, one of which, Limnephilus flavicornis, moves by crawling, and the other, Triaenodes bicolor, by swimming. One of the greatest difficulties in this kind of study is to reduce the very large mass of facts relating to insect morphology to some reasonably consistent scheme, which can be used as a datum of reference. This is not possible in any complete sense at present mainly because so many papers relate to only one species and the interpretations are applicable to only the given species, or those closely related. Moreover, comparative studies of the exoskeleton, without any reference to the musculature and the functional adaptations of the two systems, are the rule rather than the exception, and the exceptions usually relate to adult insects. The limitations of such papers on the skeletal morphology reduces their value. In this study, although the correlations between the skeletal and muscular systems have been emphasised, few conclusions can be drawn which are widely applicable. A much wider appreciation of the functional adaptations of the insect body is necessary before this can be usefully attempted. Much use has been made here of the work of Carpentier and Barlet (1946-1955), who have paid great attention in their papers to the
functional aspects of the musculo-skeletal systems of Apterygota. Their ideas are basic both in the sense of being derived from a study of primitive insects, and because they throw much light on the morphology of higher insects. By utilising their work as a framework of reference for interpreting the morphology of the insects studied here, it is hoped that in time this work will come to fit into a more general body of studies of functional morphology.

No studies of the muscles of larval Trichoptera are known to the writer, and the only description of the muscles of an adult trichopteran occurs in the comparative study of Maki (1938), who deals with Stenopsyche grisseipennis. Barlet (1951, 1953, 1954) has given a comprehensive account of the skeleton and musculature of the thoracic region of Lepisma saccharina and Kéler (1955) gives a description of the hypothetical musculature of a generalised insect.

The exoskeleton of larval Trichoptera has been described by taxonomists and ecologists rather than by morphologists. One exception to this statement is the account by Raciecka (1950) of the mouth parts and legs of larvae of Molanna angustata. Nielsen (1942, 1943, 1948) has given descriptions of all stages of development of various species of Trichoptera, and Lloyd (1921) illustrates some larval Trichoptera. Unfortunately his illustration of the animal makes it quite certain that it is not a limnephilid. Khalil (1953), studied the larvae of Hydropsyche app. with particular
particular reference to their thoracic sclerites.

Among the works of those morphologists who do consider
the exoskeleton of insects are several large comparative studies,
which regrettably usually deal with the skeletal system divorced
from the rest of the body. Some of the main papers in this
field are by Crampton (1909, 1914, 1917, 1918, 1926), Martin
(1916), Snodgrass (1909, 1927), and Weber (1924a, 1924b, 1926-1927,
1928, 1954). Ferris (1940, 1953), and Henry (1958) have more
recently re-examined some of the problems of skeletal morphology
taking the musculature and other body systems into account, and
they have proposed various far-reaching modifications to the older
theories, although all these morphologists have been primarily
concerned with adult insects. Several new hypotheses have also
been proposed by Barlet (1948, 1950, 1951, 1952), Carpentier (1949,
1955) and Carpentier and Barlet (1951) as a result of their work
on the Apterygota.

The main purpose of this thesis is concerned with the
comparative morphology and mechanics of two caddis larvae. As so
little is known about this, it has been essential to treat in some
detail the structure of the limbs, and also the thoracic musculature
which moves the limbs. At first it was hoped to limit description
of the extrinsic muscles to those which are concerned solely with
moving the limbs, but it became obvious that all the somatic
musculature is involved and therefore a full description of this
is included.
To keep this necessary mass of detail in reasonable compass and to avoid repetition, the description of Limnephilus is given first followed by that of Triaenodes. The remarks applicable to Limnephilus also apply to Triaenodes, except where this is specifically contradicted, and in the section devoted to Triaenodes only those points solely applicable to this animal have been mentioned in the comments.

The thoracic exoskeleton and the musculature of the two larvae are briefly compared and the general discussion which follows is concerned with those principles of wider application which have become clear from the comparative study of these two larvae.

TAXONOMY

There is a considerable number of keys available for the identification of the larvae of Trichoptera. Most of them do not extend to specific differences, but keys to families or genera may be found in the papers of Krafka (1915), Hickin (1946) and Betrand (1954). Other papers cover a more limited field in the taxonomy of Trichoptera larvae. These include Morton (1890), Martynov (1934), Betten (1934), Hayes (1941), and Nielsen (1942).

More comprehensive accounts of the larval stages of caddis-flies and keys to their identification are given by Klapalek (1888, 1893), Siltala (Silvenius) (1903, 1904, 1907), Ulmer (1903, 1907, 1925), Esben-Petersen (1916), and Lestage in Rousseau (1921). Hickin (1942 to 1958) in a long series of papers has described the /larvae
larvae of many species.

Identification of *T. bicolor* is relatively easy, in spite of differences in the accounts given by various writers. Esben-Petersen (1916) and Lestage (in Rousseau 1921), for example, state that the maxillary palp has four segments, Hickin (1942) and Klapalek (1888) say that it has three; again Hickin (1942) claims the labial palp has a single article, whilst all the others state it has two. Accounts of the distribution of the abdominal gills, of the proportions of the leg-lengths and of the case dimensions, also disagree. It is therefore fortunate that *Triaenodes* includes only two British species, and that it is a genus with a unique kind of case, and with swimming larvae - characters which enable it to be picked out very readily. The two British species are easily separated by the head markings, illustrated by Lestage (in Rousseau 1921) and Esben-Petersen (1916).

In the genus *Limnephilus* there are at least 27 British species, and the identification of these is very difficult. The seven species, *L. nigriceps, L. decipiens, L. rhombicus, L. politus, L. marmoratus, L. flavicornis* and *L. stigma* form a group which can be distinguished with some confidence, because the colouration of the anterior third of the prototum is darker than the middle third in these species, but not in the other species. These seven species fall into two groups: (a) one which includes *L. nigriceps, L. decipiens*, and *L. rhombicus*; and (b) one which contains *L. politus, L. marmoratus, L. flavicornis*, and *L. stigma*. These groups may also be separated with some confidence because the median clypeal band is enlarged anteriorly.
anteriorly in the former group, but not in the latter. Within the latter group, however, the species may be very easily confused with one another, and this proved a serious problem as it was intended at the outset of this work to use *L. flavicornis*, which needs therefore to be separated from the other three species of this group.

Nearly all the published keys utilise the following scheme:

1. *L. marmoratus* and *L. politus* have the hypostome dark.

   *L. flavicornis* and *L. stigma* " " light.

2. *L. flavicornis* does not make a case like that of *L. stigma* which has a characteristic form in which the pieces are laid face to face at right angles to the length of the case.

   It was assumed at the beginning that this key was reliable because it was repeated with minor differences in so many books, but as familiarity with the larvae grew, it became clear, as Hanna (1956) correctly points out that the hypostome can be light or dark in any one of these species. Use must therefore be made of subsidiary characters such as the distribution of the abdominal gills, and the shape of the hypostome. In fact these features are too irregular to be of any taxonomic value. Under these circumstances only the form and materials of the case gives any indication of the identity of the larva in it. *L. flavicornis* sometimes makes its cases entirely of shells while the other species do not, although they may utilise them to some extent. When a colony was found in which all the cases were solely of shells it was these larvae /which
which were utilised for the study of the musculature. Probably
*L. politus* and *L. marmoratus* were used for the observations on
the behaviour of the larvae.

It may be added that the keys state that *L. politus* and
*L. marmoratus* can be separated by the anterior end of the clypeal
band having a patch of a yellowish colour in the former, but not
in the latter. There is, however, a complete series from larvae
with clear yellow patches through larvae with pitchy-red patches
(in the sense as used by Joy (1931)) to larvae with no lighter
patch at all.

It is clear then that it is not possible to identify the
larvae of this group of Limnephilidae with any certainty, and indeed
the whole genus requires a new examination. Mackereth (1960) agrees
with this, and states that she found it impossible to give trust-
worthy names to the larvae of Limnephilidae. Even when a described
larva is bred out and the adult identified, one is only justified
in concluding that that particular larva was of that species. It
may be that the species is polymorphic in its larval stage, so that
larvae of more than one description give rise to one species of
adult. Thus the only sure method of establishing the character-
istics of the given species is to breed from a pair of imagines
which have been identified with certainty. It may be possible to
do this in the future.

It is quite certain that the scheme used is at best doubtful,
and at worst erroneous. Nevertheless, the lack of discrepancies in
the anatomy of the larvae examined shows that in practice it has worked reasonably well for the limited purpose for which it was designed.
Fig. 1. Apparatus used for breeding out the larvae.
MATERIALS AND METHODS

1. Collection and breeding of Larvae.

All larvae have been collected from the canal between Wigston and Saddington lying south and south-east of Leicester. Some of the larvae were kept in aquaria and others were kept in the breeding cages illustrated in fig. 1 so that their pupal and imaginal stages could be observed. The breeding apparatus consisted of a series of wide tubes (c. 1 in. diam.) aerated by small glass tubes supplied from the compressed air line of the laboratory. Each tube was surrounded by a piece of black paper, outside which was a muslin tube supported by a wire frame. When the insects hatched out they show a positive phototactic and a negative geotactic response and so climb up into the muslin tube where they may be easily seen.

This apparatus worked satisfactorily with Triaenodes, but only moderately so with Limnephilus.

2. Direct observations on swimming larvae.

Observations were made on the living animals using a hand-lens and a binocular microscope. The swimming larvae were observed in an annular vessel mounted on a slide-ringing turntable, raised above the level of the wooden frame by a ball-bearing beneath its spindle. The annular vessel consists of a large beaker placed inside a larger dish leaving a ring between them about two cms. wide, which was filled with water. Because of the tendency of the water to swirl as the turntable is rotated, it was sometimes preferred...
Fig. 2. Diagram to show the arrangement of two vessels forming an annular channel for observation of swimming larvae.
preferred to place the inner beaker eccentrically, so forcing the water to move with the turn-table. Using a microscope, it was possible with this apparatus to observe the activities of the larvae quite easily, even though they were swimming fast, because the annular trough in which they are held is kept at a constant distance from the microscope. Hence focusing can be carried out without changing the grip on the coarse adjustment (fig. 2).

Ciné films were made at various speeds and magnifications, using a watchmaker's eyeglass attached to the camera lens, or using an ordinary microscope. An inverted microscope was used to obtain pictures from below, and a high intensity lamp illuminated the larvae. The resulting films were studied with the aid of a slow-speed ciné projector, and by a micro-projector. A number of frames were examined under a microscope and the outlines of the larvae were drawn in circles on squared paper. In this way accurate copies of the sequence of events in nineteen swimming cycles were available for inspection and analysis.

Various powders were used to see the circulation of water when _Triaenodes_ was swimming, but aluminium dust in bright light was most successful.

3. Sectioning and microscopy.

The larvae were killed and fixed by dropping them into hot DuBoscq Brasil, while they were retracted in their cases. This prevented the larvae curling up and made subsequent sectioning and dissection much more straightforward. Specimens were stored in 90% alcohol.
The larvae were embedded in a mixture of 90% paraffin wax (56°) and 10% ceresin wax, after clearing in cedar-wood oil. Transverse and longitudinal sections were cut at thicknesses between 2 and 25μ. Some sections were cut at 250μ, and although many were failures some were successful and helped to show the positions of some of the smaller muscles. The legs were sectioned separately and gelatine capsules proved valuable when preparing these small objects for sectioning, as the wax could be changed with less chance of losing them. The capsule can be sectioned also if desired, so that blocking up the objects in a separate operation can be avoided.

The thick sections were stained with van Gieson's stain; the other sections were stained in haematoxylin and eosin or Mallory's azan stain.

The musculature of the legs was studied with polarised light and a calibrated stage gave the angular measurements used in the calculation given below.

4. Amputations.

A certain number of experiments involved the amputation of limbs, the larvae being first anaesthetised by ether/water mixture.

5. Dissection.

A great deal of the information about the anatomy of the larvae
larvae studied has been obtained by dissection, and methods have been devised to make it as easy and as rewarding as possible. The larvae were prepared for dissection by frontal or sagittal section, so that dissections were carried out on half a larva.

The problem of holding the animal down is of prime importance, and partial embedding in paraffin wax before dissection has not proved very satisfactory, especially with small objects such as the legs of Limnephilus, as the objects tend to work loose from the wax usually at the most inopportune moment. Several other methods of fixation were tried and the most successful was 'Evostick', although certain details need careful attention for best results. The watch-glass to be used for the dissection must first be thoroughly cleaned and dried, then a thin smear of the adhesive is spread over the whole of the glass and allowed to become thoroughly dry. If this is not done liquid seeps between the glass and the adhesive and lifts it off. Next a bar of adhesive is extruded and the specimen ready for dissection placed in position along the bar. A drop of benzene, placed on the surface just before the half-larva is put on to the bar, helps to make a good contact. If necessary strands of adhesive may be drawn from one side to the other passing over the specimen, so tethering it down more firmly. The preparation must now be left to dry for as long as possible and it is advisable to add a small drop of glycerine to the exposed internal surface to keep it moist. As it dries, the adhesive shrinks slightly and holds /the
the specimen strongly. It is also possible to submerge the whole preparation under glycerine diluted with van Gieson's stain while the adhesive dries, so that the muscles are stained at the same time.

With the more flexible limnephilid larvae it is possible to fix the larva in the adhesive on its side so that the mid lateral line is facing the operator; cutting along this line permits the whole larva to be 'unrolled' while the adhesive is still tacky. This allows the internal structures from the mid dorsal line to the mid ventral line to be displayed undamaged.

Another advantage of this adhesive over wax is that the heat of the dissecting light does not soften it. This in turn means glycerine can be used as the dissecting medium, its viscosity reducing as it warms up, avoiding the use of alcohol which is not satisfactory with van Gieson's stain because it so readily leaches the stain out of the tissues.

In larvae about to pupate, the fat-body was very extensive, surrounding all the other organs present including the muscles. It was extremely difficult to remove this tissue without also removing the muscles, although glacial acetic acid was found to facilitate the removal of the fat-body.

The dissections were first made by fine 'mosquito' points mounted in matchsticks. These were later abandoned for tungsten needles (Tindall, 1960a) mounted in soft wood clock-cleaning sticks.

A piece of apparatus found to be very useful in microdissection was a device by which slight focussing adjustments could be
Fig. 3. Apparatus used for focussing the microscope with the thigh.
Fig. 4. Apparatus used for measuring the amount of drag on the swimming larvae and its case.
made, while leaving both hands free for dissection. Two pieces of wood are bolted together around the focussing screw. A vertical strut runs down from one of these two pieces and is attached to a strap around the thigh so that as the foot is moved backwards and forwards the resultant depression and elevation of the thigh turns the focussing screw (fig. 3).

The drawings of the musculature were made using a squared graticule. The main features were drawn from a single position so that the specimen is drawn as seen from one point only. The apparent curvature of the muscles results partly from this procedure and partly because after division of the larva some of the muscles evidently become slack and curved.

6. Measurements of drag on the larva and case of *Triaenodes*.

The apparatus used is shown in figure 4. A tank of water is allowed to empty through a wide glass tube at known rates. The object on which the drag is to be measured is suspended in the tube so that as the water flows past it a tension arises in the nylon thread suspending the object. The filament is calibrated so that the tensions at different speeds of water flow can be related graphically (graph 1). From this graph the drag on the living larva can be determined because its speed of swimming is known.

The apparatus uses a constant level device and the water inlet was found to be least disturbing if it was placed close to the water surface so the inflowing water 'spread' smoothly over the surface.
Graph 1. Measurement of drag on the larva and case of *Triaenodes*.

- **V**: speed of water flow (or swimming speed) in cms/sec.
- **D**: drag in mgrms.
- **A**: using thread alone.
- **B**: using thread, larva and case.
The filament used was glass and the calibration readings were watched to see they remained well within the elasticity of the material.

The speed of water flow was controlled by a screw-cock and was calculated from the volume of water passing through the tube in one minute. Knowing the internal diameter of the tube it is a simple matter to find the speed of water passing the object in cms. per sec.

7. Measurement of the pulling power of the larvae.

Measurements were also made of forces developed by the larvae of both Triaenodes, and limnephilids. For Triaenodes a fine glass filament was used. To the end of this a short length of nylon thread was fixed by a small spot of sealing wax. The post. end of the case was tied to the thread and the larva allowed to swim in the water. The maximum deflection of the filament was noted. After calibration of the filament, the force used by the swimming larva could be found.

A similar apparatus was used to measure the force of the crawling limnephilid larvae, although the glass filament was stouter and the larvae were allowed to crawl across a sheet of cork set in the base of a large tray. It was also found preferable to attach
Fig. 4a. Apparatus used to measure the pulling power of larvae.
the case to the thread by a small hook made from a 'mosquito' point. (fig. 4a).
Fig. 5. Skeletal anatomy of the prothorax: internal view.
The anatomy of the thorax of *L. flavicornis*.

The internal views of the thorax are taken from larvae kept in lactic acid and this has caused them to be very loosely articulated, so that the sclerites are not in contact as they are normally. The external view shows the thorax of the larva when it has been stretched slightly so that the details of the structure of the various sclerites are visible. (fig. 8.)

**The Prothorax** (fig. 5)

The prothorax is more heavily sclerotised than the other thoracic segments. Anteriorly it is connected to the head by a membrane, which extends from the post-occiput to the inflected anterior edge of the protergum. This membrane is more obvious dorsally and laterally than ventrally. There are no sclerites in this membrane. The anterior edge of the protergum extends closely over the head, extending as far as its maximum width. Ventrally the membrane is continuous with the sternal membrane, but this is extensive and allows the raising of the head. Normally the head is held retracted into the anterior face of the prothorax.

**The Tergum**

This is a large sclerite covering the prothorax dorsally and laterally. The anterior edge, as mentioned above, is inflected,

/although
although the inflection is not large and transforms into a simple thickened margin laterally. This extends round to the central tergal projection. Posteriorly the tergum is thickened to form a ridge which runs antero-ventrally from the posterior end of the mid-dorsal line (post-tergite of Cranqiton, 1918). Externally the thickening appears as a low ridge; internally it is much more clearly delineated, and at its ventral end it connects with a smaller ridge forming the ventral tergal projection. From this projection the ventral edge of the tergum extends posteriorly merging into the rest of the sclerite. Anterior to the posterior thickening, the tergum is shallowly grooved, and about one third of its length from the anterior edge, there is another shallow depression. The whole tergum is dark in colour, strong, rigid and fairly brittle. The anterior edge of the tergum bears a large number of setae of a wide range of thickness and rigidity, and at their bases a dense fringe of short fine setae.

The Pleuron.

The pleural region is defined by the presence of a pleural sclerite subdivided into episternum and epimeron and possessing a pleural ridge between these two. Such a pleural sclerite is found in the prothorax. Its dorsal edge lies against the ventral edge of the tergum so that internally the tergal process extends over the dorsal end of the pleural ridge. This forms an articulation between the two
flattened surfaces. Externally the tergum overlaps the dorsal part of the pleural sclerite. There is a clear deep sulcus externally corresponding to the pleural ridge, which extends ventrally as a pleural process. The dorsal edges of the pleural sclerite are black in colour, and this sclerotisation diminishes over the sclerite so that the postero-central region is light-coloured and flexible, although remaining as thick as the sclerotised portions. The pleural process projects a short distance over the coxal cavity and its flattened ventral surface articulates with the flattened dorsal end of the coxal process.

Ventral to the anterior end of this pleural sclerite is another smaller sclerite provisionally termed the anterior pleural sclerite. This is inflected medially so that it lies dorsal to the coxal rim and posterior to the lateral region of the head. Its dorsal edge abuts against the antero-ventral edge of the pleural sclerite and it is dark brown in colour.

Both the articulations between the coxa and pleural sclerite and between the pleural sclerite and the tergum are very strong and often the leg or sclerites will break before the articulation will part.

The other parts of the pleural region are wholly membranous and are not differentiated in any way from the sternum. Hence the coxal region is bordered by a membrane which may be pleural or sternal.
The coxal cavity is much deeper posteriorly than anteriorly. Posteriorly an extensive membrane, creased in various ways, connects the posterior (= ventral) edge of the coxa to the rim of the coxal cavity. Close to the lateral edge of the coxa a tendon to which a group of remotor muscles attach, inserts on to the narrow membrane between the coxa and the epimeron. On the opposite side of the coxal cavity, dorsal to the point where the median side of the coxa begins to be emarginated, there is a larger tendon to which the adductor muscles attach. This tendon also inserts on to the membrane and not on the coxal rim itself. Posterior to this is a small point on the otherwise smooth curve of the sternal edge, to which various muscles attach. This would seem to be the furcal branch or furca.

The Sternum.

In the posterior half of the sternum there is a sternite of thick cuticle. Its sclerotisation is patchy so that most of the sternite is tough and flexible rather than rigid. There is no obvious separated postero-lateral sternal apophysis as in the other thoracic segments, because this is merged with the rest of the extensive sternite. The anterior border of the sternite is marked by the prosternal horn, and anterior to this is thin flexible cuticle. McFarlane (1951) says that in the early instars of the rhyacophilid Hydrobiosis umbripennis there are three pro sternites, but in the
Fig. 6. Skeletal anatomy of the mesothorax: internal view.
later instars only one. It is possible this is true of other species of Trichoptera too, but I have not yet examined early instars of limnephilids and Triaenodes.

There is an apophysis present in the mid ventral line at the posterior margin of the sternum. This is the spina. As in other segments, the spina appears to be quite different in the drawings of the musculature and the drawings of the skeleton. This is because the tension of the muscle pulls their attachments into prominence. When the larvae are stored in lactic acid this tension is removed and the apodemes are minimised.

The intersegmental membrane between the pro- and meso-thorax is not normally visible externally, nor is it very wide, dorsally and laterally. The mesothorax overlaps the prothorax.

The Mesothorax (fig. 6).

This segment is less fully sclerotised than the prothorax mainly because the mesotergum does not extend so far ventrally as the protergum. Anteriorly it overlaps the prothorax to a small extent, and posteriorly the dorsal edge of the tergum covers the dorsal region of the intersegmental fold. Apart from this slight overlap the two segments simply abut against one another.

/The Tergum.
The Tergum.

The tergum is covered by the tergal sclerite which extends ventrally to the region of the mid lateral line so that the tergal and pleural regions are subequal in area. The sclerite is not thickened anteriorly, but its posterior edge is sharply ridged. Just anterior to this posterior ridge there is a narrow groove. The ridge and groove extend ventrally close to the posterior ventral angle of the sclerite, where they turn anteriorly and merge into the rest of the sclerite.

Another shallow depression is present in the mid dorsal region which extends antero-ventrally, to give the sclerite something of a saddle-shape. The sclerite is dark coloured, fairly uniformly, and bears scattered setae some of which are very long.

The Pleuron.

This region is membranous apart from the pleural sclerite. This is a large, roughly triangular-shaped sclerite clearly divided by a pleural ridge into episternum and epimeron. The pleural ridge is easily seen externally as a dark sulcus, and its dorsal third is bent at an angle of about 60° to the ventral two thirds. Dorsally the pleural sclerite is median to the tergum so that there is no contact between the two, and the tergum overlaps the pleuron externally. It is in the internal pocket so formed that the wing...
bud occurs. Ventrally the pleural ridge projects internally beyond the edge of the sclerite to form a peg overhanging the rim of the coxa. This is the pleuro-coxal articulation which is very strong. At this projection the darker sclerotisation of the ridge extends in a triangular-shaped area over the episternum and epimeron. Otherwise the sclerite is lighter in colour, and less sclerotised. Close to its ventral edge the pleural sclerite bears several setae some of which are exceedingly long. The rest of the pleuran is unsclerotised membrane and this is creased arbitrarily as movements occur. It extends anteriorly and posteriorly to the adjacent segments and ventrally with the sternum.

The coxal cavity.

This is much deeper posteriorly than anteriorly. Posteriorly there is an extensive membrane which allows wide leg movements. The internal edge of the cavity is somewhat narrower than the rim of the coxa itself, and it is confluent anteriorly with the coxal rim. Posteriorly as the coxal rim dips ventrally, the edge of the coxal cavity extends round from one side of the coxal rim to the other. Laterally the tendon of the remotor muscle runs to the junction of the membrane with the coxal rim at the point where the emargination begins.

The Sternum.

This is not greatly sclerotised, although there is a sternal sclerite present which is only visible in sections. It is tough and flexible.
Fig. 7. Skeletal anatomy of the metathorax: internal view.
flexible. Postero-laterally there are small areas of dark rigid sclerotisation, usually one large and one small. Laterally the sternum extends to a sharply projecting apodeme, the furcal branch, posterior to which is another invagination giving another apodeme, the posterior sternal apodeme. Both apodemes have small patches of sclerotisation. In the mid ventral line the spinasternal apophysis projects into the metathorax.

The Metathorax (fig. 7).

The Tergum.

The segment as a whole is but little sclerotised and the tergum bears only three sclerites. The anterior one ('cephalic' of Lloyd, 1921), placed close to the anterior line, is oval in shape. The posterior ('caudal' of Lloyd), is more irregular in shape and is situated in the middle of the lateral wall of the segment. The ventral one ('lateral' of Lloyd) is the largest of the three almost stretching across the segment dorsal to the pleural sclerite. All three sclerites bear setae of various lengths.

The Pleuron

The pleural sclerite is the conspicuous feature of this part of the thorax, and is very similar to that of the mesothorax. The pleural ridge is not so dark dorsally as in the mesothorax, but /ventrally
Limnephilus

Fig. 8. Skeletal anatomy of the thorax: external view.
ventrally it articulated with the coxa at a very similar joint. The external ventral edge bears many long setae. The coxal cavity is very like that of the mesothorax, save that the furca is not so definite, and the posterior sternal apophysis is not so sclerotised.

The Sternum.

This is strengthened by a chitinous plate which is normally invisible except for some small dark sclerotised patches where muscles attach. Postero-laterally the furcal branch is represented by a slight, poorly defined, projection, posterior to which is the posterior sternal apodeme, formed as in the mesothorax by an invagination of the membrane.

There is no spinasternal apophysis posteriorly in the mid ventral line, although the intersegmental fold in this region behaves as one when the muscles are attached to it.

There is no overlapping between the metathorax and the first abdominal segment.
The Thoracic musculature.

Studies on the musculature of insects are numerous but few authors have defined what they mean by the origin and by the insertion of a muscle. Frequently the end of a muscle attached to a moveable part of the skeleton is more compact and is provided with tendonous tissue which encloses the tip of the muscle. This end may be termed the insertion of the muscle (Weber 1954): the opposite end therefore becomes the origin - a term not related to development, and therefore somewhat unfortunate. Moreover, this distinction is inapplicable in several cases. For example, many of the longitudinal muscles are attached to the intersegmental fold immediately adjacent to those of the next segment; indeed some become virtually continuous in spite of being attached at the intersegmental line and the fibres interconnect with those of adjacent segments.

Ferris (1953) discusses this problem and suggests a definition which is based on the innervation of a muscle. He says: "In the instance of a muscle extending between two segments, the insertion of the muscle is that end which attaches upon the segment to which belongs the center from which that muscle is innervated. A muscle is never innervated from two sources." This is not quite so useful as it sounds, however, because the second sentence is untrue. Nuesch shows muscles of the mesothorax of Telea polyphemus innervated from /both
both prothoracic and mesothoracic ganglia (in Pringle, 1957).
The first sentence of his definition therefore cannot be used with
absolute confidence, although where a muscle is known to be innervated
by one nerve only, it could prove valuable. On the other hand,
it is a difficult criterion to apply in practice because of the
detailed study of the nervous system which is necessary. Furthermore
it does not cover those cases where a muscle lies within one segment
and yet is isotelic, i.e. its two ends are undifferentiated. Until
a better criterion can be suggested it is proposed to use an arbitrary
convention, which may be of at least temporary value. This
convention is that if the ends are not differentiated, the anterior
end, or dorsal end is called the origin, and the posterior or ventral
end is called the insertion. Although such a convention is entirely
free from any morphological, phylogenetic, or ontogenetic support,
it does give a practical simple method for describing some of the
muscles, which makes for accuracy in description and ease of compre­
hension. This problem is discussed further in the section below in
which the musculatures of the two larvae are compared.

Where a muscle is attached to what seems obviously to be an
intersegmental boundary, it is deemed not to cross this.

Nomenclature.

The nomenclature of the muscles used by other workers is
based on three systems; the function of the muscle; the position of
the muscle; and the attachments of the muscle. The objection to the first is that a given muscle has several functions according to which other muscles it is acting with. The second has the disadvantage of considerable vagueness. The third is the best, but does not indicate all that it is desirable to know about a muscle—what group it is related to, usually functioning with; and so forth.

An attempt has been made here to follow the method of, for example, Keler, 1954, which it is believed makes a useful combination of the best of all three methods. The muscles are grouped into sets such as those which are attached to the coxa and move the leg; or those attached to the pleural sclerite and brace this against the surrounding parts of the thorax. Each set is given its own number, and the subgroups and individual muscles are shown by the figures which follow after the decimal point. The name, origin, insertion and function of each muscle is given.

O. : origin.
I. : insertion.
F. : function.

Apophyses and apodemes.

Snodgrass (1935) defines an apodeme as "Any cuticular ingrowth of the body wall, usually formed in a multicellular matrix, but sometimes in a single cell". This definition is unsatisfactory because it is /unsusable
**Limnephilus**

Fig. 9. Muscles of prothorax: first stage of dissection, median view.
unusable if the ontogeny of the structure concerned is not known.

Snodgrass also defines "apophysis", which he says is "Any tubercular or elongate process of the body wall, external or internal". This is a much wider definition and is more easily applied. Kéler (1955) limits the term "apodeme" to the internal ridge of the pleural sclerite, and agrees with Snodgrass on the definition of "apophysis". It seems better therefore to follow Kéler's usage or to drop the term "apodeme" altogether, in spite of its frequent misuse in such contexts as 'ungtractor apodeme'. In this work the latter plan has been adopted.

The thoracic musculature of Limnephilus.

Prothorax.

1. Dorsal longitudinal muscles, internal. Three large and wide muscles, all very strongly connected on to the head capsule. All are wider and flatter posteriorly; narrower and more cylindrical anteriorly. All are levators of the head.

1.10. First internal dorsal longitudinal muscle (fig. 9).
Origin. Posterior dorsal intersegmental fold, close to the mid dorsal line.
Insertion. Posterior dorsal region of post occiput.

1.11. Second internal dorsal longitudinal muscle (fig. 9).
0. and I. Immediately adjacent to 1.10, latero-ventrally.

1.12. Third internal dorsal longitudinal muscle (fig. 9).
0. and I. Latero-ventral to 1.11.
2. Ventral longitudinal muscles, internal. Four to five very large wide muscles, the first three oblique. All wider and flatter posteriorly; narrower and more cylindrical anteriorly. All are depressors of the head. At this point the head capsule is inflected; this appears to be the rudiment of the tentorium which otherwise is not to be found.

2.10. First internal ventral longitudinal muscle (fig. 9). This muscle is often partly fused with 2.11.

0. Posterior intersegmental fold, close to the mid ventral line.

I. Ventral posterior region of post occiput of the head.

2.11. Second internal ventral longitudinal muscle, (fig. 9).

0. Lateral posterior sternal intersegmental fold, near to 2.10.

I. As 2.10.

2.13. Third internal ventral longitudinal muscle (fig. 9).

0. Lateral region of posterior intersegmental fold.

I. As 2.10 and 2.11.

2.14. Fourth internal longitudinal muscle (fig. 9).

0. Dorso-lateral region of the tergum, towards the posterior.

I. With 2.10-2.13.

2.15. Fifth internal ventral longitudinal muscle (fig. 9).

0. Dorso-lateral region of the tergum just dorsal to 2.14.

I. As 2.14.
Limnephilus

Fig. 10. Muscles of prothorax: second stage of dissection, median view.
3. Dorsal longitudinal muscle, external. This set includes various groups of muscles which are perhaps not closely related, and therefore they have been given different first-place figures.

3.10. First external dorsal longitudinal muscle (fig. 9). A fine muscle – the most dorsal of the segment.

0. Posterior intersegmental fold, near the mid dorsal line.
I. Posterior dorsal region of head, alongside set 1.

Function. Levation of the head.

3.15. Second external dorsal longitudinal muscle (fig. 9). Runs immediately external to 1.12.

0. Dorsal lateral intersegmental fold ventro-lateral to 1.12.
I. Adjacent to 1.12.
F. Levator of head.

3.17. Third external dorsal longitudinal muscle, (fig. 10). With 3.18, is a large muscle with broad flat origin and thick narrow insertion.

0. Mid dorsal region of tergum, towards posterior, just in front of tergal rib.
I. Lateral region of head capsule.
F. Rotator of head.

3.18. Fourth external dorsal longitudinal muscle (fig. 10).

0. Immediately antero-lateral to 3.17.
I. and F. As 3.17.


0. Central dorso-lateral region of tergum.
I. and F. As 3.17 and 3.18.
3.30. Sixth external dorsal longitudinal muscle (fig. 10). A fine muscle of two strands.

0. Dorsal region of the anterior intersegmental fold.
I. Dorsal region of the posterior intersegmental fold.
F. Retractor of intersegmental membranes.

3.31. Seventh external dorsal longitudinal muscle (fig. 11).

0. Centro-lateral region of tergum.
I. Dorso-lateral region of intersegmental membrane adjacent to the head.
F. Retractor of anterior intersegmental membrane.

3.40. Eighth external dorsal longitudinal muscle (fig. 9). This is the only muscle which runs freely between two segments.

0. Mid dorsal region of anterior part of mesotergum.
I. Posterior dorsal region of head capsule adjacent to 3.10.
F. As 3.10.

4. Ventral longitudinal muscle, external. All are depressors of the head.

4.12. First external ventral longitudinal muscle (fig. 10). In none of this set is the insertion of the muscle so clearly marked as in the earlier sets, nor is the change in shape so obvious.

0. Postero-lateral region of sternum, by four branches, all fusing to form the main mass of the muscle.
I. Posterior ventro-lateral region of head capsule lateral to set 2.

4.13. Second external ventral longitudinal muscle (fig. 10).

0. Postero-lateral sternal apophysis.
I. Dorsal to and slightly lateral to 4.12.
4.14. Third external ventral longitudinal muscle (fig. 10).
0. Postero-lateral region of sternite lateral to 4.12.
I. Ventro-lateral to 4.12 on head capsule.

4.15. Fourth external ventral longitudinal muscle (fig. 10).
0. Postero-lateral region of sternite, median to 4.12.
I. Median to 4.14.

5. Dorso-ventral muscles.

(i) Anterior.

5.20 to 5.23. This group of fine muscles is also difficult to homologise and in fact does not seem to have close affinities to any muscles in the meso- and meta-thorax, although it is likely it corresponds in a general way with the dorso-ventral intersegmental muscles in these segments. (But see further discussion below). All are rotators of the head.

5.20. First anterior dorso-ventral muscle (fig. 10).
0. Midlateral intersegmental membrane posterior to the head.
I. Along with 5.21.

5.21. Second anterior dorso-ventral muscle (fig. 9).
0. Membrane just posterior to junction of membrane and post occiput, dorsal to insertion of muscles 2.10 - 2.15.
I. Dorsal region of post occiput, median to insertion of muscle 1.12.

5.22 and 5.23. Third and fourth anterior dorso-ventral muscle (fig. 9).
Limnephilus

Fig. 11. Muscles of prothorax: third stage of dissection, median view.
0. Close together on the anterior region of the sternum.

I. " " " dorsal region of post occiput near 5.41.

(ii) Posterior.

5.34. Posterior dorso-ventral muscle (fig. 10). This is a difficult muscle to place, but it appears to be most easily homologised with muscles 5.34 in the meso- and meta-thorax.

0. Postero-lateral sternal apophysis.

I. Lateral region of head capsule close to insertion of 3.16 and 3.17.

F. Rotator of head.


7. Bracing muscles to the pleurites.

(i) To episternum. (a) Anterior.

7.13. First pleural bracing muscle (fig. 11). A pair of muscles fused alongside one another.

0. Postero-dorsal region of the head capsule.

I. Dorsal border of inflected tip of anterior pleural sclerite.

7.14. Second pleural bracing muscle (fig. 11).

0. Centro-lateral region of tergum.

I. Dorsal anterior border of first pleural sclerite, adjacent to 7.13.

7.15 and 7.16. Third and fourth pleural bracing muscles (fig. 11). A pair of broad muscles with flat sides adjacent.

0. Central dorso-lateral region of tergum.

I. Anterior dorsal edge of second pleural sclerite.
(b) Posterior.

7.30. Fifth pleural bracing muscle (fig. 11).
0. Dorsal region of post occiput just external to 7.13.
I. Dorsal edge of posterior part of episternum.

7.31. Sixth pleural bracing muscle (fig. 11). A large broad muscle.
0. Posterior dorso-lateral region of ternum, arising as two branches which soon join.
I. Dorsal edge of second pleural sclerite.

(ii) to epimeron.

7.40. Seventh pleural bracing muscle (fig. 11). Usually this muscle is subdivided ventrally into two or three poorly defined branches.
0. Ventral lateral part of tergum, posterior to the rib.
I. Dorsal edge of epimeron.

(iii) to pleural apodeme.

7.50. Eighth pleural bracing muscle (fig. 11).
0. Dorsal half of the pleural apodeme, spread out dorso-ventrally by a series of short branches.
I. Furcal apodeme on centro-lateral edge of sternum.
8. Muscles to coxa.

(i) to region of basicoxal rim.

8.10 to 8.13. First to fourth coxal muscles (fig. 10).
0. Four branches inserting on to dorso-posterior region of tergum, branch 8.10 being slightly lateral to the other three branches.
I. On to apophysis of pericoxal membrane in the anterior median region close to the sclerotised coxal rim.

The four branches fuse together, and also fuse with the /pericoxal
pericoxal membrane so that the junction is very intimate. This con-
nection will not separate but only tear, leaving ragged fibres.
F. Adductor of coxa.

8.20. Fifth coxal muscle (fig. 11). This muscle is orientated dorso-
ventrally distally, and twists to approximately antero-posterior proximally.
0. By several separate short branches, along the whole dorso-
ventral extent of the pleural apodeme.
I. Broadly on the anterior median edge of the coxa.
F. Promotor and adductor of coxa.

8.22. Sixth coxal muscle (fig. 11). A wedge-shaped muscle.
0. Internal or posterior face of the first pleural sclerite.
I. Anterior tip of coxal rim.
F. Promotor of coxa.

8.23. Seventh coxal muscle (fig. 11).
0. Anterior internal face of second pleural sclerite.
I. Anterior lateral edge of coxa.
F. Promotor and abductor of coxa.

8.50 to 8.54. Eighth to twelfth coxal muscles (fig. 11). A group of
large muscles.
0. Posterior dorsal region of tergum lateral to 8.10-8.13.
I. Postero-lateral region of pericoxal membrane very close to
coxal rim. There is no obvious apophysis here and muscle 8.51 inserts
independently just lateral to the others.
F. Remotors and abductors of the leg.

8.56. Thirteenth coxal muscle (fig. 11).
0. Posterior latero-ventral region of tergum, close to tergal ridge.

I. Close to the insertion of 8.51.

F. As 8.50 to 8.54.

(ii) muscles passing into the coxa.

8.60. Fourteenth coxal muscle (fig. 11). A fine two-stranded muscle.

0. Lateral sternal border, anterior to the furca.

I. Anterior internal face of coxa, median to the oblique ridge.

F. Rotator of coxa.

8.61. Fifteenth coxal muscle (fig. 11).

0. Posterior lateral region of sternum.

I. Anterior internal face of coxa on the proximal region of the coxal ridge.

F. Remotor of coxa.

9. Trochanteral muscles.

9.10. First trochanteral muscle (fig. 11).

0. On sternum, just lateral to origin of 8.61 and curving sharply down into the coxa.

I. Tendon running to ventral trochanteral apophysis.

F. Extensor of trochanter and femur.

9.11. Second trochanteral muscle (fig. 11).

0. Postero-ventral region of the tergum.

I. and F. As 9.10.

The Mesothoracic Muscles.

1. Dorsal longitudinal muscles, internal. Large broad muscles
Limnephilus

Fig. 12. Muscles of mesothorax: first stage of dissection, median view.
running from one intersegmental line to the other with the anterior ends somewhat constricted and forming a tendinous insertion. All are retractors of the prothorax.

1.10. First internal dorsal longitudinal muscle (fig. 12).
   0. Posterior intersegmental fold, close to dorsal mid-line.
   I. Anterior intersegmental fold, close to dorsal mid line.

1.11. Second internal dorsal longitudinal muscle (fig. 12).
   0. Ventro-lateral to 1.10.
   I. Ventro-lateral to 1.10.

1.12. Third internal dorsal longitudinal muscle (fig. 12).
   0. Ventral end of posterior dorsal intersegmental membrane.
   I. " " " anterior " " "

2. Ventral longitudinal muscles, internal. Three muscles, two very wide and stout, covering all sternal region of segment. They are ventral retractors of the prothorax.

2.10. First internal ventral longitudinal muscle (fig. 12.)
   0. Posterior intersegmental fold close to ventral mid line.
   I. Anterior " " " " " "

2.11. Second internal ventral longitudinal muscle (fig. 12).
   0. Ventral posterior intersegmental fold, lateral to 2.11.
   I. " anterior " " " " 

2.2. Spinal muscles.

2.20. First spinal muscle (fig. 12). This muscle runs dorsal to 2.10. and ventral to 2.11.
   0. Posterior edge of sternum, close to posterior intersegmental fold.
I. Posterior part of spina between pro- and meso-thorax.

F. As 2.21 and 2.22.

2.21. and 2.22. Second and third spinal muscle (fig. 12).

Two fine muscles, one or both of which may be prothoracic.

0. Lateral tip of anterior sternal intersegmental fold.

I. Lateral region of spina between pro- and meso-thorax.

F. Bracing muscles across sternal intersegmental fold (?)

2.23. Third spinal muscle (fig. 13). A fine muscle lying external to 5.20 and 5.21.

0. Middle of anterior sternal intersegmental fold.

I. With 2.20 and 2.21 on spina.

F. As 2.21 and 2.22.

3.10. First external longitudinal muscle (fig. 12). A broad muscle.

0. Posterior intersegmental fold, partly dorsal to 1.10.

I. Anterior " " " " 1.10.


0. Dorso-lateral region of posterior intersegmental fold.

I. Anterior intersegmental fold, external to insertion of 1.10.


0. Lateral region of posterior intersegmental fold.

I. Immediately ventral to the insertion of 3.11.

3.13. Fourth external dorsal longitudinal muscle (fig. 12).

0. Posterior intersegmental fold, just ventral to 3.12.

I. Anterior " " ventral to 1.11.
0. Posterior intersegmental fold, dorsal to 3.12.
1. Lateral region of the anterior intersegmental fold, external to 1.12.

3.15. Sixth external dorsal longitudinal muscle (fig. 12). This muscle lies external and parallel to 1.12, to which it is attached by a little connective tissue; it is much narrower than 1.12.
0. Posterior intersegmental fold, immediately anterior to 1.12.
1. Anterior " " " posterior " "

3.20, 3.21. and 3.22. Seventh, eighth and ninth external dorsal longitudinal muscles (fig. 13). All these are adjacent, and might almost be three fascicles of the same muscle.
0. Posterior intersegmental fold, close to insertions of 1.10. and 3.10.
1. Central region of tergite close to mid dorsal line.

3.23. and 3.24. Tenth and eleventh external dorsal longitudinal muscles (fig. 13). These are quite separate posteriorly, but fuse anteriorly.
0. Dorsal region of the posterior intersegmental fold.
1. Central dorsal region of the tergite just ventral to 3.20-3.22.

4.10. First external ventral longitudinal muscle (fig. 13). This muscle is shown by dotted lines only since it is found against the external surface of muscle 2.10.
0. Posterior sternal intersegmental fold, on postero-lateral sternal apodeme.
1. Lateral part of anterior sternal intersegmental fold. /4.11.
Fig. 13. Muscles of mesothorax, second stage of dissection, median view.
4.11. Second external ventral longitudinal muscle (fig. 13).
0. Lateral part of anterior sternal intersegmental fold.
I. Posterior region of sternum, where this muscle divides into four branches inserting separately external and anterior to those of 4.12.

4.12. Third external ventral longitudinal muscle (fig. 13).
0. Middle of anterior sternal intersegmental fold.
I. Posterior region of sternum, also by four branches.

4.13. Fourth external ventral longitudinal muscle (fig. 13). This muscle runs ventral to 4.12 and dorsal to muscle 4.11.
0. Middle part of anterior sternal intersegmental fold, just external to 4.12.
I. Lateral part of posterior sternal intersegmental fold by three branches.

4.20. Fifth external ventral longitudinal muscle (fig. 13). A very delicate fine muscle.
0. Postero-lateral sternal apodeme.
I. Slightly anterior of mid lateral region of sternum.
F. The function of this muscle is not very clear, and it seems to be a much reduced and almost functionless homologue of muscle 4.20 in the metathorax.

5. Dorso-ventral muscles.
(i) anterior.

5.10. First anterior dorso-ventral muscle (fig. 13). A thick muscle running internal to 1.12, 3.12-3.14 and external to 1.11.
0. Central dorso-lateral region of tergum.

/1.
I. Lateral tip of anterior sternal intersegmental fold, i.e. postero-lateral sternal apodeme of the prothorax.

F. Depression of the prothorax.


O. Lateral region of anterior intersegmental fold.

I. Antero-lateral region of sternum, close to coxal cavity.

F. Helps to keep anterior sternal and tergal areas in correct relationship.

(ii) posterior.

5.30. First posterior dorso-ventral muscle (fig. 13). This muscle spans the gap between the dorsal and the ventral posterior intersegmental folds. External to it is a small cavity caused by the convexity of the body wall in this region.

O. Ventral end of dorsal posterior intersegmental fold.

I. Dorsal " " ventral " " "

F. This muscle resists the separation of the tergal and sternal posterior intersegmental regions.

5.31. Second posterior dorso-ventral muscle (fig. 13).

O. Postero-lateral region of tergum.

I. " " tip of sternal intersegmental fold.

F. As 5.30.

5.34. Third posterior dorso-ventral muscle (fig. 13). A large muscle.

O. Antero-dorsal region of tergum.

I. As 5.30 and 5.31.

F. As 5.30.
Fig. 14. Muscles of mesothorax: third stage of dissection, median view.

6.10, 6.11 and 6.12. First, second and third sternal muscles (fig. 14). These three short and yet, proportionately, broad muscles lie in the antero-lateral region of the sternum, anterior to the coxal cavity.

0. Anterior to I., and both on the sternum.
F. Nil?


0. Sternum anterior to coxa.
I. Pericoxal membrane close to insertions of 8.20 and 8.21.
F. Nil?

7. Bracing muscles to pleurite.

7.10. First pleural bracing muscle (fig. 14). A muscle of two fine strands.

0. Dorso-lateral tip of ventral intersegmental fold.
I. Anterior tip of episternum.

7.11. and 7.12. Second and third pleural bracing muscles (fig. 14).

A pair of muscle strands, here considered separate, because of corresponding muscles in the metathorax.

0. Lateral part of anterior dorsal intersegmental fold, next to 5.11.
I. Anterior tip of episternum with 7.1- - 7.13.

7.13. Fourth pleural bracing muscle (fig. 14).

0. Dorsal region of anterior intersegmental fold.
I. Dorsal anterior tip of episternum.


0. Central dorso-lateral region of tergum.
I. Median surface of anterior tip of episternum.
7.15. Sixth pleural bracing muscle (fig. 14).
0. Antero-dorsal part of tergum.
I. Adjacent to 7.13.

7.16. Seventh pleural bracing muscle (fig. 14).
0. Slightly ventral to origin of 7.11.
I. With 7.15.

7.20. Eighth pleural bracing muscle (fig. 13).
0. Median surface of anterior tip of epistemum.
I. Postero-lateral region of sternal intersegmental fold.

(b) posterior.

7.30. Ninth pleural bracing muscle (fig. 13). A very oblique muscle.
0. Anterior dorsal region of tergum.
I. Posterior dorsal edge of epistemum.

7.31. Tenth pleural bracing muscle (fig. 14).
0. Posterior dorso-lateral region of tergum.
I. As 7.30.

7.32. Eleventh pleural bracing muscle (fig. 14).
0. and I. Adjacent to, and posterior of, 7.31.

7.33. Twelfth pleural bracing muscle (fig. 14).
0. Adjacent posteriorly, and slightly dorsal, to 7.32.
I. Next to 7.32.

7.34. Thirteenth pleural bracing muscle (fig. 14). A much finer muscle than 7.30 - 7.33.
0. Postero-dorsal region of tergum.
I. Next to 7.34.
(ii) to epimeron: nil.

(iii) to pleural apodema.

7.50. Fourteenth pleural bracing muscle (fig. 13). A large muscle of five fascicles arranged dorso-ventrally along the pleural apodema. At the sternal end this muscle is cylindrical but a little elongated antero-posteriorly.

0. Centro-lateral region of sternum median to the attachments of muscles 8.41 and 9.10 on a separate fold of the pericoxal membrane. This is the furca.

I. Pleural apodeme.

8. Coxal muscles.

(i) to region of the basicoxal rim.

8.10. First coxal muscle (fig. 13). A fine muscle.

0. Antero-dorsal region of tergum.

I. Apophysis of pericoxal membrane in the anterior median region close to the coxal rim.

F. Abductor of coxa.


0. Central dorsal region of tergum.

I. With 8.10 on coxal apophysis.

F. As 8.10.

8.20. Fourth coxal muscle (fig. 14). A large muscle.

0. By four branches over postero-dorsal region of episternum.

I. Anterior tip of coxal rim.

F. Promotor of coxa.

/8.21.
8.21. Fifth coxal muscle (fig. 14). Another large muscle, lying external to 8.20.

O. By four branches over postero-ventral region of episternum.
I. Anterior tip of coxa, next to the insertion of 8.20.
F. As 8.20.

8.22. Sixth coxal muscle (fig. 14).

O. Spread by three branches over antero-dorsal region of episternum.
I. Anterior tip of coxal rim, next to 8.21.
F. As 8.20.

8.23. Seventh coxal muscle (fig. 14).

O. Spread by three branches over centro-dorsal region of episternum.
I. Antero-lateral tip of coxa, next to 8.22.
F. As 8.20, and probably also a coxal abductor.


O. Anterior spine.
I. Centro-lateral edge of coxal rim.
F. Adductor of coxa.

8.41. Ninth coxal muscle (fig. 14).

O. Fold of pericoxal membrane in centro-lateral region of sternum median to furca.
I. Coxal rim, adjacent posteriorly to 8.40.
F. As 8.40.
8.50. Tenth coxal muscle (fig. 14).

0. Centro-dorsal region of tergum.

I. Postero-lateral region of membrane very close to coxal rim.

F. Remotor and abductor of coxa.

8.51 and 8.52. Eleventh and twelfth coxal muscles (fig. 14). Two muscles lying very close together.

0. Postero-dorsal region of tergum.

I. Near to 8.50.

F. As 8.50.

8.53. Thirteenth coxal muscle (fig. 14).

0. By two or three branches in the postero-lateral region of the tergum.

I. Between insertions of 8.50 and 8.51-2.

F. As 8.50-8.52.

8.55. Fourteenth coxal muscle (fig. 14).

0. Lateral region of posterior intersegmental fold.

I. Between insertions of 8.53 and 8.51-2.

F. As 8.50-8.53.

(ii) muscles passing into the coxa.

8.60. Fifteenth coxal muscle (fig. 14).

0. Centro-lateral region of sternum.

I. Internal face of coxa, median to coxal ridge.

F. Rotator of coxa.

8.61. Sixteenth coxal muscle (fig. 14).

0. Postero-lateral sternal intersegmental fold.

I. Internal face of coxa on the proximal region of coxal ridge.
F. Remotor of coxa.

9. Trochanteral muscles.

9.10. First trochanteral muscle (fig. 14).

0. Pericoxal membrane anterior to 8.41.

1. Trochanteral apophysis to posterior tip of proximal and of trochanter.

F. Extensor of trochanter.

The Metathorax.

1. Dorsal longitudinal muscles, internal. Three very wide muscles in which the ends are undifferentiated and hence named accordingly to the convention stated above. All are contractors of the segment.

1.10. First internal dorsal longitudinal muscle (fig. 15).

0. Dorsal region of anterior intersegmental fold.

I. " " " posterior " "

1.11. Second internal dorsal longitudinal muscle (fig. 15).

0. Anterior intersegmental fold, ventral to 1.10.

I. Posterior intersegmental fold, ventral to 1.10.

1.12. Third internal dorsal longitudinal muscle (fig. 15).

0. Lateral region of anterior intersegmental fold.

I. " " " posterior " "

2. Ventral longitudinal muscles, internal. Three broad muscles covering the sternal region of the segment. These are ventral contractors of the segment.

2.10. First internal ventral longitudinal muscle (fig. 15).

0. Anterior sternal intersegmental fold, near to ventral mid line.

I. Posterior " " " " " " " " /2.11.
2.11. Second internal ventral longitudinal muscle (fig. 15).
0. Anterior sternal intersegmental fold, adjacent to 2.10.
I. Posterior " " " " " 

2.12. Third internal ventral longitudinal muscle (fig. 15).
0. As 2.10 and 2.11, lateral to 2.11.
I. " " " " " 

2.2. Spinal muscles.
2.20. First spinal muscle (fig. 15). This muscle runs dorsal to 2.10 and ventral to 2.11.
0. Postero-lateral region of sternal intersegmental fold, anterior to intersegmental line.
I. Spina between meso- and meta-thorax.
F. This muscle acts as a bracing muscle for the spina.
2.21. Second spinal muscle (fig. 15).
0. Lateral tip of sternal anterior intersegmental fold.
I. Lateral region of spina between meso- and meta-thorax.
3. Dorsal longitudinal muscle, external. A complex set of muscles similar to those of the mesothorax, with group 3.10-3.15 more or less as long as the segment, and group 3.20-3.27. in the posterior half of the segment only, the first group are additional muscles contracting and bending the body; the second group perhaps assist in this.
3.10. First external dorsal longitudinal muscle (fig. 15). This muscle is shown only by dotted lines since it lies immediately external to 1.10.
0. Dorsal region of the anterior intersegmental fold very close to 1.10.
I. " " " " posterior " " " " " 

/3.11.
3.11. Second external dorsal longitudinal muscle (fig. 15).

0. Dorsal region of anterior intersegmental fold, slightly dorsal to 1.10. and 3.10.

I. Dorso-lateral region of posterior intersegmental fold, external to 1.11.

3.13. Third external longitudinal muscle (fig. 15).

0. Dorso-lateral region of anterior intersegmental fold, ventral to 1.11.

I. Lateral region of posterior intersegmental fold, external to 3.15.

3.14. Fourth external dorsal longitudinal muscle (fig. 15).

0. Ventral end of dorsal anterior intersegmental fold, ventral and external to 1.12. and internal to 3.15.

I. Dorso-lateral region of posterior intersegmental fold, between 1.11. and 1.12.

3.15. Fifth external dorsal longitudinal muscle (fig. 15). This wide muscle is subdivided anteriorly into three, and posteriorly into four, branches.

0. Ventral region of dorsal anterior intersegmental fold, external to 3.14.

I. Ventral region of dorsal posterior intersegmental fold, external to 1.12 and internal to 3.13.

3.20. Sixth external dorsal longitudinal muscle (fig. 16). A short muscle.

0. Dorsal region of posterior intersegmental fold.

I. Posterior region of tergum, near to dorsal mid line.

3.21. Seventh external dorsal longitudinal muscle (fig. 16).
Fig. 16. Muscles of metathorax: second stage of dissection, median view.
0. Posterior intersegmental fold, just ventral to 3.20.

I. Tergum, just dorsal to posterior tergite.

3.22. Eighth external dorsal longitudinal muscle (fig. 16). This muscle is nearly parallel to 3.21.

0. Ventral to 3.21.

I. " "

3.23 and 3.24. Ninth and tenth external dorsal longitudinal muscles (fig. 16). Two flat muscles very close together throughout their length.

0. Dorso-lateral region of posterior intersegmental fold.

I. Centro-dorsal region of the tergum.

3.25, 3.26 and 3.27. Eleventh, twelfth and thirteenth external dorsal longitudinal muscle (fig. 16). Three muscles lying parallel to one another.

0. Dorso-lateral region of posterior intersegmental fold, ventral to 3.23 and 3.24.

I. Dorso-lateral end of line in tergal cuticle anterior to posterior tergite.

4. Ventral longitudinal muscle external. This group of muscles helps the internal ventral longitudinal muscles, to anchor the anterior intersegmental fold posteriorly. (An exception is 4.20).

4.10. First external ventral longitudinal muscle (fig. 15). This muscle is close to 2.10 and is shown by dotted lines.

0. Anterior intersegmental fold, external to 2.10.

I. Posterior " " " "

4.11. Second external ventral longitudinal muscle (fig. 16). This /muscle
muscle is exactly as 4.11 of mesothorax, except it inserts by five branches, not four.

4.12. Third external ventral longitudinal muscle (fig. 16). As in the mesothorax, although the insertion of this muscle and of 4.11 are somewhat more posterior than those of the mesothorax.

4.13. Fourth external longitudinal muscle (fig. 16). This is like that of the mesothorax, but it is not divided posteriorly.

4.20. Fifth external ventral longitudinal muscle (fig. 16). A much broader muscle than that of the mesothorax.

0. Centro-lateral region of median pericoxal membrane anterior to origins of 8.41 and 9.10.

I. Postero-lateral region of posterior intersegmental fold, external to 4.13.

F. Contraction of this muscle must tend to turn the metathorax laterally and depress it with respect to the abdomen.

5. Dorso-ventral muscles.

(i) anterior.

5.10. First dorso-ventral muscle (fig. 16). A very fine long muscle.

0. Antero-lateral region of tergum, close to oblique line in tergal cuticle.

I. Lateral tip of anterior sternal intersegmental fold.

F. ?

5.11. Second dorso-ventral muscle (fig. 16). A very fine muscle.

0. Ventral tip of dorsal anterior intersegmental fold.

I. Antero-lateral region of sternum close to anterior intersegmental membrane.

F. ?
(ii) posterior. These muscles must play a part in the turning and bending of the body, and also holding the posterior ventral region in place against the tergal region.

5.30. First posterior dorso-ventral muscle (fig. 15).
0. Ventral end of posterior dorsal intersegmental fold.
1. Dorsal " " ventral " "

5.31. Second posterior dorso-ventral muscle (fig. 16). A very fine muscle.
0. Posterolateral region of tergum.
1. Dorsal tip of sternal intersegmental fold, external to 5.33.

5.32. Third posterior dorso-ventral muscle (fig. 16). Another very fine muscle.
0. Posterior ventral edge of ventral tergite.
1. As 5.31.

5.33. Fourth posterior dorso-ventral muscle (fig. 16). A narrow muscle subdivided dorsally into two branches.
0. Centro-dorsal edge of ventral tergite.
1. Dorsal tip of posterior sternal intersegmental fold.

5.34. Fifth posterior dorso-ventral muscle (fig. 16). A long narrow muscle, slightly divided dorsally into two branches.
0. Antero-lateral part of tergum.
1. With 5.30 - 5.33.


6.10, 6.11 and 6.12. First, Second and Third sternal muscles (fig. 17). Three small muscles arranged as in the meso-thorax.
6.13. Fourth sternal muscle. (fig. 17).
Fig. 17. Muscles of metathorax: third stage of dissection, median view.
0. and I. As in the mesothorax; may be a coxal muscle.

7. Bracing muscles to pleurite.
   (i) to episternum. (a) anterior.


0. Lateral tip of anterior sternal intersegmental fold.
I. Anterior tip of episternum close to 7.13.

7.11. Second pleural bracing muscle (fig. 17).

0. Ventro-lateral region of dorsal anterior intersegmental fold, ventral to 7.12.
I. Anterior tip of episternum, external to 7.13.

7.12. Third pleural bracing muscle (fig. 17).

0. Lateral region of dorsal anterior intersegmental fold.

7.13. Fourth pleural bracing muscle (fig. 16).

0. Anterior dorso-lateral region of tergum.
I. " dorsal tip of episternum.

7.14. Fifth pleural bracing muscle (fig. 17).

0. Anterior dorsal edge of ventral tergite.
I. Internal face of episternum close to anterior tip.

7.15. Sixth pleural bracing muscle (fig. 16).

0. Anterior dorso-lateral region of tergum, ventral to 7.13.
and 7.16.
I. As 7.10.

7.16. Seventh pleural bracing muscle (fig. 16).

0. Anterior dorso-lateral region of tergum, posterior to 7.13.
I. As 7.13 and 7.15.
7.20. Eighth pleural bracing muscle (fig. 16).
0. Internal face of anterior tip of episternum.
I. Posterior lateral tip of sternal intersegmental fold.

(b) posterior.

7.30. Ninth pleural bracing muscle (fig. 16).
0. Centro-lateral region of tergum.
I. Posterior dorsal edge of episternum.

7.31. Tenth pleural bracing muscle (fig. 16). This muscle lies internal to 7.32 - 7.34.
0. Postero-ventral edge of posterior tergite.
I. Dorsal tip of episternum.

7.32, 7.33 and 7.34. Eleventh, twelfth, and thirteenth pleural bracing muscles (fig. 17). Three parallel muscles of the same size.
0. Ventral edge of posterior tergite.
I. Postero-dorsal edge of episternum.

7.50. Fourteenth pleural bracing muscle (fig. 16).
0. Centro-lateral part of sternum, just median to 8.41 and 9.10 at the furca.
I. As in the mesothorax this muscle arises on the pleural ridge by several branches arranged dorso-ventrally.

8. Coxal muscles.

8.10. First coxal muscle (fig. 16). This muscle is external to anterior branch of 8.11. and closely bound to it.
0. Tergum, immediately ventral to anterior end of posterior tergite.
I. Apodeme of pericoxal membrane in antero-median region of
coxal rim.

F. Adductor of coxa.

8.11. Second coxal muscle (fig. 16). This muscle is divided
into two branches in its dorsal half.

0. One branch arises on the tergum just anterior to the anterior
tip of the posterior tergite. The other branch arises on the ventral
edge of the posterior tergite.

I. With 8.10.

F. As 8.10.

8.20 - 8.23. Third to sixth coxal muscles (fig. 17). This group
of muscles is identical to those of the mesothorax, except that
8.21. is not entirely covered in a median view by 8.20.

8.40. Eighth coxal muscle (fig. 17). As in mesothorax, except that
it is not in two clear strands.

8.41. Ninth coxal muscle (fig. 17). As in mesothorax.

8.50. Tenth coxal muscle (fig. 17).

0. Anterior ventral edge of posterior tergite.

I. Postero-lateral region of pericoxal membrane close to the
coxal rim.

F. Remotor and abductor of coxa.

8.51. Eleventh coxal muscle (fig. 17).

0. Posterior ventral edge of posterior tergite.

I. Near to 8.50.

F. As 8.50.

8.53 Twelfth coxal muscle (fig. 17). A muscle of two strands.

0. Posterior dorsal edge of ventral part of tergite.
I. Anterior to 8.50.

F. As 8.50.

8.54. Thirteenth coxal muscle (fig. 17). A fine muscle.

O. Posterior ventral region of tergum.

I. Fuses with 8.53.

8.55. Fourteenth coxal muscle (fig. 17). A muscle with four branches posteriorly.

O. Ventral region of posterior dorsal intersegmental fold.

I. Between 8.50 and 8.51.

F. As 8.50.

(ii) muscles passing into the coxa.

8.60. Fifteenth coxal muscle (fig. 17). As in the mesothorax.

8.61. Sixteenth " " " " " " "

9. Trochanteral muscles.

9.10. First trochanteral muscle (fig. 17). As in mesothorax.

Abdominal muscles.

It is not possible to correlate the muscles of the abdominal segment with those of the thoracic segments more closely than into the groups indicated by the units figures. To avoid any suggestion of unwarranted homologising, letters have been adopted instead of the figures after the decimal point. The fourth abdominal segment was chosen for comparison with the thoracic segments. This was, firstly, because the anterior segments may be modified by the presence of the protruberances of which the dorsal and two lateral
Fig. 18. Muscles of fourth abdominal segment: first stage of dissection, median view.
are very obvious, although there is a wide fold ventrally which also
forms a protruberance when the larva is swollen to a maximum.
Secondly, the more posterior segments are modified by the presence
of the anal hooks. The middle region of the abdomen is therefore
in as generalised state as it is possible to find in the larva. The
fourth segment has been described in other larvae by other writers
so that the choice of this segment in *Limnephilus* allows a comparison
to be made.

1. Dorsal longitudinal muscles, internal.
   1a, 1b, 1c. First, second and third internal dorsal longitudinal
   muscles (fig. 18).
   
   Three dorsal muscles running from the anterior intersegmental
   line to the posterior intersegmental line.

1d and 1e. Fourth and fifth internal longitudinal muscles (fig. 18).
   These muscles also run from one intersegmental line to the
   other but they lie across the region of the tergo-pleural boundary.

2. Ventral longitudinal muscles, internal.
   2a, 2b, 2c and 2d. First to fourth internal ventral longitudinal
   muscles (fig. 18).
   Four muscles in sternal region passing across the full length of
   the segment.

3. Dorsal longitudinal muscles, external.
   3a. First external dorsal longitudinal muscle (fig. 18).
   This muscle runs across the segment immediately external to 1b.

3b. Second external dorsal longitudinal muscle (fig. 19).
muscle crosses 3c and 3d internally.
0. Anterior pleuro-tergal boundary.
1. Dorsal posterior tergal intersegmental line.
3c. Third external dorsal longitudinal muscle (fig. 19). A very fine muscle which crosses 3d internally.
0. Anterior dorsal region of the tergum.
1. Dorsal to 3d.
3d. Fourth external dorsal longitudinal muscle (fig. 19).
0. Dorsal anterior intersegmental line.
1. Ventral end of the posterior dorsal intersegmental line.
3e. Fifth external dorsal longitudinal muscle (fig. 19).
0. Posterior dorsal region of tergum, near to the intersegmental line.
1. Centro-dorsal " " " " " " " "
3f. Sixth external dorsal longitudinal muscle (fig. 19).
0. Ventral to 3e.
1. Antero-ventral to 3e.
4. Dorsal longitudinal muscles, external.
4a. and 4b. First and second external longitudinal muscles (fig. 18). Much as in 4c and 4d, but close to the mid ventral lines and external to 2a and 2b respectively.
4c and 4d. Third and fourth external dorsal longitudinal muscles (fig. 18). Two muscles very close to 2d, but external to it, running across the ventro-lateral region of segment.
4e and 4f. Fifth and sixth external dorsal longitudinal muscles (fig. 19). Two parallel muscles running obliquely and internally across 4g - 4i.
0. Ventral anterior intersegmental membrane.

I. Ventro-lateral posterior intersegmental membrane.

4g to 4i. Seventh to ninth external longitudinal muscle (fig. 19).

Three parallel muscles.

0. Ventro-lateral anterior intersegmental membrane.

I. Ventral posterior intersegmental membrane.

4j to 4o. Tenth to fifteenth external dorsal longitudinal muscles (fig 19).

Six muscles radiating across posterior half of sternum from posterior ventral intersegmental membrane close to mid ventral line.

5. Dorso-ventral muscles.

5a. First dorso-ventral muscle (fig. 18).

0. Ventral end of anterior tergal intersegmental line.

I. By several branches to region of dorsal end of anterior intersegmental line.

In one specimen this muscle on the right hand side of the body was as shown, while on the left it was fully divided into five separate muscle strands. The muscle is shown twice in the same segment because it overlaps the intersegmental line.

5b. Second dorso-ventral muscle (fig. 18).

0. Anterior dorso-lateral region of tergum.

I. Antero-lateral region of sternum close to the dorsal end of the sternal intersegmental membrane.

5c. Third dorso-ventral muscle (fig. 19).

0. Ventral tip of anterior tergal intersegmental line.

I. Dorsal tip of anterior sternal intersegmental line.
Fig. 19. Muscles of fourth abdominal segment: second stage of dissection, median view.
5d. Fourth dorso-ventral muscle (fig. 19).
0. Antero-ventral region of the tergum near to 5c.
I. As 5c.

5e. Fifth dorso-ventral muscle (fig. 19).
0. Antero-ventral region of tergum.
I. " " " " sternum.

5f. Sixth dorso-ventral muscle (fig. 19).
0. Centro-dorsal region of tergum.
I. " lateral " " sternum.

5g. Seventh dorso-ventral muscle (fig. 19).
0. Centro-lateral region of tergum.
I. " ventral " " sternum.

5h. Eighth dorso-ventral muscle (fig. 19).
0. Postero-ventral region of tergum.
I. " lateral " " sternum.

5i. Ninth dorso-ventral muscle (fig. 19).
0. Ventral tip of posterior tergal intersegmental membrane, adjacent to 3d.
I. Postero-lateral region of sternum.

5j. Tenth dorso-ventral muscle (fig. 19).
0. Posterior intersegmental pleural region.
I. " region of pleuron.

5k to 5m. Eleventh and twelfth dorso-ventral muscles (fig. 19).
Three radiating muscles running from centro-ventral region of tergum to dorsal end of posterior sternal intersegmental membrane.
There are no muscles of sets 6, 7 or 8.
Remarks on the musculature, and the homologies of the muscles.
The concept of homology is itself difficult to define, and being so, it is even more difficult to apply. Owen (1843) gave a definition of homology and of analogy, in which he said that a homologue is "the same organ in different animals under every variety of form and function", a definition which today would be held to include much of analogy also. He defines an analogue as "a part or organ in one animal which has the same function as another part or organ in a different animal". In 1870, Mivart and Lankester published a series of papers dealing with Lankester's (1870) claim that many supposed homologies are really analogies and proposing the term homogeny for 'true' homology. Mivart (1870) enumerated twenty-five different kinds of homology, but some of these are really analogies. Hertwig (1906, 1909) also discusses the problem, and Willey (1911) used Lankester's term homoplasy but confined it to examples of convergence in animals and plants. Crow (1926) emphasizes the ontogenetic aspects of homology.

Modern embryological work has provided much information on which homologies can be established in the sense of close similarities in the pattern of embryonic origin and development. The concept of homology is asymptotic: the more surely the homology is established the more nearly do the structures involved coincide. This is the weakness in Owen's definition. He considers the "same organ" in different animals. But if it is really the same organ, it cannot be in two animals. Two animals may possess similar organs but not the same organs. Hence Owen is actually meaning the homologous organs are: "similar organs in different animals under every variety of form and function".

"But
But since the judgement of their similarities depends on the forms they take, the definition is for the most part tautologous.

This asymptotic nature of the term homology, however, has as its necessary corollary the fact that no homology can ever be absolute.

Homology as a relative term can be applied more easily to large organs of different animals; the arm of the man and the wing of the bird being a common example. The more restricted the structures chosen for comparison the more difficult it is to make a correlation. The term as used here, therefore, applies only to a comparative consideration of the morphology of segments of one instar of two larvae, and in the absence of full ontogenetic information, it must be more descriptive than indicative.

In Limnophilus, the homologies of the muscles in the three thoracic segments are indicated by their enumeration, but some difficulties and doubts involved are considered below.

The thoracic muscles.

Set 1.

In the prothorax, muscles 1.10, 1.11 and 1.12 all insert close together, and are therefore unlike those of the meso- and metathorax. This is because of the arrangements demanded by the presence of the head. But also it should be noticed that muscle 5.10 passes external to 1.12 in the metathorax and internal to it in the mesothorax, as in the abdomen, where 5b is internal to 1d and 1e. Such a small variation cannot be held to upset the correspondences given above but is useful as an example of the kind of minor change which can occur.
It emphasizes the danger of relying completely on the musculature for the homologising of structures of other body systems.

Set 2.

Muscles 2.13, 2.14 and 2.15 of the prothorax are placed in this set because it seems more likely that they belong here with the others i.e. 2.10 and 2.11. It is, of course, possible that 2.14 and 2.15 at least, ought to be homologised with 5.10. If this was so, then the problem of 2.13 would remain. It is more rational to seek an explanation in the morphology of the segment. As has been remarked above, one of the obvious facts about the prothorax is the reduction of the sternum in proportion to the other regions of the segment. This has left so little room for muscle attachment that these very large muscles have been compelled to adopt an origin on a different part of the skeleton. In addition these muscles are in the best position for retracting the ventral part of the head, a movement which is useful in tearing through tough plant fibres, when the jaw tips are locked within the plant stem and the retraction of the head is used to break the fibres. Although this action has not been observed in limnephilids it is frequently employed by *T. bicolor* (Tindall, 1960b) in which the muscles are arranged in substantially the same pattern. The unsclerotised anterior part of the sternum allows this particular head movement.

The group of muscles attached to the spinae, group 2.2, is of interest and might well be considered as bracing muscles between sternum and intersegmental membranes. Their differential contractions would also tend to rotate the segment, while equal contractions would
flex the body ventrally.

Set 3.

Muscle 3.15 in the prothorax may belong to set 1. In general this group is poorly represented in the prothorax. The mesothorax and to a less extent the metathorax has many more muscles in this group but the muscles themselves are smaller. These differences are correlated with the functions of these muscles. The head fits into the prothoracic cavity to form a large ball and socket joint. There is no one point or axis of articulation and the full analysis of the head movement is complex. The retention of the head against the prothorax depends on the large muscles and if these are cut the head moves away from the prothorax to the extent of the large intersegmental membrane. The muscles therefore must be strong and long to retain the head and to move it widely. The prothorax fits against the mesothorax with very little membrane between them, which only permits relatively small movements between the two segments. Hence the muscles of this group in the mesothorax can be reduced in size. But in the metathorax the muscles are very similar to those of the mesothorax in spite of what amounts to a very extensive flexible intersegmental membrane. Such contradictions are bound to arise when muscles are treated as isolated effectors. It is probably more accurate, in spite of being more vague, to say that these muscles help in bending and turning the body in co-operation with the other longitudinal muscles. Muscles 3.17, 3.18 and 3.19. The function of these muscles is difficult to deduce. In the metathorax of *Limnephilus* it may be thought that they help to retract/
the anterior end of the body or to assist the turning or levation of
the body. In the mesothorax, however, where they also occur, they
insert on to the central region of the tergum and cannot act in the
same way at all. In both meta- and meso-thorax their sole function may
be to draw the posterior intersegmental membrane inwards when contraction
of the body takes place.

Set 4.

It is remarkable that in this set there is no thoracic represent-
ative of muscles 4f to 4o of the abdominal segment.

The insertion of 4*11 and 4.12 by four or five separate insertions
is another striking feature of this set of muscles. The separation
must reduce the stress on any one part of the sternite, but it is dif-
ficult to see why this is necessary in the prothorax where the sternite
is so thick. It may be that this arrangement is the result of the
partial fusion of originally entirely separate muscles, or alternatively,
of just the opposite. Only study of the embryology and development,
together with a comparative study of more primitive Trichoptera could
decide this point.

The different sizes of muscle 4.20 in meso- and meta-thorax remains
a puzzle for which no explanation can be suggested, unless it is related
to the importance of hydrostatic pressure in a relatively flexible
segment. It is also possible that this muscle is concerned with the
stability of the sternite against an intersegmental membrane. That
might account for its reduction in the mesothorax and its absence in the
prothorax.

/Set 5.
Set 5.

Muscles 5.20 - 5.23 which are only found in the prothorax, have no counterpart in the other two segments. They appear to correspond to muscles 68, 69 and 70 of Lepisma (Barlet, 1954). Unfortunately there are no homologous muscles in the meso- and metathorax of Lepisma either, so one cannot infer much about limnephilids from the apterygote condition. The presence of the head in both cases evidently disturbs the pattern of the anterior dorso-ventral muscles, and no reliable suggestions can be given as to the homologies of this group, although they may have some affinities with those of group 2.2 in the Trichoptera.

Muscle 5.34 of the prothorax may be equivalent to muscle 7.20 in the meso- and metathorax may really belong to set 5, in which case 5.34 in the prothorax would fit in very well. The reason this change has not been adopted is that 7.20 is a muscle inserting on the pleurite in the meso- and meta-thorax and therefore is classed as pleural bracing muscle.

Set 6.

These three minor muscles also seem to be without purpose but they are undoubtedly homologous to the spiracular muscles in Perla abdominalis (Wittig, 1955), Gryllus and Vespa (Berlese, 1909). One explanation for their presence would be that Trichoptera have retained traces of non-aquatic ancestry. It would be interesting to know if such muscles occur in Ironoquia or Enocyla, and if so whether they act as functional spiracular muscles in these animals. It would also be interesting
to know whether other apneustic Holometabola larvae have them, especially the aquatic larvae of the *Pyraustidae* (Lepidoptera). A comparative study of the incidence of these structures might throw some light on the ancestral relationship between the Trichoptera and the other Orders of the panorpoid complex. An alternative explanation could be that these are structures anticipating imaginal development.

Set 7.

This group is complicated and varied. Functionally, all the muscles are concerned with the anchoring of the pleurites relative to the rest of the segment; but this has imposed its own arrangement on the muscles which perhaps does coincide well with morphological factors. It has already been mentioned that muscle 7.20 may really belong to set 5, especially as its insertion is on the posterior sternal apophysis and its origin on the pleurite - the opposite way round to all the others, except 7.50. In the absence of developmental work this point is, of course, a matter of convention combined with some guesswork, but it must be borne in mind.

The anterior group inserting on to the episternum are interesting. Those of the meso- and meta-thorax seem to homologise quite well, the chief difference being that in the metathorax the anterior point of the episternum is relatively more ventral than that of the mesothorax. Thus the metathoracic muscles are relatively longer, and those of the mesothorax relative shorter.

Muscles 7.13 to 7.16 are also much longer in the meta-thorax, but the reason for this is not clear, since they do not have to be long enough to reach to a sclerite, originating instead from the unsclerotised /flexible/
flexible part of the tergum. Usually longer muscles suggest a larger movement, and it looks as though the tergum is pulled inwards and downwards towards the pleurite. This is a problem of the hydrodynamics of the larva. The shortening of the body is relatively easy the contraction of the longitudinal muscles, but in the absence of a system of circular muscles, elongation becomes more complex. The contraction of muscles which run between flexible areas of the body wall and rigid sclerites such as those of groups 7.1 and 7.3 and the dorso-ventral muscles in both thorax and abdomen, have the same effect as circular muscles providing there is liquid to transmit the pressures set up by the muscles.

The homology of muscle 7.13 of the prothorax is doubtful. It is possible it is an homologue of 7.11 and 7.12 of the other segments but if this is so, there is then no equivalent, in the prothorax, of muscle 7.13, of the meso- and meta-thorax. On the other hand, muscle 7.13 of the posterior two segments seems to be much more clearly related to muscles 7.15 and 7.16 than it does in the prothorax.

Muscle 7.14 is also somewhat problematical, but it is hoped that any difference in its insertion in the prothorax is not sufficient to invalidate its suggested homologies.

Similarly prothorax muscles 7.30 and 7.31 are probably correctly numbered, but this implies a shifting of the origin of 7.30 from tergum to head, and that the insertion of 7.31 has moved until it is anterior to 7.30. Neither such move is difficult to envisage. Muscle 7.31 is relatively large and would appear to function as a muscle restraining the second pleural sclerite from moving ventrally when muscles 8.20,
8.22 and 8.23 are contracting to promote leg 1. If nothing were stopping this movement, the promotor muscles would be much less efficient because the pleural sclerite would move towards the leg instead of the leg rising up towards the sclerite. In the mesothorax, however, where muscles of group 8.2 are large, the muscles equivalent to 7.31 are not especially conspicuous. This is all the more surprising because the tergum of the prothorax would tend to hold the pleural sclerite much more firmly than the mesothorax holds the mesopleurite. Similar considerations apply to the metathorax. Clearly, therefore, other factors must play a part in the functioning of these groups of muscles, but their full analysis has not yet become possible.

Muscle 7.40 of the prothorax is also a rather unexpected muscle. No homologous muscle occurs in the other thoracic segments yet the joint between the tergum and the second pleural sclerite is very strong and permits little movement. Nevertheless the closeness of the insertion of 7.40 to the joint shows that if it does contract it will pull the anterior end of the second pleural sclerite ventrally to a noticeable degree. This suggests that such a movement occurs when the larva crawls and if this is so it would suggest that the presence of the large muscle 7.31 causes the opposite rotation of the sclerite. When the larva is crawling its stride can therefore be lengthened by the movement of the coxifer (and the sclerite) and this compensates in part for the shortness of leg 1.

Muscle 7.50 is held to be the muscle which represents the pleurofurcal apophyses, (see further: p.88) and as such is of considerable importance. Many insects have these apophyses as rigid endoskeletal
arms but some have a small muscle between them. In Trichoptera the arms are not present, and a large muscle is found instead. Rigid skeletal structures seem to occur only where compression stresses are common and muscular or tendonous connections where stresses are tensional. This would suggest that the function of muscle 7.50 is to resist and control the lateral displacement of the pleurite away from the sternite. If this is true, it would explain the relative slenderness of this muscle in the prothorax since here the pleurite has a strong articulation to the tergite which greatly reduces its tendency to move. At the same time, it is difficult to see from whence comes the thrust which would tend to push the pleurite laterally, and the explanation may equally well lie in the need to keep the sternite steady. Probably, however, it is the presence of the coxal articulation which causes the pleurite to tend to be moved outwards, when muscles 8.10 to 8.13 and 8.50 to 8.55 contract. In the meso- and meta-thorax the long muscles of group 8.5 run down from the tergum to the pericoxal membrane around this muscle. The point of origin of this muscle is the furca, although this is not differentiated as a specialized part of the exoskeleton.

Set 8.

The groups of muscles of this set homologise well in the three segments.

The first group, 8.10 to 8.13 is most compact in the pro-thorax; in the other two segments it is longer and narrower.

The second group, 8.20 to 8.23 homologises very well in all three segments.
segments, except that 8.21 is missing from the prothorax, probably for lack of room on the episternum to accommodate any more muscles. The similarity amongst this group of muscles is of great service in determining the nature of the first pleural sclerite in the prothorax (see further below above).

The third group, 8.50 to 8.55 are in general homologous although 8.56 in the prothorax appears to have no equivalent in the other two segments.

The other coxal muscles also homologise quite well. Muscles 8.40 and 8.41 are absent from the prothorax while 8.60 has not the twist in its length which is found in the meso- and meta-thorax.

In the prothorax, muscle 8.61 does not arise on the posterior sternal apophysis, as in the other segments, but close to the origin of muscle 9.10. This may suggest that muscle 8.61 is really equivalent to 8.41; but if this were so, the insertions would not coincide.

Muscle 6.13 may belong to this group and it would then be muscle 8.30.

Set 9.

Muscle 9.10 consists of two apposed fascicles, and is the only representative of this set in the two posterior segments. In the first segment this muscle does not arise with muscle 8.41 close to the insertion of muscle 7.50 and it is joined by the tergo-trochanteral muscle 9.11.

The abdominal muscles.

Attempts to relate in detail abdominal musculature to that of the thoracic
thoracic segments results only in frustration. In general sets 1 to 5 of the muscles, correspond fairly well. There are, of course, no trochanteral and coxal muscles, but perhaps it is surprising that there is so little resemblance in the pleural regions of the thorax and abdomen.

Of set 4, muscles 4.10 to 4.13 are not clearly represented, while muscles 4j to 4o are not found in the thorax. It is possible this is something to do with the need to flex the posterior part of the body ventrally, so that the anal hooks can grip on to the case. A similar situation is found where muscles 3.20 to 3.25 in the mesothorax and metathorax are required to flex the body dorsally.

Another feature of the abdominal musculature is the two very definite chiasmata of muscles 3b over 3c+d, and 4e+f over 4g+h+i. In the thoracic segments the dorsal chiasma is lost although there may be traces of it in the external dorsal longitudinal muscles; while ventrally, 2.13 appears to be the only remnant left. This is probably correlated with the greater rigidity in the thorax which reduces the need for muscles to bend the larva. The only other muscles present, the dorso-ventral muscles, cannot be homologised easily with those of the thoracic segments. They are fairly large muscles and have their ends widened where they attach to the cuticle.

Although the details of the abdominal musculature do not allow much fruitful comparison with the thoracic musculature, they are described here because they have been used in other parts of this thesis.
Remarks on the skeletal morphology of the thorax of Linnephilus.

The thorax has three segments and it has no intersegmental regions, apart from the very limited sense of a boundary line between two segments. The use of the term 'neck' or 'cervicum' therefore should be one of convenience betraying our ignorance of the exact boundary between the ultimate posterior segment of the head and the prothorax. Many authors describe the neck as though it is an independent entity, labelling the muscles therein separately from the prothoracic muscles. Usually this separation is based on the fact that the innervation of some of the muscles in this region is from the suboesophageal ganglion, while other muscles are innervated from the prothoracic ganglion. Ewer (1957) for example, writes "However it is now clear that only a few of the muscles in the neck region are innervated by nerves from the suboesophageal and that the majority ... are truly prothoracic" (p. 204). Wittig (1955), Mayer (1954), Fuller (1955), and Müller (1955) are other recent writers who show a lingering sympathy with the old idea of Voss (1905) of a cervical "microthorax".

The use of the innervation of the muscles to separate them into the two groups 'cervical' and 'prothoracic' rests on the assumptions that (i) a nerve remains associated with a particular muscle throughout its evolution and (ii) that a muscle is innervated by only one nerve. These assumptions are undermined by the work of Marquardt (1940) and Nüesch (1953). Marquardt shows that in Carausius morosus nerve fibres run from the mesothoracic ganglion to muscles of both prothorax and metathorax. Nüesch shows in the thorax of Telea polyphemus
nerve fibres from the prothoracic ganglion passing to the muscles of the mesothorax. Henry (1958) supports her use of the term 'cervicum', by the separation of the muscles between head and mesothorax into two groups, cervical and prothoracic according to their innervation. She adds, "In no instance have nerves from two sources been found innervating a single cervical muscle bundle" (p. 98). But Nüesch shows in the above quoted paper that some of the mesothoracic muscles of the lepidopteron are innervated from both pro- and meso-thoracic ganglia, while Popham (1959) in a paper discussing the neck region of some Dermaptera, has stated that the innervation of the muscles is an invalid guide to their affinities. It seems doubtful that what can occur in one part of the insect thorax cannot occur in another, and the grounds for the separation of some of the prothoracic muscles as 'cervical' muscles are very weak. Rather may one agree with Korschelt (1924), Samtleben (1929) and Barlet (1954) that all the muscles found in the prothorax are prothoracic muscles; and it is in accord with this proposition that the labelling of the muscleshas been carried out. In the adult pterygote insect the segments of the thorax are usually considered to have been derived from a primitive condition by the transposition of elements in the intersegmental region from one segment to another. This gives the secondary segmentation of the thorax (Snodgrass, 1935). Much of the terminology applied to the secondarily segmented definitive adult thoracic exoskeleton cannot be satisfactorily applied to the immature stages especially those of the Holometabola. For example, in the Trichoptera larvae studied there is no doubt where the intersegmental lines lie between the
thoracic segments, since they are shown clearly by the appositions of the internal longitudinal muscles, as in many larvae, e.g. *Rhagoletis pomonella* (Snodgrass, 1924). There are no phragmata, nor postnota, nor obvious usable subdivisions of the sternum to complicate the simple segmentation. It seems possible that much of the morphological terminology has been derived from a study of pterygote insects, with too little attention to their early stage and to the Apterygota. Hence the detailed study recorded in this thesis serves not only to elucidate the immediate problem, but also to fill a gap in larval morphology.

Carpentier and Barlet have given detailed accounts of the morphology and musculature of some apterygotes, and criticize strongly the subcoxal theory of the origin of the pleuron, pointing out that an interpretation based on the incorporation into the lateral body wall of two basal leg articles, rather than one, would correlate much better with the known details of their musculature. Indeed Carpentier hints at a third ring in the pleuron, which may perhaps be from a third podomere. In general their work sheds considerable light on the morphology and musculature of the caddis-larvae.

All animals are under the invariant factor of natural selection and all morphology must be considered with this in mind. Although it is possible to suppose some structures occur in animals which have no functional significance, it is better to assume that they have and to try to discover this rather than assuming there is nothing hidden to be understood.

Prothorax.

The prothorax is well designed to fulfil its various functions.
It is narrower in front, mainly by the reduction in size of the sternum. This is a common feature of larval insects: it occurs in *Rhagoletis pomonella* (Snodgrass, 1924), *Apis mellifica* (Needham, 1924), *Telea polyphemus* (Nüesch, 1953), *Dytiscus marginalis* (Korschelt, 1924) and many others. Barlet's study of *Lepisma saccharina* (1951, 1953, 1954) shows two muscles which cross the mid ventral line of the sternum and these may also indicate a reduction in the sternal region. If such a reduction occurs it may be one of the reasons for the divergence of opinions about the origin of the sternum amongst morphologists, the extreme view being expressed by Perris (1940) who thought that the sternum was entirely derived from subcoxal elements.

The Tergum.

The prothorax as befits the most exposed of the segments of the thorax has deep lateral extensions to its tergite, which is hard and strong. It extends anteriorly over the posterior part of the head, so that when contracted, the head fits very closely against the anterior extension of the tergite both dorsally and laterally, so protecting the more delicate membrane connecting the anterior edge of the tergite to the posterior edge of the head capsule. The posterior rib of the protergite probably provides the required strength and rigidity to resist the stresses of the large powerful promotor and remotor muscles of the leg and also the levators and dorsal depressor muscles of the head. Without this the protergite would tend to be deformed which would immediately reduce the effectiveness of these muscles in moving the legs and head. The depressor muscles in particular are those
responsible for bending the head into a hypognathous position when the animal retracts into its case, so that the vertex of the head fills the opening into the case and presents as strong a shield as the animal possesses to any marauder attempting to enter from the anterior end. These muscles also act in feeding (cf. feeding in T. bicolor Tindall (1960b)). Any weakness therefore in the protergite especially the posterior region, would clearly have wide and deleterious consequences for the animal's efficiency.

The tergal ridge also seems to help to support the tergal projection which in turn supports the second pleural sclerite, with which the coxa articulates. The inflected anterior edge, or protergite (Crampton 1914), ventrally becomes a major factor in the support of this projection. Any stresses from the legs are transmitted by this means to the tergite. Since such stresses will come from both legs, there will be a tendency to cause the ventral edges of the tergite to move dorso-laterally so that it becomes rather less arched than it is at rest. This is particularly true because the thrust comes in the middle of the ventral edge, dorsal to which the tergite is least sclerotised and least rigid. Evidently, therefore the anterior and posterior tergal ribs stiffen the structure without adding unnecessary weight. That this is not the main reason however for the strongly sclerotised prothorax may be seen when considering the meso- and meta-thorax. In the latter the coxal thrust from the leg movements still passes to the pleurite but this has no strong tergal shield to sustain it. It might be thought that the first legs are very much stronger than the other two pairs, but this will be shown below to be incorrect.
The shallow depression in the centre of the tergite occurs where the sclerotisation is least. Whether this reflects muscular distortion of this part of the skeleton before it is hardened after ecdysis, it is impossible to say. It may, however, correspond with the division of the tergum into scutum and scutellum in adult insects. Nüesch (1953) has shown that the exoskeleton develops normally without its usual muscle attachments, so denying the theory suggested by Malouf (1935) that the muscular tension influences the shape of the exoskeleton. Nevertheless the muscles and skeleton are closely interrelated from a functional point of view, even if one is not essential for the other in an experimental situation. Over an evolutionary period of time, there must be a detailed correlation between musculature and skeleton which is perfected by natural selection, if the species is going to remain extant. Such detailed correspondence in the early stages of the insect's evolution could have occurred by mutual accommodation between musculature and exoskeleton. During evolution such interaction could have been superseded by genetic determination of both systems. In this way the observation of both Malouf and Nüesch could be reconciled.

Although he says it is not clearly visible in the pro-tergite, such a depression is shown in the illustration Barlet (1950) gives of the pseudo-foetus of Dilta hibernica, indicating that it may be a very primitive feature of the tergites. On the other hand, what he calls the antenotum of the mesothorax corresponds
to what Crampton (1918) termed the post-tergite and what I call
the post-tergal rib. Thus the segmentation of Barlet is a half-
segment anterior to my description of Limnophilus. If, however, the
segmentation of Barlet's description of Dilta is made to coincide
with that of the limnophilid, by the homologising of his anterior
groove with the typical antecostal suture of other insects, the meso-
thoracic antenotum would be the homologue of the limnophilid post-
tergite, and would bring the very early pseudo-foetal stage of the
primitive insect into almost exact correspondence with the limnophilid.
It would mean for example that muscles LD1, LD2, LD3, TE.NT1, TE.NT2,
and TE.NT3 of Dilta (as shown in Barlet's illustration (1950)), would
correspond exactly with muscles 3.40, 1.10, 3.16, 2.10, 2.11, and
2.13 of the prothorax of Limnophilus. Further similarities can be
shown in other segments also. It is a very striking tribute to the
persistence of a pattern of skeleton and musculature that such a
detailed correspondence is possible.

More recently Barlet (personal correspondence) has agreed that
the suggested alterations to his account of the segmentation of
Dilta render this more satisfactory.

There is no structure which could correspond to what Verhoeff
(1903), Snodgrass (1909) and Crampton (1914) call the post-scute
lum of adult insects.

The Pleuron.

Snodgrass (1927, 1935), Heymon (1895, 1897, 1899), Ewing (1928),
Weber (1928), DuPorte (1959) and many other morphologists have

/accepted
accepted the theory that the pleuron is, at least mainly a derivative of the sub-coxal of the primitive Arthropod limb which has become flattened out as part of the insect body wall. There are some slight varieties of detail in their views such as the exact process of sclerotisation, but these may be ignored here. Much of the evidence for this theory is based on the Pterygota: indeed Snodgrass says of the Apterygota: "... The subcoxal sclerites of the thorax are small and variable and do not form definite pleural structures"; and that "In the Diplura and Thysanura the pleurites are variable and more or less degenerate..." (p. 163, 1935).

Hansen, (1930) expressed doubts, however, about the validity of the subcoxal theory of the derivation of the pleuron, while Barlet (1950 and 1952) and Carpentier and Barlet (1951) consider that the theory breaks down when applied to Lepisma. They suggest that the pleuron is composed of at least two basal articles of the primitive leg. Carpentier (1955) even hints at the presence of three basal podomeres giving the anapleural, catapleural and trochantinal arcs of the pleuron. In this paper also he makes a most convincing comparison between the pleural regions of Lepisma and the blattids Blatta orientalis and Periplaneta americana.

In spite of this divergence, all authors agree that the typical and basic pleural sclerite is a structure lying dorsal to the coxa, and usually having a coxal articulation ventrally. It is generally subdivided into an episternum anteriorly, and an epimeron posteriorly by a dorso-ventral implex, showing as a sulcus externally. Such
sclerites are found in the pleura of caddis-fly larvae as in most other insects. In the pro-thorax there are two sclerites and this has caused difficulties of interpretation. Hickin (1946) for example, describes the black pleural implex as a trochantin in *T. bicolour*, while Lloyd (1921) in a figure of a theoretical larva calls it an epimeron, considering the first pleural sclerite as the episternum. Paulian (1944) illustrates a larva which he says is a species of *Limnephilus*, but which has no mesotergite and cannot therefore be one. He also says that the two sclerites of the pleural region dorsal to the coxa are the anapleurite and coxopleurite. Unfortunately his figure shows three sclerites in each segment of the thorax, while in the metathorax one of the three appears to have become part of the coxa. Khalil (1953) and Crampton (1926) consider that in *Hydropsyche instabilis* the first pleural sclerite is a trochantin.

It is obvious therefore that there is an urgent need for reducing this wide disagreement by defining some terms, utilising the work of Crampton, Barlet and Carpentier.

(i) Dorsal to the coxa there are three arcs: the trochantinal, catapleural and the anapleural.

(ii) The catapleural arc bears the primary pleural sclerotisation, the eupleurite; this may be implicated dorso-ventrally to divide it into an anterior episternum and an epimeron posteriorly. The anapleurite may be involved in the formation of this structure to a minor extent.

(iii) Both episternum and epimeron may be subdivided, and what is most relevant to the interpretation of the structure of caddis larvae,
the episternum may be divided anteriorly forming a latero-sternite and/or a latero-pleurite.

(iv) The anapleurite may be sclerotised but often remains membranous.

(v) The trochantin is often reduced, or absent, or it may become fused with the basicoxal rim.

(vi) The tergal promotor muscle inserts on or close to the trochantin.

(vii) There are frequently small sclerites in the 'neck' region, the 'cervicalia', having a very wide range of shape, size distribution and number. Their origin or origins are at present quite unknown.

With such principles in mind we can now begin to decide the nature of the sclerites of the caddis-larva pleuron. The main (second) propleurite, the mesopleurite and the metapleurite are clearly homologous to the eupleurite of the typical insects. The implex is the pleural sulcus (DuPorte, 1959) and divides it into episternum and epimeron. Ventrally the pleural implex projects to form a pleural process or coxifer (Crampton 1926), with which the coxa articulates. Parsons (1960) and Martin (1916) call this the coxal process, a term which should be reserved for the process in the coxa which is the other part of the pleuro-coxal joint. Snodgrass (1935) uses the term pleural coxal process, which is descriptive but rather clumsy.

In the prothorax the small first pleural sclerite does not bear the insertion of the tergal promotor muscles (8.10 - 8.13), nor are they inserted close to it. There is a prima facie case therefore
for thinking that the sclerite is not a trochantin. Its true nature is revealed by a comparison of the coxal muscles which have their origins on the episternum, muscles of group 8.2. In the meso- and meta-thorax there are four of these, of which three are represented in the prothorax. Of these three, one (8.22) arises from the first pleural sclerite which must therefore be part of the episternum. This has become divided into a small anterior portion (the first pleural sclerite) and a larger posterior portion which remains as the second pleural sclerite. The first pleural sclerite is therefore what Crampton has termed in other insects a latero-pleurite, and Snodgrass (1909) a pre-episternum.

Attempts have been made to confirm this deduction by reference to the musculature of other insects. This has proved most difficult. There have been no studies on the musculature of larval Trichoptera and very few on larvae of other Orders. The large work of Maki (1938) is unfortunately unreliable; Barlet for example, describes 203 muscles in the thorax of Lepisma saccharina while Maki only mentions 129 in the same species. In any case he only deals with adult Pterygota. Wittig (1954) has described the nymphal and adult musculature of Perla abdominalis & Korschelt (1924) has dealt with that of Dytiscus marginalis, larva and adult. Forbes (1914) has described the morphology of some caterpillars but gives no data on the prothorax, and gives his results in such a diagrammatic way that they are not usable. To a certain extent the adult musculature resembles that of the immature stages sufficiently to make comparison fruitful. Muscles, however, are not rigidly determined structures
and vary in the details of their origin and insertion, a point stressed by Matsuda (1956) and Forbes (1914). This makes the homologising of muscles a somewhat uncertain business, especially when individual muscles are being considered, so that the homologies suggested below are not to be taken as of overriding importance.

In the larva of Dytiscus marginalis, the prefurco-coxalis muscles numbered 14a and b by Korschelt (1924) would correspond to those of group 8.2 of the limnophilid in all the thoracic segments. (The pre-furco is equivalent to the episternum). In the nymph of Perla abdominalis, it is possible that the muscles labelled by Wittig Icpm 28 in the prothorax and muscles II and III cpm 52 in the meso- and metathorax correspond with those of the caddis. In the only description of the muscles of a trichopteran, either larval or adult, known to me, that of the imago of Stenopsyche griseipennis, by Maki (1938) the muscles which correspond fairly well with those in Limnophilus, are the pleural abductor muscles of the coxa, nos. 24 and 25 in the prothorax. In the mesothorax Maki gives no equivalent muscles, and in the metathorax he numbers the only corresponding muscle present, no. 75. Such an unsatisfactory comparison with other insects leaves the confirmation of the hypothesis of the nature of the first pleural sclerite of the prothorax impossible, and emphasizes the need for the study of the musculature before asserting the nature and homologies of parts of the exoskeleton.

The function of this anterior subdivision of the episternum is probably to resist the excessive withdrawal of the head. The fulcrum of head movement is approximately in the dorso-lateral region, so that
a sudden contraction of the ventral retractor muscles brings the ventral posterior surface of the head against the antero-medial surface of the inflected part of these first pleural sclerites. These are not displaced themselves because of the muscles which run to the coxal rim. They may also give an indication to the larva of the degree of flexion of the head and of other head movements. The larvae of hydrophycheids, polycentropids and rhyacophilids, have a similar sclerite, but it does not occur in other Orders. Several workers have described sensory structures on the sides of the cervical region in insects. Mittelstaedt (1957) described them in mantids and considers their function in prey capture. Popham (1959) thinks there are sensory structures in Forficula auricularia, and Wittig (1955) gives details of the "lateral cervical hair plates" in Perla abdominalis. Crome (1957) thinks the "latero-cervicalia" in the larvae of Oryctes nasicornis may have a similar function, and Roeder (1936) calls them prosternal organs. Thorough searches of the sclerite and the surrounding area have failed to reveal any structures which could be construed as sensory either in limnephilids or in T. bicolor and so the function of this first pleural sclerite remains uncertain. It is also curious that muscle 7.20 is missing from the prothorax. In the other two segments this muscle runs from the antero-dorsal tip of the episternum across the lateral wall of the body cavity, and is well placed to pull inwards the anterior end of the episternum or to resist its lateral displacement. The fact that it is missing in the prothorax suggests that either there is no lateral thrust; or that the cuticular attachment of the sclerite to the head is itself sufficient
to resist any lateral thrust; or that there is no necessity to
draw the episternum inwards. Which, if any, of these possibilities
is the applicable one remains unknown.

There remains the problem of the position of the trochantin.
As stated above, the trochantin is to be considered as that part of
the pleuron which primitively lies next to the coxa, and on which the
tergal promotor or adductor muscles usually insert. These muscles
(group 8.1) in limnephilids insert close to the coxa which suggests
the trochantin is not to be found as an independent sclerite. Muscles
insertions often wander from ahypothetical position, however, and
it is probable that the trochantin may be close to this muscle
insertion; in fact it may well be fused to the basicoxal rim. This
would agree remarkable well with the condition in the collembolan
_Tetrodontophora gigas_, (Carpentier, 1949), with _Dilta hibernica_
(Barlet, 1950), _Petrobius sp._ (Carpentier, 1949), and with
_Nicoletia neotropicalis_ (Barlet, 1952). The tergal promotor muscles
would then insert close to the trochantin and the other muscles would
fall into line with those of other insects much more easily. On
this hypothesis the proximal densely sclerotised edge of the coxa is
either wholly or partly derived from the trochantin. Parsons (1960),
however, shows that in the prothorax of _Gelastocoris_ there is a
separate sclerite which she calls the trochantin, as well as a
heavily sclerotised addition to the proximal rim of the coxa, cor-
responding to the structure found in limnephilids. The insertion of
the tergal promotor muscle, her number 13 moreover, bears just the
same relationship to the coxa as in limnephilids. Hence the condition
/
in limnephilids is in some ways more like that of the hemipteran than the Apterygota, but much more comparative study is required before these different positions can be reconciled.

The Sternum.

In adult insects the sternum may be subdivided into basisternum anteriorly, a sternellum or furcasternum posterior to it, and often a spinasternum posterior again (Snodgrass, 1935; Weber, 1954; Crampton, 1914). The basisternum may itself be subdivided by a presternal suture anteriorly, or by a laterosternal suture laterally. Little of this complication is present in the caddis larvae. There are no sutures, not even the Y-shaped endosternal ridge described by Weber (1933), which seems to have a precursor in the machilid *Ctenolepisma* and the dipluran *Campodea* (Carpentier and Barlet 1951).

The presternum bears laterally two points of muscle attachment, and posteriorly another apophysis, the posterior lateral sternal apophysis, in addition to the muscle attachments at the intersegmental line. One of these three lateral points of muscle attachment must be the furcal arm, homologous with the furca of the adult insect. The problem of determining which is the true furca is complicated by the great lack of sclerotisation which does not permit sutures and sulci to become visible. Furthermore the musculature of the prothorax is greatly modified by the muscles actuating the head, and therefore reference has to be made not only to the muscles of the prothorax but to the meso- and meta-thorax as well.

One of the most constant features of the furcal complex is
some connection between the furca and the pleural apodeme. This often takes the form of endoskeletal projections: the furcal arm and the pleural arm, which form a 'flying buttress' over the coxal cavity. Sometimes the two are fused together, e.g. in the prothorax of *Locusta migratoria* (Albrecht, 1953) and *Dissosteira* (Snodgrass, 1929). In other insects the connection is muscular e.g. *Vespa* (Weber, 1927), *Psylla* (Weber, 1929), *Periplaneta* (Maki, 1938) and *Lepisma* (Barlet 1954). In *Perla*, Wittig (1955) describes an intermediate condition with a very short "zwischenmuskel" between the two arms. In yet other examples there is no connection either endoskeletal or muscular e.g. *Anax* (Malceuf 1935), and *Locusta migratoria manilensis* (Maki, 1938), while in beetles no pleural apophyses are found (Balfour-Browne, 1961). If then such a muscle can be found in the Trichoptera larvae, it immediately tends to identify the two apophyses. There is here a great danger of arguing in a circle. The apophyses are determined in part at least by connection between them, and the connection, if muscular, is used to label the muscle. Nevertheless, each part helps to confirm the identity of the others, and the complex as a whole stands out from the other structures of the thorax.

In *Limnephilus* larvae such a muscle is numbered 7.50 in all three thorax segments, and it is considered that the mid lateral aternal apodeme is the homologue of the typical pterygote furcal arm. If this is accepted, there remains the problem of the identity of the apodeme immediately anterior to the furca, from which muscle 8.60 originates. It is possible, or even likely, that this is an anterior prolongation of the furcal region, and is only separate...
because the lack of sclerotisation in this region precludes the attachment of several muscles which are not diametrically opposed in action. A similar situation appears to be the case in the prothorax of Gelastocoris in which Parsons (1960) describes each furca as being subdivided into a lateral and medial part. From these, two muscles, six and seven (M. prosterni primus and secundus) originate, inserting on the ventral occipital condyle. There are, of course, no homologous muscles in the limnephilid. Comparison with the situation in the meso- and meta-thorax, and in other insect larvae shows that the situation is much more complicated, so that the point will be considered again below.

Finally in the sternal region we have to consider the posterior sternal apodeme. It is possible that this is the vestige of what in the Apterygota is an elaborate endoskeleton, and indeed the muscles homologise much better if this assumed. In this case this apodeme would represent the fusion of points 'g', 'b', and 'm' of the prothoracic endosternites of Lepisma as given by Barlet (1951).

In the prothorax of Dytiscus, Korschelt (1924) describes a very similar apophysis and calls it the 'furcilla'. He shows and describes a ligament passing between the furcilla and the median spina. Such a ligament would be homologous to the muscles of group 2.2, and this would suggest that their function in limnophilids is one of more active contraction, while the ligament in Dytiscus larvae is only for a passive resistance to separation. This proposal implies that the furcillae of Korschelt are on the intersegmental line, and this seems likely;
likely; as they are asymmetrically arranged, however, it is not possible to be sure about this.

The spinae are found in the mesothorax and metathorax, in the mid-ventral line. Both lie close to the anterior intersegmental line and are invaginations of the cuticle of the intersegmental fold. Snodgrass (1935), Crampton (1914), and Korschelt (1924), consider them to mark the ventral intersegmental boundary but here they are held to belong to the segment posterior to this boundary as a matter of convenience only.

The lack of sclerotisation of the sternum is remarkable in view of the number and size of the muscles attached to it. It will be seen that the most ventral muscles, muscles 4.12 - 4.15, arise on its posterior edge where it is most strongly sclerotised. This sclerotisation will be strong enough to take the primary tension of the muscles so that they are not torn from their setting but it will not be an effective arrangement if the sternal plate as a whole is free to move forwards. This sternite therefore must be held in place posteriorly, and this is the reason for the lack of membrane between the posterior edge of the sternal plate and the attachment of the mesothoracic internal longitudinal muscles at the intersegmental line. These large muscles hold the intersegmental fold and thus in turn the posterior edge of the sternal plate. They also fix the posterior ends of muscles 2.14 and 2.15 which insert at the intersegmental line. These mesothoracic muscles are themselves held by the corresponding muscles in the more posterior segments. There will of course be a changeover somewhere along the length of the body where, instead of
resisting a pull from the anterior they resist a pull from the posterior. In practice, however, this does not happen when the posterior end is held by the anal hooks. Similarly the dorsal longitudinal muscles interconnect and those of the mesothorax fix the posterior edge of the protergite much as for the protergite. This kind of arrangement applies to many insect larvae, and is associated with the presence of some method of posterior attachment, for example, the anal hooks of caddis larvae, or the posterior prolegs of caterpillars. Animals without such posterior appendages cannot withdraw themselves by such longitudinal muscles although these muscles may be retained for other purposes, e.g. breathing movements, or raising the posterior end of the abdomen in the threat posture of *Ocypus olens* and other Staphylinocidae.

The Mesothorax.

The mesotergite is neither so strongly reinforced nor so extensive as the protergite, although it has a strengthening ridge posteriorly. The pleural region is larger, because of the reduced ventral extension of the tergite, with a large pleurite of typical morphology. The mesosternum is less sclerotised than the protergum, and the same principle of transferred muscular stresses will apply more strongly here also. There is, however, a tough flexible transparent plate which extends over most of the sternal region, as in the protergum, anterior to the posterior dark part.

The pleural ridges of the meso- and meta-thorax are angled. This may be because it is acting as a spring so that there is a small distortion
distortion of the sclerite under stress. This has not been observed. Again it may be that the bend is connected with the need to keep the articulation with the coxa anterior, so that the leg may be easily swung up out of the way, when the animal retreats into its case. Thirdly it may be of some significance that the alignment of the ridge in the two thoracic segments is so close. One might have supposed that they would be oppositely orientated rather than parallel, in view of the fact that the swing and pace of the mesothoracic leg is mainly anterior to its articulation, and in the metathoracic leg it is mainly posterior.

The external dorsal longitudinal muscles 3.20 to 3.24 run from the mesotergite to the posterior intersegmental membrane. They appear to help in the retention of this sclerite against forward pulls from the coxal promotors for example, and perhaps are necessary because the tergum is not sclerotised as far back as the intersegmental membrane.

This explanation does not unfortunately apply very well to the corresponding muscle of the metathorax for here they insert on the membranous region of the metathorax rather than on the posterior sclerite to which several of the dorso-ventral muscles attach.

The Metathorax.

In the metathorax sclerotisation is weakest and the tergum bears only the three pairs of tergites mentioned above. The pleuron is the largest of the thorax because the segment itself has a larger diameter. The sternum is, as in the mesothorax, not sclerotised to any extent, although there is a similar transparent plate present.
The thoracic segments are notable for the large number of setae which they bear. Many of these are very long, not as shown by Hickin (1946, etc.) and they nearly all project across those regions of the body which are most vulnerable to attack or damage. The fine basal setae on the anterior edge of the protergite, emitted by Hickin, perhaps serve to filter the water so that irritant particles do not get swept into the fold of the intersegmental membrane between the prothorax and the head.

It is characteristic that the setae are found based on a sclerotised part of the body. Those of the head, the thorax, the legs, and the anal plates — none occur on unsclerotised areas. It is likely therefore that this has a functional significance and it is suggested that the displacement of a seta, which is the essence of extero-reception, can only be an effective stimulus if its base is inserted in a flexible ring surrounded by a more rigid and relatively immovable sclerite. Thus the anterior tergal sclerite, has no muscles attached to it, nor is it very much protection to the metathorax. Can it be then that it is necessitated by the need to carry setae in order to detect unwelcome visitors entering the case dorsally? It seems quite possible that this may be the reason for isolated sclerites in other insects too. (But cf Triaenodes/.

The whole thorax is covered by many minute microsetae, (microtrichia of Köler, (1955)) which Henseval (1895) called "papilles cuticulaires". They are not easily seen on the sclerotised parts of the thorax, but they are easily seen on the membranous regions. Henseval states that they are absent from the prosternal horn surface,
but although they are difficult to see, sections show that there are some present and that they are arranged in a spiral. They are not set in membranous sockets as the larger setae are, but appear to project into the cuticle basally. They are probably protective devices rendering the unsclerotised surface unpalatable to such predators as large planarians, which Bebutova (1941) states often attach Trichoptera larvae. This author also suggests that the presence or absence of the 'prickles' should be used as a character for taxonomic purposes. Similar microsetae are shown by Barth (1945) on the folds of the cuticle of the caterpillar of *Catocala* sp.
Fig. 21. Prothoracic leg, posterior view.
Limnephilus

Fig. 20. Prothoracic leg, anterior view.
The anatomy and musculature of the legs of Limnephilus.

The terms anterior and posterior, dorsal and ventral, when used in connection with the legs, are applied as though the leg extended laterally from the thorax. When the leg is swung forward close to the body the anterior side is therefore median and the posterior side is lateral.

The legs are all provided with a large number of setae and spurs or spines. The setae may be very long, as in Triaenodes. The spines of the ventral edges of the trochanter and femur are not sharply differentiated from the setae in their dimensions and rigidity, and there is a continuous range from the spurs to the finest setae. The basal spur on the claws is heavily sclerotised and it is hollow, as is the claw itself. The setae borne on the ventral distal edge of the trochanter are usually the finest and most delicate of those found on the legs. The positions of the setae are shown on the drawings, and are not described further.

The whole of the thorax, and to some extent the legs, especially the arthrodial membranes, are covered by a dense covering of minute points, the microsetae.

The Prothoracic leg (fig. 20 and 21).

The leg is short and stoutly built and inserted ventrally on to the prothorax. It does not all lie in one plane, so that the figures of it are very slightly distorted due to slight compression. The coxa articulates with a ventral projection on the second pleural sclerite,
Fig. 22b. Coxo-trochanteral articulation of prothoracic leg, internal view.
Fig. 22a. Pleuro-coxal articulation of prothoracic leg, internal view.
sclerite, the coxifer. The rim of the coxa is heavily sclerotised and on the postero-dorsal surface of the coxa there is an implex running obliquely from the articulation. The antero-ventral side of the proximal rim of the coxa is widely emarginated and from it extends the flexible ventral sternum of the prothorax.

Distally the coxa bears two inflected points of articulation giving a typical transverse pivot type of joint. Dorsally it is widely emarginated. The ventral side, and the anterior margin of the distal rim of the coxa are thickened with sclerotised cuticle. A large articular membrane is present which is more extensive dorsally. The coxa articulates with the trochanter.

The trochanter is divided by an annular line which is not due to the presence of a joint. The word 'trochanter' has therefore been used throughout in the singular although it refers to what some authors call the first and second trochanters or even the first trochanter and the prefemur. The trochanter is wider distally than proximally and proximally it has a sclerotised rim especially in the areas adjacent to the articulations. Distally it has a broad, oblique articulation with the proximal end of the femur which it obscures from view of the posterior side. The ventral tip of the proximal rim is heavily sclerotised where the extensor muscles insert.

The trochantero-femoral articulation is oblique, with a considerable overlap between the distal end of the trochanter and the proximal end of the femur. This articulation does not consist of direct contact between two hard parts, as in a normal joint, but
Fig. 23. Tibio-tarsal articulation of prothoracic leg, internal view.
of a limited flexibility.

The femur is also wider distally than proximally. The distal end of the femur is emarginated ventrally, especially on the anterior side. It bears two inflected sclerotised points on which the proximal rim of the tibia pivots. These inflected points are not visible in side view but may be seen if the limb is turned so that the distal end of the femur can be seen end-on (fig. 23).

The articulation of the femur and the tibia is also placed transversely so that the movement of the tibia on the femur is in the same plane as that of the trochanter and femur on the coxa.

The tibia is smaller in diameter than the femur and proximally it is bent round in the dorso-ventral plane, particularly ventrally. (This is best seen on the figure showing the muscles of this leg.) The proximal end is oblique also. Distally the tibia articulates with the tarsus in a typical single dorsal hinge joint, and the articular membrane present is restricted in area.

The tarsus is narrower than the tibia and bears a distal claw which it also articulates at a hinge joint. Again there is little articular membrane present at this joint.

The lengths of the various parts of the legs are given in the table below. The lengths are overall measurements of the parts named, except in the last line in which the effective length of the leg has been found by measuring the length from coxifer to claw-tip via the pivotal points of the articulations.
Fig. 26b. Coxo-trochanteral articulation of mesothoracic leg, internal view.
Fig. 26a. Pleuro-coxal articulation of mesothoracic leg, internal view.
**Limnephilus**

Fig. 25. Mesothoracic leg, posterior view.
Limnephilus

Fig. 24. Mesothoracic leg, anterior view.
B. Mesothoracic leg (fig. 24 and fig. 25).

This is the longest leg of the limnephilid larva, is of slender appearance and lies in one plane. It is inserted laterally on the thorax at the end of a squat boss-like structure which is covered by the pleural sclerite. The dorsal or lateral part of the heavily sclerotised coxal rim articulated with this sclerite, and this is the most proximal or dorsal point on the rim. The antero-ventral or inner region of the proximal end of the coxa is greatly emarginated.

Distally the coxa bears inflected projections like those seen in leg 1 but the trochanter also carries proximally internal bars extending alongside, and firmly bound to, the coxal pivot projections (fig. 26). The distal end of the coxa is emarginated dorsally.

The trochanter is similar to that of the first leg, although the articulation with the femur is more oblique and extensive. The distal section of the trochanter is much longer than the proximal.

The femur is almost parallel sided, but distally the ventral edge curves outwards slightly, before turning dorsalwards at the emargination of the distal end.

The tibia articulates with the femur on two inflected points.
Fig. 28. Metathoracic leg, posterior view.
Fig. 27. Metathoracic leg, anterior view.
as in the first leg. Its proximal end is very oblique and distally it is a little swollen. It articulates with the tarsus in a dorsal hinge joint. There is a normal amount of articular membrane present at the joint.

The tarsus is narrower than the tibia and parallel sided, but also slightly curved and bears a claw hinged dorsally.

Although this leg by its length appears slender it is not therefore also weak. In fact it is well sclerotised throughout and quite strong.

C. Metathoracic leg (figs. 27 and 28).

This leg is almost as long as the mesothoracic leg, and is similar to it in its proportions, shape and structure. It articulates with the pleural sclerite of the thorax wall which, as in the mesothoracic leg, projects antero-laterally. The ventral projection borne by the pleural sclerite articulates with the dorsal edge of the coxal rim. The inner or anterior side of the proximal end of the coxa is more acutely oblique than in the second leg, and the emargination has encroached more widely around the rim. This has left only a small region of the proximal end adjacent to the coxo-pleural articulation on the anterior side, which is more or less transverse. The articular membrane here is also more extensive than the corresponding one of the second leg.

Distally the coxa is much as in the meso-thoracic leg, except that the dorsal emargination is somewhat larger.

The trochanter is again elongate, broader distally than proximally. Its distal part is, on the anterior side, almost wholly membranous.
**Limnephilus**

*Fig. 29.* Vertical section of trochanteral annulus to show details of its structure.
proximally than the distal part of the femur, originates in the larva of *Oryctes nasicornis* in the coxa. This is a good example of the need to bear in mind the possible adaptations which the musculature can show, and which may make definitions based on muscle insertion and origin quite invalid. As Crome points out, the reason for this abnormality is the extreme shortness of both the trochanter and the femur in this insect, being together shorter than the coxa. If, therefore, the podomere distal to the coxa is to be called trochanter, it must be recognised that the evidence for this being based on the musculature is not so strong as it is sometimes suggested.

The nature of the annular line is difficult to see clearly, but from sections stained with azan it seems to consist of elastic material wider internally than externally, and not extending through to the surface layer; which according to the terminology of Lower (1959), is probably the epicuticle and the amphion, (fig. 29).

Superficially the line suggests a plane of autotomy similar to that of crustaceans, and attempts were made to test this bysubjecting the legs of an anaesthetised limnephilid larva to severe stresses. In no case did the break occur at this line, however, so that this hypothesis is incorrect.

Possibly this line is one of elasticity, which, combined with the
Fig. 30. The muscles of the prothoracic leg.
trochantero-femoral muscle, gives a springiness between the thorax and coxa and the rest of the leg. A similar subdivision occurs in the trochanters of the larvae of *Molanna angustata* (Raciecka, 1953)\textsuperscript{end} and Hickin (1946) says that in *Leptocerus atterinus* the trochanter of the metathoracic legs is subdivided into three parts.

A similar annulus is described by Manton (1958a) on the trochanter of Scolopendromorpha and Lithibiomorpha, and she states that it has a breaking plane lying across it.

The muscles of the prothoracic leg (fig. 30).

1.0. The coxo-trochanteral flexor muscle consists of two branches arising close to the postero-dorsal rim of the coxa, and five branches arising on its posterior face. These seven branches sweep down to insert on the dorsal edge of the proximal rim of the trochanter.

1.1. The coxo-trochanteral extensor muscle consists of five branches arising on the antero-ventral region inserting on the ventral tip of the proximal end of the trochanter.

9.10 and 9.11. Also inserting here are the two fine branches of the pleuro-trochanteral muscle. They arise in the thorax.

2.0. The trochantero-femoral muscle consists of three short muscle branches based on the ventral edge of the trochanter and inserting on
the antero-dorsal proximal tip of the femur.

3.0. The femoro-tibial flexor muscle consists of a large mass of muscle lying in two series, one slightly anterior to the other. The anterior group consists of ten branches and the posterior one of eight branches. In addition there is a single branch extending into the trochanter. This muscle inserts on to the apophysis running to the ventral proximal tip of the tibia.

3.1. The femoro-tibial extensor muscle is a single muscle with its origin on the dorsal edge of the femur and its insertion on the dorsal proximal tip of the tibia.

4.0. The tibio-tarsal flexor muscle consists of two small branches arising on the ventral region of the tibia, and inserting on the ventral proximal end of the tarsus.

4.1. Eleven branches of the tibio-claw flexor muscle are present in the tibia, five arising on its antero-dorsal edge, and six posterio-dorsally; all insert on to the claw tendon.

4.2. There is also the femoro-claw flexor muscle which consists of five branches, four of which arise close to 3.1 on the dorsal edge of the femur. The fifth arises just within the ventral margin of the proximal end of the femur. This muscle passes into the tibia where it inserts on to the proximal end of the ungulltractor tendon. /Intrinsic
Limnephilus

Fig. 31. The muscles of the mesothoracic leg.
Intrinsic muscles of the second leg (fig. 31).

1.0. The coxo-trochanteral flexor muscle consists of eight branches, two of which are more slender and dorsal than the other six. All originate near to the proximal rim of the coxa spreading in a broad arc over the posterior face of the coxa. They insert dorsally on to the proximal face of the coxa.

1.1. The coxo-trochanteral extensor muscle consists of two fine and three broad branches originating on the anterior face of the coxa and inserting on to the ventral proximal tip of the trochanter.

9.10. The pleuro-trochanteral muscle, which arises in the thorax, also inserts here, with 1.1.

2.0. The trochantero-femoral muscle consists of two longer and two shorter branches arising in the antero-ventral region of the trochanter and inserting on the antero-dorsal edge of the femur.

3.0. The femoro-tibial flexor muscle is very large and consists of twelve branches arising from the postero-dorsal region of the femur and inserting on to an apophysis running to the ventral proximal edge of the tibia.

3.1. The femoro-tibial extensor muscle is a small muscle with its origin on the antero-dorsal region of the femur and insertion dorsally on the proximal rim of the tibia.
Fig. 32. The muscles of the metathoracic leg.
4.0. The tibio-tarsal flexor muscle is a small muscle arising ventrally nearer to the distal end of the tibia and inserting ventrally on to the proximal rim of the tarsus.

4.1. The tibio-claw flexor muscle has fifteen branches. Eight arise on the postero-dorsal and seven on the antero-dorsal regions of the tibia and insert on to the unguitractor tendon.

4.2. The femoro-claw flexor muscle consists of two fine branches originating on the dorsal wall of the femur, distal to the origins of the other muscles. They pass into the tibia where they insert to the claw tendon.

Intrinsic muscles of the third leg (fig. 32).

1.0. The coxo-trochanteral flexor muscle consists of seven large branches arising in an arc on the posterior face of the coxa from its proximal tip. The most dorsal of these seven branches is not so closely bound to the other six as they are to one another. These branches, as before, insert dorsally on to the proximal end of the trochanter.

1.1. The coxo-trochanteral extensor muscle has two short fine branches, all arising from the anterior surface of the coxa and inserting ventrally on the proximal end of the trochanter.

9.10. The pleuro-trochanteral extensor muscle consists of two fine branches arising in the thorax and inserting on the trochanter with muscle 1.1.

2.0. The trochantero-femoral muscle consists of six small branches running from the anterior face of the trochanter to the dorsal edge of the proximal end of the femur.
3.0. The femoro-tibial flexor muscle consists of ten branches, nine arising along the dorsal edge of the femur, and one from the proximal tip of the femur. It inserts ventrally on the proximal tip of the tibia.

3.1. The femoro-tibial extensor muscle is a group of five branches arising on the antero-dorsal surface towards the distal end of the femur, and inserting dorsally on the proximal end of the tibia.

4.0. The tibio-tarsal flexor muscle is a small two-branched muscle arising near the distal end of the tibia on its ventro-posterior region. It inserts on the ventral edge of the tibia.

4.1. The tibio-claw muscle consists of fourteen branches all spaced out in the tibia and not closely adjacent as in the other legs. Eight branches arise on the postero-dorsal, and six on the antero-dorsal regions of the tibia, and insert on the claw tendon.

4.2. The femoro-claw flexor muscle consists of three small branches, one of which more ventral than the other two, arises from the anterior wall of the femur. The other two arise from the posterior wall.
The use of the legs in limnephilids.

The legs are used principally in connection with case-building, feeding, and locomotion.

Case-building.

Limnephilids build cases mainly with pieces of plants, and experiments have been made to determine their method of case building. The larvae are not easy to keep in captivity, especially where no decaying plant debris is available for food. In *L. marmoratus* and *L. politus* the stem fragments used are of various thicknesses and lengths (up to 3 cms. long). *L. stigma* uses leaves of duckweed if available, while *L. flavicornis* uses mollusc shells. In this last it is almost certain that the case material and food material are different, especially when it is common to find both living bivalves and living gastropods used for building the case. In some caddis there is evidence that the food and the case material are alike even to the shape of the pieces bitten off for food and the case (Professor H.P. Moon, pers. comm.).

Cases occupied by living larvae were partially destroyed and the larvae left to rebuild the missing part. They remain still for a time before they commence repairs. Eventually, however, they add to the case until it is as long as before. Several specimens with cases made entirely of shells and stones had the anterior part of their cases removed. Some had this part broken up and returned to them while others had access to plant material only. In all the trials the cases were rebuilt with the available materials, the original material being preferred. When the posterior end of a case is removed, the silk...
membrane across the posterior opening is also removed. When this is done, the larva builds on to the anterior end of the case until the case is long enough, and then it reverses within the case and reformsthe posterior end. After again reversing the head of the larva is at the anterior end of the case. The whole process from damage to the case to its full repair took two hours of fairly continuous activity in one specimen.

When adding a new piece of stem or other material to the case, it is held by the legs while silk is used to fix it into place on the case. As may be expected, the legs are not limited in the tasks for which they are used, all of them are sometimes used for holding the case or the new piece, or the plants in the vicinity. The fore-legs, being so much shorter than the other two pairs, are usually used to grip the edge of the case while the longer legs extend past them to hold the piece to be added. Larvae are very dextrous even in their handling of such awkwardly shaped objects as a shell of a pond snail of bivalve and, gripping it with 3, 4, or even 5 legs, they can reverse or rotate the shell with complete assurance.

Objects are gripped by the raptorial action of the folding of the tibia, tarsus and claw against the femur at the femoro-tibial joint. Usually, but not always, the larva inspects an object suitable for case-building by gripping it so that it is in the dorso-ventral plane, sticking upright before the head of the larva. This involves a considerable rotation of the leg from its normal plane of movement, and, by its ventral insertion, the fore-legs are best fitted for this. The piece may be
raised or lowered relative to the larva by a step-wise movement of the legs up or down it. The larva is almost "walking" up and down the stem with small strides, although of course the legs are rotated more medially than in true walking.

In the inspection the piece is turned to the horizontal plane (approximately) and now the fore-legs become less advantageous. Very often legs of the second and third pairs take over the holding of the piece, while the fore-legs get a grip on the existing case, often only by the tip of the claw being inserted into the interstices of the case structure and its silken lining.

At the same time too much should not be deduced from this, for a larva can use the fore-legs when the stem is held horizontally and the other legs can hold it vertically. Moreover, a larva without fore-legs has been watched and is able to build and repair its case as well as a normal animal.

Feeding.

Larvae have been observed feeding in a variety of circumstances both in the field and the laboratory. They have been noted as feeding frequently on the algal growth found on submerged masonry, and other objects. They also feed readily on the plentiful partially decayed plant remains found amongst the canal reed beds.

In taking plant food such as a reed leaf, a larva grasps the leaf on either side with its two long pairs of legs and moves along hugging the leaf in a "bear-hug". The fore-legs play least part here, although they may reach to the edge of the leaf, or their claws may use /irregularities
Fig. 33. Reed nibbled by larvae.
irregularities in the surface of the leaf to get a grip. As may be seen in the illustrations (fig. 3J) a leaf may be attacked at the edge or a hole may be bitten directly into it. It is easy to see how the larva manages to bite the edge of a leaf and nibble its way inwards, since the mandibles are very efficient cutting tools. The breaking into the surface of a leaf, however, is not as straightforward: there is no edge to bite on and generally one would expect the mandibles to slip on the surface. Possibly the surface irregularities are utilised to facilitate an entry; unfortunately I have not been able to observe this feeding process so far.

When eating softer food such as algae, or parts of decayed pulpy reeds, the disposition of the legs is less definite and the food is scraped readily into the mouth without needing to be held by the legs. From this it would seem the limnephilid larvae are herbivorous, and indeed many authors have stated this conclusion (Wesemberg-Lund, 1913, 1943). Examination of the gut contents of several larvae showed that they had all eaten some food of animal origin. The majority of the gut contents was plant fragments but embedded in these were numerous rotifers and a number of gills and setae, almost certainly from limnephilid larvae. Other fragments found included (insect) muscle tissue still attached to a piece of an arthropod leg which appeared to be the trochanteral region of a limnephilid and the cuticular covering from a group of ocelli from a limnephilid larva. Hence there is a strong case for believing that limnephilid larvae are not only carnivorous but also cannibalistic. This confirms the statement by Wiggins (1959) that larvae which are normally herbivorous
become cannibalistic when crowded. Some of the fragments, however, may have come from dead animals or even perhaps from the moulted skins of larvae. Larvae are frequently seen holding firmly on to the case of another larva, usually at one of the terminal openings (Moretti, 1942). If they do eat one another it is probable that the best position for attack is at the posterior end. Perhaps the frequency with which the gills turn up in the stomach contents is one reason for the variation in the gill counts on these larvae!

The carnivorous nature of the diet has also been confirmed by direct observation. A limnephilid larva was seen to take a chironomid larva, grasping it proximally with its fore-legs, and eat it end-on, from the tail end. The head was discarded. The lashing of the body of the victim was reduced by the two posterior pairs of legs which were wrapped around the chironomid and held it against the ventral edge of the limnephilid's case. In this example, the limnephilid attacked the moving chironomid without 'prompting'. On a later occasion another limnephilid was offered on oligochaete (probably a tubificid) of about 4 cms. long. The worm was held in forceps in front of the caddis larva, and the lashing of the worm could be seen to attract the limnephilid's attention. Suddenly in one snap, the worm had been grasped and bitten into two parts, one of which remained in the grip of the forceps, and the other in the grip of the fore-legs of the caddis, with the second and third legs wrapped around it more ventrally. The caddis proceeded to eat the worm as it had eaten the chironomid. The speed of this attack was astonishing, and such rapid movement is difficult to describe. For comparison,
Fig. 34. Diagram to show grip of prothoracic legs on prey, etc.
however, it may be said that it was quicker than the speed of a frog's tongue when taking food, and far quicker than could be followed by the observer. Limnephilids generally appear to be somewhat like tortoises in the matter of speed (and cumbersomeness), and the change on this occasion was very impressive.

The use of the legs in holding wriggling prey is of importance. As has been mentioned, the fore-legs grip the proximal part of the body of the prey while the end of it is nibbled. One fore-leg is just dorsal to the other one, but both are very close together along the length of the body of the prey. The flexing of the distal part of the legs against the proximal part gives the vice-like grip required. But in fact the grip is more effective than even this would suggest because the fore-legs are both swung inwards and the flexed limbs form a four sided grip: the opposite sides of the grip from each leg, (fig.34). Such a grip is obviously most effective, especially in view of the spiny ventral margins of the legs.

Locomotion.

The larvae of many Trichoptera are encumbered by a case which they must transport with them wherever they go. The case of limnephilids is usually large and very irregular in shape often with projecting pieces of woody stem. Such a case must reduce the speed of an animal bearing it especially when passing amongst dense vegetation. Indeed it would seem likely that there are many situations in which the larva can pass through a gap but is unable to drag the wider case after it. Attempts have been made to simulate such a situation by placing the two prongs of
a pair of forceps so that the case became stuck between them. On no occasion when this was done did a larva retreat and try elsewhere. They always go on trying for a time and then withdraw into their cases. It was also found that if the cases were held tightly enough to prevent forward movement, the cases had to be squeezed too hard, and this influenced the larva within to exhibit abnormal behaviour. This may take the form of the withdrawal into the case just mentioned, or the larva may stretch out of its case and bite the surrounding materials or even the outside of its case. At the same time, none was seen to bite at the obstruction deliberately. On the other hand when stretching out and arching over its case backwards, a larva sometimes touched the forceps, and then it would climb up one of the limbs of the forceps if it could get a grip. In this way it sometimes got round the problem. If the case was not held so tightly as to deform it, the larvae were able to get it through by very sharp and strong jerks which not only drew the case forwards but also rotated it in various directions, by twists of the abdomen aided by alternate grips with the swellings on the first abdominal segment and the posterior hooks. It is likely therefore, that in natural conditions the larva rarely, if ever, gets its case stuck either being able to wrench it through, or not attempting a gap which is too small. How the larva determines which gaps are too small is not at present clear, although the setose body and the extended legs must surely play a part. On the other hand the ocelli may well be concerned in this.

stepping pattern of the animals she was working with. Such detail is not possible with limnephilid larvae; they are more like the Geophilomorpha which Manton describes, where the stepping is irregular because of the irregular nature of the environment. Sometimes a limnephilid larva may be ploughing through mud, or crawling along a leaf, or amongst dense vegetation, or even climbing a vertical surface of stone or brick. In such an environment, the animal requires the ability to place its feet where the suitable footholds are available, and its stepping must often be very irregular. In a less natural and more even environment the stepping movements could be more easily observed and understood.

A dish with a piece of paper covering the bottom was filled with water and the larvae then introduced. After a time, some of the larvae began to crawl about in the dish. Unfortunately the larvae never crawled for any distance in a straight line, turning aside with exasperating frequency. A strong light was focussed on them and this did improve matters as the larvae show negative phototaxis to a certain extent. In this way some details were obtained on the crawling of limnephilid larvae.

The sequence of steps is basically that of alternate tripod positions, first left, second right, third left and then first right, second left, third right, and so on. This simple pattern is, however rarely seen and the first legs may step together, while the second right and third left legs alternate with the second left and third right legs. The third legs may also step together, and only the second legs alternate. At other times, the first right and second
left were moving forwards while all the other legs were on the ground. The animal can pass through a period of instability, and one sequence which was observed was as follows:

(i) On the right hand side the legs in contact with the ground were the second and third, and on the left, the first and third legs.

(ii) First, second and third on the right and none on the left.

(iii) First, second and third on the right and the first on the left.

In other words it can balance for a short period on the legs of one side only.

There is a tendency for the second group of tripod arrangements to be slightly out of phase with the first, so that after the first left, second right and third left legs are put down, the first right is picked up just before the second left, and this just before third right. From this stage other irregularities creep in and the scheme becomes completely arbitrary.

From animals which had been deprived of one or more legs, it could be deduced that each pair of legs has its own part to play in locomotion. The first legs pull downwards, and the third legs perhaps push upwards. This causes the larva and case to tilt up at an angle. The second legs seem to be mainly responsible for the changes in direction, although they are very important in the pulling power exerted by the larva. Progression in this tilted position is probably easier than if the case is left parallel with the substratum since it is less likely to foul the latter. A larva without fore-legs is seriously handicapped in a dish, making little progress, continually /extending
extending the other two pairs in all directions and stretching out of its case. No doubt in a more natural environment, with plants near at hand it would survive quite well. Its turning movements were not impaired.

A larva without the claws and tarsi of the second legs progressed fairly well, but more slowly. When the entire second legs were removed the larva modified the movement of the third legs so that they extended further forward than normally. In this way it was able to compensate for the damage to a large extent.

A larva in which the third legs were removed was able to crawl almost normally, which does not necessarily mean that the third legs play no important part in locomotion. Rather is it that the animal can compensate very well for its mutilation.

A larva taken out of water and placed so that it is not buoyed up is faced with a much more strenuous task. Under these circumstances it uses its jaws as well as its legs to haul itself and its case along. The body is elongated; the jaws and first and second legs get a grip and then the body is shortened and the head flexed, with a sharp jerk. The third legs act mainly as stabilisers, particularly when the animal was induced to crawl on a sloping surface, so that this is a clue to their use under more normal conditions. This method of extension, grip and contraction is also seen when the animal is under water but where the case is obstructed in some way, and was commonly seen in the pulling experiments. (See below).

The first leg steps in a plane passing through or close to
Fig. 35. Diagram to show the pacing of the legs of one side, as seen in dorsal view.
its insertion. Because it is only half the length of the other legs it usually either steps once and waits until the two long pairs of legs have finished their steps, or it steps twice to one pace of the long legs. There are times when it steps in time with the other legs. In this case the long legs have a reduced stride and the short legs have a maximum stride.

The planes of movement of the tips of legs 2 and 3 are widely lateral to the pleuro-coxal articulations. Leg 3 steps just inside leg 2 and has a slightly longer pace \( \frac{\text{pace}}{2} \). Leg 2 swings in an arc extending from the lateral position forwards, and leg 3 swings from the lateral position backwards (Figs. 3 and 5).

Other important leg dispositions.

Although not strictly a 'use' of the legs, we may also consider here the manipulation of the legs which are necessary for retreat into the larval case for safety and also for pupation.

If a larva is disturbed it can very rapidly retreat into its case. If, for example, a larva is feeding on a leaf which is jarred, the larva immediately contracts its body and draws the case up to the leaf with the aid of the anal hooks. In this way the animal is protected to a large extent and yet it can retain its grip on the leaf. When further interference occurs, the larva will release its grip and retreat much further into its case. In either condition the larva must ensure the correct positioning of the legs so that they get into the case in the correct order and position. Normally this involves (i) the raising of leg 3 and leg 2 until they are closely apposed.
Fig. 36. Position of the legs when a larva is withdrawn into its case.
apposed to the body wall; and (ii) their folding which brings legs 2 and 3 to lie along the body dorsally. Leg 1 is ventro-lateral to the prothorax and head, with the claws approximately level with the mouth parts (fig. 36).
Analysis of leg movements.

1. The swing of the pleural sclerite.

In the meso- and metathorax muscles 7.20 and 7.30 rotate (the anterior end of the pleurite ventro-posteriorly). Muscles of group 7.1 and muscle 7.50 rotate it in the opposite sense. This produces a to and fro movement of the coxifer and helps in the swing of these legs, acting as an extra unit in the effective length of the leg.

In the prothorax the situation is slightly different because muscle 7.20 is not present. The antero-dorsal movement of the second pleural sclerite is brought about by muscles 7.1 and 7.31. This movement allows the forelegs to be brought up alongside the head where they are used in feeding and case-building. The return movement of the sclerite is brought about by muscle 7.40 which is on the posterior side of the boss on the postero-ventral angle of the tergum on which the second pleurite sclerite rocks. The contraction of this muscle turns the anterior end of the second pleural sclerite ventro-posteriorly.

The small size of this muscle is a reflection of the weakness of this movement and shows it is only needed for returning the leg to its original position.

The differences in the muscle arrangements of the segments shows how its pattern is adapted to the leg movements: the foreleg reaching forwards in front of the head, and the other legs using a long stride both anterior and posterior to the coxifer for walking.

In some centipedes the katapleure and the eucoxa also swing to and fro in the locomotion but they move forwards on the backstroke.
**Limnophilus**

**Fig. 37.** Plane of articulation of the prothoracic leg.
of the leg and backwards on the forwards stroke (Manton, 1958a).

2. Rotation of the leg on the coxifer.

Leg 1 is not so free to move about on the coxifer as legs 2 and 3 because its articulation is flattened and elongated. This design of articulation limits the movements of the leg relative to the thorax, mainly to an antero-posterior direction, although the plane in which it moves is not quite parallel to the long axis of the body because the articulation is somewhat oblique to the transverse axis (fig. 37).

In legs 2 and 3 the articulation is between a less pronounced coxifer with a slight ventral curve and the basicoxal rim; there is no special socket on the coxa to receive it.

The nature of the connective tissue in these articulations is of some interest. It is obviously not rigid sclerotised cuticle, although it can hardly be the same as that of the general body surface. Evidently the arthropod cuticle can be very tough without being rigid. Manton (1958) in discussing the cuticle of myriapods, describes its staining reaction with Mallory's stain, and on this basis classifies the cuticle into several types. Those which stain red or dark blue with Mallory, are nearest in properties to the cuticle of the limnephilid articulation, being less sclerotised, less rigid, particularly elastic and slightly extensible. Weis-Fogh (1959) described the tendon of the third subalar muscle of dragon-flies as behaving as "an ideal rubber" and being "ideally suited for elastic loaded pads like the principal hinges". Although this author was
thinking of the insect thorax from the point of view of the energetics of flight, his remarks apply very well to the nature of the articular connection between the coxal rim and the coxifer. Such cuticle is also found between some of the podomeres and will be mentioned below.

The movements of the legs are brought about by the extrinsic muscles which have been described above. The functions of the individual muscles have been indicated above also. Only one or two points remain to be mentioned in this connection.

Leg 1 cannot move very far from the plane of its usual movement because of its articulation with the coxifer. In addition it is attached to the sternum of the prothorax with very little sternal region left between the two coxae. Thus muscles 8.40 and 8.14 are not present and only 8.60 remains to rotate the coxa to a slight degree towards the median plane. This movement must be assisted by muscles 8.10 to 8.13. The opposite movement in which leg 1 is pulled backwards is brought about by muscles 8.50 to 8.55 and 8.60, with the latter perhaps tending to correct the abduction component in the former group. Muscles 8.20 to 8.23 promote the coxa and the very short leverage of these muscles means that they can bring the leg forwards and upwards very quickly. Such swift movements are clearly of importance for the catching of prey and when retreating into the case.

The muscles of legs 2 and 3 are basically similar to those of leg 1. Because these legs are inserted more laterally than leg 1, they are more free to move against the body. Their freedom is also enhanced by the nature of the coxiferal articulation. Muscles 8.40
and 8.41 are found in the meso- and meta-thorax, are inserted posterior to the coxifer and are coxal rotators, turning the leg outwards. In the metathorax their insertions are also ventral to the pivot, so they must also act here as adductors pulling the leg below the thorax. In the mesothorax this is not quite so marked because the emargination is not so extensive on the median side of the coxa as it is in the meta-thorax, so that their insertions are hardly below the level of the coxifer.

3. Walking movements.

The main promotor muscles in all three thoracic segments are those of group 8.2, and the main remotor muscles are group 8.5. It is perhaps surprising that the arrangement of these muscles is so similar in all three legs for, as was pointed out in the description of the use of the legs, the first leg takes only a small part in walking movements, the second leg paces mostly anterior to its pivot, and the third leg mostly posterior to its pivot. This may be an example of the insignificance of normal optimal activities in determining the course of evolution of a species of animal. The legs have similar musculature because the abnormal demands which are a matter of life and death, need that pattern of musculature, while the everyday activities manage with it. Also as mentioned earlier limnephilid larvae live where the footholds are bound to be irregular, so that the musculature is adapted to irregular movements of the legs. In any case the use of the legs in building the case and feeding /precludes
Fig. 38. Successive positions in one pace of the prothoracic leg.
precludes any absolute differentiation in structure. The mus­
culature is, therefore, just as often called upon to move the second
leg posterior to its coxifer and the third leg anterior to its, and,
as a result, is very similar in both segments.

The walking movements in limnephilid larvae are not, however,
simply one of promotion and remotion, except perhaps in leg 1.
The claw tip of this leg moves, when the larva is walking, in a plane
passing through or close to, its coxiferal joint. Because of the
nature of this joint, rotation of the coxa is greatly reduced, so
that rotation of the leg during its swing cannot occur. (Cf. with
legs 2 and 3). As the body moves forward relative to the claw of
the leg, the leg begins to flex. As it does so the claw, slowly
rotates on its tip, so that, instead of the ventral surface being
apposed to the substratum, the dorsal side becomes nearer. Con­
sequently the claw loses its grip (fig. 38). Thus the first leg is
principally concerned with traction. In addition it is unable to
straighten fully because of the limitation of the articular membranes
at the joints and this limits the length of its pace. Legs 2 and 3
extend laterally and their paces are some distance from the plane of
their coxiferal joints (fig. 35). As the larva moves forward,
point Y approaches and becomes opposite to C. This means leg 2
must flex as this movement occurs, because YP is clearly shorter than
YC. Once Y is opposite to C, further movement means leg 2 must begin
to extend until it reaches the end of its pace, D. At the same time Z
approaches and becomes opposite to E, so that at first leg 3 must flex.
Fig. 39. Change of position of the plane of the leg at the beginning and at the end of the typical pace of an insect.
When Z passes E leg 3 begins to extend until its pace is completed at F. On the recovery stroke both legs rotate forwards again, leg 2 extending and leg 3 flexing. From this it would appear that the power developed by leg 2 is applied mainly during flexion, while leg 3 works largely during extension. It cannot, however, be concluded that the legs exert their maximum power in these positions. In the first place damage to one leg initiates compensatory movements by the others: and secondly, there is no doubt that a limnephilid larva is normally utilising only a very small part of its available power. Under conditions of difficulty, a larva exerts maximum effort and the third legs extend far forward, parallel to the second legs, so that they are now putting forth most power in flexion.

The next things to consider are the planes of the forces acting on the leg which tend to deform it and which must be resisted.

These are the planes in which the forces generated by the musculature and the weight of the animal, are acting. At the beginning of the stroke, when a leg is in the anterior position, the weight of the body acts on the tip of the claw on the substratum (here considered horizontal) (fig. 39). This causes an equal and opposite reaction in the limb acting along the leg and directly through its articulations. Similarly the muscular forces flexing the limb cause the claw tip to be pressed against the ground which will cause similar stresses to be set up in the limb. These two forces exist in a vertical plane (A) turned anteriorly at an angle to the main axis of the body. Such a plane passes through the claw tip on the ground and the pleuro-coxal joint.
Fig. 40(a) and (b). Diagrams to show the torque applied to the leg at the end of its pace by gravity.
and the leg also lies within it. As the leg moves backwards relative to the body moving forwards, the weight of the animal will continue to act in a vertical plane. This plane will turn on a vertical axis. See fig. 35, where YC, ZE and YD, ZF are the planes of force due to the weight in dorsal view at the beginning and the end of the pace respectively.

The second way in which the legs move on the thorax is one in which the plane of the leg is itself rotated about a horizontal axis passing through the pleurocoxal joint on each side of a segment (fig. 398). This rotation occurs as the legs move backwards, and allows the muscular forces generating the forward propulsive power to continue to act through the podomeres and their articulations. That is, the plane in which the muscular forces are working still is aligned with the leg and passes through its articulations, but this plane is no longer vertical. The forces generated by the weight of the animal naturally cannot rotate with the limb because gravity continues to act vertically downwards. Thus the weight of the animal causes forces still in a vertical plane passing through the claw tip and the coxo-pleural articulation. These forces cause a torque to be applied to the leg, and in particular the trochanter-femur, (fig. 40). This torque tends to twist the dorsal proximal edge of the femur away from the distal edge of the trochanter, here assumed to be rigid, and the trochanter-femoral muscles are bracing muscles designed to resist it.

This torque must be very weak in aquatic larvae, because of the buoyancy of the water so that they can afford to have the remarkable oblique joints between the trochanter and the femur seen in caddis-fly larvae.
larvae. No doubt on land such joints could not be strong enough to stand the stresses exerted on them. Manton (1958) does not consider this point, but in an animal where the weight is spread over several legs as in the Myriapoda, the forces involved may also be negligible in any one limb.

The muscles responsible for the remotion of the leg are mainly those of group 8.5. These muscles insert on the pericoxal membrane slightly lateral to the coxifer so that they slightly rotate the leg as well as remote it. Muscles 8.40 and 8.41 also are of importance in this rotation. The correction of the rotation on the forward recovery stroke is due to muscle 8.60, which curls round on to the median anterior inner face of the coxa as described above. (Muscle 8.20 may be involved too). In the prothorax where the coxa does not undergo such rotation, it is significant that (i) the remotor muscles group 8.5 insert much closer to the coxal rim, and not properly lateral to the coxifer, (ii) muscles 8.40 and 8.41 are not found: and (iii) muscles 8.61 does not curl round into the coxa, but is a straight muscle.

4. Flexion and extension of the legs.

This is a vital part of the movement of the legs in any walking animal, but in those caddis-larvae which have a case to retract into, whether larval or pupal, the folding of the legs to accommodate them within the case is also a necessity.

The folding of the legs takes place at two points: the coxo-trochanteral and the femoro-tibial joints, and this subdivides the limb
Fig. 41(a), (b) and (c). Diagrams to show possible arrangements for folding of the legs in order to accommodate them within a case.
into three parts; the coxa; the trochanter and femur; and the tibia, tarsus and claw. Since the arthropod limb is built of rigid units it is only by such folding that the limbs can be fitted into a confined space such as a case. Moreover, the joints at which it is folded, and the direction of the folds must be arranged to give the maximum length of limb in the minimum space. This is achieved by placing the joints so that the three subdivisions are subequal (fig. 41a) unless the attachment of the leg is half-way along one fold. In this case the first subdivision may be about half the length of the other two (fig. 41b). In limnephilids the position taken by the fore-legs is as in figure 41a, while that of legs 2 and 3 is more as in figure 41b. Such acute folding probably brings its own problems, of circulation and aeration perhaps, especially in narrow legs. It is necessary in the forelegs, otherwise they would be projecting in a vulnerable position when the larva had retreated into its case in danger. In the second and third legs it is not so pronounced for they attach more posteriorly. They lie alongside and above the body, the femoro-tibial joint not being so strongly fixed.

Another problem which has to be overcome when the legs are taken into the case is that the length of the coxa cannot be greater than the distance from its articulation with the thorax to the ventral surface of the case. If it were, then the coxa could not be placed in a more-or-less vertical position and the rest of the leg could not be fitted in. This may be one reason why the coxifer of the long posterior two pairs of legs are so high up on the sides of the body (fig. 41c).
The speed of withdrawal suggests that there is mechanism for making the withdrawal movements automatically draw up the legs into the proper positions. At one time it was suspected that the same muscles might be used for both movements, but this cannot be so. It would therefore be of interest to know whether the nervous system is so integrated that a defence reaction via the giant fibres of the ventral nerve cord directly activates both the muscles folding the legs and the muscles contracting the body.

The pivot joints.

The flexor and extensor muscles are responsible for the bending and straightening of the leg. They work in opposed groups in the coxa and femur actuating the trochanter and tibia respectively. When one of these muscles contracts the other relaxes, and, presuming they function as in vertebrates (a large assumption and certainly not fully justified), the tone of the muscles is important in the smoothness of the muscle action.

The other pivot joint of the legs is that between the coxa and the trochanter. Much of the foregoing applies equally well to this joint, but in addition mention must be made of the extrinsic muscle from the thorax to the trochanter. That the prothorax has two such muscles (9.10 and 9.11), while the meso- and meta-thorax have only one each suggests that this muscle is of greater importance in the functioning of leg 1 than in legs 2 and 3.
The muscles together with the intrinsic coxal muscle, are the extensor muscles of the trochantero-femur, so that some action must be sought which results from contraction of these muscles and which is more important or better developed, in leg 1 than in legs 2 and 3. The only action which fits these criteria is that of extending the leg when the larva catches its prey. Perhaps here also the fact of having one branch elongated and arising on the tergum is because a long muscle can contract over a given distance more quickly. On the other hand, it is normal in insects to find a tergo-trochanteral muscle, so actually legs 2 and 3 are reduced in this respect. One could therefore look at it as though the normal function of this muscle is only required by leg 1. What then is missing from the activities of legs 2 and 3 which can allow the reduction of this muscle to one branch? These legs also need to be extended, and also take part in holding the prey, but they do not take part in that swift snap by which the forelegs first capture their food. Hence even from this viewpoint the first suggestion is borne out.

In the femur, the pivot is close to the dorsal side of the joint, and the extensor muscle is short and lies dorsally, while the longer flexor muscle occupies much of the available space. The exact shape of the ends of the podomeres has a great bearing on the degree to which a limb can be bent and consequently its whole usefulness. A more extended discussion of this point is given below.

The Trochantero-femoral joint.

The mechanism of this joint remains one of the most obscure aspects.
Fig. 42 Diagram to show twisting motion at the trochanterofemoral articulation.

Limnophilus

Fig. 43. Diagram to show turning motion at the trochanterofemoral articulation.
aspects of the functioning of all the larval legs so far examined. In the first place its movement is clearly very limited; and secondly there is only one set of muscles with no opposing set. From observations made on the living animals, the movement at this joint can be separated into two kinds, although each grades into and modifies the other.

The femur is able to rotate on its longitudinal axis on the trochanter (fig. 42). This rotation is the result of stress on the distal end of the leg such as would result from the torque due to the weight of the larva as described above. The trochantero-femoral muscle is in a position to resist this twisting. On the other hand, if there was no stress from the distal end of the leg, contraction of this muscle would twist the femur in the opposite direction, and this does happen.

The other component of the action at this joint is a lateral turning of the femur on the trochanter (fig. 43). The other arrangement of the trochantero-femoral muscle is not easy to reconcile with this movement, except for those branches which insert on to the extreme tip of the femur. In leg 1 these include more or less all the branches of the muscle, but in legs 2 and 3 it applies to only one or two small branches, so that it can only be a very weak movement in these legs.

The lack of any clear pivot for these movements is interesting. Pivots confine any movements to planes passing through them, but here, the movements can be unconfined and yet they do not become too vague and inaccurate by the restriction of the articular membrane at this joint.

The mechanism of the restoration of the position of the podomeres at this joint after muscle contraction remains unknown. The articular membrane
membrane is very thin and quite flexible, and there is no hinge with elastic properties. Where the limb has undergone twisting shown in figure 42, it seems likely that the weight of the body at the end of the pace of the leg would correct the displacement, as explained above. Where it has undergone the turning movement as in figure 43, it is only possible to suggest that internal fluid pressure is the mechanism which straightened out the leg. At the moment experimental evidence for this is lacking.

A similar oblique trochantero-femoral articulation is mentioned by Brinkhurst (1960) in the legs of Gerris najas.

Hinge joints.

These joints occur between tibia and tarsus, and tarsus and claw. They provide some interesting features but these will be considered in the general discussion.

The extension of the distal parts of the leg.

The absence of any tarsal extensor muscle raises the problem of how the tarsus and claw are extended again after flexion. This is a problem which has been debated for some years, and Manton (1956) gives an extended discussion of it in myriapods, spiders and other arthropods. Undoubtedly it is the muscles which press the tip of the leg on the ground towards the end of its backstroke which inevitably cause the extension of the leg. When the leg is not in contact with the substratum other explanations must be sought. Two hypotheses have been suggested; that the extension is due to the elasticity of the cuticle at the joint, or /that
that it is due to the internal hydrostatic pressure. Detached legs of caddis larvae show a certain amount of elasticity in their hinge joints, but it is almost certain that in the larvae haemocoelic pressure is also important, as it is in spiders (Parry and Brown, 1959) and the larvae of Catocala (Barth, 1945) and many other arthropods in this kind of passive extension. Manton (1958a) mentions the elastic storage of energy as a probable reason for the slight distortion of the trochanter in locomotion, and the thick hinge joints in fast centipedes.
Fig. 44. Skeletal anatomy of the prothorax: internal view.
Triaenodes bicolor.

Having given an account of the functional morphology of the thorax of the larval Limnephilus, that of Triaenodes bicolor will now be considered. Because this animal swims the details of its morphology can be expected to be different from that of Limnephilus, and a comparison between the two larvae will illustrate the morphological changes which functional adaptations have brought about.

The descriptions follow almost the same sequence as those of Limnephilus, although where warranted a comparison is made between the various aspects of the structures of the two larvae.

Thoracic skeleton of Triaenodes bicolor.

This is similar to that of the limnephilid with the pro- and meso-thorax more or less sclerotised, while the metathorax is relatively unsclerotised.

The Prothorax (figs. 44 and 47).

The tergum is extensively and strongly sclerotised so that the tergal shield extends ventrally over the pleural region, and anteriorly over the cervical region. Posteriorly, the tergite is strengthened by a cylindrical internal rib which runs from one tergal articulation to that on the other side. Ventrally the ends of this rib merge into an area of more sclerotised cuticle lying in the postero-ventral angle of the tergite. This postero-ventral sclerotisation is roughly triangular in shape and its dorsal apex is sometimes extended to form a dark band along the posterior edge of the tergite. Ventrally it articulates with the second pleural sclerite by a blunt boss.
boss which fits into a broad groove on the inner dorsal face of the second pleural sclerite. The tergite is fairly uniform in colour though darker antero-dorsally, with additional darker marks where muscles are attached. The marks are variable to a slight degree and are not shown on the figures. Long setae are found as in limnephilids, most of them projecting anteriorly from the anterior border of the tergite.

The pleural region is also unsclerotised apart from two sclerites. The second of these bears internally a broadly triangular ridge, with the vertex ventral, forming the coxifer. Dorsally this triangular ridge is hollowed out leaving its edge approximately in the form of a semi-circle. Anteriorly it articulates with the first pleural sclerite. This projects ventro-laterally from the pleural region of the thorax alongside the head and its internal surface is thin smooth cuticle shaped exactly to receive the head by being slightly concave. Externally the first pleural sclerite is more sclerotised and darker, and bears a single long seta. Dorsally the sclerite is narrowed to a knife-edge; ventro-medially it is broader. The posterior edges of the first pleural sclerite are connected to the flexible cuticle of the sternal and cervical regions but in the figures this may not be clear because these membranes have been partly removed to allow other details to be shown.

The sternal region of the prothorax is unsclerotised flexible cuticle which merges anteriorly with the wide membrane between the head and the prothorax. The posterior intersegmental line forms a
Triadenodes

Fig. 45. Skeletal anatomy of the mesothorax: internal view.
stronger region than the rest of the sternal membrane for muscle attachment, but the main resistance to deformation is the chain of broad muscles which run throughout the length of the animal. The large coxae approach close together in the mid ventral line so that the area of the sternum is greatly reduced. This is therefore a similar situation to that of the limnephilids and other insects, with a reduction of the thoracic sterna anteriorly.

The Mesothorax (figs. 45 & 47).

The tergum is sclerotised but not so extensively as in the prothorax, not reaching ventrally to the mid lateral line. Anteriorly it is connected by a membrane to the metathorax with no overlapping dorsally, although laterally there tends to be some overlapping owing to the attachment of leg 3. In the folds of the dorso-posterior membrane there is a narrow patch of slightly stiffer cuticle. The ventral edge of the developing wing bud lies immediately internal to the ventral edge of the tergite. The tergite has two or three setae along its anterior edge and one or two more posteriorly.

The pleuron is not differentiated from the tergum and sternum except for the pleural sclerite. This is a large sclerite which is mostly pale in colour and not strongly sclerotised. Like the epimeron of the second pleural sclerite of the prothorax, that of the meso-thoracic pleural sclerite is easily deformed when pressed. The pleural ridge is on the other hand dense and strong and is extended anteriorly to form a projection which acts as a coxifer. It engages with the internal hook developed on the posterior or
lateral side of the proximal coxal rim. Posteriorly the pleural ridge curves dorsally and at this point it projects into the thorax. The apex of the dorsal curve of the pleural ridge connects with the dorsal edge of the episternum which is more clearly sclerotised than the other parts of it. In this segment the pleural ridge lies at approximately 60° to the vertical and is therefore more nearly horizontal than that of the prothorax (50° to the vertical).

Some of the posterior part of the mesopleurite is not shown in the figure (fig.47), because of the position of the metathoracic leg, but its external appearance is similar to its internal appearance.

The pleurite bears two setae on its anterior angle.

The sternum is wholly unsclerotised and bears a single seta projecting ventrally. It is wider than in the prothorax and internally the rim of the coxal cavity runs posteriorly to form a postero-lateral sternal apophysis as in the meso- and meta-thorax of limnephilids, although it remains unsclerotised like the rest of the sternum. The rim of the coxal cavity is rather more definite in nature than mere folds of the integument. Even when all the muscles have been removed and the cuticle is stretched out flat the rim is still visible as a narrow line, a little darker in colour than the surrounding membrane. These narrow linear "strong-points" are found wherever muscles attach to unsclerotised cuticle: for example, at the broad ends of the muscles of the abdomen of *L. flavicornis*. The anterior part of the meso-sternum of *T. bicolor* bears such lines, here called "attachment lines". (The
Triagenodes

Fig. 46. Skeletal anatomy of the metathorax: internal view.
pro-sternum does not because only muscle 7,5 inserts on to it).
There is an elongate spina, which lies in the mid ventral line just
posterior to the anterior intersegmental line.

The Metathorax. (Figs. 46 and 47).

The tergum and the sternum are covered by unsclerotised thin
cuticle. The tergum bears a single dorsal setae and one or two
anterior setae. The sternum bears two setae ventrally, and one is
present in the pleuro-sternal region. Internally the sternum bears
a few attachment lines.

The pleurite consists of an extensive strong pleural ridge,
with lateral areas of slightly sclerotised cuticle forming the
episternum dorsally and epimeron ventrally. The latter appears to
merge into the general cuticle ventrally when seen from outside, but
is more definite when seen in internal view. The former has an
anterior region which is slightly darker than the rest; this part
being adjacent to the pleural ridge.

The pleural ridge lies at approximately 90° to the vertical
and extends anteriorly to form a long curved coxiferal projection,
which articulates with the hook on the coxa as in the mesothorax.
At the posterior end the pleural ridge changes into a transparent
disc which projects internally. This remarkable disc is wider in
diameter than the width of the posterior end of the sclerotised part
of the pleurite, and is about 20 μ thick. It is quite amorphous in
sections and has the consistency of stiff hyaline cartilage (fig. 46).

The pleurite bears a single seta near to the anterior angle.
Fig. 47. Skeletal anatomy of the thorax: external view.
Remarks on the thoracic skeleton of *Triaenodes*.

Discussion of the details of the skeletal anatomy of the thorax of *Triaenodes* can be confined to those points which have not been considered in connection with the more or less identical structures of *Limnephilus*. For example, reference to the muscles of the three thoracic segments shows that in *Triaenodes* the first pleural sclerite of the prothorax bears just the same relationships to the other pleural sclerites as in *Limnephilus*, and it is not necessary to repeat the details to be convinced that it is a similar pre-episternum. It is not inflected anteriorly as it is in *Limnephilus*, but extends alongside the head where it probably functions in the same way as in *Limnephilus*.

The body as a whole in *Triaenodes* is stiffer than in *Limnephilus*. This probably results from a higher turgor pressure in the former, and this also is more evenly spread throughout the body. In *Limnephilus* there are times when the turgor in some segments is as high as it appears to be in *Triaenodes*, but then there are other segments which are partly flaccid. The turgor is perhaps reinforced in *Triaenodes* by the nature of the cuticle, which may be stiffer and less flexible. This is suggested by the presence of setae on the metathorax of *Triaenodes* without a basal ring of sclerotised cuticle. In *Limnephilus* it was seen that such a basal ring was probably a necessary condition for the full and proper working of the setae. Unless the setae of *Triaenodes* are supposed to be different from those of *Limnephilus* in this respect, it seems likely that the conclusion...
reached above, that the cuticle of Triaenodes is more rigid than that of Limnephilus, is indicated by this absence of a special basal ring. It is also necessary to bear in mind the fact that the small diameter of the body of Triaenodes automatically gives it greater resistance to deformation than that of Limnephilus.

For these reasons then, the body of Triaenodes is not very flexible, and this may assist it in its swimming as described below.

The coxo-pleural articulations.

The coxiferal articulations of the meso- and meta-thoracic segments are of a specialised nature. Although in limnephilids the coxiferal projections of these two segments overlap the edge of the coxa, they do not bear the curvature which is seen in those of Triaenodes. The functional importance of their shape will be considered below when the legs themselves are dealt with.

The posterior pleural disc.

This structure is very unusual since it is so transparent, so large relative to other parts of the pleurite, and so amorphous. It has attached to it the posterior ends of some of the retractor muscles, including the largest and thickest one. On contraction of these muscles it is stressed anteriorly and it is against its resistance to this stress that the anterior ends of these muscles can in fact draw the leg posteriorly. The posterior pleural disc is not, however, simply a rigid piece of skeleton for muscle attachment because it has some degree of elasticity. In recent years work of great interest has revealed the presence in
many insects of a rubber-like protein which can be hyaline like this pleural disc. Described by La Greca (1947) in locusts, this substance has been called resilin (Bailey and Weis-Fogh, 1961) and it is found at joints where its elasticity contributes to the efficiency of the mechanics of movements (Weis-Fogh, 1959, 1960). As in locust wing ligaments the resilin of the pleural disc must store energy from the power stroke and release it in the recovery stroke so that the extension of the remotor muscles is brought about swiftly enough for them to be in a position to start the next cycle at the proper time. It is possible that the same material is involved in the ligamentous links at the coxo-pleural joints of legs 2 and 3 of Triaenodes (see below) but they are so small that it is not possible to make any definite assertions on this point. Probably histochemical tests would reveal something further of their nature and this is a problem which it would be interesting to investigate in the future. It is also of importance to know what is the elasticity of the 'tendons' of muscles for this has important bearings on both the mechanics of actions as well as the physiology of isometric muscle contractions.

The disc projects internally into the segment and is therefore seen nearly edge-on in figure 46. It is remarkable that in spite of great stresses it is not anchored by any posterior muscles attached to its internal edge, a fact which emphasizes its strength and toughness.
Tri aes nodes

Fig. 48. Muscles of the prothorax: first stage of dissection: median view.
The muscles of the thorax of *T. bicolor*.

The illustrations of the musculature of the thorax of *T. bicolor* are drawn from animals sagitally bisected. In limnephilids the size and relative flexibility of most of the body allowed the bisected animal to be pressed almost flat, so that the figures could show the intersegmental, the mid dorsal, and the mid ventral lines quite easily. With *T. bicolor* this is not possible and at the dorsal extremities, the intersegmental folds had to be broken to allow the dorsal muscles to be seen. It is for this reason that the most dorsal muscles appear to end some distance from the adjacent segments. The nomenclature and descriptions of the origins, insertions and functions of the muscles are on the same basis as in *Limnephilus*.

Prothorax.

1. Dorsal longitudinal muscles, internal. Three broad muscles, which are levators of the head.

1.10 to 1.12. First, second and third internal dorsal longitudinal muscles (fig. 48).

0. Posterior intersegmental fold.

I. Posterior border of head capsule, dorsally and dorso-laterally.

2. Ventral longitudinal muscles, internal. Six large head depressors, three oblique rather than transverse, which narrow anteriorly where they insert on to the head capsule. At this point the head capsule is inflected and this would appear to represent the tentorium which otherwise is absent.
2.10 and 2.11. First and second internal ventral longitudinal muscles (fig. 48). These two muscles are parallel and closely adjacent, and may also be one muscle in two bands.

0. Ventral posterior intersegmental fold.

I. Ventral border of posterior rim of head capsule.

2.12. Third internal ventral longitudinal muscle (fig. 48). This muscle is broader posteriorly than anteriorly.

0. Ventro-lateral pleural intersegmental fold.

I. Lateral to 2.10 and 2.11.

2.13. Fourth internal ventral longitudinal muscle (fig. 48).

0. Postero-ventral region of tergum dorsal to origin of 8.53.

I. Ventro-lateral part of post occiput.

2.14. Fifth internal ventral longitudinal muscle (fig. 48).

0. Postero-dorsal intersegmental fold between the insertions of 1.12 and 8.12.

I. As 2.13, but external to the insertions of 2.13 and 2.15.

2.15. Sixth internal ventral longitudinal muscle (fig. 48). The most oblique muscle of the group.

0. Centro-lateral region of the tergum.

I. As 2.13 and 2.14.

3. Dorsal longitudinal muscles, external. These muscles are all concerned with the levation and rotation of the head and the retention of the intersegmental membrane in its proper place.

3.10. First external dorsal longitudinal muscle (fig. 48). A broad muscle immediately external to 1.10.

0. Posterior intersegmental fold, close to dorsal mid line and
external to 1.10.

I. Dorsal post occiput adjacent to 1.10.

3.11. Second external dorsal longitudinal muscle (fig. 48). A narrow muscle.

0. Posterior intersegmental fold near dorsal mid line.

I. Anterior intersegmental membrane, just external to the insertion of 3.10.

3.12. Third external dorsal longitudinal muscle (fig. 48). A double banded oblique muscle.

0. Postero-dorsal intersegmental fold.

I. Anterior membrane dorsal to insertion of 3.11. and closest to the mid dorsal line.

3.13. Sixth external dorsal longitudinal muscle (fig. 49). This muscle consists of two bands lying adjacent latero-medially.

0. Postero-dorsal intersegmental fold.

I. Postero-dorsal margin of the foramen magnum.

3.14. Fourth external dorsal longitudinal muscle (fig. 48). A broad muscle which lies very close to 1.12, as 3.10 does to 1.10.

0. Postero-lateral intersegmental fold, adjacent to 1.12.

I. Postero-lateral border of post occiput adjacent to 1.12.

3.15. Fifth external dorsal longitudinal muscle (fig. 48). A narrow muscle.

0. Postero-lateral intersegmental fold, external to 3.14.

I. Anterior intersegmental fold, external to 3.14.

3.17. Seventh external dorsal longitudinal muscle (fig. 49). A
Triaenodes

Fig. 49. Muscles of the prothorax: second stage of dissection: median view.
broad muscle.

0. Posterior mid dorsal part of tergum.

I. Just internal to 3.16 and external to 1.11.

3.30. Eighth external dorsal longitudinal muscle (fig. 49). A narrow oblique muscle, which, with the following two muscles, holds the anterior intersegmental membrane in position.

0. Postero-dorsal intersegmental fold, ventral to the origin of 3.30.

I. Antero-lateral intersegmental membrane passing internal to 5.34 and 7.30.

3.31. Ninth external dorsal longitudinal muscle (fig. 49) A muscle of two parallel bundles.

0. Centro-lateral wall of tergum.

I. Anterior intersegmental membrane, passing external to 5.44 and 7.30.

3.40. Tenth external dorsal longitudinal muscle (fig. 49). A fine muscle, which unlike that of L. flavicornis does not extend into the mesothorax, without sometimes being attached at the intersegmental line. See II, 3.11.

0. Posterior intersegmental fold, near the mid dorsal line.

I. Posterior margin of the head capsule.

4. Ventral longitudinal muscles, external. Only a single muscle represents this group in the prothorax.

4.10. First external ventral longitudinal muscle (fig. 48). A narrow muscle.

0. Postero-ventral intersegmental fold adjacent to 2.12.
I. Ventro-lateral part of post occiput close to 2.12.

F. Assists the muscles of group 2 in depression of head.

5. Dorso-ventral muscles.
   (i) anterior
   (ii) posterior.

5.2. This group of four fine muscles, shown in the figures as single lines, are all rotators of the head.

5.20. First anterior dorso-ventral muscle (fig. 49).
   0. Lateral region of the fold of membrane posterior to the head.
   I. Dorso-lateral region of posterior occiput.

5.21. Second anterior dorso-ventral muscle (fig. 49).
   0. Anterior region of rim of coxal cavity.
   I. Immediately dorsal to 5.30.

5.22 and 5.23. Third and fourth anterior dorso-ventral muscle (fig. 49).
   0. Inner edge of anterior part of rim of coxal cavity.
   I. Dorsal edge of post occiput, median to insertion of 3.17 and 7.30.

5.34. First posterior dorso-ventral muscle (fig. 49). A two-stranded muscle.
   0. Postero-lateral sternal intersegmental fold.
   I. Postero-dorsal region of post occiput, lateral to the insertion of 7.30.


7. Bracing muscles to the pleurites.
   (i) to episternum. (a) anterior.

7.13. First pleural bracing muscle (fig. 50). A very fine muscle.
Fig. 50. Muscles of the prothorax: third stage of dissection:

median view.
0. Lateral region of post occiput.

I. Dorsal median tip of first pleural sclerite in either side of the insertion of 7.14.


0. Centro-lateral region of tergum, posterior to the origin of 7.16.

I. Median dorsal tip of first pleural sclerite.

7.15. Third pleural bracing muscle (fig. 50). A very fine muscle, lying parallel to 7.13.

0. Post occiput, dorsal to origin of 7.13.

I. Dorsal tip of first pleural sclerite, lateral to insertion of 7.14.

7.16. Fourth pleural bracing muscle (fig. 50). A large muscle.

0. Anterior lateral region of tergum.

I. Anterior dorsal edge of second pleural sclerite.

(b) Posterior.

7.30. Fifth pleural bracing muscle (fig. 49).

0. Dorsal region of post occiput, internal to 5.44.

I. Mid dorsal edge of the episternum.

7.31. Sixth pleural bracing muscle (fig. 50). A broad muscle both at origin and insertion.

0. Posterior dorso-lateral region of tergum.

I. Dorsal edge of episternum.

7.40. Seventh pleural bracing muscle (fig. 50).

0. More densely sclerotised part of postero-ventral angle of tergum, just ventral to origin of 8.52 and 8.53.
I. Postero-dorsal edge of episternum.

7.50. Eighth pleural bracing muscle (fig. 49).

0. Furcasternum close to coxal rim.

1. Anterior dorsal face of pleural ridge at its posterior end.

8. Muscles to coxa.

(i) To region of basicoxal rim.

8.10. First coxal muscle (fig. 49). A large muscle.

0. Postero-dorsal region of tergum anterior to tergal ridge.

1. Apophysis of pericoxal membrane which arises close to anterior (or dorsal) edge of coxal on the median side. This apophysis is so much closer to the sclerotised rim of the coxa in T. bicolor than it is in L. flavicornis that this muscle might equally well be said to insert on to the coxal rim itself.

F. Promotor and adductor of coxa.

8.11. Second coxal muscle (fig. 49). A larger muscle than 8.10.

0. Postero-dorsal edge of tergum, posterior to tergal ridge.

1. and F. As 8.10.

8.20 and 8.21. Third and fourth coxal muscles (fig. 50). Two muscles lying very closely together, broad dorsally and narrow ventrally.

0. Postero-dorsal internal face of episternum, 8.20. arising posterior to 8.21.

1. Both muscles insert on the median anterior tip of the coxal rim.

F. Both muscles adduct and promote the coxa.

8.22/
8.22. Fifth coxal muscle (fig. 50).
0. Postero-dorsal internal face of first pleural sclerite.
I. Extreme anterior tip of coxal rim.
F. Promotion of coxa.
8.23. Sixth coxal muscle (fig. 50).
0. Anterior internal face of episternum.
I. Lateral anterior tip of coxal rim.
F. Promotor and abductor of coxa.
8.50 to 8.53. Four muscles of the major coxal remotor complex.
8.50. Seventh coxal muscle (fig. 50). A narrow muscle.
0. Postero-dorsal tergum, anterior to tergal ridge.
I. Mid lateral region of the coxal rim, posterior to the coxifer.
8.51. Eighth coxal muscle (fig. 50). A large broad muscle.
0. Postero-dorsal tergum, posterior to tergal ridge and lateral to the origin of 8.12.
I. As 8.50.
8.52 and 8.53. Ninth and tenth coxal muscles (fig. 50). These two muscles lie immediately external to 8.51.
0. Postero-ventral angle of tergum just dorsal, and internal, to the origin of 7.40.
I. As 8.50 and 8.51.
8.56. Eleventh coxal muscle (fig. 50).
0. Spread out along the postero-ventral edge of the pleural ridge.
I. Lateral basicoxal rim between pivot and insertion of 8.50 to 8.53.

F. As 8.50 to 8.53.

(ii) Inserting into the coxa.

8.60. Twelfth coxal muscle (fig. 50). A fine two-stranded muscle.

O. Posterior ventral intersegmental fold, near to 8.60.

I. Posterior edge of dorsal end of internal coxal ridge close to pivot.

F. Remotor (and rotator ?) of coxa.

8.61. Thirteenth coxal muscle (fig. 50).

O. Posterior ventral intersegmental fold.

I. Anterior internal face of coxa, ventral to the dorsal tip.

F. Remotor (and rotator ?) of coxa.

9. Trochanteral muscles.

9.10. First trochanteral muscle (fig. 50).

O. Just anterior of postero-ventral intersegmental fold and antero-dorsal to origin of 8.61.

I. Trochanteral tendon.

F. Extension of the trochanter.

9.11. Second trochanteral muscle (fig. 50).

O. Extreme postero-ventral part of the tergum.

I. and F. As 9.10.

These two muscles are the same as muscle 1 and 2 of the intrinsic muscles of the leg.

Mesothoracic muscles.

1. Dorsal longitudinal muscles, internal. All are dorsal retractor/
Fig. 51. Muscles of the mesothorax: first stage of dissection; median view.
retractors of the prothorax.

1.10. First internal dorsal longitudinal muscle (fig. 51). A broad muscle.

0. Posterior intersegmental fold, close to dorsal mid line.
I. Anterior " " " " " " "

1.11. Second internal dorsal longitudinal muscle (fig. 51). A broad muscle, but separated from the previous muscle by a gap approximately equal to its own width.

0. Dorso-lateral region of posterior intersegmental fold.
I. " " " " anterior " "

2. Ventral longitudinal muscles, internal. All are ventral retractors of the prothorax.

2.10. First internal ventral longitudinal muscle (fig. 51). A very wide large muscle.

0. Posterior intersegmental fold, close to mid ventral line.
I. Anterior " " " " " " "

2.11. Second internal ventral muscle (fig. 51). A broad muscle.

0. Posterior intersegmental fold, adjacent to 2.10.
I. Anterior " " " " 2.10.

2.2. Spinal muscles. Bracing muscles of ventral intersegmental fold.

2.20. First spinal muscle (fig. 51).

0. Mesospina.
I. Posterior intersegmental fold, external to 2.11.

2.21. Second spinal muscle (fig. 51).

0. Metapina.
Triamenodes

Fig. 52. Muscles of the mesothorax: in second stage of dissection: median view.
I. Lateral anterior intersegmental fold.

3. Dorsal longitudinal muscles, external. Several fine muscles, some oblique and all are retractors and rotators of the prothorax.

3.10. First external dorsal longitudinal muscle (fig. 52). This muscle and the next are sometimes fused into one.

0. Posterior intersegmental fold, close to mid dorsal line.

I. Anterior " " " " " "

3.11. Second external dorsal longitudinal muscle (fig. 52). A fine muscle, which is equivalent to the mesothoracic part of 3.40. in *L. flavicornis*, and is a continuation of 3.40 from prothorax of *T. bicolor*.

0. As 3.10.

I. Slightly lateral to 3.10.

3.12. Third external dorsal longitudinal muscle (fig. 52). A fine muscle divided anteriorly into two strands.

0. Mid lateral region of posterior intersegmental fold.

I. Anterior dorsal intersegmental fold, external to 3.10 and 3.11.

3.13. Fourth external dorsal longitudinal muscle (fig. 52).

0. Posterior intersegmental fold, adjacent to 3.12.

I. Mid lateral region of anterior intersegmental fold.

3.14. Fifth external dorsal longitudinal muscle (fig. 52). A very oblique muscle with posterior and bifid.

0. Posterior intersegmental fold, close to 3.11.

I. Anterior " " " " mid lateral line and external to 5.12.

3.15. Sixth external dorsal longitudinal muscle (fig. 51). A broad oblique muscle.

0./
0. Posterior intersegmental fold, external to 1.11.

I. Anterior " " in pleuro-tergal region ventral to 1.11.

3.17. Seventh external dorsal longitudinal muscle (fig. 52).

0. Central tergum close to mid dorsal line.

I. Anterior dorsal intersegmental fold.

4. Ventral longitudinal muscles, external. This group of muscles assists group 2 as ventral retractors and rotators of the prothorax.

4.10. First external ventral longitudinal muscle (fig. 52).

0. Postero-lateral sternal apophysis, which is also the postero-median part of the rim of the coxal cavity.

I. Lateral part of the sternal anterior intersegmental fold.

4.11. Second external ventral longitudinal muscle (fig. 52).

0. Posterior intersegmental fold, close to 4.12.

I. As 4.10.

4.12. Third external ventral longitudinal muscle (fig. 52). A rather broader muscle which is subdivided into two equal parallel strands.

0. Posterior intersegmental fold, close to ventral mid line.

I. Median anterior intersegmental fold.

4.13. Fourth external ventral longitudinal muscle (fig. 52).

0. As 4.10.

I. Adjacent, and median to, 4.12.

5. Dorso-ventral muscle.
(i) Anterior

5.10. First anterior dorso-ventral muscle (fig. 52).
0. Anterior tergum, near mid dorsal line.
I. Postero-lateral region of sternum of prothorax just anterior to 5.14.
F. Rotation of prothorax on mesothorax. (?).

5.11. Second anterior dorso-ventral muscle (fig. 52).
0. and I. Mid lateral region of posterior intersegmental fold.
F. ?

5.12. Third anterior dorso-ventral muscle (fig. 52).
0. Lateral anterior intersegmental fold.
I. Dorso-lateral region of anterior intersegmental membrane just posterior to the intersegmental line.
F. As 5.11.

(ii) Posterior

5.30. First posterior dorso-ventral muscle (fig. 52).
0. Postero-lateral sternal apophysis.
I. Mid pleural region of posterior intersegmental fold.
F. Helps to hold posterior part of sternum in position against stresses from other muscle. It also helps to depress the body which may have value in inflating swellings of first abdominal segment.

5.31. Second posterior dorso-ventral muscle (fig. 52).
0. As 5.30.
I. Posterior pleural intersegmental fold, dorsal to 5.30.
F. As 5.30.
5.32. Third posterior dorso-ventral muscle (fig. 52).

0. As 5.30 and 5.31.
I. Posterior pleuro-tergal intersegmental fold, dorsal to 5.31.
F. As 5.30 and 5.31.

5.33. Fourth posterior dorso-ventral muscle (fig. 52).

0. As 5.30 to 5.32.
I. Posterior dorso-lateral region of tergum.
F. As 5.30 to 5.32.

5.34. Fifth posterior dorso-ventral muscle (fig. 52).

0. As 5.30 to 5.33, but crossing these muscles internally.
I. Centro-lateral region of tergum.
F. As 5.30 to 5.33.


6.10. First sternal muscles, (fig. 53). A small muscle of doubtful affinity.

0. and I. Pericoxal membrane close to median side of the coxa.
F. Probably helps to maintain the position of the coxal rim.

7. Bracing muscles to the pleurite.

7.10. First pleural bracing muscle (fig. 53).

0. Lateral part of anterior intersegmental fold.
I. Anterior edge of episternum.

7.11 and 7.12. Third and fourth pleural bracing muscles (fig. 53). A muscle of two fine strands.

0. Dorso-lateral anterior intersegmental fold.
I. As 7.13 and 7.15.

7.13. Fifth pleural bracing muscle (fig. 53).
Fig. 53. Muscles of the mesothorax: third stage of dissection: median view.
0. Dorsal anterior intersegmental fold.

I. Antero-dorsal tip of episternum.

7.15 and 7.16. Seventh and eighth pleural bracing muscles (fig. 53).

0. Antero-dorsal part of the tergum.

I. Adjacent to 7.13.

7.20. Ninth pleural bracing muscle (fig. 52).

0. Postero-lateral sternal intersegmental fold.

I. Inner surface of anterior dorsal tip of episternum.

7.30. Tenth pleural bracing muscle (fig. 53).

0. Central dorso-lateral region of tergum.

I. Dorsal edge of episternum towards posterior.

7.31. Eleventh pleural bracing muscle (fig. 53). A broader muscle.

0. Central dorso-lateral region of the tergum.

I. Postero-dorsal tip of episternum.

7.35. Twelfth, pleural bracing muscle (fig. 53).

0. Tergo-pleural region of posterior intersegmental fold.

I. As 7.31.

7.36. Thirteenth pleural bracing muscle (fig. 53).

0. Postero-lateral sternal apophysis.

I. Posterior tip of pleurite, posterior to curved end of pleural ridge.

7.37. Fourteenth pleural bracing muscle (fig. 53).

0. Close to origin of 7.35.

I. Ventral to insertion of 7.35.

7.50. Fifteenth pleural bracing muscle (fig. 53). This muscle
makes a sharp bend to curl round muscle 8.50.

0. Just inside coxal cavity, on postero-median wall.

I. Posterior tip of pleural ridge.

There are two further muscles attached to the postero-dorsal tip of the pleural sclerite and these are dealt with below: see 1.13 and 5.15 in the metathorax.

8. Coxal muscles.

(i) to region of the basicoxal rim.

8.10 and 8.11. First and second coxal muscles (fig. 52). Two parallel muscles.

0. Central dorso-lateral region of the tergum, dorsal to the wing bud.

I. Apophysis on coxal rim, on median side opposite to pivot.

F. Adductor of coxa.

8.20. Third coxal muscle (fig. 53).

0. Postero-dorsal episternum and curve of pleural ridge.

I. Antero-median tip of coxal rim.

F. Promotor of coxa.


0. Anterior internal face of episternum.

I. Anterior tip of coxa.

F. As 8.20.

8.23. Fifth coxal muscle (fig. 53).

0. Postero-dorsal part of episternum, extending close to origin of 8.20.
I. Antero-lateral tip of coxa.

F. As 8.20 and 8.22.

8.50. Sixth coxal muscle (fig. 53).

O. Central dorso-lateral region of tergum, close to 8.10, 8.11 and 5.44.

I. Lateral pericoxal membrane very close to coxal rim, approximately half-way between pivot and posterior of coxal rim.

F. Remotor and abductor of coxa.

8.52. Seventh coxal muscle (fig. 53).

O. Postero-dorsal part of epimeron, very close to the pleural ridge.

I. With 8.50.

F. As 8.50.

8.53 and 8.54. Eighth and ninth coxal muscles (fig. 53). Two parallel muscles.

O. Immediately dorsal to 8.52, and external to 7.50.

I. Lateral coxal rim, just posterior to pivot.

F. As 8.50 and 8.52.

(ii) inserting into the coxa

8.60. Tenth coxal muscle (fig. 53). A fine muscle.

O. Central median edge of coxal rim.

I. Lateral proximal face of coxa, close to pivotal hook.

F. Rotator of coxa.

8.61. 11th coxal muscle (fig. 53).

O. Postero-central region of edge of coxal cavity, close to origin of 7.50.

I. Anterior internal face of coxa.
F. Rotator and remotor of coxa.

9. Trochanteral muscles.

9.10. First trochanteral muscle (fig. 53). A two-stranded muscle.

0. Rim of coxal cavity next to 8.61.

I. Trochanteral tendon.

F. Extensor of trochanter.

10. Ventral transverse muscle.

10.10. First ventral transverse muscle (fig. 52).

0. Central part of mid ventral line, passing dorsal to nerve connective.

I. Centro-median edge of coxal cavity opposite to 8.60 and 6.10.

F. Holds median edge of coxal cavity in place against tensions of 8.60 and (?) 6.10.

Metathorax

1. Dorsal longitudinal muscles, internal. All these large muscles are retractor of the mesothorax and also shorten the metathoracic segment.

1.10, 1.11 and 1.12. First, second and third internal dorsal longitudinal muscles (fig. 54). Three broad muscles lying adjacent to one another.

0. Dorsal posterior intersegmental fold.

I. " anterior "

1.13. Fourth internal dorsal longitudinal muscle (fig. 54).

0. Lateral region of posterior intersegmental fold.
Fig. 54. Muscles of the metathorax: first stage of dissection: median view.
I. Postero-dorsal tip of pleural sclerite of mesothorax.

2. Ventral longitudinal muscles, internal. Ventral retractors of the mesothorax.

2.10. First internal ventral longitudinal muscle (fig. 54).
A broad muscle especially at the posterior end.

0. Posterior intersegmental fold, near to mid ventral line.
I. Anterior " " " " " "

2.11. Second internal ventral longitudinal muscle (fig. 54).
A broad and somewhat oblique muscle.

0. Latero-ventral region of sternal posterior intersegmental fold.
I. Anterior intersegmental fold, close to 2.10.

2.12. Third internal ventral longitudinal muscle (fig. 54).
A broad muscle.

0. Posterior intersegmental fold, in lateral region.
I. Anterior " " " " "

2.2. Spinal muscles. Bracing muscles to ventral intersegmental fold.

2.20. First spinal muscle (fig. 54).

0. Metaspina.
I. Posterior intersegmental fold, just external to 2.11.

2.21. Second spinal muscle (fig. 54).

0. Metaspina.
I. Lateral region of anterior sternal intersegmental fold.

3. Dorsal longitudinal muscles, external. This group of fine muscles assists group 1, and is probably of importance in the turning of/
Fig. 55. Muscles of the metathorax: second stage of dissection: median view.

Triaenodes

0.25 mm
of the body.

3.10. First external dorsal longitudinal muscle (fig. 54).

0. Posterior intersegmental fold, against the dorsal mid line.

I. Anterior " " external to 1.10.

3.11. Second external dorsal longitudinal muscle (fig. 55). 

Runs parallel to 3.10.

0. Dorsal posterior intersegmental fold, external to 1.10.

I. " anterior " " " "


0. Dorso-lateral region posterior intersegmental fold.

I. Dorsal anterior intersegmental fold, passing internal to 3.11.


0. Tergo-pleural region of posterior intersegmental fold.

I. Anterior intersegmental fold, close to dorsal mid line and the insertion of 3.12, passing external 3.11 and 3.12.


0. Adjacent to 3.13.

I. Anterior intersegmental fold, ventro-lateral to 3.11.

3.15. Sixth external dorsal longitudinal muscle (fig. 54). An oblique muscle, not quite parallel to 3.14.

0. Posterior intersegmental fold, close to 1.13.

I. Anterior " " external to 1.12.

3.17./
3.17. Seventh external dorsal longitudinal muscle (fig. 56).

0. Centro-dorsal edge of coxal cavity on the tergum.

I. Dorsal anterior intersegmental fold.

3.18. Eighth external dorsal longitudinal muscle (fig. 56).

0. As 3.17.

I. Anterior edge of coxal cavity.

3.20. Ninth external longitudinal muscle (fig. 55).

0. Dorsal posterior intersegmental fold.

I. Centro-dorsal edge of coxal cavity.

4. Ventral longitudinal muscle, external. These muscles assist muscles of group 2.

4.10. First external ventral longitudinal muscle (fig. 55).

0. Posterior lateral sternal apophysis.

I. Lateral region of anterior sternal intersegmental fold.

4.11. Second external ventral longitudinal muscles (fig. 55).

An oblique muscle.

0. Posterior sternal intersegmental fold, external to 4.12. and 2.12.

I. Anterior " " " " " 4.10. " 2.12.

4.12. Third external ventral muscle (fig. 55).

0. Posterior intersegmental fold, between 4.11 and 2.11.

I. Anterior " " close to ventral mid line.


0. Postero-lateral sternal intersegmental fold, external to 4.10 and 2.12.

I. Anterior sternal intersegmental fold, adjacent to 4.12. and external to 2.10.
5. Dorso-ventral muscles. Several of these muscles, all of which are small in size, like some of this group in the mesothorax, extend into adjacent segments. Their enumeration is not intended to show exact segmental associations, for there is no evidence available on which this can be done. The functions of these muscles are not clear, but presumably they help to hold the various parts to which they are attached in their correct relative positions. They are all bracing muscles, but they probably help to twist the body.

(i) anterior

5.10. First anterior dorso-ventral muscle (fig. 55).
0. Anterior part of tergum, near to the mid dorsal line.
I. Postero-lateral region of mesosternum, close to intersegmental line.

5.11. Second anterior dorso-ventral muscles (fig. 55).
0. Anterior dorso-lateral part of tergum, on antero-dorsal edge of coxal cavity.
I. Alongside 5.10.

5.12. Third anterior dorso-ventral muscle (fig. 55).
0. Anterior intersegmental fold in pleural region.
I. Centro-dorsal edge of coxal cavity.

5.13. Fourth anterior dorso-ventral muscle (fig. 55).
0. Adjacent to origin of 5.12.
I. Dorsal region of anterior intersegmental fold.

5.14. Fifth anterior dorso-ventral muscle (fig. 55).
0. Anterior dorsal part of tergum.
I. Mid lateral region of attachment line between anterior edge of coxal cavity and the anterior intersegmental line.
5.15. Sixth anterior dorso-ventral muscle (fig. 55).

0. Ventral end of anterior attachment line of stergum.

I. Postero-dorsal tip of pleural sclerite of mesothorax.

(ii) posterior

5.30. First posterior dorso-ventral muscle (fig. 56). A fine muscle.

0. and I. Posterior pleural intersegmental fold.

5.31. Second posterior dorso-ventral muscle (fig. 55).

0. Mid lateral posterior intersegmental fold.

I. Dorsal edge of coxal cavity, adjacent to 5.34 and 5.12.

5.34. Third posterior dorso-ventral muscle (fig. 56).

0. Postero-lateral sternal apophysis on the posterior intersegmental fold.

I. Dorsal edge of coxal cavity between 5.12. and 5.32.

(iii) abdominal

A5.10. First special posterior dorso-ventral muscle (fig. 55).

0. Anterior dorsal region of tergum of first abdominal segment.

I. Lateral sternal apophysis close to the origin of 7.50.

A5.11. Second special dorso-ventral muscle (fig. 55).

0. Anterior dorso-lateral region of tergum of first abdominal segment.

I. As 5.10.

A5.15. Third special posterior dorso-ventral muscle (fig. 55).

0. Attachment line in anterior region of sternum of first abdominal segment.

I. Just within dorso-posterior margin of coxal cavity.

6. Sternal muscles. The affinities and functions of this group of muscles are very doubtful.

6.10/.
Fig. 57. Muscles of the metathorax: fourth stage of dissection; median view.
6.10. First sternal muscle (fig. 56).
0. Anterior sternal attachment line.
I. Antero-ventral edge of coxal cavity.

6.11. Second sternal muscle (fig. 56).
0. & I. Dorsal to 6.10.

6.12 and 6.13. Third and fourth sternal muscles (fig. 56). Two adjacent muscles.
0. Antero-dorsal region of tergum.
I. " " edge of coxal cavity.

7. Bracing muscles to pleurite.

(i) Anterior

7.14. First pleural bracing muscle (fig. 56). A very large muscle, of several branches.
0. Anterior mid dorsal line.
I. " dorsal edge of pleural ridge.

7.15. Second pleural bracing muscle (fig. 56).
0. Anterior dorsal tergum.
I. Dorsal edge of episternum.

7.16. Third pleural bracing muscle (fig. 56).
0. Dorsal edge of coxal cavity close to 5.12, 5.44. etc.
I. Postero-dorsal edge of episternum.

7.20. Fourth pleural bracing muscle (fig. 56). A large muscle of two wide branches ventrally, and narrowing dorsally.
0. One branch arises on the attachment line running obliquely across the posterior half of the sternum. The second branch arises on the/.
the postero-ventral edge of the coxal cavity which is modified to form
an apophysis at this point, the furcal apophysis.
I. Anterior dorsal tip of the episternum.

(ii) Posterior

7.30. Fifth pleural bracing muscle (fig. 56). A small muscle.
0. Postero-dorsal part of tergum external to 7.32.
I. External postero-dorsal edge of episternum.
7.31. Sixth pleural bracing muscle (fig. 56). A small muscle.
0. Central dorsal edge of coxal cavity.
I. External postero-dorsal edge of episternum, posterior to
insertion of 7.30.
7.32. Seventh pleural bracing muscle (fig. 56). A large muscle.
0. Central posterior dorsal mid line.
I. External postero-dorsal edge of episternum, posterior to
insertion of 7.31.
7.33. Eighth pleural bracing muscle (fig. 56). A large muscle.
0. Dorsal mid line, posterior to origin of 7.32.
I. Posterior and adjacent to insertion of 7.32.
7.34. Ninth pleural bracing muscle (fig. 56). A small muscle
lying external to 7.32, and internal to 7.30.
0. Postero-dorsal region of tergum.
I. External postero-dorsal region of episternum.
7.35. Tenth pleural bracing muscle (fig. 57). This muscle and/or
the two following muscles may belong to series 7.4.
0. Postero-dorsal intersegmental fold.

I./
I. External edge of posterior edge of pleural sclerite.

7.36. Eleventh pleural bracing muscle (fig. 57).

0. Dorso-lateral region of the posterior intersegmental fold.

I. Adjacent to 7.34.

7.37. Twelfth pleural bracing muscle (fig. 57).

0. Lateral region of posterior intersegmental fold.

I. Just ventral to 7.34 and 7.35.

7.50. Thirteenth pleural bracing muscle (fig. 56). This muscle acts as a pulley round which 8.50 curls.

0. Postero-lateral sternal apophysis (furca).

I. Posterior end of pleurite.

8. Coxal muscles.

(i) To region of basicoxal rim

8.10. First coxal muscle (fig. 56). A narrow muscle.

0. Centro-dorsal rim of coxal cavity.

I. Ventro-median edge of pericoxal membrane.

F. Remotor and adductor of coxa.

8.11. Second coxal muscle (fig. 56).

0. Ventral part of posterior transparent disc of pleural sclerite.

I. Central region of median edge of coxa.

F. Promotor.

8.12. Third coxal muscle (fig. 56). A narrow muscle passing diagonally across the median face of 8.11.

0. and I. As 8.11.

8.20. Fourth coxal muscle (fig. 57). A large thick muscle.
Fig. 56. Muscles of the metathorax: third stage of dissection: median view.
Dorsal-part of posterior disc of pleurite.

Antero-lateral tip of coxa.

Remotor of coxa.

Fifth coxal muscle (fig. 57). A smaller muscle.

Antero-central region of dorso-lateral wall of coxal cavity.

Adjacent and external to insertion of 8.21.

As 8.20.

Sixth coxal muscle (fig. 57). A large muscle, which curls round 7.50.

Posterior dorsal mid line.

Lateral pericoxal membrane, a short distance from the coxal rim.

Remotor and rotator of coxa.

Seventh coxal muscle (fig. 57). Probably the thickest and most powerful muscle in the body.

Ventral part of posterior transverse disc of pleurite.

Lateral rim of coxa, adjacent to the pivot.

As 8.50.

Eighth coxal muscle (fig. 57). A thick muscle.

Posterior intersegmental fold, ventral to origin of 7.35.

Lateral rim to coxa adjacent to 8.51.

As 8.50.

(ii) Muscles inserting into the coxa

Ninth coxal muscle (fig. 57). Four fine strands shown on the figure as single lines. Their origins and insertions are, from ventral to dorsal, as follows:
8.60a.
0. Anterior lateral attachment line.
I. Lateral proximal face of coxa.

8.60b.
0. Furcal apophysis.
I. As 8.60a.

8.60c.
0. and I. As 8.60b.

8.60d.
0. Posterior edge of coxal rim dorsal to origin of 8.61.
I. Pericoxal membrane very close to the coxifer.

The function of these strands is obscure.

8.61. Tenth coxal muscle (fig. 57). A wide thick muscle.
0. Postero-ventral edge of coxal cavity.
I. Antero-median internal face of coxa, distal to 8.60.
F. Retractor of coxa.

9. Trochanteral muscles.

9.10. First trochanteral muscle (fig. 57). A muscle of two parallel strands.
0. Antero-ventral sternal attachment line.
I. Trochanteral tendon.
F. Extensor of trochanter.

9.11. Second trochanteral muscle. (fig. 57). Also of two fine strands.
0. Both strands arise in the region of the furcal apophysis, one on either side of 8.61.
I. and F. As 9.10.
10. Ventral transverse muscles.

10.10. First ventral transverse muscle (fig. 57).

1. Central mid ventral line, passing dorsal to nerve connectives.

Remarks on the musculature of the thorax of *Triaenodes*.

Set 1.

It is noticeable that the muscles of this set in all the thoracic segments of *Triaenodes* are isotelic, that is, one end is not differentiated by a more cylindrical form with a definite tendinous attachment. Both ends are broad, and splay out to attach to the skeleton in a linear manner with no obvious tendinous specialisation. In this respect they are like the homologous muscles of the metathorax and abdomen of *Limnephilus*.

Muscle 1.13 of the metathorax is an example of a muscle which extends beyond the segmental boundaries because it inserts on the mesopleurite. No doubt its function is to anchor the posterior end of the mesopleurite but it is curious that this is necessary when there are muscles 7.35, 7.36 and 7.37 of the mesothorax to do just this. Intersegmental muscles like this clearly have far more effect in bending the body than one confined to a segment; this well-known effect may be recalled in the relationships of the myotomes and vertebrae of the developing vertebrate. Nevertheless soft-bodied larvae are not vertebrates and this special arrangement is not obligatory for their turning and bending movements since in many cases there are no such intersegmental muscles. It is not possible to give any explanation why
the insertion of this muscle should have "migrated" forward in this way.

The extra length of intersegmental muscles, where they occur, may be connected with the fact that longer muscles effect a faster intrinsic displacement (see section on the mechanics of the skeleto-muscular system below, for a fuller discussion of this), although it is not necessary for the extra length to be accommodated by extending the muscle into an adjacent segment. In the metathorax of Triagenodes, for example, there is the remarkable muscle 8.50, which is certainly very long in order to effect a quick movement and yet its relatively enormous length is contained in the segment by being bent at right angles halfway along its length. It is difficult to see why one solution is adopted in one case, and another in the other.

Set 2.

The three oblique muscles of this set are arranged as in Limnephilus, and the remarks applied to them in that animal apply to those of Triagenodes.

The muscles of the spina are more easily seen in Triagenodes than in Limnephilus because the spinae are longer in the latter.

Set 3.

As in Limnephilus this set of muscles is complex in its details with considerable variations from segment to segment. In the prothorax there are as many as in the other two segments, although muscles 3.18 and 3.19 are not present in the prothorax. In some degree this difference is the result of muscles of group 1.1 in Triagenodes having muscles of the
same width lying external to them. In the limnephilid each pair is probably fused together and hence only counted as a muscle of group 1.1.

Some of the numbering may suggest homologies which are not intended. It is not possible to correlate every muscle of the group with the others of other segments, but the overall pattern remains fairly constant. Muscle 3.30. is one example of where the similarity between the prothorax of Limnephilus and that of Triaenodes is not very close, and this muscle may belong in Triaenodes to group 3.1. Again the different widths and obliqueness of muscles of the same number shows how variable this set of muscle is. It also shows that if the explanation, given for the paucity of these muscles in Limnephilus, is applied to Triaenodes, the only conclusion possible is that the head of Triaenodes is more mobile than that of Limnephilus, a conclusion which is likely to be true.

Muscle 3.40 in Limnephilus is continuous from head to mesotergum; in Triaenodes it is attached at the membrane between pro- and meso-thorax. This attachment is sometimes very definite so that each part of this muscle can be removed independently of the other part. In other cases the attachment is much less definite, and only the external fibres of the muscle are discontinuous. When an attempt is made to remove one part of the muscle under these conditions, it tears longitudinally and the inner part is of continuous fibres. Such a situation precludes any true homologising and the part lying in the mesothorax has been numbered 3.11. This is, of course, not very consistent because it ought to be numbered 3.40 as in the mesothorax of Limnephilus. Since it can exist as an independent muscle, however, it has been thought best to retain the/
the number which it was given before its probable connection with muscle 3.40 had been discovered. Only further comparative work could decide whether this is correct.

Muscles 3.17 and 3.18 in the metathorax are difficult to homologise, particularly 3.18 because of its insertion on the anterior rim of the coxal cavity. It is just possible that this is the anterior half of a muscle of group 3.1 which became attached centrally and formed 3.20 and 3.18.

It is very striking that there are no representatives of group 3.2 in Triaenodes with the single exception of one fine muscle in the metathorax, 3.20. This muscle crosses the internal surfaces of 8.50, 7.32 and 7.33, and appears to hold them in place. It is, of course, possible that this belongs to group 3.1, but, in the absence of any indication to the contrary, the former enumeration is preferred.

Set 4.

This set of muscles is remarkable because it has only one representative, 4.10, in the prothorax, and this is slender. In connection with Set 2 it was suggested that the retraction of the head was important for the breaking of tough plant fibres which the larva was unable to bite through directly. It is surprising to find so few muscles of Set 4 in the prothorax and it suggests that the other longitudinal muscles of the prothorax are concerned in this action, together possibly with those of more posterior segments.

In the meso- and meta-thorax, no muscles are present with specialised subdivided insertions on the posterior region of the sternum.
as in 4.11 and 4.12 in Limnephilus. The numbering of this set proved
difficult because of the lack of any detailed correspondence between the
individual muscles, and 4.20 is not represented at all.

Set 5.

In this set also, the numbers must be taken as indicating
general similarities not exact homologies. There are so many of these
muscles and they are so variable in origin and insertion that they have
proved very difficult to correlate.

Group 5.1 This group in the mesothorax and metathorax correspond fairly
well with the exception of 5.12. It is quite likely that there is no
muscle 5.12 in the mesothorax, and that the muscle so numbered should be
5.1x. Muscle 5.15 is noteworthy because it crosses the segmental
boundary, and shows that there is an antero-dorsal thrust on the posterior
end of the mesopleurite which requires a muscle to the angle of attach­
ment to counteract it.

Group 5.2. This group remains as enigmatic as in Limnephilus. They
are very fine and seem to be attached along their whole length to creases
in the cervical membrane so that if they do have any function it must
be a very minor one.

Muscle 5.31 in the metathorax is longer than its corresponding
muscle in the mesothorax and is also unusual because its origin is
dorsal to the origin of comparable muscles and lies on the mid lateral
intersegmental fold.

Muscle A5.15 is a muscle homologous to 5.15 and clearly belongs
to the first abdominal segment. As such it should not be included in this account of the thoracic muscles, but just as 5.15 comes into the functioning of the mesopleurite, so this muscle must be considered in any account of the working of the metathorax. Similarly muscles A5.10 and A5.11 are included. These three muscles help to hold the posterior end of the metapleurite in position.

Set 6.

As in Limnephilus this set defies sure interpretation. In Triaenodes these muscles are very irregular in distribution, especially in the metathorax, although the general disturbance due to the unusual position of the leg articulation in this segment may partly explain this.

Set 7.

This set of muscles is very complex and each group will be considered in turn.

Group 7.1. In the pro- and meso-thorax these muscles follow the same basic pattern, except for the absence of 7.10 and 7.11 from the former. The two small muscles 7.13 and 7.15 in the prothorax have been so numbered in order to fit into the pattern found in the prothorax of Limnephilus, although a comparison with the mesothorax of Triaenodes might suggest that they should be 7.10 and 7.11 respectively. The main objection to this is that muscle 7.14 would not then insert between 7.13 and 7.15, but it must be admitted that 7.15 in the prothorax of Triaenodes is unlike 7.15 in the mesothorax of Triaenodes or in any segment of Limnephilus.

In the metathorax the pattern is not very similar and it seems as/
as though some muscles have become abnormally large while others have
become reduced and subdivided into several minor muscles. Such is the
peculiarity of this group that its numbering has to be rather arbitrary.

Group 7.2. The only important feature of muscle 7.20 is its large
size in the metathorax. Having two origins also shows the difficulties
of effective muscular action when there are no sclerotised areas for
muscles to attach to. The furcal region evidently has insufficient
strength to cope with the pull of both parts of this powerful muscle
and the anterior branch extends on to the apophysis of the sternal
attachment line.

Group 7.3. The homologies of this group are not very clear and the
insertions rather than their origins have been used as the basis for
their numbering. In the prothorax muscle 7.30 is very oblique and runs
from the head while in the mesothorax it is almost vertical and arises
on the tergum posterior to the origin of 7.31. In the prothorax muscle
7.31 is very large and muscle 7.40 is also present. This suggests that
these muscles are acting as it is thought they do in Limnephilus, varying
the position of the coxifer as the larva is crawling.

It is possible that muscles 7.35, 7.36 and 7.37 in the meso-
and metathoracic segments belong to group 7.4. Furthermore muscle 7.36
and 7.37 in the mesothorax are not really equivalent to 7.36 and 7.37
in the metathorax. Hence the numbering of these three muscles is of
doubtful significance, and in the mesothoracic 7.36 and 7.37 may be
muscles of group 5.4.

Group 7.5. As in limnephilids this muscle is of great interest as the
pleuro-furcal connector. In the prothorax it is a slender muscle and only its ventral end is shown in the figures. Its insertion is on the pleural sclerite opposite to that of 7.40 and lateral to 8.5. In the other two segments this muscle acts as a pulley under which the tergal remotor muscle passes. Muscles acting as a pulley seem to be rare in animals although the trochlear muscle of the vertebrate eye is one example, and the tendon of the levator muscle of the wing of a bird is another. In the mesothorax the muscle is strongly angled and muscle 8.50 is slender. In the metathorax 7.50 is less strongly angled while 8.50 is thick and bent at right angles round it. In the mesothorax the origin of 7.50 is not on the coxal cavity rim but just inside it; in the prothorax it is just outside it; in the metathorax it is on it. One can only conclude that the coxal cavity is sometimes so placed as to encompass the furca, but at other times it is lateral to it.

Set 8.

Group 8.1. In the pro- and meso-thorax the muscles of this group follow the expected pattern. In the prothorax the two muscles share the same long tendon and arise on opposite sides of the post-tergal rib. In the mesothorax the muscles are parallel and of a constant width. In both segments the insertion of these muscles is opposite to the coxiferal pivot and their contraction must adduct the leg under the body.

In the metathorax, the coxa and the coxifer have become more dorsal so that the coxa, in the dead animal, projects anteriorly along the mesothorax. The muscles have for the most part followed this change and have remained in the same relationship to the articulation.
Muscle 8.10 arises on the tergal region as usual, but it is odd because its insertion, which is not opposite to the coxifer, is not with the other muscles of this group and because its insertion is on to the pericoxal membrane close to the coxal rim, and not on to the rim itself. Muscles 8.11 and 8.12 are the other two muscles of this group and they have no counterpart in other segments because instead of arising on the tergum they arise on the pleurite. Their main function is to swing the leg forwards during swimming, while 8.10 is used to flex the coxa ventral when the larva is in its case. It seems difficult to see why 8.12 is required at all in view of its relative fineness but presumably it is a minor modifying factor in the movement of the limb.

Group 8.2. In the prothorax there are two muscles, 8.20 and 8.21, inserting on the median edge of the coxa. In the mesothorax there is only one, and muscle 8.23, inserting on to the lateral edge of the coxa, is almost as long as 8.20. In the metathorax there are only two muscles which are probably 8.20 and 8.23, and which insert on to the anterior tip of the coxa. The reason for these differences is not clear, except in the metathorax where the arrangement of these muscles is determined by the swimming movements of the leg.

Group 8.3. No representatives are found in Triaenodes, unless some of the muscles of Set 6 belong here.

Group 8.4. No muscles belonging to this group are found in Triaenodes a rather surprising situation which suggests that these muscles may only be important, as in Limnephilus, where strong leg actions are used.
Group 8.5. This group is complex in the prothorax with five muscles all inserting on to a very well defined tendon. In the mesothorax the muscles are not as stoutly built as in the prothorax, and their axis of contraction is not parallel to the pleural ridges, so that 8.50 curls round 7.50 from the tergum, as mentioned above. In the metathorax this bend from the tergum is even more pronounced, and in this segment this muscle, 8.50, does not insert by a tendon, nor together with the other muscle of the group, nor on to the actual coxal rim, but on to the pericoxal membrane a short distance from it. Muscles 8.51 and 8.52 are straightforward in their positions and insert very close to the pivot.

Group 8.6. In the mesothorax the two muscles of this group, 8.60 and 8.61, have the expected origins and insertions. In the prothorax, both originate on the posterior intersegmental fold and so once again it is their insertions which determines their homologies. The origin of 8.60 has moved from its normal position and come to be dorsal to that of 8.61. This is almost certainly a response to the need to rotate the fore-leg in a particular direction which would be impossible if the muscle ran nearly transversely instead of longitudinally. In the metathorax, there are four fine strands (8.60 a-d) which are impossible to relate to any other muscle with any certainty. Muscle 8.61 is large and clear, so these four strands have been given the number 8.60 because this seems to indicate their most probable affinities. It is possible, nevertheless, that 8.60d may correspond to/
to $8.41$ in *L.flavicorns*. These muscles are so fine, like group 5.2 in the prothorax, that it is hard to believe they can play much part in the functioning of the leg. Comparison with later stages of the life-history of the larva might show that they are precursors of more important muscles.

Set 9.

The prothorax has two branches of this muscle which are quite large. Evidently the extension of the trochanter needs muscles of considerable power at times as in *Limnophilus*. In the mesothorax the two strands of 9.10 may represent the fused homologues of 9.10 a and 9.11, but without further evidence it is impossible to know. In the metathorax the muscles 9.10 and 9.11 arise separately and although they fuse together in the coxa, it has been thought desirable to give each part the status of a separate number. It is hard to see why this arrangement is needed but it may be to reduce the tension on one point of the sternum. This does not accord with the origins of such massive muscles as 8.61 and 7.20 on to the same unsclerotised cuticle. Rather is it that the different origins of 9.10 and 9.11 allow them to give different degrees of tension as the coxa is flexed or extended. There may be here a situation similar to that in the distal podomeres of the legs (see below) in which there is a point of zero torque beyond which the one muscle takes over extending the trochanter from the other.

Set 10.

This set includes only one muscle which runs transversely across/
across the central region of the sternum to the ventral mid line. Here the muscles from both sides arise opposite one another so that when they contract their tensions balance each other. This muscle appears to be a direct response to the need to hold the coxal rim in place against the powerful pull of muscles 8.61 and 7.20 and it is surprising that it is not present in Limnephilus. It may be involved in the maintenance of turgor, holding the body more rigidly for swimming.
Comparison of the thoracic musculature of *Limnephilus* and *Triaenodes*.

In the following table (Table 1) the homologies of the muscles of the thorax of the two larvae are indicated. Each muscle is numbered, and the presence of a muscle in a segment of the thorax is shown by L for *Limnephilus* and T for *Triaenodes*.

**Table 1. Homologies of the muscles of the thorax of *Limnephilus* and *Triaenodes***.

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Set 1.

In Triaenodes there are two muscles of this set in the mesothorax. In Limnephilus there are three, but the mesothorax of Limnephilus is the only segment in which 5.10 passes internal to a muscle of set 1. It is possible, therefore, that the ventral muscle of this set in the mesothorax of Limnephilus belongs to set 3. It is not so numbered because it extends from the extreme limits of the segment; it connects with the ends of the longitudinal muscles of the adjacent segments; and it is external to the anterior end of 3.14 and 3.15. Looking at the problem from the opposite point of view, in the mesothorax of Triaenodes the muscle numbered 3.15 may belong to set 1, in which case the pattern of set 1 and 5.10 in the mesothoracic segments of Triaenodes and Limnephilus would be alike. Muscle 3.15 is not in fact placed in set 1 because its posterior end is external to 1.11.

In the abdominal segment of Limnephilus, the muscle obviously homologous to 5.10 i.e. 5b, passes internal to the two ventral lateral muscles of the dorsal longitudinal muscles i.e. 1d and 1e. Here also, unfortunately, 1d or 1d and 1e may correspond to muscles of either set 1 or set 3. There is therefore no conclusive evidence which allows an absolute answer on this point.

Set 2. All the muscles of this set in Limnephilus and Triaenodes and in the abdominal segment of Limnephilus, are arranged in a similar pattern, except, of course, that there are no spinal muscles in the abdominal segment in the absence of a spina. The minor similarities
and differences cannot be ascribed to particular causes in the present state of knowledge; only the inactivation of individual muscles would indicate their individual effects and so lead to a deeper understanding of their arrangement.

Set 3.

Detailed comparisons of muscles in this set are impossible, although in general, they are in homologous groups. Certain differences stand out, however, and an account of these will make the situation clearer.

Firstly, there are wide differences amongst this set of muscles particularly in group 3.1, of width, number present, and angle with respect to the long axis of the segment. This makes comparisons between individual muscles at the best highly problematical and at the worst misleading.

Secondly, there is a tendency towards a cruciform arrangement of some of these muscles best seen in the abdominal segment of Limnephilus (3b and 3d) and in the metathorax of Limnephilus (3.13 and 3.14). The crossing over may be shifted anteriorly as in the metathorax of Triaenodes (3.11 and 3.13) and the mesothorax of Limnephilus (3.11 and 3.12), or posteriorly as in the mesothorax of Triaenodes (3.12 and 3.14).

It may be noticed that the number 3.16 is missing from the sequence of numbers of group 3.1. This is because there is the possibility that the muscle numbered 3.17 in the prothorax of Triaenodes
is not homologous with the other muscles of that number, and may require a separate number on its own.

Thirdly, muscle 3.40 presents a special problem. As mentioned above, this muscle in *Triaenodes* is usually not continuous into the mesothorax as in *Limnephilus*, and neither does it originate in the central mid dorsal region of the tergum, as in *Limnephilus*. Possibly the continuation of this muscle in the mesothorax of *Triaenodes* should have been numbered 3.40, but it is hard to deny its equal status with the other dorsal longitudinal muscles which cross the full width of the segment.

Fourthly, the absence of all but one representative of group 3.2 in *Triaenodes*, is very striking. It immediately suggests that the explanation for the presence of these muscles in the thorax of *Limnephilus* cannot be very sound because it can hardly be denied that the correct positioning of the intersegmental fold when contraction of the body takes place, is of no less importance to *Triaenodes* than to *Limnephilus*.

Fifthly, in the prothorax of *Limnephilus*, 3.30 is a dorsal muscle and there is no corresponding muscle in the prothorax of *Triaenodes*. The muscle numbered 3.30 in *Triaenodes* is quite possibly related to group 3.1.

Set 4.

The prothorax of *Triaenodes* has only one muscle of this set, and that of *Limnephilus* has four. One can only conclude that the rotation of the head into the hypognathous position needs to be more powerful/
powerful in Limnephilus than in Triaenodes. This may be correlated with the fact that Limnephilus may have to bite through much tougher plants than Triaenodes to get its case-building material and its food. Indeed the whole system of external ventral longitudinal muscles in Limnephilus is more strongly built and more firmly based on more sclerotised sterna, and reflects the problem which the larva faces when biting through a woody twig rather than a herbaceous leaf or stem.

Triaenodes, like Limnephilus, has no muscle resembling the series 4j - 4o in the abdominal segment of Limnephilus and no muscle comparable with 4.20 in Limnephilus.

Set 5.

The pattern of this set of muscles is basically similar in both larvae. In the anterior group 5.1, only the mesothorax of Triaenodes is unusual by not having either 5.10 or 5.12 originating in the centro-lateral region of the tergum. It is quite likely that 5.10 is not homologous in all cases; in Limnephilus perhaps 5.10 is more similar to 5.12 in Triaenodes.

In the posterior group 5.3, it may be seen that 5.34 is found in all segments and is a useful landmark in the pattern of the musculature in both larvae. The other muscle of the group are numbered without regard to detailed correspondences. As in Limnephilus, any muscles lying along the posterior intersegmental fold of the prothorax have been arbitrarily considered as mesothoracic.

The special group of posterior muscles 5.51 have no representative in Limnephilus and they are evident adaptations to stresses set up in the metathorax.
metathorax by the swimming of *Triaenodes*. Whether this applies to the anterior extension of 1.13 in the mesothorax is doubtful: it may be used to anchor the posterior intersegmental fold, but it seems more likely that it restricts the anterior displacement of the mesopleurite. Probably A 5.10 and A 5.11 are homologues of 5b and 5d of the abdominal segment, while A 5.15 corresponds to 5e.

Set 6.

Little useful can be added about these muscles. It is doubtful if they all belong together, and 6.13 in the meso- and meta-thorax of *Limnephilus* may belong to a group of set 8, i.e. 8.3. 6.12 and 6.13 in the metathorax of *Triaenodes* are also difficult to relate to the others.

Set 7.

This set presents several problems. The muscles of group 7.1 homologies very well. Only in the metathoracic segments is there much difference, *Limnephilus* having seven muscles and *Triaenodes* three.

Group 7.2, with its single muscle 7.20, is interesting because it is absent only in the prothorax of both larvae. Since in the meso- and meta-thorax of both *Limnephilus* and *Triaenodes* it restricts the antero-dorsal movement of the pleurite, either the stress causing such movement is absent from the second pleural sclerite in the prothorax, or this sclerite is restrained by the position of the first pleural sclerite against the back of the head. On the other hand, the homologue of the insertion of this muscle in the prothorax is on the first pleural sclerite projecting anteriorly, and is therefore not available/
available to this muscle. It is likely that there is truth in both these explanations.

Group 7.3 is less easy to homologise in the different segments than the others of this set, mainly because of 7.35, 7.36 and 7.37 which may belong to groups 7.4 or 5.3. Furthermore 1.13 in the metathorax of Triaenodes may be a combination of 7.40 in the mesothorax and 1.13 in the metathorax, in the same way that 3.40 and 3.11 are related in Triaenodes. It is clear, nevertheless that in their functioning these muscles are very similar. They are all concerned with anchoring or bracing the pleurite against excessive play.

Groups 7.4 and 7.5. No further comment needs to be added here.

Set 8.

The homologous muscles of this set stand out very well, and there are few difficulties. The sizes of corresponding muscles vary enormously, but their mutual relationships remain astonishingly constant in spite of the wide variety of uses to which their legs are put. In group 8.5, however, the numbers do no more than indicate the general affinities amongst the muscles. 8.60 in the metathorax of Triaenodes is obviously very irregular.

Set 9.

Apart from the presence of two muscles in this set in the metathorax of Triaenodes, the muscles of this set are similar in the two larvae.
It is difficult to suggest any convincing reason for the presence of this muscle only in the meso- and metathorax of *Triaenodes*. Possibly it is concerned with the maintenance of a high turgor, or perhaps with the stresses involved in swimming.

From this comparison of the two musculatures, certain conclusions can be drawn. In general terms, the two systems of muscles differ less than might be expected, taking into account the very different methods of locomotion, feeding and case-building. In the metathorax of *Triaenodes*, however, naturally the differences are more accentuated because of the arrangement of the swimming leg. Yet even here there remains enough of the general pattern to permit a reasonable attempt to be made to homologise the majority of the muscles with those of the other two segments, and with those of *Limnephilus*.

It is of some interest here to speculate on the derivation of the muscular pattern exemplified by these two larvae. Berlese (1909) has considered this problem, and he suggests that the primitive stages of insect evolution possessed an internal longitudinal, and an external circular, layer of muscle. It may also be assumed that originally the insect precursors possessed metameric appendages and that there were muscles evolved to actuate these. Berlese (1909) suggested that they arose from a third layer which was ' tegumentary', but there seems to be no evidence for this. In the Symphyla (Tiegs, 1945), the Onychophers (Fauvel, 1923) and the Polychaeta (Grassé, 1959/
1959), there is no real circular layer of muscles, but a longitudinal layer outside which are the locomotor muscles, nearest to the bases of the appendages. This also appears to be true of insects so that one may discount Berlese's hypothesis and suggest that in the primitive precursor of insects more or less every segment had this arrangement of musculature, since every segment probably bore appendages.

In earthworms the circular layer is of course well developed and this is associated with their method of progression. Such opposed layers of muscles are usually thought to be most suitable where the animal depends for its shape on its turgidity and where its main movements are extension and shortening of the body. Such movements are typical of the abdominal segments of the caddis larvae, especially limnephilids, yet they do not possess a circular layer of muscle in spite of the fact that they have no appendages requiring separate muscles. It seems odd that they have not evolved a more definite layer of circular muscles with which to work against the longitudinal muscles. It may be that the demands of the imaginal stage cannot be met if the musculature is too different in the larval stage even though the musculature is one system of larval insect which is known to undergo profound changes during metamorphosis.

The longitudinal muscles themselves are not arranged in a continuous layer, being divided into four main blocks, two dorsal and two ventral. This pattern is quite general in the Arthropoda.
and even in some polychaetes. In caddis larvae these dorsal and
ventral pairs of longitudinal muscle are of great importance especially
in the abdominal segments, because they cause the dorsal and ventral
undulations of the body which drive the water through the case over
the abdominal gills. A similar quadripartite subdivision of the
longitudinal muscles occurs in the tubicolous polychaetes (Grassé
1959), which have the same need for a respiratory current. Here
again, therefore, all the evidence points to muscles arising as single
functional units, later grouped together, and later still fused into
virtually continuous layers in highly specialised animals.

Another feature exemplified by this comparison of Limnephilus
and Triaenodes is the wisdom of using a flexible system of criteria
by which to judge similarities. Quite often one group of muscles
can be said to be homologous to another group and some attempt can
be made to indicate homologies between individual muscles of each
group. Usually this cannot be anything but an approximation, but that
does not mean it is useless. Certainly exact parallels would be
more pleasing but the fact that group homologies can be asserted shows
that there is a basic pattern which is common to both larvae. The
differences which exist in the details of the pattern can be ascribed
to functional adaptations in the species concerned; sometimes these
adaptations are easily understood, sometimes less easily. Again
although it is easier to work on the principle that only the origin
of a muscle can be of use in determining its homology, it is surely
better to use all the available evidence, even though this increases
the/
the number of factors which have to be taken into account. For example, muscles of groups 7.1 and 7.3. in Limnophilus and Triaenodes are best numbered by taking their insertions in order from anterior to posterior although there are difficulties in the metathorax of Triaenodes. Similarly a comparison of insertions of the muscles of the spinae, shows that muscles 2.21 - 2.23 of the mesothorax of Limnophilus belong to this group rather than to group 5.1.

A notable difference between the thoracic musculatures of the larvae is caused by the peculiar position of the coxifer in the metathorax of Triaenodes. The pleural sclerite is rotated in its position on the side of the thorax until it lies at about 90° to the vertical, and this has necessitated a rotation of most of the extrinsic muscles which are concerned with leg movements. They run antero-posteriorly rather than obliquely from dorsal to ventral. In spite of this new orientation, the relative positions of muscles and sclerites are not greatly altered, and this exemplifies the balance between the genetically determined pattern and the phenotypic changes caused by the adoption of swimming as a means of locomotion.
Fig. 59. Prothoracic leg: posterior view.
Fig. 58. Prothoracic leg: anterior view.
Morphology of the legs of *Triaenodes*.

1. The prothoracic leg (figs. 58 & 59).

Leg 1 is inserted ventrally on the thorax and is a stout short limb. It does not lie in one plane: cf. leg 1 in limnephilids. It articulates with a projection on the second pleural sclerite in the dorso-posterior region of the coxa, where the proximal rim is heavily sclerotised. At this point an internal ridge is present in the coxa, with a broad external sulcus marking this infolding. The articulation is therefore between the two faces of the pleural peg and the coxal ridge. The two faces are elongated triangles projecting over the cavity of the coxa (fig. 60).

The proximal margin of the coxa is emarginated, particularly ventrally and anteriorly. The dorsal part of the coxal rim is more proximal than the point of articulation with the pleuron. This region is heavily sclerotised. The coxa tapers distally and ends with some emargination dorsally, and with two lateral inflected points, on which the trochanter articulates. The inflected point on the anterior side is more conspicuous and heavily sclerotised than that on the posterior side.

The trochanter is apparently in two parts. Proximally it is sclerotised; distally it ends obliquely although not to the same degree as in the other legs. Ventrally it bears five stout spines. It articulates with the femur by the oblique membranous joint as in limnephilids, the femur overlapping the trochanter posteriorly.

The/
Fig. 60. Pleuro-coxal articulation of prothoracic leg, internal view.
Fig. 61(a). Femoro-tibial articulation of prothoracic leg, dorsal view.

Fig. 61(b). Femoro-tibial articulation of prothoracic leg, lateral view.
The femur is a large conspicuous unit of the leg approximately twice as wide distally as proximally. It has two regions of dense sclerotisation at the proximal and distal tips. Ventrally the femur bears two stout spines.

The femur articulates with the tibia at a joint with considerable articular membrane yet where points of direct contact between the sclerotised parts of the podomeres appear to be absent. There are two very slight thickenings on the distal rim of the femur, but they do not reach to the tibia. On the proximal end of the tibia there are two small projections which are close to the distal rim of the femur approximately where this has its local thickenings. Manipulation of the limb shows that this region is indeed the region of the fulcrum. Nevertheless there is a clear band of arthrodial membrane between the two parts of this pivot. It may be thought that under muscular contraction the projections on the tibia would be brought into contact with the thickenings on the femur. This is not the case because the tibia even with its projections is too narrow to touch the femur, at least on both sides at once (fig. 61(a)). Possibly the tips of the projections on the femur being unsclerotised are transparent, as is the posterior end of the pleural apodeme in the metathorax. Such transparent cuticle is elastic and in this joint would give a certain degree of flexibility.

Ventral to this femero-tibial joint, the femur extends in a large distal lobe against which the tibia can fold.

The tibia is also much wider distally than proximally and the
Fig. 63. Mesothoracic leg: posterior view.
Fig. 62. Mesothoracic leg: anterior view.
proximal end is curved round from the rest of its length. Ventrally the tibia has two spines, of which one stands on its distal tip.

The tibia articulates with the tarsus by a dorsal hinge joint, as does the tarsus with the claw. The extent of the arthrodial membrane is minimal and allows only very limited movement at these joints.

The tarsus is almost cylindrical. The claw is long and bears the usual basal spur. Both claw and spur are hollow.

2. The mesothoracic leg (figs. 62 & 63).

Leg 2 is longer than leg 1 and is not so stoutly built. It lies in one plane when at rest.

The coxal articulates with a ventral projection on a rod-like pleural sclerite at a point on the coxal rim just posterior to its most dorsal tip. The proximal end is widely emarginated except dorsally, where there is an area of densely sclerotised cuticle. The dense sclerotisation at the point of articulation is inflected towards the dorsal side forming a small hook. Into this hook, the projection on the pleural sclerite fits, which is itself not straight but also hooked, curving away ventrally. These two hooks intertwine as two little fingers, each hooked round the other (fig. 64).

Distally the coxa is not emarginated dorsally to any great extent, it is sclerotised more heavily ventrally, and bears two inflected points, the anterior being more sclerotised. On these the trochanter articulates.

The trochanter is broader distally than proximally, the dividing annulus being close to the proximal end. It is sclerotised mainly/
Fig. 64. Pleuro-coxal articulation of mesothoracic leg, internal view.
mainly at the coxal articulation and distally the articulation with the femur is as before, without direct contact. The emargination is dorsal and anterior, and the tapered femur is apposed to it. The femur does not, however, cover it completely. The proximal end of the femur is closer to the trochanter ventrally than dorsally. In the drawing (fig. 62) it appears to fit within the trochanter ventrally, but this is fortuitous and actually the two podomeres are connected by a narrow flexible arthrodiial membrane. The trochanter bears five small spines.

The femur is tapered proximally and the distal end is oblique. It is sclerotised dorsally particularly at the distal end, but proximally, in the region of the distal posterior margin of the trochanter, there is a break in the dorsal sclerotisation which extends across the anterior face of the femur. This forms a line of flexibility allowing the femur to bend one way only (anteriorly) at this point. Lloyd (1921) describes this as cutting off a very short basal piece from the rest of the femur. It is not a true joint, but a pseudo-joint; there is no 'pre-femur'.

The tibia is curved proximally but otherwise is parallel-sided, and it is more sclerotised ventrally. The articulation between the femur and tibia is almost identical to that of leg 1, and further description is unnecessary (fig. 62).

The tibio-tarsal joint is a simple dorsal hinge joint. The tarsus is cylindrical, bears several spines, and is more sclerotised centrally. The claw articulates with it also at a hinge joint. The claw is long and sharply pointed and has a basal spur; both are hollow.
Fig. 68. Pleuro-coxal articulation of metathoracic leg, internal view.
Fig. 67. Metathoracic leg, posterior view.
Fig. 66. Metathoracic leg, anterior view.
3. The metathoracic leg (figs. 66 & 67).

Leg 3, the swimming leg, is one of the most remarkable of limbs of the larvae of insects. It is greatly elongated and both slender and flexible. The distal parts of the leg bear a very large number of long fine setae, which are of a rigidity incommensurate with their thinness.

The coxa articulates with the pleural sclerite by a joint similar to that of leg 2 but the projection on the pleural sclerite is more elongated than in the latter. As in leg 2 also, only the dorsal tip of the proximal rim is sclerotised, and ventrally it is similarly emarginated (fig. 68).

Distally the coxa bears the same points of articulation with the trochanter as in legs 1 and 2. On its anterior face it bears a number of short minute spines, or microsetae, arranged in fairly regular tracts.

The trochanter is extremely long although the division occurs close to the proximal end. The proximal end and the dorsal edge are the most sclerotised regions, and distally, the dorso-anterior region is deeply emarginated to give a V-shaped notch. Into this notch the steeply tapered proximal end of the femur fits.

As in leg 2, this junction is not a direct articulation, a large expanse of arthrodial membrane being present. As in leg 2 also, the femur, proximally, has a gap in the heavier sclerotisation of the dorsal edge and this line of flexibility continues across its anterior face, forming a pseudo-joint (fig. 66).
Fig. 65(a). Femoro-tibial articulation of metathoracic leg, dorsal view.

Fig. 65(b). Femoro-tibial articulation of metathoracic leg, posterior view.
not very definite. In dorsal view (fig. 65a) it appears to be similar to that of leg 2, and the projections and thickenings are as in that leg. In lateral view, however, the thickening of the distal rim of the femur is not opposite to, but more dorsal, than the two more small projections on the proximal edge of the tibia (fig. 65b). It is possible that on extension the more dorsal pivot is used, while on flexion the ventral projections become the fulcrum. When the limb is extended manually, it can be seen that the former statement is true. When it is flexed manually, it is probable that the latter statement is also true, but it is not possible to be quite certain. The difficulty lies in the fact that in flexion the proximal tip of the tibia passes within the end of the femur and the actual place of articulation becomes hidden from view. Also in manipulation it is very easy to influence the arrangement of the very delicate arthrodial membrane to make it appear as though the articulation is in any one of several positions. Nevertheless, working from the relative positions of the axes of femur and tibia, the probability is that there are two pivotal places at this articulation, and one is used in flexion and one in extension.

The tibia is very long and is slightly bent at approximately its mid point. Here there is a short region of less sclerotised cuticle, lighter than the rest. This is the tibial pseudo-joint. The antero-ventral border is more sclerotised proximally than distally, but the postero-dorsal border is entirely sclerotised.

The distal end of the tibia is nearly transverse, and the tibiotarsal and tarso-claw articulations are both typical dorsal hinge joints.
Triaenodes

Fig. 69. Muscles of the prothoracic leg.
Both tarsus and claw are elongated. The claw is sharp, bears a basal spur and as before claw and spur are hollow.

**Intrinsic muscles of the legs of Triaenodes.**

**Leg 1 (fig. 69).**

1.0. The coxo-trochanteral flexor muscle consists of a radiating series of branches arising just within the rim of the coxa and inserting on the dorsal proximal part of the trochanter. These radiating fascicles are grouped into two major subdivisions, one of which is more anterior and dorsal than the other.

1.1. The coxo-trochanteral extensor muscle is also in two major subdivisions. The first, more dorsal one consists of a broad branch arising as three separate branches, which soon fuse to form the single branch. The second, more ventral one is a single branch, whose origin extends along the ventral region of the coxa. This muscle inserts on the ventral condyle of the trochanter.

9.10 & 9.11. Also inserting with muscle 1.1. is the pleuro-trochanteral muscle inserting on a long apodeme which runs to the trochanter and arising in the thorax.

2.0. The trochantero-femoral muscle is a two-branched short muscle arising in the ventral region of the trochanter and inserting on the antero-dorsal proximal rim of the femur.

3.0. The femero-tibial flexor muscle is a trifid muscle; one branch arises dorsally, and the second arises on the posterior face of the coxa. The most ventral of the three arises from the distal posterior edge of the trochanter. It inserts on the ventral proximal end of the tibia.
Triaenodes

Fig. 70. Muscles of the mesothoracic leg.
3.1. The femoro-tibial extensor muscle arises from the dorsal edge of the femur and inserts on the dorsal condyle of the tibia.

4.0. The tibio-tarsal flexor muscle is a narrow muscle arising ventrally close to the proximal end of the tibia and inserting on the proximal ventral edge of the tarsus.

4.1. The tibio-claw flexor muscle consists of four large branches, arising along the dorsal edge of the tibia and extending through the tarsus along the claw tendon to insert ventrally on the base of the claw.

4.2. The femoro-claw flexor muscle is three branched. Of these three, two branches insert upon the unguitractor tendon independently of the third. One of these two branches is longer than the other, arising dorsally on the anterior face of the femur; the second branch arises ventral to the first. The third branch is a small muscle arising on the posterior face of the femur and runs into the mass of the tibio-claw muscle.

Leg 2 (fig. 70).

1.0. The coxo-trochanteral flexor muscle consists of three branches arising on the posterior face near to the proximal rim and inserting dorsally on to the proximal end of the trochanter.

1.1. The coxo-trochanteral extensor muscle consists of two branches: one, very large, arising on the anterior face; and one arising in the proximal ventral corner of the coxa. This muscle inserts on the ventral end of the trochanter.

9.10. The pleuro-trochanter extensor muscle running from the thorax to the trochanter also inserts with muscle 1.1.
2.0. The trochantero-femoral muscle consists of three short branches passing from the ventral distal region of the trochanter to the antero-dorsal proximal edge of the taper of the femur. The most distal of these three branches crosses the middle one.

3.0. The femoro-tibial flexor muscle is less extensive than in leg 1 and is of three branches. Two larger branches arise on the posterior face of the coxa and the third finer branch arises in the extreme tip of the proximal end of the femur. This muscle inserts on to the ventral region of the proximal end of the tibia.

3.1. The femoro-tibial extensor muscle is a small muscle arising dorsally in the femur and inserting on the dorsal region of the proximal end of the tibia.

4.0. The tibio-tarsal flexor muscle is a small muscle arising in the ventral distal region of the tibia and inserting ventrally on the proximal end of the tarsus.

4.1. The tibio-claw flexor muscle consists of three branches; two with their origin in the dorsal region of the proximal half, and one arising dorsally close to the tibio-tarsus joint. This muscle inserts on to the claw tendon.

4.2. The femoro-claw flexor is a long muscle arising proximally in the dorsal region of the femur and passing into the tibia where it inserts on the proximal end of the claw tendon.

Leg 3 (fig. 71).

1.0. The coxo-trochanteral flexor muscle consists of two large branches with their origin on the posterior proximal region of the coxa, and a small branch arising on the posterior face closer to the muscle insertion.
Triaenodes

Fig. 71. Muscles of the metathoracic leg.
insertion. These branches insert upon an apodeme from the dorsal region of the proximal end of the trochanter.

1.1. The coxo-trochanteral extensor muscle arises on the ventro-anterior region of the coxa and inserts on the trochanter opposite to muscle 1.0.

9.10. The pleuro-trochanteral extensor muscle is also present as a fine muscle running from the thorax to the trochanter with muscle 1.1.

2.0. The trochantero-femoral muscle is three short branches arising in the ventro-anterior region of the distal part of the trochanter and inserting on the dorsal edge of the proximal end of the femur.

3.0. The femoro-tibial flexor muscle is a small three branched muscle. Two branches arise on the proximal face of the femur and the third arises close to the proximal tip of the femur. It inserts ventrally on the proximal end of the tibia.

3.1. The femoro-tibial extensor muscle is a small muscle arising in the dorsal region of the femur and inserting dorsally on the proximal end of the tibia.

4.0. The tibio-tarsus flexor muscle is small, arises in the distal ventral region of the tibia, and inserts ventrally on the proximal end of the tarsus.

4.1. The tibio-claw flexor muscle consists of four small branches; one arises dorsally in the most proximal part of the tibia and inserting on to its own branch of the claw tendon: two arise close together on the posterior wall of the tibia and insert on to the tendon of the first branch close to where this joins on to the main apodeme: and one arises on the dorsal region of the distal end of the tibia, and which passes into/
into the tarsus before inserting on to the tendon to the base of the claw.
A comparison of the legs and leg muscles of *Limnephilus* and *Triaenodes*.

1. The lengths of the legs of *Triaenodes* and a comparison with those of *Limnephilus*.

The lengths of the legs of a larva of *Triaenodes* were measured as described for *Limnephilus*, and the figures are given below.

<table>
<thead>
<tr>
<th>Triaenodes</th>
<th>Leg 1</th>
<th>Leg 2</th>
<th>Leg 3</th>
</tr>
</thead>
<tbody>
<tr>
<td>coxa</td>
<td>0.41</td>
<td>0.45</td>
<td>0.65</td>
</tr>
<tr>
<td>trochanter</td>
<td>0.25</td>
<td>0.33</td>
<td>0.7</td>
</tr>
<tr>
<td>femur</td>
<td>0.35</td>
<td>0.48</td>
<td>0.7</td>
</tr>
<tr>
<td>tibia</td>
<td>0.25</td>
<td>0.4</td>
<td>1.0</td>
</tr>
<tr>
<td>tarsus</td>
<td>0.14</td>
<td>0.25</td>
<td>0.6</td>
</tr>
<tr>
<td>claw</td>
<td>0.6</td>
<td>0.25</td>
<td>0.47</td>
</tr>
<tr>
<td>trochanter and femur</td>
<td>0.5</td>
<td>0.6</td>
<td>1.13</td>
</tr>
</tbody>
</table>

Total measured through the articulations: 1.37  1.6  3.8

To enable a comparison to be made between *Triaenodes* and *Limnephilus*, the figures for the latter are repeated here. Now the length of the *Triaenodes* larva from which these figures were taken was 7 mms., and the larva of *Limnephilus* from which its figures were taken, was 21 mms.

Therefore if the lengths of the legs of the *Triaenodes* larva are multiplied by three, the sets of figures become directly comparable. These figures are given below, and they emphasize the differences between the two larvae. In *Limnephilus*, leg 1 is a little greater than half the length of both legs 2 and 3; in *Triaenodes* leg 1 is not very much smaller than leg 2 while leg 3 is more than twice the length of leg 2. The length of each leg as a percentage of the
total lengths of the three legs of a larva is:

<table>
<thead>
<tr>
<th></th>
<th>Limnephilus</th>
<th>Leg 1</th>
<th>Leg 2</th>
<th>Leg 3</th>
<th>Triaenodes</th>
<th>Leg 1</th>
<th>Leg 2</th>
<th>Leg 3</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>22.0%</td>
<td>39.7%</td>
<td>38.3%</td>
<td></td>
<td>20.2%</td>
<td>23.6%</td>
<td>56.2%</td>
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### Limnephilus

<table>
<thead>
<tr>
<th></th>
<th>Coxa</th>
<th>1.25</th>
<th>2.13</th>
<th>2.0 mm</th>
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<tbody>
<tr>
<td>Trochanter</td>
<td>1.0</td>
<td>1.25</td>
<td>1.25</td>
<td></td>
</tr>
<tr>
<td>Femur</td>
<td>1.2</td>
<td>1.75</td>
<td>1.63</td>
<td></td>
</tr>
<tr>
<td>Tibia</td>
<td>0.63</td>
<td>1.38</td>
<td>1.25</td>
<td></td>
</tr>
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<td>0.31</td>
<td>0.88</td>
<td>0.75</td>
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</tr>
<tr>
<td>Claw</td>
<td>0.25</td>
<td>0.38</td>
<td>0.38</td>
<td></td>
</tr>
<tr>
<td>Trochanter and Femur</td>
<td>1.69</td>
<td>2.5</td>
<td>2.5</td>
<td></td>
</tr>
</tbody>
</table>

Total measured through the articulations: 3.9 7.0 6.75

### Triaenodes x 3; i.e. on the same scale.

<table>
<thead>
<tr>
<th></th>
<th>Coxa</th>
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<th>1.35</th>
<th>1.95 mm</th>
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<tr>
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<td>1.0</td>
<td>2.1</td>
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</tr>
<tr>
<td>Femur</td>
<td>1.05</td>
<td>1.44</td>
<td>2.1</td>
<td></td>
</tr>
<tr>
<td>Tibia</td>
<td>0.75</td>
<td>1.2</td>
<td>3.0</td>
<td></td>
</tr>
<tr>
<td>Tarsus</td>
<td>0.42</td>
<td>0.75</td>
<td>1.8</td>
<td></td>
</tr>
<tr>
<td>Claw</td>
<td>0.6</td>
<td>0.75</td>
<td>1.4</td>
<td></td>
</tr>
<tr>
<td>Trochanter and Femur</td>
<td>1.5</td>
<td>1.8</td>
<td>3.4</td>
<td></td>
</tr>
</tbody>
</table>

Total measured through the articulations: 4.1 5.8 11.4

2. The exoskeleton of the legs.

Although the legs of the two larvae have widely different proportions their basic plan has remained common to them both.
The differing lengths of the various podomeres is clearly related to their functions and it is only in rather minor details that functional adaptation has occurred. At the same time these small modifications play a most important role in the work of a leg, so that it can be seen how readily functional needs can be satisfied from the basic pattern found in the leg morphology. For example, in Limnephilus the coxo-pleural articulation of leg 1 is broader and more triangular than that of either leg 2 or 3. The extra width gives a firm base to a leg with considerable strength working through a short leverage (i.e. the leg length) and one moreover which can work quite well with the increased rigidity this entails. At the other extreme, leg 3 of Triaenodes has a coxo-pleural articulation which allows an almost unlimited freedom of movement, necessary for its many functions, and yet has sufficient strength for the forces involved in swimming.

3. The muscles of the legs.

The muscles in Limnephilus tend to be more subdivided than those of Triaenodes, although this effect is probably exaggerated in the drawings because of the different scales used. The legs of Limnephilus have a much greater mass of muscles, and this accounts for their different appearances. In leg 2 of Triaenodes, for example, the muscles inserting on to the claw tendon, muscles 4.2 and 4.1, are much less extensive than those of leg 2 of Limnephilus. This applies with even more force to muscle 3.0 in the legs of Triaenodes, compared with the same muscle in the legs of Limnephilus.
These differences of quantity of musculature are of course related to the different sizes of the larvae but they are also indicative of absolute differences as well as relative ones. *Triaenodes* does not require the same power for its activities as *Limnephilus*. It does not move amongst tangled weeds: its case is perfectly smooth and regular; its case building pieces are small and manœuvreable; its feeding is easier also. Furthermore, it may be postulated that the decrease in the size of the skeleton and of the musculature from a larger to a smaller animal should be proportionate. If this is accepted, one would expect that both the limbs and the muscles would be reduced to the same extent in *Triaenodes*. In fact the muscles are smaller in relation to the skeleton than those of *Limnephilus* showing that in all probability the power needed by *Triaenodes* even allowing for the differences of its mode of life mentioned above, is smaller relative to body size than in *Limnephilus*. Moreover, although it is less easy to see, a comparison of the relevant figures shows that these differences are not compensated by a proportionately larger quantity of extrinsic musculature within the segments of the thorax and one can only conclude that *Triaenodes* requires in proportion to its size, less locomotive power than *Limnephilus*.

The muscles of the legs usually insert on to the skeleton by lesser or greater apophyses. Some of these are very long such as the unguitractor tendon or claw tendon and allow action remote from the site of the contraction muscles.
The pattern of leg muscles found in Limnephilus and Trienodes is also present in the legs of other insects. Kéler has given a list of the muscles of the typical insect leg. These names are given below, together with the number and name used in this work of each muscle.

Name & Number used here. Equivalent of Kéler.

1.0. Coxo-trochanteral flexor. 161M. Coxotrochanteralis lateralis.
1.1. "  " extensor. 162M. "  medialis.
2.0. Trochantero-femoral. 163M. Trochanterofemoralis.
3.0. Femoro-tibial flexor. 165M. Femorotibialis ventralis.
3.1. "  " extensor. 164M. "  dorsalis.
4.0. Tibio-tarsal flexor. 169M. Tibiotarsalis ventralis.
4.2. Femoro-claw " 166M. Femoropretarsalis.

In order to demonstrate the regularity of the pattern of musculature in the legs of different insects, the following table has been compiled. The numbers used in this work (1), and the numbers of Kéler (2) are given first, followed by those of:

(3) Malouf (1932) in Nezara viridula (Hemiptera).
(4) Korschelt (1924) in Dytiscus nasicornis (Coleoptera).
(6) Crome (1957) in Oryctes nasicornis (Coleoptera).
(7) Füller (1954) in Boreus westwoodi (Mecoptera).
(8) Wittig (1955) in Perla abdominalis (Ephemeroptera).
(9) Albrecht (1953) in Locusta migratoria (Orthoptera).

Füller's/
Filler’s nomenclature coincides with that of Weber (1954), and Albrecht has followed the nomenclature of Snodgrass (1927).

Table 2. Designations of leg muscles according to various authors.

<table>
<thead>
<tr>
<th>Source no.</th>
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</tr>
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<tbody>
<tr>
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<tr>
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<td>4</td>
<td>A4 and A5</td>
</tr>
<tr>
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<td>m. cox. 1</td>
</tr>
<tr>
<td>6</td>
<td>162, from opposite side</td>
</tr>
<tr>
<td>7</td>
<td>cxm 1 and 2</td>
</tr>
<tr>
<td>8</td>
<td>mcx 1</td>
</tr>
<tr>
<td>9</td>
<td>70 (prothorax), 102 (mesothorax), 131 and 132 (metathorax).</td>
</tr>
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<td>1.1</td>
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<td>A1 to A3 (part)</td>
</tr>
<tr>
<td>5</td>
<td>m. cox. 2</td>
</tr>
<tr>
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<td>161, from opposite side</td>
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<td>8</td>
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<tr>
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<td>71 (prothorax), 103 (mesothorax), 133 (metathorax); (parts).</td>
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<td>---------------------</td>
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</tr>
<tr>
<td>3</td>
<td>A2 to A3 (part).</td>
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<tr>
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<td>7</td>
<td>dvm 18 and cpm 29 (prothorax), dvm 42 and cpm 50 (mesothorax)</td>
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<tr>
<td>8</td>
<td>? and ? (metathorax).</td>
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<tr>
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</tr>
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</tr>
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<td>m. rem. fem.</td>
</tr>
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<td>163</td>
</tr>
<tr>
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<td>m. rem. fem.</td>
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<td>17</td>
<td>m. tr. 1,2,3 and 4</td>
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<td>3</td>
<td>11</td>
</tr>
<tr>
<td>4</td>
<td>C2</td>
</tr>
<tr>
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</tr>
<tr>
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<td>165</td>
</tr>
<tr>
<td>7</td>
<td>m. fl. ti. 1 and 2</td>
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<tr>
<td>8</td>
<td>m. fem. 2</td>
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<tr>
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<td>C1</td>
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<td>m. fl. ta.</td>
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<tr>
<td>8</td>
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<tr>
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<td>E</td>
</tr>
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<td>5</td>
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</tr>
<tr>
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<td>167</td>
</tr>
<tr>
<td>7</td>
<td>m. fl. part 2, inferior</td>
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<td>m. ti. 1 and 2</td>
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<td>78b and c (prothorax), 110 (mesothorax), 139 (metathorax)</td>
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<td>4.2</td>
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<td>E</td>
</tr>
<tr>
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<td>m. fl., part 1</td>
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<tr>
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<td>166a from coxa. 166b from femur</td>
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<tr>
<td>7</td>
<td>m. fl. part 1, superior</td>
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<td>8</td>
<td>m. fem. 3</td>
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<td>78a (prothorax), 110 (mesothorax), 139 (metathorax)</td>
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Fig. 72. Diagram to show grip of prothoracic legs on plant stem, etc.
The use of the legs by *Triaenodes*.

As in limnephilids the main functions of the legs are in connection with case-building, feeding and locomotion.

1. Case-building.

The case is built from a large number of separate pieces of plant leaf or stem arranged in a dextral or sinistral spiral.

Although the legs are used in a wide variety of ways, each pair has its own chief function. The first leg is responsible for holding the plant which is being utilised. Because of their ventral insertion these legs are able to bring the plant close to the head. The larva is able to grip objects of a very small diameter and when doing so the fore-legs co-operate to form an effective grip in front of the head. The coxae are parallel and touching, while the ventral edges of the trochanter and femora are close together. The tibiae, tarsi and claws are strongly flexed and press the object against the spiny edges of the femora (fig. 72).

When one leg only is holding a plant stem or leaf, the distal end is flexed against the ventral edges of the femur and trochanter is able to form a good grip. The ventral lobe of the femur helps to grip flat objects such as leaves because it fits very closely to the tibia which flexes against it (fig. 73). When utilising stems, these are usually gripped in the curve of the flexed tarsus and claw.

As the larva clambers about amongst the vegetation the...
Fig. 73. Diagram to show grip of prothoracic legs on plant leaf.
second and third legs are brought into play. The third legs being so disproportionately long tend to get in the way and are repeatedly drawn back, straightened and extended, so touching different pieces of neighbouring vegetation. These legs are used to hold the larva in position but bend the plants so slightly that they can play little part in drawing fresh plant material close to the larva's head. This is done by the second legs, which are strong enough to pull surrounding plants up to the larva where they can be used in feeding or case-building. Sometimes one of the fore-legs holds the leaf or stem being bitten, while the other one holds on to the ventral edge of the case. At other times the middle legs hold the plant and both fore legs hold the case.

When actually fitting a new piece of leaf or stem into position on the end of the case, the long third legs are extended laterally and suspend the larva from the surrounding plants. The first and second pairs of legs between them hold the new piece and the case in their proper relative positions. Since the details of the movements of the legs will change according to whether the case is sinistral or dextral, further description will be limited to the process when the case is sinistral (Fig. 74).

The anterior end of such a case is much more open on the right hand side than on the left hand side. The third left leg, therefore, has to be held either more anterior or more dorsal than the right one. Similarly the left second leg also tends to get in the way and usually is found holding on to the edge of the case close to the termination of the spiral. The right second leg holds the piece/
Fig. 74. Diagram to show a typical arrangement of the legs in case building.
piece to be added on the right hand side. The fore-legs may hold on to the existing edge of the case, or on to the new piece, or both. While the piece of weed is so held a silk thread is spun over its inner edge. Next the piece is moved so that its lateral and posterior edges are touching the case. The first leg is moved to allow this and it usually grips the inner lining of the case by its sharp claw; or it may join left leg 2 on the edge of the case. The right first leg may be moved further to the right on the case edge, or it may remain where it is until the anterior end of the new piece is fixed into place, not moving until the last moment. These processes require very little strength but they do need a very precise and accurate manipulation. No doubt the setae on the body and legs play a considerable part in this, but the ocelli may also be of use at such short range. The ocelli of T. bicolor larvae are similar to those of limnephilids.

2. Feeding.

Most authors state that the larva of Triaenodes are herbivorous. Moretti (1942) who describes the damage to young rice plants by the larvae in Northern Italy, states that the gut contents include material of animal origin as well as plant material. Examination of the gut contents and the faecal pellets of some larvae collected for this study has failed to reveal animal fragments, nor has any larva been observed to eat anything except vegetation. Indeed much of the faecal material was bright green and undigested, indicating that perhaps they eat more than they immediately require. On the other/
other hand some larvae kept in a clean tank in clean tap-water with no
food, survived for over two weeks.

The larvae collected for this study have been found amongst
masses of Callitriche and in aquaria have been found to feed on this
plant readily. They will also attack other delicate plants but do
not touch reeds unless these are very decayed. The larvae bite ir-
regular portions out of leaves and frequently discard the piece they
have removed. As they treat stems in the same way, they soon reduce
a plant of numerous stems and leaves to a mass of small pieces. They
attack a leaf from the edge outwards. They seem to be unable to attack
the surface of a leaf although since the leaves of Callitriche are so
narrow they have little incentive to do so.

The limbs are used in much the same way when the larva is
feeding as when it is building its case. The fore-legs grip the piece
being eaten; the second legs drag plants medially with a scooping
action; and the third legs suspend the larva amongst the vegetation.

A larva of Triaenodes frequently crawls along the case of
another larva and may be seen to nibble at its surface. It may be
inferred that the larva is eating epiphytes and epizoites, and so
incidentally keeping the outside of the case clean. A larva has not
been seen to eat algal growths as such, but experiments in which the
larvae were placed in a pure culture of algae show that they readily
eat Oedogonium, Hydrodictyon and Cladophora, but do not eat Ulothrix
and Closterium. When crawling along another's case, the first legs of
the larva are used mainly for pulling it along, the second legs for turning


to one side or the other and the third legs are placed where convenient.

3. Locomotion.

_Triaenodes_ swims, utilising the very long third legs (which are so setose). This fact dominates so much of the life of the larva, that other methods of locomotion are entirely subsidiary.

Crawling.

Like limnephilids, the larvae of _Triaenodes_ are found in situations where the foot-holds on the substratum are placed entirely irregularly so that regular stepping is rarely observed. Even in experimental situations where the substratum is a submerged sheet of rough paper the larva of _Triaenodes_ does not show walking movements if it can help it, preferring to swim. Hence the water covering the paper must be shallow enough to discourage, if not prevent, swimming. Under these conditions the larva will walk, but then the third leg on its forward return stroke nearly always touches the water surface and, with its many setae and hydrophobic cuticle, becomes trapped in the surface tension of the water surface. The larva usually cannot free the leg directly, but has to retreat into its case and drag the leg into the case gradually. As it does so the case rises (the extremity of the leg being held in the surface tension layer) until the anterior end of the case comes to the surface. The case is, however, hydrophilic and its angle of contact with the water is very low. Thus the case does not get trapped in the surface tension film, and when the leg is pulled into the case below the water, case and larva sink/
Fig. 75. Diagram to show the pacing of the legs of one side, as seen in dorsal view.
sink from the surface again. This interference with the normal progression naturally breaks any stepping pattern. The following observations are not therefore intended to be taken as from fully continuous movements.

The tripod type of progression is rarely seen. Leg 3 being so long and weak probably plays little part in forward movement; it is placed in an anterior position so that it steps alongside leg 1. Leg 2 extends laterally and has a large angle of swing. It also rotates on a horizontal axis so that the dorsal surface faces anteriorly, at the end of its pace. Leg 1 is not, as in limnephilids, held so far under the head but has a very similar orientation and behaviour to leg 2. The degree of rotation on the horizontal axis is reduced, however, because its pace rarely extends more posteriorly than its thoracic insertion (fig. 75). Leg 3 shows little longitudinal rotation because its pace is so far anterior. It is very striking that legs of such unequal lengths can be used together in walking, and their pace lengths are approximately the same.

When stepping is not in a regular alternate tripod sequence leg 1 may be unused; leg 2 often extends its pace to a very posterior position, and leg 3 can extend laterally rather than anteriorly. Leg 3 has also been seen to bend near the trochanter-femoral joint. The bending takes place not at the oblique overlap of these two podomeres, but at the plane of unsclerotised cuticle just distal to it (fig. 76), and sometimes is due to its pressing on the substratum; sometimes it occurs when free in the water, however. These facts are further considered below.
Fig. 76. Shape of the femur when it is bent at the pseudo-joint.
The larvae have been observed to walk backwards by a true reversal of the stepping movements. This is clearly a slower and more laboured process than forward movement. Alternatively, a larva will progress backwards by extending out of its case to one side, and by using its legs crab-wise. This is the method also used for turning round, when the anterior end of the case moves through an arc whose radius is approximately equal to the case length.

When a larva which is on the bottom of a dish begins to swim, legs 1 and 2 are extended sideways and move rapidly to and fro, so that left leg 1 and right leg 2 alternate their stroke with right leg 1 and left leg 2. The larva appears to be running along the bottom, much as a water bird runs on the water when taking flight. The third legs are, of course, beating more rapidly throughout. As the larva gets clear of the bottom, legs 1 and 2 usually cease to move to any great extent. Leg 2 remains outstretched while leg 1 is folded in alongside the head. From its position, leg 2 could be acting as a balancing organ during swimming, but a larva without the second legs is able to swim perfectly well.

The larvae are able to use the setose third legs for walking inverted on the underside of the surface tension film.

Swimming.

The larvae of *Triaenodes* swim with remarkable facility although with rather a jerky motion. They can swim inverted as well as normally orientated and can perform turning and rolling movements in the water. They can swim vertically upwards and downwards as well as horizontally.
They swim amongst the water weeds from one place to another, bumping into anything in their path, grasping it with the first two pairs of legs. In an aquarium when they swim to the sides, they cannot get a grip when the glass is clean. Instead they exude a drop of silk from the labial spinneret and this sticks the larva to the glass. Presumably when moving away the silk thread is broken off at the spinneret.

Lestage (in Rousseau, 1921) quotes Buchner (no ref.) in an account of the swimming of the larvae. They are said to swim forwards in such a position that the anterior end describes a spiral equidistant from the line of motion while the posterior end remains on the line of motion. The larva and its case are said to turn upon their own axis so that the same side of the case faces the line of motion, and it is even stated that the angle of the case to the line of movement is $10^\circ$. Lestage says he has never observed this kind of swimming himself.

Moretti (1942) confirms the account of Buchner, and although he does not state any particular angle of orientation, his figure shows the same side of the case facing the line of motion as described by Buchner.

Observations made in the present work show that the larvae can swim in the manner described by Buchner and Moretti, except that the posterior end of the case is not always on the line of movement. It tends to be thrown off it by the violence of the swimming movements, so that it also moves through a narrow spiral close to the direction of movement. However, it is rare for this type of swimming to be seen at all. If a rotary kind of progression is adopted, and this is not
Fig. 78. Lateral view of a swimming larva, to show the position of the plane of action of the swimming leg.
Fig. 77. Diagram to indicate successive positions of the larva in two kinds of spiral swimming path. The left one shows that described by Buchner and the right that observed by the writer. For further description see text.
common, it is more usual for it to be without the rotation of the larvae and its case on its own axis, so that its dorsal side is always dorsal and its ventral side ventral. This means that all surfaces of the case become adjacent to the line of motion through one turn of the spiral. In addition the posterior end of the case does not remain on the line of motion but describes a smaller spiral round it.

Figure 77 shows both the movement as described by Buchner and that described by the present writer. This diagram can be more easily understood if it is held so that a fore-shortened view is obtained from the lower end.

It has been noticed that both types of rotary swimming may occur when the swimming legs are damaged, but they also have been observed between periods of perfectly normal linear swimming by the intact larva.

It must be emphasized that, when swimming normally, the larva progresses without rotation. The head and thorax extend out beyond the case and are curved ventrally. The third legs sweep to and fro in a plane dorsal to the anterior part of the body and directed obliquely from antero-ventral to postero-dorsal. In other words when the direction of movement is horizontal the legs beat to drive the larva downwards (fig. 78).

Because the case is built of a spiral of plant pieces, the last few additions to the case form a projection at the anterior end. This projection has two important effects on the swimming of the larva. Firstly, a larva always orientates its case so that the projection is dorsal/
Fig. 79. Diagram to show the position of swimming legs in relation to the anterior dorsal hood of the case: anterior view.
dorsal. If the case is turned over so that the larva lies upside down it will after a little struggling right itself, so that now the projection lies ventrally. In this position the larva cannot swim properly and immediately it is free to do so it rotates its case again until the projection is restored to its dorsal position. Only now can it use its swimming legs properly, because, in order to avoid stretching too far out of its case, it must have one leg extended just ventral to the most anterior projecting piece of the spiral (fig. 79). This is the only position which gives the legs maximum freedom to move, since when one leg is just ventral to the anterior projection, the opposite leg has enough room to sweep to and fro without knocking against the case on the backward movement. In any other position one or other of the legs would have less freedom, because any change in the relative positions of the larva and the anterior end of the spirally built case would cause one side of the case to be nearer to one of the legs (fig. 80).

The second effect of the dorsal projection is that it produces an upward lift i.e. a positive pitch at the anterior end as the larva swims through the water. This positive pitch is cancelled out by the negative pitch caused by the downward direction of the metathoracic legs when swimming (fig. 78). Alteration of the angle of attack of the legs allows the larva to swim upwards or downwards. Something of the forces at work in the movement of the larva through the water may be seen in the behaviour of a model of the case pulled through the water. A scale model was made of varnished paper, and this was towed through water on a slender thread. The thread was attached at first at the anterior end of the/
Fig. 80. Diagram of swimming larva to show normal sweep of the swimming legs: dorsal view.
the model by three hooks made from mosquito points, one being placed dorsal and two latero-ventral. This was to imitate the three swellings of the first abdominal segment of a larva, which, as in limnephilids wedge a larva of *Triaenodes* in its case when it swims. With the thread attached in this position the model simply rotated when drawn through the water and showed no stability. Indeed this is to be expected with the asymmetry of a spirally built case, because the larger overhang on one side gives a turning moment to the case, about its longitudinal axis, owing to the thrust of the water against it as the larva swims.

The thread was then attached by two hooks placed posteriorly to imitate the anal hooks of a larva. The model turned until the anterior projection or hood became dorsal and the thread crossed the ventral edge of the anterior end, against which it pressed, opposing the upward lift from the dorsal hood. The model was now stable and travelled forwards without rotation. When a *Triaenodes* larva swims it extends out of its case curling ventrally as described above (fig. 78) and shows exactly the same position over the ventral edge of the anterior end of the case as did the thread of the model. This suggests that the larva grips the case by its anal hooks, and that its position is to counteract the lift caused by the dorsal hood. It shows too how the structure of the case influences the swimming position, although the larvae can adapt themselves to swim with a square ended case, or without a case at all. The stability of a swimming larva must be difficult to attain. There are no median fins to correct a tendency to roll and no paired fins to act as hydroplanes for adjusting the pitch. It may be that the fact that the anterior projection must
be dorsal to allow the larva to use its swimming legs properly, has, in turn, given the larva a definite lift force against which it can react. This means that it has one main vector component in the forces acting on it which tends to localise the reactions needed to keep it on an even keel. It is not suggested that a larva does not need other sensory information in order to swim. Clearly it needs other stimuli to remain orientated to its environment, though whether these include light and gravity or both it is not possible to say. No structures have been found which might act as gravity receptors but larvae swimming in dishes with the light below do not turn over and swim inverted, so that it seems unlikely that only the ocelli are used to determine its proper orientation. In the honey bee there are sensory structures between the head and prothorax as well as between the thorax and abdomen, which indicate the vertical plane (Lindauer and Nedel, 1939). It may be that similar structures are present in Triaenodes, but in spite of much searching it has not been possible to locate any.

There is another feature of the swimming larva which probably contributes to its stability. This is the elongated case trailing behind which acts like a fixed rudder, and perhaps plays a role analogous to the threads which, tied to flies with their halteres removed, enables them to fly more successfully (Fraenkel, 1939).

The experiments with the model show rotation if the thread is attached anteriorly to simulate the grip of the swellings of the first abdominal segment. It seems likely that the rotation of the larva/
Fig. 81. Diagram to show the details of the movements of leg 3 during one cycle of its maximum swimming action.
larva and its case which sometimes occurs when swimming, and which is
described above, is a result of the larva gripping the case with
these swellings and releasing the grip of its anal hooks. At the
same time it must be borne in mind that the model case used in the
experiments had no model larva in it, and the presence of a larva in
the case could affect its behaviour in motion, although it is unlikely
this would seriously invalidate the above discussion.

The swimming larvae have been photographed at various speeds
through both a simple lens and through a microscope. The films have
revealed how the shape of the leg varies in the swimming action.
Stroboscopic examination has proved almost fruitless because the legs
are not moved with a sufficiently regular frequency and only glimpses
of their movements are obtained by this method. Such glimpses as
have been seen all tend to confirm the film records.

Figure 81 has been compiled from a series of 19 cycles
photographed at 64 frames per second while the larva was held so that
the swimming legs remained in the correct place. Because of this,
figure 81 shows the maximum sweep (and probably the maximum power)
used by the larvae. In free swimming the sweep of the leg is less
as in figure 80. To get the photographs of the freely swimming larvae
they were held as described until they were making vigorous swimming
movements and then released so that they swam across the field of
the camera.

It can be seen in figure 81 that at the beginning of the
back stroke the distal part of the leg (the claw, tarsus and tibia)
is held at an angle to the proximal part (the femur, trochanter and coxa). As the leg is drawn backwards this angle increases until it is 180° and the whole leg is in a straight line.

At the end of the back stroke the forward stroke begins with a rapid decrease in the angle at the femoral-tibial joint so that the distal part of the leg trails behind in the water. As the forward stroke is completed the distal part of the leg is extended again ready for the next back stroke. This movement is in some ways similar to that of the swimming leg of Acilia (Nachtigall, 1960), and to the movement of a cillum. This shape is determined no doubt by the density of the medium in which it occurs and is much less pronounced in bird wings moving in air.

Films of the freely swimming larvae show that one complete cycle occupies five frames at 64 frames/sec. - three for the forward stroke and two for the back stroke. These figures are the average from five successive cycles on the film and show that the rate of beating is in the region of thirteen cycles per second. The films also show the swimming speed of the larvae since the background was squared paper giving a figure of 1.7 cms/sec. Direct observation of larvae swimming in a dish over squared paper gave the speed as being 2 cms/sec. The discrepancy may be explained on two grounds. The result obtained on the films was for larvae just starting off and may be low for lack of momentum; and secondly the difficulty of deciding the length of the irregular path of the swimming larvae as they passed over the graph paper, was a possible source of error.
Fig. 83. Diagram to show banking (?) of swimming larva.
Fig. 82. Diagram to show turning of swimming larva.

Triatnodes

Correction:— the arrow on this figure should point to the left.
It is suggested that the film result is the one which is more reliable.

Turning.

A swimming larva can turn by banking or by veering. Attempts to photograph the larva laterally have not been successful, and direct observation shows only limited details of these manoeuvres because of the speed with which they occur. Dilute glycerine was used to slow down the legs, but was not satisfactory because its chief affect was to reduce the sweep of the legs rather than their speed. When turning in the horizontal plane leg 3 of one side beats faster than the other and so causes the animal to turn away from the faster side (fig. 82). Larvae have been observed to beat only one leg when making a very sharp turn.

When an aeroplane or bird turns it is necessary for it to bank while Acilius, like many water beetles, uses its broad ventral surface in the same manner as an aerofoil when making sharp turns (Nachtigall, 1960). When Triaenodes turns it cannot utilise the stability given by banking since it has no plane which could act as an aquafoil, and it therefore turns by a veering motion in the horizontal plane.

Neverthelesss, banking does sometimes occur when Triaenodes larvae are swimming. It is brought about by the plane of action of the two swimming legs being altered so that the outer leg beats in a plane more dorsal than normal and the inner leg in a more ventral plane (fig. 83). Theoretically this should not cause a banking movement to occur and the larvae should simply swim straight forwards with
Triaenodes

Fig. 85. Diagram to show larva swimming vertically upwards.
Fig. 84. Diagram to show pitching of swimming larva,

(a) positive (b) negative.
one leg higher than the other. It is obvious, therefore, that the
exact nature of this action remains obscure.

Positive and negative pitching movements occur when the
plane of the beating of both third legs is tilted up or down
respectively (fig. 84a & b). The larvae can swim vertically upwards
by this method (fig. 85).

It is also possible that the further extension of the body
from the anterior end of the case so displaces the centre of gravity
that it automatically swims downwards. But Zeiser (1934) shows that
in Dytiscus weighting the anterior end of the swimming beetle causes
it to respond in such a way that it counteracts the change in the
position of its centre of gravity and swims upwards. It is not
impossible therefore that Triaenodes when it extends out of its case
responds by swimming upwards, and not downwards. The force of
gravity has not simply a mechanical effect but it provokes an
adjustment reaction in the swimming animal.

Other observations related to swimming.

A larva taken out of its case is able to swim in a straight
horizontal direction, but only rarely does so. Usually it curls up
ventrally so that its head is close to its anal region, and the
beating of the swimming legs causes it to become a rotating annulus.
It moves more quickly without its case. Often it touches the surface
of the water, and being unwettable it is there trapped, unless it can
find something such as a plant stem by which it can pull itself under
the water surface.

Removal of parts of the third legs shows that a larva is
Fig. 86. The position of the legs when a larva is crawling into its case.
able to swim without the claws, and tarsi and even to a slight extent
without the tibiae. With half of each tibia present, swimming is
greatly impaired, but not completely prohibited. There is a definite
speeding up of leg movements when part of it is removed. This means
that removal of the claw and tarsus on one side does not necessarily
cause the animal to swim in circles, because the increased rate of
beating by the damaged leg compensates for its reduced length - a
good neat example of homeostasis. It would be interesting to know
whether this increased frequency when the leg is shortened is purely
the expected effect of shortening a pendulum, or whether the larva is
also striving to beat faster on the damaged side in order to progress
in a straight line. The complete removal of one of the metathoracic
legs does make the larva swim in circles as would be expected.

Miscellaneous leg movements.

It often happens that because of its dense setae leg 3
becomes fouled by microscopic organisms and debris. To clean the
leg, the larva draws it through leg 1, which is flexed so that its
claw, tarsus and tibia enclose leg 3 against its femur. This takes
place in front of the head, and larvae have been seen to eat the
material removed.

A larva dispossessed of its case will re-enter it head first.
The first and second pairs of legs pull the animal forward assisting
the peristaltic contraction and elongation of the body. The third
legs take no part in this and are drawn in passively. They are
folded at the coxo-trochanteral joint so that they lie dorsally along
Triasenodes

Fig. 87. The position of the legs of a pupa in its case.
the abdomen (fig. 86). As the head of the larva emerges at the end of the case, legs 1 and 2 are in their normal position. To free the third legs, the larva stretches out anteriorly until the trochanter-femoral part of the leg is clear of the case edge and draws the rest of the leg out of the case.

In the pupa a very similar situation occurs, although both second and third legs are folded and directed posteriorly (fig. 87). Presumably this position is attained by the animal leaving its case and drawing itself into its case with its first pair of legs only.
Further analysis of the leg movements and actions in *Triaenodes*.

Although much of the discussion of the details of the leg mechanisms in *Limnephilus* applies to *Triaenodes*, there are some points of difference between the legs of the two larvae. The action of leg 3 in swimming is the most obvious of these and this process is considered in more detail below. In most respects the integration of form and function in legs 1 and 2 is similar in *Triaenodes* to that of *Limnephilus*, but salient points of difference, or of different emphasis, are considered.

1. The prothoracic leg (figs. 58 to 61).

The coxo-pleural articulation of this leg readily permits movements in a plane at an angle to the long axis so that the distal part of the limb can be brought across in front of the head. Rotation of the leg as a whole on this articulation is largely prevented by the strong connection between the two surfaces of the articulation which are elongated transversely. Nevertheless some rotation of the leg does take place, and this is by the mobility of the second pleural sclerite itself as well as in the more distal parts of the leg. The fold in the posterior wall of the coxa, opposite to the coxifer is presumably to strengthen the coxa against the stresses at this joint. That such folding is necessary when other parts of the exoskeleton are made more or less equally strong by sclerotisation at the point of muscle attachment, is probably because in the former case the stress is in compression, while in the latter it is in tension.

The trochantero-femoral joint permits only very limited movements of...
of the two podomers, correlated with the use of this leg for gripping hard, especially by the distal parts against the femur and trochanter. The femur is very wide distally and as in limnephilids, this swollen end is used in conjunction with the ventral enlargement of the tibia to grip thin objects such as leaves.

The general form of the leg then, is very like that of limnephilids, although it is less heavily sclerotised. The claw is proportionately longer, and appears more slender. The nature of the articulations, and the mechanics of the leg are as in *L. flavicornis*. One of the striking features of the prolegs of both animals lies in the wide range of setae found on the ventral edge of the trochanter and femur. These range from fine delicate threads to very large stout spines. Obviously the stout spines can pierce objects and help the larvae to grip them more surely. The slender thread-like setae are less easy to explain. Probably they are sensory but if this is so, their length is surprisingly great.

2. The mesothoracic leg (figs. 62 to 65.)

This leg again is very similar to the corresponding leg of the limnephilid in structure and function. The articulation of the whole leg with the thorax is both free and stable. The hooked projection and the curved tip of the coxifer together make an articulation which gives very wide lateral and transverse ranges of movement, yet retains the parts in their correct relationship. This joint is specialised and is clearly more effective than a typical vertebrate ball-and-socket joint in which displacement of the parts is mechanically easy. The vertebrate has overcome this by an elaborate system of ligaments and...
and lubricated surfaces enclosed in a sinovial capsule. In these insect joints no such elaborate additional apparatus is required and the system has been refined to great simplicity. Surprisingly, however, much of the action of this articulation relies not so much on the interactions between the two curved sclerotised parts, as on a tough flexible ligament which unites them. An exactly similar joint occurs between the coxifer and leg 3. In this leg it is easy to see its value in the swimming movement, allowing the leg to rotate until it sweeps horizontally and brings a maximum forward thrust to the larva. Such an explanation cannot apply to leg 2, although even here, the leg does move very widely alongside the body so that a similar freedom of movement is desirable (see above, page 216 and fig. 75).

It is also possible that having this fulcrum slightly median to the insertions of the protractor and retractor muscles causes a rotation of the leg, particularly on the backward stroke, into a more horizontal position. In Limnophilus this same effect would occur because there the inflexion of the coxa which forms its internal ridge brings the coxiferal fulcrum slightly median to the insertion of the retractor muscles although the effect in this animal is much less pronounced.

Another reason for this specialised joint may be that the fine manipulations required for the building of the spiral case of Triaenodes requires a freer type of articulation than the relatively coarse type of case built by Limnophilus.

Again it may be that it is of value in allowing the legs to be more compactly folded when the larva retreats into its case; a consideration which weighs more with Triaenodes than with Limnophilus.
The femur is curious because it has a line of lightly coloured cuticle near to the proximal end, where it begins to taper at the trochantero-femoral joint. This is a line of flexure of the limb and permits the distal parts of the leg to be bent anteriorly. Since this band of flexible cuticle is only present on the anterior surface of the femur, it only allows the leg to be bent forwards. The leg cannot bend posteriorly because the flexible cuticle on the anterior side will not stretch and the stiffer cuticle on the posterior side will not buckle, probably because of its curvature. This feature of the femur is exploited to the full in the metathoracic leg, and its importance and significance will be considered below.

The leg is without adaptation for raptorial action and indeed is not able to do more than grip things between the tip of its claw and the ventral edge of the femur and trochanter. Even this limited ability, however, enables the larva to manipulate the pieces of plant with which it builds its case.

The metathoracic leg (figs. 66 to 68).

The features of this leg most worthy of attention are the presence of a weak band across the anterior face of the femur, and a second area of flexibility in the centre of the tibia. Manton (1958a) describes a similar structure in the tarsus of Lysiopetaloida (Myriapoda, Diplopoda) and terms it an "incipient joint". In so far that this implies that it is the beginning of a new true leg joint, it is perhaps better at present to call it a "pseudo-joint" in the Insecta.

The weak band across the femur allows the distal part of the leg/
leg to swing forwards relative to the proximal part of the leg. Usually this bending is passive; i.e. the distal part of the leg is caught against a piece of weed and the proximal part continues to move posteriorly. Such passive bending could be of use in extrication of the elongated legs from entanglement amongst the plants. Bending at this point, however, is sometimes active so that muscles must be used. Which muscles bring about this in both meso- and meta-thoracic legs is not easy to see. One muscle (the middle slender branch of muscle 3.0) arises in the proximal tip of the femur and when it contracts, it could be responsible for the bending of the femur at this weak band. If this is the case, it must be inferred that the tibia must of necessity be flexed also, because this muscle is part of the tibial flexor muscle. But in fact the tibia does not flex when the femur is bent, and so one is driven to postulate that the hydrostatic pressure of the leg and the resistance of the cuticle is sufficient to keep the tibia extended while this muscle contracts to bend the femur.

This explanation of active bending of the leg at the pseudo-joint on the femur is not felt to be a very sound one. When observed the action looks as though the internal pressure in the leg was suddenly reduced, and the leg collapses slightly at the weakest point. This explanation seems less likely to be true than the previous one, for it is difficult to conceive any insect mechanism which could reduce the internal pressure of a limb suddenly. Only more information is likely to solve this problem.

The tibial region of pale cuticle occurs slightly distal to its mid point. It does not extend into the dorsal sclerotised edge of the leg.
leg, and this acts as a hinge. The flexible cuticle allows the leg to flex on this hinge and this is utilised in the swimming movements of the leg (see below, page 240).

These pseudo-joints are of considerable interest from the point of view of the origin of the joints between the podomeres of arthropod limbs. In the myriapods there is clear affinity between true joints of some species and the incipient joints described by Manton (1958) in the Lysiopetaloidea. It may be that some of the unusual 'extra joints' found in the legs of some insects have arisen in the same way, and that in Triaenodes an intermediate stage in the evolution of the larval legs had been reached. Hickin (1946) mentions such a pseudo-joint in the tarsus and tibia of Mystacides, and Lestage (in Rousseau, 1921) states that the posterior tibia is of two pieces in both this genus and Exotelia.

The principal function of this very long leg is for swimming. Its great length is a disadvantage in a larva which lives and pupates in a case because of the difficulty of folding it up to fit into the case. This point was discussed in connection with Limnophilus but in Triaenodes the problem is greatly accentuated. The first and second legs fit in quite easily as in Limnophilus but leg 3 has to be so sharply folded at the coxo-trochanteral joint that the two podomeres in fact lie in contiguity throughout their length. The trochanterofemur is held alongside the body pointing obliquely backwards, and the rest of the leg extends forwards over the body. Even so it is only just possible for the legs to be completely withdrawn into the case.

The manipulation of the legs when withdrawn into the case would/
would be easier with these extra points of flexure. This is even more true when one remembers that a larva may leave its case. On returning, the larva enters its case pulled by legs 1 and 2, while leg 3 trails alongside its body. On reaching the opposite end of its case, the larva has to extricate its long legs from a position in which they point posteriorly to the normal one. This manipulation of the legs raises some interesting problems. Extra points of flexure will help to make it easier and it is instructive to consider the measurements involved.

The diameter of the anterior end of the case of a large Triaenodes larva is 1.8 mms. When the larva is in the case it occupies the central region and any rigid unit of a leg lying at 90° to the longitudinal axis of the body must become a chord less than a diameter in length. Suppose this chord lies half-way between the centre and the circumference then it would be about 1.5 mms. long. In practice this is too large, since the larva is greater than half the internal diameter of the case. Suppose then the figure of 1 mm. is taken for Triaenodes, it means that any unit of the leg greater than this length can only be arranged obliquely or parallel to the body. Reference to the measurements of the lengths of the legs (pg. 204) shows that the length of the trochanter and femur of leg 3 is slightly greater than this, and it is possible that it will just succeed in squeezing in with slight distortion. Evidently the pseudo-joint of the femur and the limited freedom of the trochantero-femoral joint gives just the right amount of play. In leg 2 the same considerations apply, but here there is no unit of the leg which is too long to fit in easily/...
easily, so that the necessity for a femoral pseudo-joint should not arise. Why such a specialised structure is present remains a mystery.

In *Limnephilus* the maximum internal diameter of the case is 4 mms. This by the same reasoning as above gives a figure of about 2.3 mms. as the maximum leg unit length, while the lengths of the trochanter and femur of legs 2 and 3 are both 2.5 mms., again slightly larger than the theoretical maximum. Yet here no pseudo-joint is present. Presumably in this larva, the leg must be slightly oblique, and it suggests that there is in fact no simple correlation between the folding of the legs and the case into which they are fitted. It does, however, strongly suggest that there is correlation between the lengths of the rigid units of the legs and the sizes of the larva and its case.

Analysis of the swimming process in *Triaenodes*.

A description of this process has been given above (page 218). This section is an attempt to analyse the underlying muscular actions and some of the mechanical processes at work in the leg when swimming is taking place. In short all aspects of the third leg are examined in so far as they take any part in the use of the leg in swimming.

An exact account of swimming necessitates detailed description of several complex processes. Although in fact these processes are all wholly integrated, the account given here considers them separately in order to make them more understandable. The extrinsic musculature of the leg, lying in the metathorax is dealt with first, and this is shown in figures 54 to 57. Some of this explanation is based on direct manipulation of the larger muscles, but some is by inference from the relationships of the parts.
The coxo-pleural joint is a curved pleural peg in a coxal hook, and it looks as though the hook turns round the peg when the coxa is rotated on its long axis. Manipulation shows that this is not the case; the actual articulation is a small link of tough flexible more or less transparent cuticle between the peg and the hook. This link is postero-lateral and is indicated in figure 68. It allows the coxa to be rotated simultaneously: (i) on its own axis so that the dorso-ventral plane of the leg comes to be roughly antero-posterior and (ii) in the horizontal plane so that the leg sweeps in the antero-posterior plane. If muscle 8.51 or 8.52 is cut posteriorly, pulling the anterior end of it produces just these two rotations and the leg swings backwards as in the power stroke of swimming. The main remotor muscles therefore include these two muscles and their remotor effect causes automatically the rotation of the coxa so that the leg gives maximum effect to the water.

This coxo-pleural link is similar to the trochantericoxal articulation in the leg of the swift centipede Lithobius which Manton (1958b) describes and points out is the type of joint adapted to fast movement, but weak stresses.

The other main remotor muscle is 8.61. This muscle lies against the lateral wall of the coxal cavity and inserts on to the median internal face of the coxa. Its contraction rotates the coxa on its own axis and pulls back the leg in the horizontal plane as before.

The return of the leg on the forward stroke is brought about by muscles 8.11 and 8.12, and possibly by 8.20 and 8.23. The rotation
of the coxa is maintained during the forward stroke by muscle 8.10.

With these two sets of balanced muscles the leg is driven backwards and pulled forwards, when the animal swims.

In addition to this movement, the pleurite itself moves, as in the other legs of both Limnephilus and Triaenodes (see p. 118). In the metathorax of Triaenodes its position is such that its anterior end moves first postero-laterally, then antero-medially (fig. 81.). These movements, which are noticeable in a dorsal view of a swimming larva, are brought about by two further opposed systems of muscles. The displacement postero-laterally is by contraction of muscles 7.20 (and 7.32 and 7.33), together with the pull of the remotor muscles acting themselves on the posterior part of the pleural sclerite. The return movement is the effect of the contraction of muscles 7.14 (and 7.50?), together with the relaxation of the remotor muscles. By this swing outwards and backwards of the coxifer, the whole articulation of the leg moves and this allows the leg room to move so far posteriorly that the coxa is turned until it lies parallel to the side of the metathorax. It obviously also helps in the to and fro movement of the leg, just as it does in the other segments of Limnephilus and Triaenodes.

The precise effects of the contraction of muscle 8.50 is less easy to assert. Certainly it is a remotor muscle like 8.51 and 8.52, but the position of its insertion shows that the intrinsic displacement of its insertion is greater than that of 8.51 and 8.52, because of its distance from the coxifer. This is no doubt correlated with its greater/...
greater length, but it is also important to recognise that this greater distance between its insertion and the coxifer gives it greater leverage. This suggests that its greater mechanical advantage is sometimes needed to provide additional power to the swimming stroke. This would be an example of a structure adapted to the emergencies of life, like the abnormal power output possible in *Acilius* (Nachtigall, 1960).

The greater length of this muscle is accommodated within the segment and does not necessitate its extension into the first abdominal segment. There may be several reasons for this but two appear most likely to be correct. The first is that the pull of this muscle would be too great for the flexible cuticle of the abdominal segment to resist and its contraction would deform the abdominal segment rather than move the leg. It may be objected that it is attached to unsclerotised cuticle in the metathorax so there is no reason why it could not be so in the abdominal segment. However the two muscles of the segment, one from each side, curve transversely and dorsalwards to meet in the mid-dorsal line. This means that tensions created by their contractions are counter-balanced provided they both contract more or less together and with approximately the same strength, and they do not need further anchorage to be effective. If the two muscles passed into the abdominal segment this would not be possible, because they would be extending posteriorly more or less parallel. Secondly it seems likely that the mutual curvature of 7.50 and 8.50 has effects, particularly on 7.50, which are too indefinite to delineate, such as modifying the position of the posterior end of the pleural sclerite. This would not be possible if 7.50 came directly from the furca because...
Fig. 89. Diagram to show movements of the long setae during swimming.
Fig. 88. Diagram to show details of the action of the tibial pseudo-joint in the swimming movements.
of the relative positions of sclerite and furca.

Summarising so far then, the remotion of the third leg is by muscles 8.50, 8.51, 8.52, and 8.61, assisted by displacement of the coxifer by muscle 7.20. The promotion of the leg is by muscles 8.10, 8.11, 8.12, 8.20 and 8.23, assisted by the replacement of the coxifer by muscle 7.14.

Turning now to the behaviour of the leg itself during the swimming movement several features of its construction are adaptations to this, its chief function.

Firstly, the rotation of the leg about its own axis, mentioned above as resulting from the pull of the remotor muscles, is enhanced by the spreading of the setae on the backstroke. They spread out widely as the leg moves backwards and form a wide 'paddle' which gives maximum effect to the power of the swimming stroke. The setae occur on the podomeres asymmetrically so that once they begin to open they also twist the leg round.

On the return stroke the setae trail passively in the water, giving minimum resistance to the forward stroke (fig. 89).

Secondly, the tibial pseudo-joint allows the extension of the leg at the end of the return stroke to be made smoothly and with a more curved appearance than would otherwise be possible (fig. 88). The fact that the pseudo-joint does not allow forward bending, prevents loss of efficiency due to loss of rigidity on the leg during the power stroke.

Thirdly, during both the forward and backward movements the straightness of the leg at the coxo-trochanteral joint depends on the/...
the intrinsic coxal muscles. The trochanteral extensors keep this part of the leg straight for the power stroke and the flexors keep it straight on the recovery strike.

Fourthly, in an animal performing rapid reciprocating movements elasticity can reduce the energy required for each stroke by retaining part of the energy at the end of one stroke and releasing it at the beginning of the next. It has been shown that in the flight muscles of locusts it is the muscle itself in which this elasticity resides (Buchthal, Weis-Fogh, and Rosenfalk, 1957). This probably applies to *Triaenodes* larvae, because the lack of rigidity of the metathoracic wall would certainly prevent this playing any part in an elastic recoil system, although the posterior pleural disc probably does have a part to play. At the same time it may be illegitimate to compare flight muscles, which are relatively specialised, with the leg muscles of larval *Triaenodes*, which are not so specialised although they are involved in fairly quick movements.

Fifthly, on the return stroke, the bending of the leg at the femoro-tibial joint, causes the tibia, tarsus and claw to trail behind. This shortens the effective length of the leg and so reduces its inertia. This reinforces the effect of the closing of the setae in allowing the smaller promotor muscles to make the recovery stroke as quickly as they do.

A very striking feature of the third leg is the very small amount of musculature present in it. One might expect a limb of such/...
such importance to possess a highly developed and differentiated series of muscles, and the fact that the muscles are reduced, in all but the coxa, to what is probably the minimum, emphasizes the over-riding importance of reducing the inertia of the limb. The joints of the limb are such that on the power stroke they open to the proper degree automatically and close up automatically on the recovery stroke. The only exception to this is the coxo-trochanteral joint, and it is only here that any quantity of intrinsic leg muscles are found. It is noteworthy that in horses, fast running Myriapoda and in Triaenodes the need to minimise the inertia of the limbs and to maximise their locomotor efficiency has led to the concentration of the weight of the musculature at the proximal end of the leg, to the use of tendons to transmit the pull of the muscles, and to the elongation of the distal parts of the leg.

The traction of a swimming larva and the drag it has to overcome.

Using the apparatus described on page 14, the drag on a case containing a dead larva was determined for various speeds of water flow. It was not possible to use a living larva in these experiments because its swimming would have made readings impossible, and an anaesthetised larva would not have remained so long enough for all the necessary readings to be made. The drag on the thread and hook was determined first and this was later subtracted from that for the thread, hook, and case with larva. Graph 1 shows these measurements and shows that at the maximum swimming speed of 1.7 cms./sec. The drag/...
drag on the larva and case must be approximately 0.95 mgrms.

Using the apparatus described on page 15 (fig. 4a) the effective pull, i.e. the tractive power, of larvae was found to reach a value of 2 mgrms. Larvae therefore have a forward thrust when swimming of about twice the drag on the case, and have power enough available to account for acceleration from rest or, in emergencies, to above the normal maximum speed.

It is interesting to compare the swimming of Triaenodes larvae with that of Acilius and other dytiscids, described by Nachtigall (1960, 1961). This author has shown that the streamlined shape of this beetle causes very low drag even at the fastest of its swimming speeds, whereas the shape of the swimming larva and case of Triaenodes with its maximum diameter anteriorly, its posterior extension, and its anterior opening into the tapering case, all combine to make it one of the worst possible for movement through water. Whereas Acilius has a resistance of only one fifth that of a disc of the same surface area as the front elevation of its body, it seems likely that the resistance to the movement of Triaenodes larva through the water, must be approximately equal to that of such a disc. The drag on the beetle would be decreased if it were of the optimum "drop-shape" of a fully streamlined object, but as Nachtigall points out, this would reduce its stability. Its broad abdomen gives stability to both rolling and pitching movements but it still suffers from yawing instability which makes its movements tend towards being a zig-zag. Being almost cylindrical and not dorso-ventrally flattened like Acilius it/...
it is hardly surprising therefore that the stability of *Triaenodes* is sometimes upset and the rotatory motion described above (page 219) occurs. However, yawing and pitching are probably reduced by the elongation of the case, and the extended swimming legs help to reduce rolling.

The coxo-pleural articulations of the second and third legs are quite different in *Acilius*, both to one another and to those of *Triaenodes* and *Limmophilus* larvae (Nachtigall, 1960). That of the second leg is a joint which permits rotation in a plane parallel to the longitudinal axis of the body. That of the third leg is fused and permits no movement. Nachtigall states that this predetermines the plane of action of the swimming leg of the beetle while the tibiotarsal joint is a complex joint which he describes as being partly a ball-and-socket and partly a hinge joint and which, he states, gives a certain degree of positional variation to the distal part of the leg. It is most unfortunate that this joint is not fully described, because it must have evolved to compensate for the rigidity of the action at the coxo-pleural articulation and the details of the functional adaptations of such a limbe would be most instructive, and relevant to swimming appendages in general.
General discussion.

A. The Morphology of the Thorax.

"The form and function of a living organism are mutually self-determinative", (Engels in Gilarov, 1960), and in the larvae studied here nothing could be more true. Their bodies are very flexible, extensible and contractible for life in a case, and the anterior parts of those bodies are protected by large sclerites. Their legs are strong for feeding, locomotion, and case-building, and yet they have enough joints to allow them to be tucked into their cases with speed and simplicity. Their musculature is closely integrated with their exoskeleton and yet is sufficiently adaptable to actuate a swimming leg while retaining the basic pattern seen in the other segments of the larvae.

The sclerotisation of the anterior parts of the body is clearly protective. This is the most exposed part of the body when the larva is crawling about, and the head particularly is the structure which closes the anterior entrance to the case when the larva retreats into it and which prevents marauders reaching the softer parts of the body. The protergite is noticeably extended on the lateral walls of the prothorax compared with the other two thoracic segments, and this situation occurs in a considerable number of holometabolous larvae (Dytiscus, Gyrinus, helmid-larvae). This is somewhat surprising because, although the prothorax is the thoracic segment most liable to attack, being furthest out of the case, the meso- and meta-thorax might well also benefit by extended tergal protection. In these two posterior/...
posterior segments, however, there are developing wing primordia at the junction of tergum and pleuron. Possibly the need to have the wings developing not too far from their definitive positions has prevented the ventral extension of the mesotergite to the same degree as in the protergite. It is also possible that it would interfere with the easy rotation of the coxa and withdrawal of the legs when the larva retreats into its case. In the meta-thorax the sclerotisation is so reduced as to be negligible or absent and it is hard to be sure why this is of benefit to the animal. One must suppose that the contractability and extensibility of the segment is of more importance than its protection by rigid sclerites. If this is conceded, it is probable that this is correlated with the need to inflate the swellings on the first abdominal segment when the larva retreats into its case, the metathorax contracting and squeezing fluid backwards against the pressure of the fluid coming forwards from the abdominal segments. The turgor of the larvae of both Limnephilus and Triaenodes can be quite high, judged by the eversion of the tissues if the body wall is accidentally punctured. This pressure is one of distension and the body wall is under tensile stress from it. It is significant that is is just these areas of the body which are not sclerotised, indicating that unsclerotised cuticle has a considerable tensile strength. Those parts which are sclerotised are those where muscular action causes compression stresses which have to be resisted for the muscular action to be effective. Sclerites and sclerotisation therefore, occur where protection is important; where
compression stresses are found; and possibly, as mentioned elsewhere, where large setae arise.

The tapering of the body towards its anterior end is a noticeable feature of the larval body. It is mainly due to a reduction in the size of the prosternum, and is associated with the narrowness of the fore gut, which does not widen out into the mid gut until it reaches the posterior region of the mesothorax.

The meso- and meta-thoracic segments are often taken to be more typical of the body, or at least the thorax, as a whole, than the prothorax. But it could be argued that the presence of the wings or wing primordia probably causes many variations in the musculature and therefore in the skeleton, so that these segments are no more typical than the prothorax and in fact are often less so. The presence of the head unfortunately prohibits the conclusion that the prothoracic musculature is more fundamental in its total pattern than that of the other two thoracic segments, but in respect of the leg muscles it probably is. The very different pattern of muscles seen in the abdominal segments of Limnephilus unfortunately does not help at all to make any certain conclusions possible on this point.

B. The morphology of the leg joints.

One of the purposes of this thesis is to try to analyse the skeleto-muscular system of the limbs of two caddis larvae and to infer any general principles which they exemplify. A study of their construction illuminates that of the legs of other arthropods and it is now possible to visualise some of the mechanical problems which have/...
Fig. 93. Simplified diagram of figure 92.
Fig. 90. Joint with a short pivot.

Fig. 91. Joint with a longer pivot.

Fig. 92. Joint with the proximal podomere, A, wider than the distal one, B.
have had to be overcome in the evolution of legs with complex but efficient articulations.

The precise construction of the skeleton at the joints of the limbs is of very great importance to their functioning. There are wide variations in the uses of legs in insects, but the articulations used are all varieties of hinge or pivot joints, or specialised forms such as the coxiferal articulations in *Limnephilus* and *Triaenodes*. It is to the hinge and pivot joints that attention is drawn here.

(i) Hinge joints.

Consider first a hinge joint such as the femoro-tibial joint. It is easy to see why the contraction of a muscle moves the distal podomere when it starts from an intermediate resting position; it is not clear what the limits of the movement will be and why they are the limits. If the limb units A and B were of equal diameters and close together movement would be extremely limited (fig. 90). To get any noticeable movement they would have to be widely separated with a large expanse of articular membrane (fig. 91). The degree of the movement is in fact determined by the relative lengths of a and c. If, however, A is of a greater diameter than B, then B can rotate much further (fig. 92). Now the rotation, θ, is determined by the lengths of a, b, and c; in fact

\[
\tan \theta = \frac{\frac{c}{a} + \frac{c}{b}}{1 + \frac{ec}{ab}}
\]

Let \( \theta = \theta_1 + \theta_2 \) (fig. 93)
Fig. 95. Joint with podomere A swollen and podomere B curved to fit.
Fig. 94. Joint with emarginated podomeres.
\[
\tan \theta_1 = \frac{e}{a} \quad \text{(where } e = \sqrt{d^2 - a^2} \text{ and } d = \sqrt{b^2 + c^2})
\]

and \( \tan \theta_2 = \frac{c}{b} \)

\[
\tan \theta = \tan (\theta_1 + \theta_2) = \frac{\frac{e}{a} + \frac{c}{b}}{1 - \frac{ec}{ab}}
\]

When the corners of the podomeres are emarginated, still further rotation is possible (fig. 94), but the large arthrodial membrane makes the joint more vulnerable to damage. Nevertheless it is a common arrangement as in the coxo-trochanteral and femoro-tibial joints of limnephilids and Triaenodes.

Many insects use a raptorial grip, particularly by their fore-legs, well shown in mantids and Nepa and to a lesser degree, by Limnephilus and Triaenodes. In order to fold one podomere against another, one of them may be swollen to meet the other before movement is stopped by the limitations of the articulation (fig. 95). This is seen in the femoro-tibial joints of the legs of Limnephilus and Triaenodes and is clearly recognised by Raciecka (1950) in his study of Molenna angustata. It is approximately midway between full extension and full flexion that the point of maximum grip exists and in the larvae of the caddis flies Hydrobiosis parumbripennia and Neurochronema confusum the swellings are such that the leg has a grip almost as efficient from the mechanical point of view as that of lice and fleas (McFarlane, 1951).

Alternatively, a more extreme raptorial grip can be formed if the end of the moving podomere is angled (fig. 96). One difficulty which this type of articulation has to overcome is that there is a great/...
Fig. 98. Distal podomeres of leg 3 of *Triaenodes*.
Fig. 96. Joint with podomere A straight and podomere B angled.

Fig. 97. Diagram to show the position of zero torque in a joint of the type shown in figure 96.
great likelihood that the origin and insertion of the flexor muscle and the fulcrum come to lie in one straight line before the two opposed surfaces actually meet (fig. 97). In this position no torque is applied to B and no further rotation can occur. It seems probable that in Nepa and mantids there are specialisations which overcome this problem, but it has not been possible to make any thorough examination of them yet.

(ii) Pivot joints.

The second kind of joint in the legs of Limnephilus and Triaenodes is the hinge joint at the tibio-tarsal and tarso-claw joints. Both joints flex as a result of tension in the claw tendon which runs from the proximal muscle in the tibia to the base of the claw. The tendon passes over the ventral proximal tip of the tarsus which acts as a pulley, but an interesting situation arises because the position of the pulley alters as flexion proceeds. Figure 98 shows the situation simplified, with the action of the tendon extended to meet the dorsal wall of the tibia. This is because the presence here of a muscle causes the direction of the tendon's action to be as shown; its line of action does not follow the tendon into the femur proximal to this point, although of course the tendon itself does pass into the femur. Figure 99 shows the system reduced to its simplest terms for the purpose of mathematical analysis (see appendix 1).

As the tension in AD increases, D tends to move round carrying F with it. F approaches the line AB and turning will continue until F lies on the same straight line as A and B. The angle \( \theta \)
at this point of zero torque depends therefore on the angle $\alpha$.
If $\alpha$ is $90^\circ$, i.e. the proximal end of the moving podomere is
transverse, $\theta$ when the moments of turning about $B$ is nil, is
also $90^\circ$ approx. If $\alpha = 60^\circ$, $\theta$ at equilibrium = $120^\circ$ approx.,
and vice versa.

Some measurements of the size of $\alpha$ in the legs of Limnephilus
and Triaenodes are:

<table>
<thead>
<tr>
<th>Limnephilus</th>
<th>Triaenodes</th>
</tr>
</thead>
<tbody>
<tr>
<td>Leg 1</td>
<td>Leg 1</td>
</tr>
<tr>
<td>Leg 2 - 67$^\circ$</td>
<td>Leg 2 - 53$^\circ$</td>
</tr>
<tr>
<td>Leg 3 - 59$^\circ$</td>
<td>Leg 3 - 85$^\circ$</td>
</tr>
</tbody>
</table>

The measurements for the fore legs are omitted because in life
there is no movement at this joint in either larvae. (A more
exact analysis of the size of $\theta$ at equilibrium may be made as
indicated in the appendix).

These figures indicate that the maximum angular movement ($\theta$)
of the tarsus and claw of leg 2 of Triaenodes and legs 2 and 3 of
Limnephilus is about $120^\circ$; in leg 3 of Triaenodes it is about $90^\circ$.
In other words, the architecture of the skeleton at the joint is
such that those legs which need to flex a great deal can do so,
while leg 3 of Triaenodes which does not need to flex so much has
the mechanically suitable type of joint.

C. The morphology of joints and their muscles.

Joints designed for powerful movements need to be strongly
built, whereas quick weaker movements can utilise a less massive joint/...
joint. This is clear in the myriapods from the work of Manton (1958a) and from a comparison between the first and third legs of *Triaenodes*. Here the first leg is used for actions needing strength, while the swimming movements of the third leg are quick but weak movements. The build of the joints is therefore of greater and lesser proportions respectively. Manton (1958a and b) also points out that the other two factors which determine the morphology of a joint in the myriapods are (i) the planes of movement of the limbs, and (ii) economy of muscles involved. The more freely one unit of the leg can move at a joint, the more essential it is for many muscles to make sure it moves only in the desired direction. In respect of economy of muscles therefore, it would be better to have a joint which permitted movement only in one plane, i.e. a hinge or pivot joint, although then the degree of freedom of movement is greatly limited.

This difficulty is overcome if there is a series of pivot or hinge joints along the length of the limb, and at least one of them is at right angles to the others. This arrangement acts like a gimbal mounting, where the axes of rotation are separated out from one another, and provides full freedom on movement. Yet at the same time only one pair of muscles is necessary at each joint, i.e. a flexor and an extensor muscle. Even this pattern may be simplified by the loss of the extensor muscle at hinge joints, at least at some of the distal joints.

There are examples of joints with much more freedom, such as the pleuro-coxal joint in *Scutigera* (Manton, 1958b), which has 33 extrinsic/...
extrinsic muscles involved in its control. This joint is very similar to that of the third leg in *Triaenodes*, although in this case the number of extrinsic muscles is no greater than that of the metathorax of *Limnephilus* in which the joint has not the same freedom at all. This is because there is an automatic action of some of the retractor muscles which turns the leg into the correct position for the swimming stroke and also because the numerous setae are arranged to maintain the leg in the correct position when moving. This effect of swimming setae may be seen also in *Acilius* (Nachtigall, 1960). Nevertheless in aquatic animals the behaviour and actions involved in swimming are not very different from those used in walking and it is not to be wondered that the numerical differences in the musculature of leg 3 in *Triaenodes* and *Limnephilus* are small.

It is sometimes true that the space within a limb is entirely occupied by muscles, while in other cases it is largely empty. Sometimes this can be ascribed to the need for the opposing surfaces of adjacent podomeres to meet (see above) and at other times by the need to reduce the mass of the limb to a minimum, as in the case of *Triaenodes* (see above, page 241). In many arthropods, however, the limbs may be overcrowded with muscles at key points along the length of the limb, while other parts are empty. These variations in the arrangements of the musculature in the limbs of arthropods would perhaps repay a more wide and detailed study, and give a greater understanding of their functional morphology.
Fig. 100. Muscle pattern at hinge joint.

Fig. 101. Muscle pattern at a hinge joint, displaced (i).

Fig. 102. Muscle pattern at a hinge joint, displaced (ii).
D. The correlations of the muscular and skeletal systems.

D1. The relationship between the length and the leverage of a muscle.

Manton, in her series of papers (1950-1958) points out, on several occasions, that longer muscles cause unit displacement in a shorter time than shorter muscles; (e.g. p. 499, 1958a). She deduces that long muscles are associated with rapid movements. "Rapid movements ... are effected in arthropods by relatively longer muscles giving greater displacements..." (1958b, p. 59). This is undoubtedly often true, but consideration of the musculo-skeletal system at the femoro-tibial joint in the legs ofLimnephilus and Triaenodes shows that it is by no means the full story.

For the purpose of further analysis the mesothorax and leg 2 of Limnephilus were chosen because the leg was large enough to dissect and its pace was of average position and range. In diagrammatic form the femero-tibial joint has two muscles of different lengths acting on either side of a pivot (fig. 100).

A and B are the points on the proximal end of the tibia at which the extensor muscle (e) and the flexor muscle (f) insert respectively. E is the origin of e on the femur and F is the origin of f on the femur.

When e contracts the distal end of the tibia rises and A moves closer to E at A' (fig. 101).

The distance through which A moves to A' for unit displacement...
of C, is here called the intrinsic displacement of e (i.d.e.). The movement of C is called the extrinsic movement due to e (e.d.e.).

Similarly when the flexor muscle contracts, i.d.f. is the intrinsic displacement and e.d.f. is the extrinsic displacement (fig. 102).

Now for the same extrinsic displacement downwards at C, B must move further than A and therefore muscle f contracts more than e because PB is longer than PA. Hence the speed of the effective action at the distal extremity of a limb is determined by the leverage through which a muscle works as much as by anything else. A longer muscle gives faster intrinsic movement, but if it is working on a longer leverage the extrinsic effect may be just the same as a shorter muscle acting through a shorter lever.

Measurements of the operative parts of this system in leg 2 of Limnephilus have been made while manipulating the legs of a dead larva and they show that the length of muscle and the length of the leverage through which it acts are closely interrelated. The leverage of the extensor muscle (le) is 0.0938 mms.; that of the flexor muscle (lf) is 0.2188 mms. (fig. 98). The maximum length of the extensor muscle is 0.8125 mms. and that of the flexor muscle is 1.813 mms. These figures show that the ratio of leverage to length is almost the same for the two muscles, i.e.

\[
\text{extensor muscle} = 0.1154 \\
\text{flexor muscle} = 0.1207
\]
Fig. 103. Diagram of the muscle pattern at the coxiferal articulation of leg 2 of *Limnephilus*. 
A similar musculo-skeletal pattern can be found in the thorax where the promotor and remotor muscles insert on the coxa on either side of the coxiferal pivot (fig. 103). The promotor muscles are those of group 8.2, and the remotor muscles are those of group 8.5. The other major group of muscles affecting the coxa are those of group 8.1. They are not considered in this problem because they insert opposite to the coxiferal articulation and therefore their effect will be to adduct the leg. If they have any promotor or remotor effect at all, it must be very small because the plane of their action is very close to the articulation.

The muscles of group 8.2 and those of 8.5 were dissected out of a larva without any more damage than a slight roughness at their ends where they had been detached from the cuticle. They were mounted in undiluted glycerine so that this supported the coverslip, and they were not distorted by its weight.

The maximum length of group 8.5 is 40 units (units are used for simplicity here, because the measurements were made using a squared graticule at x100; one unit was 0.0435 mms.) Its leverage is 10 units. The maximum length of group 8.2 is 17 units, and its leverage is approximately 4 units long. The ratios are therefore 40:10 and 17:4 i.e. 4 and 4.25. These are sufficiently alike to be a confirmation of the situation found in the leg. The maximum lengths of these muscles were taken because the shorter branches do not affect the principles involved since they affect only the intermediate stages of the leg movement and not its ultimate stage.

These/...
These two examples show the length of a muscle is related to the extent of its intrinsic displacement as Manton has stated, but that the extrinsic displacement may be the same in speed and size for a long muscle as for a short muscle. This means, of course, that long muscles are not necessarily associated with swiftness. In Triaenodes for example, the main muscles (8.51 and 8.52) which remote leg 3 are not long, but they have a very short leverage which makes their extrinsic speed high. The examples also show that the extrinsic displacement is the same in speed and extent, whether it is the long or the short muscles which contract.

From a theoretical point of view, there is no reason why the muscles and leverages should not be of equal length, and if greater power is required, the muscle concerned could then be increased in diameter. The fact that such a solution is rarely found shows that it is not so simple as it sounds. It may be that a narrow leg cannot accommodate two muscles of equal length which have a diameter, large enough to give adequate power, or perhaps there is not room on the skeleton for all the muscle branches to originate. In the thorax this probably does apply with the same force but another factor must be taken into consideration.

In figure 103, the power developed by the flexor muscle \( f \) is applied at \( B \). The extrinsic effect of this force at \( C \), will depend on the leverage \( 1f \). If this is large the effective power at \( C \) will be greater than if \( 1f \) was short. Thus the power required for a given movement at \( C \) will be supplied by the product of the intrinsic force/...
force developed by the muscle and the leverage of the muscle. This means that if the flexion of the leg needs to be more powerful than its extension, the leverages of the two movements become different, and therefore the lengths of the muscles must change. Further increases in the extrinsic power output at C could be made by increasing the leverage if, but this would involve increasing the length of muscle f if the same speed and extrinsic displacement are to be retained. Clearly there is a sharp limit to this in the length of the skeletal unit which contains the muscle, although there are cases where even this problem is avoided, as in muscle 8.50 in the metathorax of *Triaenodes* which is accommodated within the segment, by making a right angle bend round muscle 7.50. Normally, an increase in the extrinsic power of a muscle beyond that due to optimum leverage is brought about by enlarging the muscle. This in turn necessitates a greater area of cuticle from which it can originate and this may sometimes be a real problem. Crome (1957), for example, considers this to be one of the main reasons for the shifting of the origin of the femoro-pretarsal flexor muscle from the femur to the coxa in *Oryctes nasicornis*. In the femoro-tibial joints of *Limmophilus*, it is the need for increased power in flexion which has required the increase in leverage of the flexor muscles, and this in turn has involved commensurate increase in the length of the flexor muscle. It is in this way that the extensor and flexor muscles come to be of different lengths.

Some general principles which arise from the discussion and from the experimental work described above, may now be proposed.

They/...
They are basic to the action of the skeleto-muscular system of the animals studied here and probably to other arthropods also.

1. Longer muscles give larger and quicker intrinsic displacements.

2. Longer muscles working on longer leverages do not give larger or quicker extrinsic displacements.

3. Longer leverages give greater extrinsic force, and are important in strong movements.

4. Fast movements are brought about by muscles working on short leverages.

These principles of the action of the musculo-skeletal system immediately illuminates the reason for the fan-wise arrangement of muscles such as is seen in the muscles of group 8.5 in the mesothorax of Limnephilus (figs. 14 and 103). As movement begins all the muscles contract because even the shortest muscles have an intrinsic displacement sufficient to act at the start of the movement. As the turning of the coxa continues the shorter muscles cease to be effective since they are now shortened to a maximum and power is supplied by the medium and longer muscles. Towards the end of the movement only the longest muscles are effective. Moreover, this effect will be reinforced by the fact that muscles give their maximum force at or close to their resting or body length.

In the power stroke of a swimming leg, resistance to the movement of the leg is minimum at the beginning and end of the stroke, and maximum in the middle of the stroke when the leg is extended at right/...
Fig. 104. Femoro-tibial joint of leg 2 of *Limnephilus*:
exact measurements.
right angles to the direction of movement. Nachtigall (1960), poses the question as to how Acilius manages to adjust its muscle power output to the changing requirements during the swimming stroke; it seems likely that in this insect as well as in Triaenodes the swimming muscles have lengths which are optimum for just the power output that the swimming movement demands. Unfortunately in Triaenodes the swimming muscles do not all insert at one point so that their differing leverages complicate the picture, and Nachtigall does not give the morphological details necessary to establish whether the suggestion is correct for Acilius or not.

D2. The relation between the length of a muscle and its intrinsic displacement.

One of the assumptions involved in the account given in the previous section is that the maximum shortening of a muscle is a constant percentage of its resting length. In all muscles so far investigated this seems to be true, but it does not seem to be known what the percentage is for insect muscle. By analogy from vertebrate muscle it is usually assumed that striped muscle in insects contracts by no more than 20% (Manton, 1958b). It was thought desirable to check whether this coefficient of contraction was true of the femoro-tibial muscle of Limnephilus, and figure 104 shows the exact measurements involved in leg 2.

This figure shows the positions of the tibia with respect to the femur when the leg is fully extended and fully flexed. The angular displacement is approximately 60° and the movement of the insertion/...
insertion of the flexor muscle is 0.21 mms. This means that the flexor muscle must contract by 11.6% ($\frac{0.21}{1.813}$) of its maximum length, and by 23.1% ($\frac{0.21}{0.911}$) of its minimum length. Thus the shorter parts of this muscle may be fully contracted before the point of maximum flexure. In the case of the extensor muscle the figure is about 10% ($\frac{0.06}{0.8125}$). This probably means that this muscle can contract to a greater extent so that the leg may be more fully extended than appears from these measurements on a dead leg. It must be admitted, however, that the construction of the flexor muscle is not so simple as the above calculations assume. It consists of several nearly parallel branches as well as a few, almost coalesced branches, running from the proximal apex of the femur to the insertion on the tibia. The shorter branches probably cause the initial quick contraction which begins flexion. The longer branches give maximum movement to the flexed leg.

D) The position of a muscle and its action.

Lockhart (in Bourne, 1960) points out that "the fact that a muscle happens to be favourably placed for the execution of a movement and even the fact that it does so under electrical stimulation, provides no guarantee whatever that in the normal state the muscle does carry out this movement". (Page 17). He quotes the clavicular section of the pectoralis muscle in man as an example of such a situation, in the action of depressing the arm. In this study, as in most other published work, it is tacitly assumed that function can be deduced from position to a great extent, and, although it is undeniable...
Fig. 105. Muscle tensiometer. Figures are the lengths indicated in cms.
undeniable that this is usually true, it is perhaps desirable to make explicit the assumption involved.

E. The physiology of the muscles.

In order to gain a greater understanding of the actual performance of some of the muscles and the use made of them in normal life by the larvae, it was decided to make a fuller investigation into the magnitude of the forces which various muscle groups produce. For this purpose several designs of apparatus were tried, but the following proved most satisfactory (fig. 105).

A teak dish (w.d.) mounted on the mechanical stage of a microscope (m.s.) carried a fixed clamp (f.c.) holding one end of the specimen (f). The other end was held by another clamp soldered to a lever (u.c.). At the opposite end of the lever there was a small mirror (m.) made from a silvered cover slip which reflected light on to a scale. As the specimen contracted, the lever was moved, and this movement was magnified by the optical lever. It was also magnified because the pivot (p.) of the lever was much closer to the clamp holding the specimen than to the mirror so a small displacement of the clamp gave a larger displacement of the mirror.

In order to make the movement of the light more clearly visible a bridge of fine wire (w.) was arranged between the condensing lens of the spot light (s.l.) and another small lens of long focal length (m.g.). By correct placing, a sharp shadow of the wire fell on to the scale (sc.) and made it possible to read the movement to...
the nearest millimetre.

The lever was supported by a small hook attached to a nylon thread (n.) which ran up to a glass filament (fil.) drawn out from a glass rod. The underside of the lever was notched and by varying the position of the hook in the notches the force required to move the lever was varied.

The clamps were made from phosphor-bronze draught-sealing strip, a material which is very useful for this purpose. It can be cut by ordinary scissors, bends easily and sharply without cracking, retains great springiness, and, of course, is a good conductor of electricity. This last was of importance because the clamps also acted as electrodes. In the case of the clamp attached to the lever, the wire to the electricity source was soldered to the arm in which the lever pivoted and not the lever itself so that there was no interference to its free movement by connecting wires.

The calibration of the apparatus proved difficult because it was designed to work properly when the specimen and its tensions acted in a horizontal plane. Thus the effects of any weights hanging in the vertical plane were useless for calibration, until a pulley altered their tension to horizontal. All available pulleys, however, produced so much friction that they were unsatisfactory. To overcome this, water in a glass tube was frozen, and the resulting icicle used as a pulley. This solved the problem and allowed accurate calibration to be carried out.

The apparatus described was used in many of the experiments on...
Fig. 106. Muscle tensiometer. Modification for leg actions with turn-table.
on preparations of the abdominal musculature and was modified to find the force developed by the legs of larvae (fig. 106). A small dish filled with 'Plasticene' (P.) supported the larva, which was held in place by several small hoops, made from micro-points, pushed into the 'Plasticene'. A leg was attached to the lever by nylon thread (n.). The dish was mounted on a turn-table fixed to the mechanical stage of a microscope (m.s.). In this way a larva could be placed in any desired position so that the nylon thread conveying the tension developed by the leg to the clamp could be orientated at 180° to the intended direction of movement of the leg. It also permitted the promoter and remotor tensions of a leg to be measured one after the other without the necessity of removing the thread from the leg. This was of practical importance since it was not easy to get the slip-knot of the thread tightened on to the same place on each leg while it was being vigorously waved about by the larva.

A kymograph was used to record the results of some of the experiments on the abdominal musculature, using a straight-forward physiological lever. The preparation was held by loops of 40 S.W.G. copper wire, and the marking point was a small piece of celluloid attached to an arm of expanded polystyrene; this was lighter than a straw of the same length. Loads were applied to the muscle by attaching weights to the lever. Use was also made of chains attached to the lever, so that as the lever was displaced so the length of chain depending from it increased; in other words increase in movement/...
ment increased the load moved. The chains available were not satisfactory because they were either too light, or the links from which they were made were too large to give a smooth movement, but the method seems to be capable of further refinement. In these experiments, the lower end of the preparation was attached to a 'Prior' micromanipulator, so that it could be placed accurately in any position and so that the tension on it could be easily adjusted.

Various methods of stimulation were tried, but most satisfactory was a mains transformer with an output of 24v. passed through an induction coil. The resulting shock to the preparation could be varied from a minute value upwards. Currents of about 3v. and 2ma. were in fact used. The arrangement avoided any polarisation at the electrodes. A simple neon stimulator was also used.

E1. The extrinsic and intrinsic muscles of the legs.

During the course of this study it has been quite obvious that in general the size of muscles is related to their usual tasks. However, there is apparently an exception in the thoracic premotor and remotor muscles of the legs in Limnephilus and Triaenodes. In the mesothorax of Limnephilus for example, the promotor muscles look stronger and more powerful than the remotor muscles, although it may be believed that the backward thrust of the legs to propel the larva forwards brought about by the remotor muscles, must be greater than the returning of the leg to its anterior position at the end of its backstroke by the promotor muscles.

This/...
This discrepancy led to a more detailed consideration of these muscles and of their functioning. At first it was hoped to make a preparation from which the force developed in each group of muscles could be measured when the muscle was stimulated by an electric shock to its nerve. The larva, however, proved to be too small to make this possible.

Instead the larva were held inverted on a 'Plasticene' bed and the tensions developed in the coxa of leg 2 were found using the apparatus described above. The animals were stimulated to struggle by touching or stroking them with a fine brush, and the maximum tension developed was the measurement noted. The tensions of both the promotor and the remotor muscles of the coxae of the second legs of several larvae were taken, the turntable being used to reverse a larva so that the readings of the opposed muscles could be taken without removing the nylon thread. The results of these experiments show that the force developed by the promotor muscles acting on the coxa was 0.25 grms. (average of 19 readings), while that of the remotor muscles was 0.26 grms. (average of 25 readings). The two figures are so close that they can be considered to be equal and one is forced to the conclusion that the coxa is pulled forwards on its return stroke just as powerfully as it is pulled backwards on its power stroke.

This result suggests that the larva, for some reason, requires as much power to bring the legs forwards as it does to move them backwards. This could perhaps be so for the fore-legs...
which hold the prey or other food strongly in an anterior position; or even for all the legs, to allow rapid withdrawal into the case. Nevertheless it remains somewhat surprising, and it was felt confirmation would be desirable.

A series of measurements was therefore made to check whether this hypothesis was correct by taking the force developed at the claw of each leg. The results are shown in table 3.

<table>
<thead>
<tr>
<th>Muscles</th>
<th>Leg 1</th>
<th>Leg 2</th>
<th>Leg 3</th>
</tr>
</thead>
<tbody>
<tr>
<td>Promotor</td>
<td>0.129</td>
<td>0.19</td>
<td>0.104</td>
</tr>
<tr>
<td>Remotor</td>
<td>0.354</td>
<td>0.346</td>
<td>0.204</td>
</tr>
</tbody>
</table>

Table 3. Tension in grams developed at the tip of each leg during promotion and remotion. (Average of 6 readings). This clearly shows that in all legs, the effective force at the claw tip is much greater on the backstroke than on the return stroke, and it is in contrast to the results given above for the forces acting on the coxa. The differences between the two results indicates the effect of the intrinsic leg muscles acting on the backstroke, an effect whose efficacy is enhanced by another consideration. This is the effect of the length of leg on the magnitude of the pull found. When the promotor pull is taken at the coxa of leg 2, it is 0.25 g.; at the claw tip it is 0.19 g. This reduction may be accounted for by the lower mechanical advantage when the measurements are taken at the claw compared with the coxa, and relate only to the thoracic extrinsic coxal muscles (but see below).

Equally well the lower mechanical advantage of extrinsic muscles/...
muscles acting at the claw-tip instead of at the coxa, must be
ture of the remotion of the limb, and by the same amount. Thus it
is reasonable to suppose that the effectiveness of the thoracic
remotor muscles at the coxa (i.e. 0.26g.) is reduced at the claw-tip
by a factor of 0.19/0.25, which equals 0.198g.

Since, however, we know from Table 3 that in fact the actual
remotor pull at the claw-tip is 0.346g., it must be concluded that
the difference between these two figures is the contribution to the
remotion of the limb by the intrinsic remotor muscles. That is,
0.346 - 0.198g. = 0.148g. This represents 34% of the total remotor
force of the leg.

These calculations assume that no part of the observed
promotor pull at the claw-tip is derived from the intrinsic muscles,
although these are known to be present. If an estimate is made of
the contribution of these muscles to the promotion of the leg, (and
it cannot be large since they are relatively small) it is probably
that in remotion, the contribution of the intrinsic muscles would
rise to about 50%.

E.2. The pulling power of limnephilid legs.

Using the apparatus described above (page 15) various
limnephilid larvae were used to test their power of pulling against
a calibrated glass thread. Their maximum pull varied from 0.825
grms. to 1.95 grms. The weights of the larvae and their cases in
water varied from less than nothing to 0.113 grms., the heaviest
case being made from shells. There is little correlation between
the pull developed and the weight to be moved. Some relevant figures are:

<table>
<thead>
<tr>
<th>Pull (grams)</th>
<th>Wt. of larva &amp; case, in water (grams).</th>
</tr>
</thead>
<tbody>
<tr>
<td>1.39</td>
<td>0.0494</td>
</tr>
<tr>
<td>1.39</td>
<td>0.1130</td>
</tr>
<tr>
<td>1.14</td>
<td>0.0438</td>
</tr>
<tr>
<td>1.06</td>
<td>0.0323</td>
</tr>
<tr>
<td>1.06</td>
<td>less than zero</td>
</tr>
<tr>
<td>0.975</td>
<td>0.0674</td>
</tr>
</tbody>
</table>

The pull of the larvae is much greater than the weight they are ever called upon to move. At the same time the irregular shape of the case and the difficulty of the terrain through which it has to be moved may require an output of many times the submerged weight of the larva and case and this is available, as the figures above show.

When exerting their maximum effort the larvae used their jaws to grip the cork, and sometimes advanced all the legs on each side alternately. At other times a larva extended fully and got a grip with jaws and all the legs stretched as far forward as possible and then contracted its body to pull the case up to its usual position. This method is like that of Onychophora and Chilopoda described by Manton (1954).

The experimental results above to some extent check the accuracy of the measurements of the pull of each leg separately. The maximum total for the three legs of one side was 0.364 +
0.346 + 0.204g. = 0.904g.; or 1.808g. for the six legs of the larvae (see table 3). Remembering that the figure of 1.95g. is a maximum and that of 1.808g. is an average one, the agreement seems quite close.

When the pulling force of limnephilid larvae was measured, the opportunity was taken to attempt to find out what proportion of the total was derived from each pair of legs. A larva was taken and its maximum pull determined while it was intact, and also after it had had the claws of one pair of legs removed. The removal of the claws and possibly the distal tip of the tarsus, was preferred to the removal of the whole leg, because since the grip is by the claw only, it was unnecessary to remove the whole leg. Also, in spite of being anaesthetised, the shock of amputation was so great that the larvae would refuse to come out of their cases for twelve or twenty-four hours, which was obviously inconvenient. It was in any case difficult enough to get readings from intact larvae which one could feel represented their true full power output. The results were as follows:

Larva 1.

Pull when intact 0.98g.
Pull after loss of claws of first pair of legs 0.49g.
% of power attributable to the first pair of legs 50%

Larva 2.

Pull when intact 1.39g.
Pull after loss of claws of 2nd pair of legs 0.325g.
% of power attributable to second pair of legs 77% (Larva/
Larva 3.

Pull when intact 1.47g.
Pull after loss of claws of 3rd pair of legs 1.225g.
% of power attributable to 3rd pair of legs 17%

It is also possible to work out these percentages from the later experiments when the pull of individual legs was measured. From the figures given above in table 3 (Page 166) it can be calculated that the percentage contribution of each pair of legs is: first legs 39.2%, second legs 38.3% and third legs 22.6%. The differences between these two sets of figures are considerable and probably show that the measurements on the whole larvae were inaccurate because they did not allow properly for the poor cooperation of the larvae after mutilation, nor for the stepping pattern when only one leg of a pair may be effectively used or needed at any one moment. Both sets of figures however, show the relative unimportance of the third legs in forward propulsion, and the latter set indicates that the first and second pairs of legs are sub-equal in importance, in spite of the much greater length and therefore lower mechanical advantage of the second legs.

Having established that the forces applied to the coxa by the opposed groups of muscles were of the same size, it remained to consider the relationship between the size of the muscles and their power. The promotor muscles appear larger in dissections than the remotor muscles, but they have already been shown to be shorter. The other component of their size is their thickness of...
or more precisely their cross-sectional area. This was measured
to see whether this showed any correlation with other known
measurements. To do this, the two sets of muscles were dissected
from a larva which had been anaesthetised. They were embedded
in gelatine and cut on a freezing microtome so that their cross-
sectional areas could be determined unchanged by dehydration.
In this process thin dental celluloid strip was found useful for
supporting the minute muscles while they were being embedded.
Gelatine adheres quite well to this material and it cuts easily on
the microtome. A graticule showing 0.1 mm. squares was used with
a x40 objective. Because the promotor muscles are grouped into a
fan-shaped mass the outer members of the 'fan' were cut obliquely,
giving their sections an elipsoid appearance. In all cases there-
fore, where a section was not circular, the shorter axis was chosen
as the real diameter of the muscle. The muscles of two larvae
were treated in this way with several sections of both groups of
muscles and the diameters of the muscle strands measured. The
average value of several examples was found and the actual set of
muscle strands nearest in this value was chosen for the calculation
of the total cross-sectional area of the muscle. In the case of the
promotor muscles this was 0.0294 sq. mm. and in the case of the
remotor muscles it was 0.0137 sq. mm. Hence the promotor muscles
have a cross-sectional area 2.15 times as large as the remotor
muscles. It is significant that this is nearly the same as the
ratio of the leverages of the insertions of the two groups of
muscles from the coxifer, namely 1 : 2.5. It has already been shown
that/...
that the lengths of the two groups of muscles bear this relationship (see page 256). Thus, the length of a muscle is directly proportional to its leverage, while its cross-sectional area is inversely proportional to its leverage, assuming that comparable extrinsic effects are considered. This result may be added to the five principles of muscle action suggested above (page 259) and the whole summarised as follows:

1. \( f_i \propto a \) (intrinsic force developed is proportional to cross-sectional area)

2. \( f_e \propto aw \) (extrinsic force developed is proportional to the product of the cross-sectional area and the mechanical advantage employed)

3. \( v \propto lw \) (the speed of extrinsic effect is proportional to the product of the length of the muscle and the leverage used).

It is also often true that

4. \( l \propto w \) (the length of the muscles is proportional to the length of the lever it acts on).

E.3. The abdominal musculature.

Although the work which has been described on the leg muscles proved very fruitful and gave a better understanding of the working of the legs, the need was felt for a preparation in which the muscle action could be more isolated from the limitations of the skeleton. At first it was intended to use the coxal remotor muscles of group

8.5/...
8.5, but this proved impossible because of their small size. Muscles similar to the leg muscles are found in the abdomen and these proved suitable since the longitudinal muscles extending in groups or bands from one end of the abdomen to the other were large enough to use in the experiments to be performed.

Sometimes the whole abdomen was used, after the head of the larva had been removed; in other cases a longitudinal strip was cut from the abdominal body wall which included the ventral nerve cord and some of the rows of longitudinal muscles adjacent to it. The intact abdomen survived very well but the strips of the body wall were less resistant. Aquarium water and saline solutions were used to bathe the preparations. Where part of the body wall was being used, the hemocoelic fluid was kept and used mixed with 0.7% saline. No special precautions were taken to provide oxygen, and indeed the use of aquatic animals reduced this problem to negligible proportions. It was unfortunately not found possible to revive the preparation if the larva had been anaesthetised before being dissected. Because of this fewer larvae were used than would be desirable in a full scale investigation into the physiology of insect muscle.

Rhythmic movements and the nerve cord.

The rhythmic movements of the larval abdomen, so important in normal life for the current of water through the case, continued in most of the experiments, even in those in which the abdomen was divided into two. They continue after a contraction has relaxed which/...
which is in contrast to the earthworm body (Collier, 1939) where they occur usually only in response to a tactile or stretch stimulation. The contraction of the preparation when the stimulation arrived at the relaxation phase of the rhythmic contraction was less than that when the stimulation was given during the contraction phase (fig. 107). Where a second stimulation was received after an earlier one, all the records showed augmentation even when the two stimuli were nearly 10 secs. apart, and were single stimuli from a neon stimulator. A similar example occurs in the body wall of earthworm, in which Botsford (1941) found augmentation after a stimulation, although the interval between the stimulations had to be not more than 0.5 sec. except after a brief tetanus when the period extended to 30 secs. Botsford considers the relationship between the frequency and duration of shocks to the tension developed, but little can be said here about this aspect of the contraction of the larval body wall muscles. Only one experiment was performed in which the frequency and intensity (but not the duration) of the stimuli were varied, and this showed that the tension increased with both frequency and intensity. Becht and Dresden (1956) found that increase in intensity of the stimulus to the slow extensor nerve of cockroach caused a decrease in tension and concluded that an inhibitory nerve was involved. The absence of this effect in the limnephilid larva suggests that such inhibitory nerves are not present. At the same time it must be pointed out that the results given in this part of the thesis need much further investigation before any certain conclusions can be drawn.
Fig. 108. Length-tension curve of vertebrate muscle.

T = tension; L = length of muscle as a percentage of the body or resting length.
If the ventral nerve cord was removed from the preparation neither the rhythmic nor other activity was usually manifest, although on one occasion responses were obtained from a preparation of only the dorsal half of the abdominal wall. This is true of earthworm also according to Collier (1939), although Wu (1939) denies this for Lumbricus while agreeing with it for Arenicola. The part played by the nerve cord is of considerable importance in the contraction and relaxation of the body wall musculature in these experiments and clearly a better preparation to study the muscle activity would be one in which the nerve and the muscle to which it runs are isolated from the central nervous system. On a larger larva there is every likelihood that this would be possible, but in this work the larva proved too small to allow this.

The length/tension relationship.

Like all muscle tissue there is a length of the abdominal muscle at which it gives its greatest tension. In most muscles this is close to the normal body length, although there are exceptions in which the optimum length is greater than the maximum length in vivo (Fischer, 1944). One great difficulty, however, resides in the fact that the abdomen of a larval limnophilid has no obvious normal length. When extracted from its case the larva is usually contracted, or, if not, it is extending and contracting in locomotion. It is only possible to estimate the normal body length by inspection. The alternative is to find the increase in tension/...
Fig. 110. Length tension curve for abdominal muscle
(average of three experiments). T, L and L₀ as in
figure 109.
Fig. 109. Length tension curve for abdominal muscle (single experiment). $T =$ tension in grams; $L =$ length in mms.
$L_o =$ resting length.
tension at different degrees of extension. At the point where the increase is at a maximum, the muscles are at their optimum length. This point is indicated on figures 108 and 110 by the mark L₀.

In the graph given by Hill (1953) for the sartorius muscle of a frog the tension developed in maximal tetani increases to a maximum at the body length of the muscles and then decreases as the muscle is further elongated (fig. 108, curve 1). The tension developed by the passive resistance of the muscle increases as the muscle is elongated beyond its body length (fig. 108, curve 2). The summation of the two gives the tension curve for typical vertebrate skeletal muscle (fig. 108, curve 3).

Figures 109 and 110 show length/tension curves derived from experiments with the larval muscles. On both figures curve 1 is the active tension curve i.e. the tension developed on stimulation, and curve 2 is the passive tension curve. Curve 3 shows the increase in tension upon stimulation. Figure 109 is of a single experiment but it is similar to those of nine other experiments, while figure 110 shows the results of an experiment in which the preparation was extended and allowed to shorten again (at 0.1 mm. intervals) three times, the averages of the tensions at each length being found for both passive and active tensions. Both curves show a marked difference from the classic picture of figure 107. They show that in spite of ever increasing passive tension
Fig. 112. Length-tension curve for locust flight muscle; redrawn from Weis-Fogh (1956).
Hx = mistake - no record.


Free loading? b = 50s. Free loading? h = 60s. Free ordering?

KYmograph record of muscle tension under various conditions.
the preparation can give an active tension on stimulation which
is still greater. This situation can continue until the passive
tension placed upon it is sufficient to break the preparation or
to tear it from its clamps. It has proved impossible to hold it
firmly enough to obliterate all signs of contraction upon
stimulation by merely increasing the load and in the kymograph
records there is still a slight response under a free-loading of
nearly 60 grams. (fig. 111). All this is shown by the curves
approaching almost asymptotically and exactly the same pattern
was found by Weis-Fogh (1956) in his experiments with locust
flight muscle (fig. 112). In these examples of insect muscle
physiology the active tension curve is rather similar to that of
a frog muscle which is stretched during contraction (fig. 108,
curve k; and Polissar, 1952). It is also of interest that a
similar relationship between length and tension occurs in the
experiments of Csapo and Goodall (1954) on rabbit uterus muscle.

The absolute muscle force.

One very important consideration in muscle physiology is
the absolute force developed by the muscle i.e. the maximum
tension increment per cm.² cross-section at optimal muscle length
(Fischer, 1944). Unfortunately only one experiment can be quoted
from which this parameter can be determined because in only one
experiment was the cross-sectional area of the preparation found
with any certainty after the tension measurements had been made.
In this experiment, in which the ventral half of the abdomen was
used/...
used, the cross-sectional area of the main eight ventral longitudinal muscles was 0.21 sq. mms. (The small and oblique muscles were ignored as being of negligible importance in segmental shortening). This gave an absolute muscle force of approximately 1.5 kg./cm.² which is in close accord with that of 1.6 kg./cm.² for locust flight muscle (Weis-Fogh, 1956). Weis-Fogh calculates that the theoretical isometric maximal tension increase would be about 3 kg./cm.² at 25°C, and this no doubt also applies to the abdominal muscle of Limnephilus since the data given by Weis-Fogh are closely paralleled by those given here. It seems therefore that functionally the work, force, and length/tension relationship are similar in these two groups of muscles. Measurements of the absolute muscle force of other muscles have not been made very frequently, but Ramsey and Street (1940) give a figure of 3.5 kg./cm.² for single striated muscle fibre of frog, while the unstriated pharyngeal retractor muscle of the snail reaches 2.8 kg/cm.² (Abbot and Lowy, 1953).

Twitch contractions.

The latent period of a contraction is usually about 0.025 seconds, but when the preparation is fatigued it rises to as long as 0.17 seconds. (The figures given here for the latent period include the time lag due to the mechanical inertia of the recording apparatus; this would be very small.) In one example the tension reached its maximum in slightly over 1 second after stimulation/...
Fig. 14. Kymograph record of a twitch contraction (slow speed); s = stimulus.
stimulation and relaxation took about 3 minutes (fig. 113).
The preparation in this case was free-loaded to the extent of approximately 7 grams, and reached a maximum tension of 7.7 grams.
In another example, the tension reached its maximum in \(1\frac{1}{2}\) seconds after the stimulation, decayed to half this value after another second, and decayed to one third of it after a further half second, i.e. 3 seconds after stimulation. Full relaxation did not occur until several seconds later (fig. 114).

Tetanic contractions.

In tetanic contractions the rates of contraction and relaxation are both very slow. It takes anything from 20 to 40 seconds to reach a maximum, and relaxation time may be as long as 4\(\frac{1}{2}\) minutes (under a tension of 1.5 grams.). In these respects the abdominal muscles of *Limnephilus* are, of course, very different from the flight muscles of locust and are more like uterine muscles which take about 4 seconds before they reach their maximum response, (Csapo, in Bourne, 1960); or the foot muscle of *Ariolimax* which takes about 20 seconds (Carlson, 1904 in Howell, 1930). The slow relaxation of the abdominal musculature is typical of vertebrate smooth muscle and Fischer (1944) suggests that it is the cause of the tonus associated with this kind of muscle. Now once a caddis larva has withdrawn into its case, it remains contracted for a relatively long time without difficulty, and this may also be an example of tonus, i n the abdominal muscles. A similar slowness in contraction and relaxation is found/...
found in the non-striated muscles of other invertebrates as well as in the striated muscles of other insects (Becht & Dresden, 1956).

Comparison with non-striated muscles.

When a limnephilid larva stretches out of its case, the abdominal muscles show great extensibility. This is a characteristic feature of non-striated muscles such as those of the body wall of Onychophora which allows these animals to pass through very narrow cracks (Manton, 1961). Again it is striking that non-striated muscles are usually associated with action around a hollow organ, whether it is gut or mantle cavity or annelid body wall, and in the case of larval abdomen of some insects, the same functional properties have evolved in spite of the retention of muscles with a striated appearance. These two features together with the relative slowness of contraction and relaxation show that the striated abdominal muscles have properties akin to non-striated muscles, while the length/tension relationships are very like those of locust flight muscle. This confirms the growing opinion that the functional differences between muscles of different histological structure are not as absolute as was once thought. For example, Prosser, (in Bourne, 1960) points out that some striated muscles contract more slowly than some non-striated.

Even in vertebrates, Kuffler and Vaughan Williams (1953) and Hunt and Vaughan Williams (1954) have shown that many muscles previously taken to be purely striated muscles have components which show some features associated with non-striated muscle. The term smooth/...
smooth muscle is best reserved for the visceral non-striated muscle of vertebrates while other kinds of muscle which are not striated may be called non-striated. Amongst the invertebrates there are many varieties of both non-striated and striated muscles, with a wide range of properties (Prosser, and Hanson and Lowy, in Bourne, 1960). It is not surprising therefore that the abdominal muscles of a caddis larva show characteristics not usually associated with vertebrate striated muscle and it seems that muscles of all kinds form a graded series in which two of the extremes of specialisation so far evolved are the vertebrate smooth muscle and the insect flight muscle. The abdominal muscle of Limnephilus fit somewhere in between and have features pertaining to both.
Summary.

This thesis is a comparative study of the thorax of the crawling larva of *Limnephilus* and the swimming larva of *Triaenodes*. It correlates the differences in structure found in these larvae with their different modes of locomotion; this has involved a detailed study of both the skeleton and the musculature as well as an examination of their intimate functional association. Every effort has been made to take into account the details of the skeleto-muscular system because so often it is only in the details of its construction that a full explanation can be found for its actions. Wherever possible measurements have been made and the objective approach this has engendered has made the anatomical data more reliable. Measurements have led to the detection of mistakes arising by subjective, (and perhaps unconscious) pre-conceived ideas as to function, and, as in other fields of science, numerical information acts as a check against which other conclusions can be tested.

The study of the sclerites necessary for the full understanding of the skeleto-muscular interrelations has led to several interesting conclusions. There are, for example, two sclerites in the propleuron in both larvae, and it has become clear that the anterior of the two is a detached part of the episternum of the pleural sclerite. This anterior sclerite must be termed a pre-episternum, and this conclusion is probably applicable to other Trichoptera larvae apart from *Limnephilus* and *Triaenodes*. The posterior/...
posterior sclerite is the typical pleurite common to all the thoracic segments.

The prothorax is narrower than the meso- and meta-thorax. This reduction in diameter, which is a feature of many insects, occurs by a relative decrease in the size of the pleural, and particularly the sternal regions, and may be one reason for the disagreement amongst morphologists as to the exact nature of the sternum in insects. The protergum is relatively much more extensive than either the meso- or meta-tergum and it seems very probable that this is because the developing wings, which are found at the junction of the pleuron and tergum cannot grow properly if they are displaced very far from their definitive position in the imago.

In many ways the broad aspects of prothoracic anatomy of the larvae of *Limnophilus* and *Triaenodes* are no less typical of a thoracic segment, in spite of the presence of the head, than those of the other two thoracic segments. In these the wings exert their own special influence even before they are fully developed.

There are several apophyses of the sternum to which muscles attach and it has been necessary to decide which one is the furca. In the larvae studies here there is no furcal strut articulating with the pleural arm, as in many other insects, but there is a muscle which corresponds to this strut. The point of attachment of this muscle to the sternum is held to be the furca.

The sclerotised regions of the body are not only for protecting vulnerable exposed areas, but for resisting the compression stresses/...
stresses of muscular action, and for the proper working of the larger setae.

The tough resilient modification of the cuticle found in the posterior pleural disc of the metathorax of *Triadenodes*, and in ligaments at some of the leg joints, is probably the same as the resilin occurring in the tendons of flight muscle. It has great strength and elasticity and helps to make the reciprocating motion of the skeleto-muscular system mechanically more efficient in the swimming larva of *Triadenodes*.

Much of the body of both larvae, and especially the flexible unsclerotised cuticle, is covered with numerous small hard points, for which the name "microsetae" is proposed.

The muscles of the larval thorax fall into a common pattern which is repeated with various modifications in all three segments of each larva. The pattern indicates sound homologies among the muscles, but in some cases difficulties arise. A muscle which is subdivided in one segment may, for example, be a single structure in another segment, and it is not always obvious what degree of homology may be inferred from this. The concept of homology, not a concept which can be applied blindly, because no absolute definition of the term is possible, its correctness and applicability varying with the degree of similarity of the structures under consideration. Another important point is that innervation is not an infallible guide to muscle homology since in several typical thoracic segments muscles are innervated from two of the thoracic/...
thoracic ganglia. Wherever possible, variations in the muscle pattern are related to adaptations for particular functions of the larval body.

Homologising the individual muscles of the larvae of *Limnephilus* and *Triaenodes* with those of insects described by other writers, has not been very easy or satisfactory. At the same time a most interesting parallel can be drawn between the Trichopteran muscle pattern and that found in the pseudo-foetus of the primitive machilid *Dilta hibernica*. This suggests that although the muscles are a variable component of the insect body, they have a basic arrangement which has persisted from very early times. It ought to be possible to deduce from the study of other species of insects found today, especially their larval stages, the details of this fundamental common arrangement.

The abdominal muscles of *Limnephilus* have been studied, and compared with those of the thorax, partly to see how similar the musculatures of the two regions of the body are, and partly because the abdominal muscles have been used for some of the experiments on muscle physiology described in the thesis. They have also retained an ancient pattern, suitable for segmental appendages, and have not adopted a more complete circular layer, such as that found in animals with a soft-bodied abdomen. It is possible that primitive insects and their precursors had a longitudinal layer of muscles, outside which were the muscles of the (locomotor) appendages, contrary to Berlese's theory of a primitive arrangement of a longitudinal, a circular, and a tegumentary layer/...
layer of muscle.

The limbs of the two larvae and their activity in case-building, feeding and locomotion have been described in the thesis. The morphology of the exo-skeleton is exactly correlated with the needs of the animal and these larvae are extremely adept at the manipulation of awkwardly-shaped shells, and wriggling worms, in case-building and feeding respectively. The legs have many strong spurs which aid in gripping and many fine setae for sensory purposes. The long leg 3 of *Triaenodes* has a great many long setae essential for its swimming. All the legs of both larvae have to be withdrawn into the case in times of danger and this poses the problem of accommodating such structures within a case. Measurements show that even the longest podomere can fit fairly easily into the case, although in the long swimming legs of *Triaenodes* the extra flexibility of the pseudo-joints is probably of importance.

Two features of the legs which are of much interest are the oblique trochantero-femoral joint and the trochanteral annulus. The former allows only very limited movements which hardly seem necessary for the effective use of the limb. The latter is a line of elasticity, in spite of its superficial similarity to a plane of autotomy. Both these structures suggest that the legs need a small degree of flexibility at this point along their length, though the reason for this is perhaps not fully understood.

Locomotion in the larvae consists of crawling or walking in *Limnophilus*...
Limnephilus and crawling and swimming in Triaenodes. In both larvae, the stepping of the legs is irregular even on a regular substratum, and this is thought to reflect the irregularities of the normal environment amongst tangled plants. In Limnephilus, the major function of the first pair of legs is shown to be mainly one of traction; the second pair are concerned with both pulling and pushing and with lateral movements; the third pair raises the case and assists the second pair in forward progression. In Triaenodes the extreme length of leg 3 necessitates the pacing of this leg to be far forward, lateral to leg 1, rather than posterior to leg 2 as in Limnephilus. Because of this, the mesothoracic leg of Triaenodes rotates much more widely from anterior to posterior in order to support the case and posterior part of the body.

An important feature of the action of any insect leg which seems to have hitherto been overlooked, is that at the end of a pace, a leg is subject to a turning moment due to the effects of the weight of the animal, although, of course, in a submerged larva this will be very small.

A comparison between the leg muscles of Limnephilus and Triaenodes larvae and between their leg muscles and those of other insects, larval and otherwise, shows great uniformity. The skeleto-muscular system of the insect leg is adaptable and can be easily modified for such special purposes as swimming and case-building.

Limnophilid larvae can exert a much greater pull than their own/...
own weight when submerged. This enables them to take their irregular case amongst the vegetation of their habitat. Experiments show that Triaenodes larvae have a forward propulsive power of about twice that of the drag on the case and larva at the normal swimming speed. The force given by the extrinsic remotor muscles of leg 2 in Limnephilus is about 50% of the total force at the claw tip in remotion. The other 50% is due to the intrinsic remotor muscles, and the contribution of each pair of legs to the total tractive effort of the larva is given.

Neither hydrostatic pressure nor extensor muscles are necessary for the extension of the insect leg when it is pressing against a substratum; the tarsus and claw of leg 3 of Triaenodes have, however, been seen to be extended even when lifted from the substratum. This must be due to the hydrostatic pressure of the blood, since no extensor muscles are present for these two podomeres.

The swimming of Triaenodes is described in detail. The movement is jerky and sometimes appears to be unstable with rotary motion of at least two kinds. The case trails in the water and the anterior end of the larva extends ventrally over the lower edge of the case opening. The inertia of the swimming leg during the forward stroke is reduced by the folding of the long setae and by the folding of the leg itself. The tibial pseudo-joint allows the extension of leg 3 at the end of the forward stroke and the beginning of the backward stroke to be more rounded and even than...
would be possible with a totally rigid tibia. The power of the backstroke is utilised to the full by the extension of the leg and the setae which spread out widely in the water. Movement of the coxiferal articulation allows the leg to make a wide sweep from anterior to posterior. Leg 3 turns on its own axis during the back stroke, by the action of remotor muscles and the spreading setae.

The pattern of the musculature working the swimming leg can be related fairly completely both with that of the pro- and mesothorax of Triaenodes and with that of the thoracic segments of Limnephilus. There are differences in which some small muscles have become greatly developed in the metathorax of Triaenodes, e.g. 8.61, and others usually large which have become reduced or absent, e.g. 8.4. There is a parallel between the swimming leg of Triaenodes and the legs of other animals which move their legs quickly. All have the main musculature at the proximal end of the leg, have long tendons to transmit tension, and have the distal parts of the limb elongated. Larvae deprived of the claw, tarsus and part of the tibia of leg 3, can still swim, but the frequency of the beating by the damaged leg is increased. Larvae without one of the metathoracic legs, swim in circles.

Because the case is spirally built, it has an asymmetrical anterior projection. This causes an upward and a lateral thrust when the larva swims, and these forces are liable to upset the balance of the swimming animal. The former is counteracted by the ventral curvature of the anterior part of the body of the swimming larva/
larva and by the negative pitch of the swimming legs. The latter is counteracted by the fact that the larva grips the case with its anal hooks. Experiments show that if a larva grips the case by the swellings on the first abdominal segment, the case and larva move with a rotary motion. The long case probably gives stability in pitching and yawing, and the outstretched legs probably give stability in rolling. Nevertheless, larvae can swim without a case but usually in a circular motion of maximum negative pitch.

A thorough analysis of the geometrical and mechanical features of the different kinds of joints of the legs demonstrates how closely morphology and behaviour are related. In pivot joints the movement must be sufficient to allow opposing surfaces of adjacent podomeres to touch, and moreover to grip firmly. In its extreme form, this raptorial action creates geometrical and mechanical problems which different insects solve by different specialisations, some of which are mentioned in this work.

Hinge joints are more complex mechanically though simpler geometrically. In the larvae of Limnophilus and Triaenodes the structure is shown to be directly related to their action, and the mathematics of this relation is explained. Their movement is always such that they come to the end of their movement before the position of zero torque is reached.

The interrelations between the podomeres and the muscles which actuate them are considered, and this had led to four principles which may be summarised as follows:

(1)/...
(i) Intrinsic force developed is proportional to the cross-sectional area of the muscle.

(ii) Extrinsic force developed is proportional to the product of the cross-sectional area and the mechanical advantage employed.

(iii) The speed of the extrinsic effect is proportional to the product of the length of the muscle and the leverage used.

(iv) Often, the length of the muscles is proportional to the length of the lever it acts upon.

Apparatus of different designs have been devised for experiments with the abdominal muscles which show that the length-tension relation resembles that of locust flight muscle, while their twitch and tetanic contractions show characteristics usually associated with non-striated muscles.

The absolute muscle force of the abdominal muscle is about $1.5 \text{ kg./cm}^2$, at $19^\circ\text{C}$. 
Acknowledgements.

This work has been carried out in the Zoology Department of Leicester University under the guidance of Professor H.P. Moon, who has been unfailingly patient and helpful and to whom I am greatly indebted. My thanks also go to Drs. D.M. and M.G. Guthrie who have given much valuable criticism; to Mr. C. Haywood and Dr. K. Majut, who have helped so willingly with the mathematics; to Mr. A. Hall for help in numerous ways; to Messrs. I. Parker and G. Broughton for assistance with the photography; and to Miss J. Gardner who has typed it all out so carefully.

The Principal and Governors of the College of Technology and Commerce, Leicester, are thanked for their permission to carry out this work at the University.
**List of abbreviations used in the figures.**

<table>
<thead>
<tr>
<th>Abbreviation</th>
<th>Description</th>
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<tbody>
<tr>
<td>a</td>
<td>antenna</td>
</tr>
<tr>
<td>af</td>
<td>algal filament</td>
</tr>
<tr>
<td>aif</td>
<td>anterior intersegmental fold</td>
</tr>
<tr>
<td>ail</td>
<td>anterior intersegmental line</td>
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<tr>
<td>al</td>
<td>attachment line</td>
</tr>
<tr>
<td>am</td>
<td>articular membrane</td>
</tr>
<tr>
<td>as</td>
<td>air supply</td>
</tr>
<tr>
<td>at</td>
<td>anterior tergite</td>
</tr>
<tr>
<td>bb</td>
<td>ball bearing</td>
</tr>
<tr>
<td>bp</td>
<td>black paper</td>
</tr>
<tr>
<td>c</td>
<td>coxa</td>
</tr>
<tr>
<td>ca</td>
<td>case</td>
</tr>
<tr>
<td>cc</td>
<td>coxal cavity</td>
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<tr>
<td>cf</td>
<td>coxifer</td>
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<td>cl</td>
<td>claw</td>
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<td>clp</td>
<td>clamp</td>
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<tr>
<td>clt</td>
<td>claw tendon</td>
</tr>
<tr>
<td>cp</td>
<td>coxal peg or projection</td>
</tr>
<tr>
<td>cs</td>
<td>cork sheet</td>
</tr>
<tr>
<td>cv</td>
<td>collecting vessel</td>
</tr>
<tr>
<td>cy</td>
<td>clypeus</td>
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</tbody>
</table>

\( d/... \)
d - decreased

dh - dorsal hood

e - epicuticle

eco - elastic cuticle

ep - epimeron

ep - eccentric position

es - episternum

f - femur

f' - furca

fb - frontal band

fc - fixed clamp

fil - glass filament

fl - flexible link

fp - femoral pivot

f - ganglion

GA - ganglion of abdomen

ge - gena

h - head

h' - position of head

hk - hook

i - increased

ir - internal ridge of coxa

is f - intersegmental fold

isl - intersegmental line

ism/...
ism - intersegmental membrane
iv - inner vessel
l - larva
L - length (resting)
lac - locus of anterior end of case
lc - larva in case
Lf - left femur
m - mirror
mc - muslin cover
mdl - mid dorsal line
mg - lens
ml - leg 3
ms - mechanical stage
mvl - mid ventral line
n - nylon thread
nc - nerve connectives
nm - membrane between head and prothorax
p - pivot
pac - locus of posterior end of case
pb - Plasticene bed
pcm - pericoxal membrane
pif - posterior intersegmental fold
pil - posterior intersegmental line
pj - pseudo-joint
pl - plant leaf
plr - pleural ridge
pm - posterior notum
pr - prey
prm - promotor muscles
ps - pleural sclerite
psl - anterior pleural sclerite, first pleural sclerite and
pre-episternum
pt - post-tergite
r - reed
rm - remotor muscles
s - sternum
sa - posterior or lateral sternal apophysis
sc - scale
sg - suboesophageal ganglion
sh - prosternal horn
sl - light source
slc - sclerotised cuticle
sp - spina
sr - sclerotised rim
t - tergum
T - tension, in grams
ta - tarsus
td - transparent disc
te - edge of tergum
ti - tibia
tip - tibial pivot
th - thickening
tr - trochanter
tri - tergal ridge
trp - trochanteral peg
ts - thigh strap
tt - turntable
uc - moving clamp
vs - ventral sclerite
vt - ventral tergite
w - wire
wd - teak dish
ws - water supply
wt - wide tube
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Fig. 99. Diagram of figure 98.
Appendix 1

In the legs of the larvae the mechanical situation may be simplified so that the position of one part may be calculated with respect to another part, when the limb under muscular contraction is at equilibrium.

Diagrammatically the situation is shown in figure 99. The problem is to find θ, when 1₁, 1₂, 1₃, and α are known and when the leg is at equilibrium.

AB = 1₁; BD = 1₂; BF = 1₃.

XF is erected perpendicular to BF.

YF bisects angle AFD.

Now in triangle HFD, FD = \sqrt{1₁^2 + 1₂^2 - 2*1₁*1₂*cos α}, where α is a given or chosen value, and sin HFD = \frac{1₂*sin α}{FD}

which gives angle HFD = θ

In triangle ABF, AF = \sqrt{1₁^2 + 1₃^2 - 2*1₁*1₃*cos(180 - α - Θ)}; and

sin AFB = \frac{sin(180 - α - Θ)*1₁}{AF}

which gives angle AFB = θ, and this may be computed for various values of Θ.

At F, 2 γ + θ + ε = 360°; therefore γ = \frac{360 - θ - ε}{2}

and can be calculated for various values of Θ.

Also at F, δ + γ + ε = 90° = 360°, therefore δ = 270 - γ - ε

and δ may be similarly found for various values of Θ.

Now/...
Now the couple of BD about B, anticlockwise is:

\[ 1_2 (T \sin \beta) + (2T \cos \gamma \cos \delta \cdot 1_3) = 0 \text{ at equilibrium} \]

(where T is the value of the tension acting along AFD).

Dividing through by T, it is necessary to compute

\[ 1_2 \sin \beta + 2 \cos \gamma \cos \delta \cdot 1_3 \]

and plot this against the values of \( \Theta \) used. From this graph the equilibrium value of \( \Theta \) may be read off.

In the larvae of this study the measurements used for three of the legs were as follows:

**Triazenodes bicolor:** leg 3; \( 1_1 = 0.97 \text{ mms.}, 1_2 = 0.58 \text{ mms.}, 1_3 = 0.063 \text{ mms.}, \) and angle \( \alpha = 84^\circ. \)

**Limnephilus flavicornis:** leg 2; \( 1_1 = 1.375 \text{ mms.}, 1_2 = 0.9375 \text{ mms.}, 1_3 = 0.2375 \text{ mms.}, \) and angle \( \alpha = 67^\circ. \)

**Leg 3;** \( 1_1 = 1.25 \text{ mms.}, 1_2 = 0.9375 \text{ mms.}, 1_3 = 0.225 \text{ mms.}, \) and angle \( \alpha = 59^\circ. \)
Appendix 2

Since this thesis was typed, a paper by Winkler (1959), has come to my notice which describes the skeleton and muscles of the larvae of *Limnephilus flavicornis*. This paper gives a brief description of a simplified version of both systems and does not consider any of the possible implications which they may involve. The muscles shown in the figures do not include all those actually present (see list below) and as some are neither named or numbered it is not easy to give a full criticism of the figures. It is probably sufficient to enumerate those given in this thesis which Winkler omits and to mention one or two other points over which my account differs from his.

The skeleton.

Apart from lack of details of the less pronounced points of sclerotisation of the sternal region, the only important difference of the two accounts lies in Winkler's use of the 'Cervicale' for the first pleural sclerite, which has been shown in this thesis to be the anterior portion of the pleurite which has become detached, and which is termed by the present author pre-episternum.

The musculature.

(i) The prothorax.

Sets 1 and 2. These two groups are shown in Winkler's figure of the prothorax but they are insufficiently differentiated into their component muscles.
Sets 3, 4 and 5. None of these muscles are shown.

Set 7. Muscles 7.14, 7.40, and possibly 7.15, 7.16 and 7.50 are omitted.

Set 8. All the muscles of group 8.2, and muscle 8.56 are missing.

Set 9. No muscle 9.10 is shown.

(ii) The mesothorax.

Sets 1 and 2. As prothorax.

Set 3. All except one are omitted, and this one (Winkler's muscle 96), seems to be equivalent to 3.20, 3.21 and 3.22 combined.

Set 4. All of this set are also omitted except one which is shown extending too far to the posterior.

Set 5. In group 5.1, all are omitted except 5.10.

In group 5.3, there are two muscles which are not included in this thesis, and which are unnumbered in Winkler's paper.

Set 6. Three out the four muscles of this included in this thesis are missing from Winkler (1959).

Set 7. Muscles 7.10, 7.11, 7.12, 7.13, 7.16, and possibly 7.14 and 7.15 are all omitted.

Set 8. Muscles 8.10, 8.21, 8.23, 8.40, 8.41, 8.51, 8.53, 8.60 and 8.61 are omitted.

Set 9. Muscle 9.10 is omitted but a muscle is included as a trochanteral muscle which is considered here to be a coxal remotor muscle. This Winkler numbers 104, while in this thesis it is numbered 8.55.

(iii) The metathorax.
Set 1 and 2. These sets seem to be similar in both papers.

Set 3. There appears to be no mention of any of these muscles except 3.21 and possibly 3.22.

Set 4. All are omitted except one which is as in the mesothorax too far posteriorly.

Set 5. Muscles 5.16, 5.31, and 5.32 are not shown, while there is one extra muscle shown (without a number) which seems to have its origin on the surface of one of the longitudinal muscles of the first abdominal segment.

Set 6. All these muscles are apparently omitted.

Set 7. Muscles 7.10, 7.11, 7.12, 7.14, 7.15, 7.16, 7.32, 7.33, and 7.34 are not shown by Winkler, while he includes one which is not shown in my drawings.

Set 8. Muscles 8.10 and 8.11 seem to be shown arising from the wrong point of origin, and muscles 8.21, 8.22, 8.40, 8.41, 8.53, 8.54, 8.55, 8.60 and 8.61 are all omitted.

Set 9. Muscle 9.10 is omitted but a muscle is included as a muscle to the trochanter which is considered here to be a coxal remotor muscle. This is Winkler’s muscle 139, which I have shown as muscle 8.55.

Fourth abdominal segment.

Sets 1, 2 and 3. The muscles of these three sets are insufficiently differentiated to show their details adequately.

Set 4. Muscles 4a, 4b, 4c, 4d and 4j to 4o inclusive are omitted.

Set 5. Muscles 5c, 5d, and 5j are missing.
Reference: