A Comparative Morphological Study of the Tracheal System in Larval Diptera. Part I

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SUMMARY

The larval tracheal system of species representative of certain families in the Diptera Nematocera, Brachycera, and Cyclorrhapha is discussed. Detailed descriptions are given of the larval systems of members of the families Psychodidae, Trichoceridae, Anisopidae, Scatopsidae, Bibionidae, Phoridae, and Calliphoridae.

Attention is drawn to the fact that the dissimilarity between the tracheal systems of the species from the selected families—more particularly between the Diptera Nematocera and Cyclorrhapha—is superficial. The differences overlie what is in fact a series of tracheal systems in which the number and distribution of the main elements is remarkably constant. The homologies of these main elements in all three sub-orders are demonstrated. Correlation between the form of the central nervous system and the distribution of the tracheae is also shown.

Each described system is analysed into its main constituents and represented by a 'larval tracheal pattern'. On close examination the patterns or plans of each system in the various families are shown to conform to a 'general plan' common to all the species described, and probably representative of a general larval plan for the whole order; it is suggested that it approaches what must be the primitive distribution of tracheae in the Diptera. It is also suggested that this pattern may prove of phylogenetic importance should it be possible to discover similar generalized patterns for the other insect orders. It is shown how the plan can be used in interpreting previous descriptions by other workers.

The results presented illustrate the stability and remarkable constancy of the basic pattern of the tracheal system throughout the main sub-divisions of the order. No correlation is seen between the form of the internal tracheal system and the variations shown by the spiracles, the elements of the tracheal system remaining constant in number and origin in all the species described.

In a future paper it is proposed to describe the systems of species from the remaining nematoceran families; considerable deviation from this general plan is to be seen, but the systems can be interpreted in the light of the present results.

CONTENTS

INTRODUCTION .............................................. 258
MATERIALS AND METHODS .................................. 259
THE GENERALIZED DIPTERAN LARVAL SYSTEM .................. 260
THE TRACHEAL SYSTEM OF INDIVIDUAL SPECIES ................. 262
Family Psychodidae: Psychoda alternata Say ................. 262
Family Trichoceridae: Trichocera annulata Meigen .......... 263
Family Anisopidae: Anisopus fenestralis (Scopoli) .......... 265
Family Bibionidae: Dilophus febrilis (Linnaeus) .......... 266
Family Scatopsidae: Scatops notata (Linnaeus) .......... 268
Family Phoridae: Aphiochaeta (Megaselia) sp .............. 268
Family Calliphoridae: Calliphora erythrocephala (Meigen) .... 271
DISCUSSION ............................................. 272
CONCLUSION ............................................. 277
REFERENCES .............................................. 277

INTRODUCTION

Many workers have described the larval tracheal system of individual dipteran species, but no attempt has been made to present a comparative morphological account. In fact few comparative studies on this system have been made for any of the insect orders. Notable exceptions are those of Fuller for the Isoptera (1919), Landa for the Ephemeroptera (1948), and the work of Lehmann (1925) who surveyed the tracheal system of the whole class. The earlier classical work of Palmén (1877) provides the basic work on topography and anatomy of the insect tracheal system, and many of Lehmann's deductions are based on this.

The detail with which the tracheal systems of individual dipteran species have been described varies considerably. Very many accounts, both older and more recent, are very incomplete, while many of the more detailed accounts throw no light on the homologies of the individual parts. In fact, the systems vary so considerably within the order that it would appear that no consistency exists, and it is therefore not surprising that comparisons have been made only infrequently.

Older accounts, such as those of Lowne (1900) for Calliphora erythrocephala (Meigen), Hewitt (1914) for Musca domestica Linnaeus, and de Meijere (1901) for Lonchoptera sp., are often vague and incomplete. Ruhle's (1932) description of Drosophila melanogaster Meigen—which is quoted by Bodenstein (in Demerec, 1950)—and also Stammer's (1924) for Tabanus sp., give a good general account, but many details are not included, while Kemper's (1925) description for Psychoda phalaenoides (Linnaeus), and Fuerborn's (1927) description of Psychoda sexpunctata Curtis are detailed. Lehmann's (1925) survey of the insect tracheal system is based on a number of the older descriptions including the work of Palmén and those of Wahl (1900) for Eristalis tenax (Linnaeus), Taylor (1902) for Simulium latipes (Meigen), and Hewitt for Musca domestica (1914); these vary considerably in their degree of detail. Wardle (1926) describes in detail, and compares, the systems of two tipulids, Tipula flavolineata Meigen and Pedicia rivosa (L.). However, he does not attempt to homologize the individual tracheae. The account by Gäbler (1930) of the tracheal system of Eristalis tenax is very detailed, clear, and instructive. Cameron (1933), after describing the system of Haematopota pluvialis (Linnaeus), proceeds to compare it with Stammer's (1924) description for Tabanus sp. However, the anterior region is such a complicated mass of tracheae in both, that homologizing of all the parts has obviously presented difficulties. These difficulties would have been far less were the homologies of the main tracheae known.

The only recent comparative work on any aspect of the tracheal system appears to be that of Keilin (1944). He summarizes past work on the detail of the spiracles, and describes the metamerism and the process of moulting of the tracheal system in larval Diptera. He is not concerned with the detailed morphology of the individual tracheae nor with their homologies. Hence his
description of the dipteran larval system is not based on a comparative study of the detailed morphology of the individual elements.

Larvae of some thirty identified species have been studied in detail during the present investigation. The species have, as far as was possible, and as time permitted, been taken from different sub-divisions of the Diptera. The results obtained from these and other species studied, together with evidence supplied from descriptions by other workers (which as the above résumé briefly indicates, is in some cases detailed, in others fragmentary), have been pieced together and an attempt is made to give a more complete picture of the larval tracheal system in the Diptera, than has previously existed.

In the present paper descriptions are given of a number of specially selected dipteran larvae whose tracheal systems most closely approach what the results of the investigation indicate to be the generalized larval dipteran tracheal system. In a future paper descriptions will be given of the more anomalous systems found in the remaining larval Diptera which have been studied.

Species described and figured

Nematocera
Family Psychodidae: Psychoda alternata Say
Family Trichoceridae: Trichocera annulata Meigen
Family Anisopidae: Anisopus fenestralis (Scopoli)
Family Bibionidae: Dilophus febrilis (Linnaeus)
Family Scatopsidae: Scatopse notata (Linnaeus)

Brachycera and Cyclorrhapha
Family Phoridae: Aphiochaeta (Megaselia) sp.
Family Calliphoridae: Calliphora erythrocephala (Meigen)

Materials and Methods

Living larvae were obtained by either collecting or breeding through from eggs laid by females in captivity. Specimens of Psychoda alternata were obtained from the sewage beds at Cambridge; Trichocera annulata was obtained from the same habitat; Anisopus fenestralis was bred through from eggs kindly sent by Dr. Ll. Lloyd of Leeds, and others were obtained from cow-dung and rotting fruit and from eggs laid by females in captivity; Dilophus febrilis was bred right through from larvae found in cow-dung; Scatopse notata was bred from eggs laid by females which had emerged from fungi collected and kept in the laboratory; Aphiochaeta (Megaselia) sp. in all its stages was obtained from decaying recently killed cockroaches belonging to a laboratory culture.

Each was studied in the living state, either in a drop of water between slide and coverslip, or by dissection in glycerine. In a few cases, permanent preparations were made using an injecting technique (Wigglesworth, 1950). This
involves the removal of air from the tracheal system of a living larva by means of a vacuum pump, followed by immersion of the larva in cobalt naphthalate dissolved in white spirit. Subsequent rinsing in white spirit removes cobalt naphthalate from the surface of the larva. Hydrogen sulphide bubbled through white spirit containing the specimen precipitates the cobalt in the tracheae as cobalt sulphide. The larva is then fixed, cleared and mounted in canada balsam.

Illustrations

In most cases the larva is drawn from the dorsal side; where detail is obscure a portion is drawn on a larger scale. Opposite each figure is a diagrammatic representation of the particular system to show the distribution of the elements and their relation to the spiracles together with the functional or non-functional nature of these. In each plan the right half of the larval system only is given: the centre of the diagram represents the right lateral view, the left the right dorsal side, and the right the right ventral elements of the system. The diagrammatic representations enable easier comparison between one system and another, as the main elements are frequently obscured by fine tracheae, or their distribution is masked in some other way. In all cases the figures omit the finest tracheae and tracheoles.

The descriptive terms ‘dorsal’ and ‘lateral longitudinal trunks’, ‘transverse connectives’, ‘spiracular’, and ‘visceral tracheae’, are those used by previous workers. However, the terms ‘dorsal’ and ‘ventral cervical tracheae’, ‘dorsal cervical anastomosis’, ‘ventral ganglionic tracheae’, and ‘ventral thoracic anastomoses’ have not, to the writer’s knowledge, been consistently used before; they are those found to be, descriptively, the most appropriate.

According to Keilin (1944) the spiracles are intersegmental in origin. This is explained by the forward migration of the so-called ‘pro-thoracic’ spiracles, and the backward migration of all the other pairs of spiracles. The present work shows that the internal morphology of the system substantiates this view. Hence in the following descriptions the terms ‘pro-thoracic’ and ‘meta-thoracic’ spiracles (which imply the absence of a meso-thoracic spiracle) will be replaced by ‘anterior’ and ‘posterior’ thoracic or ‘first’ and ‘second thoracic’ pairs of spiracles.

The Generalized Dipteran Larval System

As mentioned previously, the only attempt at describing a generalized dipteran larval system is that by Keilin (1944). He takes Scatopse notata as a typical example and enumerates the following components.

(1) two main longitudinal latero-dorsal trunks; (2) a pair of secondary latero-ventral longitudinal trunks; (3) transverse branches which are given off laterally from the main tracheal trunks and connect them, in each segment, with the latero-ventral trunks; they continue as spiracular branches terminating in more or less developed spiracles; (4) transverse commissures which connect, in each segment, the main tracheal trunks; (5) tracheal branches or tufts, which arise principally from
the secondary latero-ventral trunks, the ramifications of which extend to various organs; (6) branches which arise from transverse commissures; (7) spiracles, functional or non-functional, and perispiracular glands.

In each of the species to be described in this paper the following parts can be distinguished (fig. 1):

1. Ten spiracles (sp.).

2. Two dorsal longitudinal trunks (d.l.t.).
3. Two lateral longitudinal trunks (l.l.t.).
4. Eight transverse connectives (tr.c.).
5. Ten dorsal anastomoses (d.a.).
6. Two dorsal cervical tracheae (d.c.).
7. One dorsal cervical anastomosis (d.c.a.).
8. Two ventral cervical tracheae (v.c.).
Whitten—Morphology of the Tracheal System in

(9) Ventral ganglionic tracheae (v.g.).
   (a) Three thoracic, with ventral anastomoses (v.a.).
   (b) Seven abdominal, without ventral anastomoses.
(10) Visceral tracheae (vcl.).

It can be seen that components (1), (2), (3), (4), and (10) are those mentioned by Keilin although the exact number of components is not given by him. Numbers (6), (7), (8), and (9) are not mentioned or figured in his paper. These latter are, moreover, the elements most frequently omitted in descriptions by other workers, but are definitely represented in all the Diptera observed by the present author. In taking Scatopsea notata as his example Keilin specified eleven as the normal number of dorsal anastomoses, whereas it will be seen that from the present results the normal number appears to be ten.

THE TRACHEAL SYSTEM OF INDIVIDUAL SPECIES
1. The tracheal system in Psychodidae

Psychoda alternata

The larva has a head capsule (in common with most Nematocera). The system figured is that of a fourth instar larva; it is amphipneustic, having the post-abdominal spiracles opening at the end of a respiratory siphon. The metameric nature of the system is clearly seen and the whole can be analysed into the following components (fig. 2):

Dorsal longitudinal trunks (d.l.t.). There are two of these extending from the first pair of thoracic spiracles to the last pair of abdominal spiracles.

Lateral longitudinal trunks (l.l.t.). These are also paired and run the whole length of the larva.

Transverse connectives (tr. c.). In addition to their anterior and posterior junctions, the dorsal and lateral longitudinal trunks of either side are linked by eight transverse connectives. It is from these that the spiracular threads arise.

Dorsal anastomoses (d.a.). The dorsal longitudinal trunks are connected by ten commissures, the first and second arising between the region of the first thoracic spiracles and first transverse connectives, and one between each of the subsequent connectives and the post abdominal spiracles.

Dorsal cervical tracheae (d.c.). On each side, a trachea arises in the region of the first thoracic spiracle, and appears almost as a continuation of the dorsal longitudinal trunk. Each passes anteriorly to the head after giving rise to two branches. The posterior one divides, one part passing to the supra-oesophageal ganglia (s. oes.) and the other to the sub-oesophageal ganglion (sb. oes.) which lie outside the head capsule. The second pair are given off medially and anastomose mid-dorsally (d.c.a.) just posterior to the head capsule.

Ventral cervical tracheae (v.c.). These also occur in the region of the first thoracic spiracle and appear as continuations of the lateral longitudinal trunks. They also pass anteriorly into the head capsule.

Ventral ganglionic tracheae (v.g.). These pass to the nerve ganglia comprising
the ventral nerve chain. The first pair is given off by the ventral cervical tracheae, and the subsequent ones by the segments of the lateral longitudinal trunk of either side. Each passes ventrally to the nerve ganglion of its segment. The first three constitute the thoracic tracheae, and are peculiar in forming mid-ventral anastomoses (v.a.); the corresponding abdominal tracheae do not anastomose mid-ventrally.

**Visceral tracheae** (v.c.l.). On both sides, and in each segment, visceral tracheae arise just anterior to the origin of the ventral ganglionic tracheae.

2. **Family Trichoceridae**

**Trichocera annulata**

The following description is of a fourth instar larva which has a head capsule and is amphipneustic; the last pair of spiracles opens at the posterior end of the
body and is surrounded by four lobes. The tracheal system consists of the following parts (fig. 3):

*Dorsal and lateral longitudinal trunks* (d.l.t., l.l.t.). Both pairs of trunks are present and are well developed.

*Dorsal anastomoses* (d.a.). The two longitudinal trunks are connected dorsally by ten commissures, the first two occurring in the region between the functional first thoracic spiracles and first transverse connectives (t.c.), while the remainder occur between each subsequent pair of connectives and the last pair of spiracles.
**Transverse connectives** (t.c.). Eight of these are present and unite the dorsal and lateral trunks of either side.

**Dorsal cervical tracheae** (d.c.). These arise just anterior to the junction of the longitudinal trunks. Before entering the head, a median branch is given off which anastomoses mid-dorsally with its fellow to form the dorsal cervical anastomosis (d.c.a.).

**Ventral cervical tracheae** (v.c.). These also arise in the region of the first thoracic spiracle and pass into the head.

**Ventral ganglionic tracheae** (v.g.). A pair of tracheae serves each nerve ganglion. The first pair arises from the ventral cervical tracheae, and the remainder from the lateral longitudinal trunks. The thoracic tracheae form three mid-ventral anastomoses (v.a.).

As only a limited number of larvae were available the system has not been studied in as great detail as the other species described. No descriptions of the tracheal system of any of the Trichoceridae have been seen in the literature.

### 3. Family Anisopidae

**Anisopus fenestralis**

The larva has a head capsule; the following description is of a fourth instar larva which is amphipneustic, having well developed first thoracic and terminal abdominal spiracles. The tracheal system is composed of the following parts (fig. 4): 

**Dorsal and lateral longitudinal trunks** (d.l.t., l.l.t.). These two pairs of trunks are present and well developed.

**Transverse connectives** (t.c.). Besides their union anteriorly and posteriorly, the dorsal and lateral trunks of either side are joined by eight transverse connectives.

**Dorsal anastomoses** (d.a.). The dorsal trunks are connected by ten dorsal anastomoses, one occurring between each pair of transverse connectives, the tenth between the last connective and the last pair of abdominal spiracles, while the first and second occur between the first thoracic spiracles and first transverse connectives.

**Dorsal cervical tracheae** (d.c.). These arise near the junction of the longitudinal trunks with the first thoracic spiracular tracheae, and pass anteriorly into the head capsule. A median branch is given off from each and this subdivides; one part anastomoses mid-dorsally with its fellow (d.c.a.) and the second runs, first in a posterior direction and then anteriorly to what are the supra-oesophageal ganglia lying outside the head capsule.

**Ventral cervical tracheae** (v.c.). These also run anteriorly into the head capsule, first giving off ventral tracheae to the pro-thoracic ganglion.

**Ventral ganglionic tracheae** (v.g.). Each ganglion is served by a pair of tracheae; the first pair arises from the ventral cervical tracheae, and the remaining pairs from the lateral trunk. Those passing to the three thoracic ganglia form mid-ventral anastomoses (v.a.).
Visceral tracheae (vcl.). These arise from the lateral trunk just anterior to its junction with each of the transverse connectives.

The tracheal system of *Anisopus* does not appear to have been described previously.

**Fig. 4.** The larval tracheal system of *Anisopus fenestralis*. A, the larval system in dorsal view. B, plan of the right half of the larval system.

4. *Family Bibionidae*

* Dilophus febrilis

The larva has a head capsule. The following description is of the fourth instar larva which is holopneustic; the first thoracic spiracles are on the second apparent segment and the second pair on the meta-thoracic segment. Of the abdominal pairs, the last is very large and is situated at the anterior margin of
the last segment. The tracheal system is composed of the following parts (fig. 5):

Dorsal and lateral longitudinal trunks (d.l.t., l.l.t). There are two well-developed pairs present.

Transverse connectives (t.c.). The two trunks of either side are connected by eight tracheae, each of which gives rise to a spiracular branch.

Dorsal anastomoses (d.a.). These trunks are connected by ten dorsal anastomoses, two occurring between the first and second thoracic spiracles and the remainder between each of the subsequent pairs of spiracles.

Dorsal cervical tracheae (d.c.). These originate near the junction of the dorsal and lateral trunks, and pass into the head capsule. Before doing so, a median branch is given off which divides; one part anastomoses mid-dorsally with its
fellow (d.c.a.), and the second passes into the head alongside the main trachea (s. oes.).

Ventral cervical tracheae (v.c.). These also pass into the head capsule.

Visceral ganglionic tracheae (v.g.). The first pair of ventral tracheae arises from the ventral cervical tracheae and passes to the first thoracic ganglion. The subsequent ventral tracheae arise from the lateral trunk. Those passing to the three thoracic ganglia form mid-ventral anastomoses (v.a.), whereas the abdominals do not.

Visceral tracheae (vcl.). These arise from the spiracular region of segments two to nine inclusive.

In the region of the first thoracic spiracles there are many other tracheae, which are figured but will not be described in detail.

5. Family Scatopsidae

Scatopse notata

The larva has a head capsule. The following description is of the fourth instar larva which is peripneustic. The last pair of spiracles is situated on slight protuberances of the last abdominal segment. The tracheal system consists of the following parts (fig. 6):

Dorsal and lateral longitudinal trunks (d.l.t., l.l.t.). Both pairs are present and extend throughout the length of the larva.

Dorsal anastomoses (d.a.). The dorsal trunks are connected by ten dorsal anastomoses. The first two occur in the region between the first thoracic spiracles and the non-functional second thoracic spiracles; the third to ninth occur in the region between successive abdominal spiracles, and the tenth and eleventh between the region of the ninth and tenth pair of spiracles.

Transverse connectives (t.c.). Eight of these join the dorsal and lateral longitudinal trunks on each side.

Dorsal cervical tracheae (d.c.). These arise at the junction of the first thoracic spiracular tracheae with the longitudinal trunks, and pass forward to enter the head. Before entering, a median trachea is given off which divides, one part passing alongside the main trachea (s. oes.) and the second anastomosing with its fellow mid-dorsally (d.c.a.).

Ventral ganglionic tracheae (v.g.). One pair of tracheae passes to each of the nerve ganglia. The first pair arises from the ventral cervical tracheae, and the remainder from the lateral longitudinal trunks. The three thoracic pairs form mid-ventral anastomoses (v.a.), whereas the abdominal ones do not.

Keilin (1944) figures the larval system of Scatopse notata, but omits the ventral cervical tracheae and all ventral ganglionic tracheae, including the three mid-ventral anastomoses.

6. Family Phoridae

Aphiochaeta (Megaselia) sp.

The larval head is non-capsular, being reduced to mouth hooks and sup-
Larval Diptera. Part I

porting skeleton. The following description is of a third instar larva which is amphipneustic; the first thoracic spiracles are distinct, and the abdominal ones terminal. The tracheal system consists of the following parts (fig. 7):

**Dorsal and lateral trunks** (d.l.t., l.l.t.). These are present and well developed.

**Transverse connectives** (t.c.). In addition to their anterior and posterior union the dorsal and lateral trunks are joined by eight transverse connectives.

![Diagram of larval system](image)

**Dorsal anastomoses** (d.a.). The dorsal trunks are connected by ten dorsal anastomoses. The first two occur between the first thoracic spiracles and the first transverse connectives, the second to ninth between the successive transverse connectives, and the tenth, which is much shorter and stouter, between the last connectives and last pair of spiracles.

**Dorsal cervical tracheae** (d.c.). These arise just posterior to the junction of the lateral and dorsal longitudinal trunks. The main trachea passes anteriorly, but shortly after its origin it gives rise to a trachea which passes posteriorly to unite with its fellow and form a deep median anastomosis (d.c.a.). From the
latter two tracheae pass to the posteriorly displaced supra-oesophageal ganglia (s. oes.).

**Ventral cervical tracheae** (v.c.). These arise slightly anterior to the dorsal cervicals. Each first gives rise to a superficial dorsal branch, then to the first ganglionic tracheae and finally passes anteriorly.

**Ventral ganglionic tracheae** (v.g.). As the nervous system is concentrated in the thoracic region, all the pairs are correspondingly displaced. The first three, which constitute the thoracic tracheae, form mid-ventral anastomoses (v.a.).

**Visceral tracheae** (vcl.). These arise from the transverse connectives in every
segment, but that arising from the lateral trunk before its posterior junction with the dorsal trunk is very much larger than the others.

As far as is known to the writer there is no existing description of the tracheal system of any of the Phoridae.

Fig. 8. The larval tracheal system of Calliphora erythrocephala. A, dorsal view of the larval system. B, the anterior end in left lateral view. C, plan of the right half of the system.

7. Family Calliphoridae

Calliphora erythrocephala

In common with other Cyclorrhapha the larval head is non-capsular, being reduced to mouth hooks and supporting skeletal elements. The third instar larva is amphipneustic, with first thoracic, and very large terminal abdominal spiracles. The tracheal system is composed of the following elements (fig. 8):

Dorsal and lateral longitudinal trunks (d.l.t., l.l.t.). Two well-developed pairs are present.
Transverse connectives (t.c.). Besides their junction anteriorly and posteriorly the dorsal and lateral trunks are also joined by eight transverse connectives.

Dorsal anastomoses (d.a.). The dorsal trunks are connected dorsally by ten dorsal anastomoses. The first and second lie between the first thoracic spiracles and the first transverse connectives, numbers three to nine between successive transverse connectives, and number ten between the eighth connective and last pairs of abdominal spiracles. The first anastomosis is wider than numbers two to nine while the tenth is very much stouter and shorter than the rest.

Dorsal cervical tracheae (d.c.). These arise just posterior to the junction of the dorsal and lateral trunks. The main trachea passes anteriorly, but shortly after its origin it gives off a trachea which passes posteriorly to unite with its fellow and form a deep median anastomosis (d.c.a.). From this, two tracheae pass to the posteriorly displaced supra-oesophageal ganglia (s. oes.).

Ventral cervical tracheae (v.c.). These arise anterior to the dorsal cervicals and pass anteriorly. A dorsal superficial trachea is first given off and then the first ganglionic.

Ventral ganglionic tracheae (v.a.). The first pair of these originates from the ventral cervical tracheae and subsequent ones from the lateral trunks. As the nervous system is concentrated in the thoracic region, the tracheae are correspondingly displaced. The three anterior thoracic pairs form mid-ventral anastomoses (v.a.), whereas the abdominals do not.

Visceral tracheae (vcl.). These spring from the transverse connectives in each segment. The trachea arising from the lateral trunk shortly before its junction posteriorly with the dorsal trunk is very much larger than are any of the others.

Although the 'typically cyclorrhaphan' larval tracheal system is a familiar one, accurate descriptions are virtually non-existent, Gäbler's (1930) being a noteworthy exception.

Larvae of undetermined species of Musca, Fannia, and Cordilura (observed by the writer), all of which are calypterates, have tracheal systems very similar to that of Calliphora. This similarity extends to the acalypterates. Ruhle's (1932) description of the development of the tracheal system in the larva of Drosophila melanogaster has been confirmed during the present investigation, and the system is seen to agree very closely with those of the Calypterae. The larva of Eristalis tenax (Cyclorrhapha, Aschiza) is described by Gäbler (1930), and his detailed account of the system is also very similar to all of the above, except for the incomplete connexion of dorsal anastomoses two and three in Eristalis. Imms' (1942) diagram of the tracheal system of the larva of Braula coeca is also 'typically Cyclorrhaphan' except that only nine dorsal anastomoses and seven transverse connectives are figured. This suggests the absence of a complete tracheal segment, which may possibly have been overlooked.

Discussion

It has been seen that the tracheal systems of the above larvae possess a remarkably similar arrangement of elements, giving almost identical larval patterns. From these the generalized larval pattern has been deduced.
The variations seen in the spiracles—which vary from the amphipneustic condition found in Psychodidae, Trichoceridae, Anisopidae, Phoridae, and Calliphoridae, through the peripneustic condition of the Scatopsidae to the holopneustic condition in the Bibionidae—are not accompanied by any corresponding modifications of the internal morphology of the tracheal system.

The ten dorsal anastomoses are seen to occupy a definite position. Numbers one and two arise from the dorsal longitudinal trunk between the first and second pairs of spiracles. The remainder arise from the trunks between each of the consecutive pairs of spiracles (second to tenth). In *Scatopse notata* an eleventh anastomosis occurs between the tenth and last pair of abdominal spiracles; this is more probably an addition to the normal complement of ten; if it were not so and the primitive number were eleven then the condition of all the other described species would be secondarily derived by the loss of the eleventh anastomosis.

Most descriptions by other workers usually include the longitudinal trunks, transverse connectives, and at least some of the dorsal anastomoses. In de Meijere’s description of *Lonchoptera* (1901) the relationship of these tracheal elements at the posterior end of the larva is clear, but at the anterior end they are very incompletely figured. Nine tracheal metameres, and not ten, are figured by Imms for *Braula coeca* (1942); that is, there are present only nine dorsal anastomoses instead of the usual ten and only seven transverse connectives instead of the normal number of eight. There would be correspondingly nine spiracles and not ten if these were functional and figured. Either this is a descriptive error or the system is remarkably peculiar in this respect. Similarly only seven transverse connectives are described for *Lonchoptera* sp. (de Meijere, 1901).

In the region anterior to the first thoracic spiracles two pairs of tracheae are seen to arise in each of the described species. Both pairs pass into the head in forms having an obvious head capsule, and in the case of those in which the head is non-capsular but reduced to mouth hooks, these elements can be recognized by the distribution of the tracheae arising from them. The ventral pair—the *ventral cervical tracheae*—in all cases give rise to tracheae which pass to the pro-thoracic ganglion. Without exception, the dorsal pair—the *dorsal cervical tracheae*—give off median branches which join mid-dorsally in the characteristic *mid-dorsal cervical anastomosis*. From the dorsal anastomosis there arise two tracheae which pass to the ‘brain’, composed of the supra-oesophageal ganglia and sub-oesophageal ganglion. This anastomosis and the cervical tracheae are not mentioned or are incompletely figured for *Calliphora* (Lowne, 1900), *Musca* (Hewitt, 1914), *Metoponia*—Stratiomyidae—(Irwin-Smith, 1923), *Haematopota* (Cameron, 1933), and *Tabanus* (Stammer, 1924), although they are almost certainly present in each of these genera.

In all of the described species the *ventral ganglionic tracheae* tracheate the thoracic and abdominal elements of the central nervous system. Typically, they arise from the lateral longitudinal trunks and each has a characteristic
position of origin. The tracheae to the pro-thoracic ganglion differ from the remainder of the ganglionic tracheae in arising from the ventral cervical tracheae; those passing to the meso-thoracic ganglion arise from the lateral trunks half-way between the first and second pairs of spiracles; those to the meta-thoracic and all abdominal ganglia arise from the lateral trunks in the region between consecutive pairs of spiracles. A remarkable feature is that the tracheae passing to the thoracic ganglia give rise to mid-ventral anastomoses. These are recorded in very few accounts given by other workers, although they have been observed in all the species described in this paper, and in numerous other species investigated by the writer; not one cyclorrhaphan or brachyceran has been found in which they are absent. The ganglionic tracheae are imperfectly represented and the ventral anastomoses are not described in most accounts, including those of Hewitt (1914), Imms (1942), de Meijere (1901), Ruhle (1932), Cameron (1933), Stammer (1924), and Irwin-Smith (1923). They are probably present though unobserved or unmentioned in the species described by these authors. The present condition in which the thoracic tracheae only form ventral anastomoses is possibly derived from an ancestral condition in which abdominal ganglionic tracheae also possess them.

The dorsal cervical anastomosis and the ventral ganglionic tracheae are constant in their origin and in the distribution of their tracheae. They do, however, vary considerably in their position. At first sight their position in the Cyclorrhapha would appear to be characteristic and diagnostic of this sub-order, being very different from the condition in the majority of Nematocera. However, the systems of the species described above show that the position is governed solely by the form of the central nervous system, which in the nematoceran species described here is in the form of distinct ganglia extending the length of the larva, but in the Cyclorrhapha is concentrated into a mass lying in the post-thoracic and anterior abdominal region. The present writer has observed both in certain of the brachyceran families such as the Leptidae—where the central nervous system may attain a nematoceran form—and in others, such as Tabanidae and Stratiomyidae—where it is concentrated—that the ganglia remain distinct and a single pair of ventral ganglionic tracheae tracheate each ganglion. In the Cyclorrhapha in which external evidence of segmentation in the nerve mass has disappeared, the segmentally arranged ganglionic tracheae are the only remaining external indication of the fundamentally segmented nature of the nervous system. The ‘brain’ can be seen to lie inside the head capsule in Trichocera, Scatopse, and Dilophus, just outside in Psychoda and Anisophas, and situated in the posterior thoracic region in Aphiochaeta, Calliphora, and all Cyclorrhapha; in general the position of the dorsal cervical anastomosis is correspondingly displaced.

It seems probable that the generalized tracheal pattern given at the beginning of this paper approaches that of the ancestral larval dipteran pattern, and it should thus possibly prove of interest in the phylogenetic relationships of the order, especially if a similar type of pattern should be discovered for other
insect orders. Improvement on Lehmann's (1925) deductions on the form of the insect tracheal system could follow only after each order of insects is thoroughly investigated. Only by first tracing the evolution of the tracheal system within each order can any fruitful attempt be made at tracing the relationships of the system within the class as a whole.

The fact that the main tracheal elements are identical in number and origin in certain nematoceran families, in the Brachycera seen to date, and in the Cyclorrhapha, is remarkable and is a positive reply to the question of the stability of the system, for the tracheal pattern composed of the main elements has remained unchanged in spite of the wide diversity of larval habits, ranging from purely terrestrial forms to wholly aquatic types. Furthermore, this consistency is maintained while, among the same species, considerable variation occurs in the condition of the spiracles.

The tracheal system is therefore seen to have remained remarkably unaltered in an order in which considerable variation has occurred in other characters. The larval head capsule and the male genitalia (Crampton, 1942), both external characters, have been used as systematic characters in tracing phylogenetic relationships within the Diptera. It is therefore conceivable that where variations in the tracheal systems are found to occur this system may also prove to be a useful systematic character. The tracheal system would appear to have a certain advantage over these other characters in being internal, and therefore less influenced by external conditions.

One example of the stability of the tracheal system may be illustrated by the 'rat tailed' larva of Eristalis tenax. The larva is strikingly adapted to live in water several inches deep, breathing by means of its last pair of spiracles which are situated at the extreme tip of a very long retractile syphon. If the tracheal system is unstable it might be expected that such a remarkably adapted larva, whose relatives are terrestrial, would have a correspondingly highly modified internal tracheal system. On the other hand, the same organs have to be supplied with tracheae in aquatic and terrestrial forms. Details taken from Gäbler's (1930) description of the larval system of this species show that, in actual fact, no great modification has taken place, and the main tracheae are identical with those of the general tracheal pattern given here for the whole of the order. Critical examination of the figures given by Gäbler makes it clear that the only modification lies in the enormous elongation of the tenth spiracular tracheae.

It is hoped that the general tracheal pattern which has been deduced will prove valuable in further studies and also in examining the descriptions of other workers. An example of the possibilities in this respect can be illustrated by taking Cameron's (1933) work on Haematopota pluvialis. He described in some detail the larval tracheal system of this species although no mention is made of the branches tracheating the nervous system. He compares the system with that of Tabanus species, described by Stammer (1924). The anterior ends of both larvae contain numerous tracheae whose relationship is described by him as being difficult to interpret. The figures and lettering of
Cameron and Stammer are reproduced here (fig. 9). Cameron concludes his comparison thus:

"... the distribution of the non-segmental branches 1-6, 8 and 9 at the anterior end of the longitudinal trunk is not easily traceable. ... identity of the branches has been established in all save two instances—7 and 9, and there are differences regarding the distribution of certain of the branches. ... Stammer and I both agree that there are eight branches in the complex. ... I have failed to trace his branch 7—a cross commissure joining the two tracheal trunks. ... to an elongated branch distributed to the muscles at the anterior end of the head capsule, which was not mentioned by Stammer, I have assigned number 9. This branch is joined to its fellow by a cross commissure in segment II. Branch 9 which was not observed by Stammer probably represents the inner branch of segment II. It is joined to its fellow and in this
respect resembles the remaining members of the series of inner branches except those of segments III and IV already noticed. . . ."

It would appear that element 7 of Stammer—'a cross commissure'—is in fact the first dorsal anastomosis as also is Cameron's element 9, which he says was not observed by Stammer. The position of the elements may vary, although the origin and distribution remain constant. The nine pairs of inner branches correspond to dorsal anastomoses two to ten, so that with element 7 or 9 there are present, in all, tracheae corresponding to the ten dorsal anastomoses, and not nine as suggested by Cameron. The second and third do not join, but the component tracheae are present. Element 8 is undoubtedly the dorsal cervical anastomosis, the difference in the form of this in Haematotopota and Tabanus possibly being a generic one: in both cases it gives rise to branches which pass to the supra-oesophageal ganglia. In order to interpret elements 3, 4, 5, and 6 it would be necessary to reinvestigate the material as too little information is given on the distribution of these elements. Almost certainly dorsal cervical, ventral cervical, and ventral ganglionic tracheal elements are present.

**CONCLUSION**

The impression gained from a study of the larvae discussed in this paper is that the Cyclorrhapha diverge very little from the generalized larval pattern. Further work is required on the systems of brachyceran species before any generalizations can be made: the scanty evidence at present available suggests that species from the few families studied also diverge little from the generalized larval pattern. This is not so in the remaining families of the Nematocera. In a future paper descriptions will be given of the tracheal systems present in representatives of these nematoceran families, and it will be shown that even these more anomalous systems can be interpreted in the light of the results given in the present paper.

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