

THE HOMOLOGIES OF THE TRACHEAL BRANCHES IN THE RESPIRATORY SYSTEM OF INSECTS

CLARENCE HAMILTON KENNEDY

Department of Zoology and Entomology, Ohio State University

The following study of the tracheation of the Zygoptera was undertaken to determine the homologies of the tracheal branches that supply parts of the genitalia of the second and third segments of the male. This full investigation will eventually appear in one of the government publications but the study brought to light points of so much greater importance that a discussion of these was given at the Toronto Meetings of which this article is the outline.

Grassi* has shown the probability that the insect tracheal system was originally a series of disconnected segmental systems which later fused into a connected whole.

Chapman† has homologized the main thoracic tracheæ which form the main air supply of the wings in the various orders of insects, and has shown us that the tracheal system can be homologized but so far no attempt has been made to refer these back to the more generalized (?) plan found in the tracheation of the abdominal segments. In the majority of the general morphological works on insects the tracheal system is described as being composed of certain longitudinal trunks with various accessory parts in the way of spiracles, air sacs, cross-connections, etc. This is true, but these are not descriptions which take into consideration the origin and homologies of the individual parts of the tracheal system.

The Zygopterous naiad, among the nymphs, of all winged insects, appears to have the abdominal segments least modified from a probable primitive condition. Its abdomen is cylindrical, therefore no parts are displaced or lost by depression. Its gills are at the apex of the abdomen, therefore their position does not modify any but the caudal parts of the system. The abdomen is elongate so that each segment can be studied individually.

* Atti dell' Accad. Gioenia d. Sci. Nat. Catania (3) T. XIX. 1885.

† In "Wings of Insects," Comstock, pp. 27-51.

The nymph of *Lestes*, which furnished the material for this study, is so abundant and so transparent that little dissection was needed.

In this article the writer will outline the homologies of the principal thoracic tracheal branches as referred back to the simpler system of an individual abdominal segment. The terms used are descriptive as far as possible and were worked out with the help of Dr. Chapman with the hope that we had terms that would be useful in future tracheal studies.

If the reader will refer to the plate he will see in Fig. 1 the simplest tracheal unit in abdominal segment 2. It is repeated in segments 3-7. Segments 1 and 8-10 have more or less modified versions of this same unit. In the thorax the tracheal branches are yet more highly modified. The diagram Fig. 3, shows what the writer considers as the hypothetical primitive unit from which the present system with its longitudinal trunks has been developed.

The studies of the primitive tracheal systems in *Peripatus* and in the embryology of the insectean tracheal system show that the spiracles develop first as pits. From the bases of these pits the tracheal branches develop. Our unit starts then with (1) the *spiracle*, sp., extending into the body wall, (2) is the *spiracular* pit, spp. From the bottom of this there develops dorsad a short stout branch, (3) the *spiracular trunk*, spt. This trunk forks and sends a branch, (4) the *anterior dorsal connective*, adc. to the muscles of the anterior end of the segment, and a branch (5) the *posterior dorsal connective*, pdc. to the posterior muscles of the dorsum of the segment. Each of these has a branched tip supplying its group of muscles, (6) (7) the *tip* of the *anterior dorsal connective*, tadc, and the *tip* of the *posterior dorsal connective*, tpdcc. These tips become landmarks later in the study.

The *spiracular pit* sends out three other branches, (8) the *anterior spiracular connective*, asc, which connects forward to the leg trachea and which gives off a small branch to the body wall, (9) the *posterior latero-tergal trachea*, plt. Opposite to this (8) is given off a larger trachea, (10) the *leg trachea*, lt, which runs caudad and ventrad. It gives off first, (11) the *anterior latero-tergal trachea*, alt, to the body wall, then (12) the *pleural trachea*, pt, to the pleural fold. Ventrad the spiracular pit gives

off a slender branch direct to the ganglion of the segment (13) the *ganglionic trachea*, gt. This has a tip which runs along the sternum caudad from the ganglion, (14) *the sternal trachea*, st.

As this hypothetical unit is derived from the tracheal system as it appears in the less modified abdominal segments these terms are directly applicable to the parts in Fig. 1. In this figure it will be seen that the anterior and posterior dorsal connective have united as they alternate along the dorsum into a large dorsal trunk. In *Lestes* it is especially large as it functions with its mate of the opposite side, as a swim bladder, while along it at regular intervals are the *tips* of the *anterior and posterior* dorsal connectives.

In the front end of the abdomen the ganglions of segments 1 and 2 have each moved cephalad one segment. In each case the *ganglionic trachea* has followed its ganglion cephalad. The ganglion of segment 1 fuses with that of the metathorax but the elements of the tracheal supply are still recognizable. See Fig. 2, which is a ventral view of the thorax.

In each segment the *anterior spiracular connective* has fused with the *leg trachea* next ahead so that in the abdomen there is a delicate but complete lateral trunk. In the thorax a pair of ventral or sternal trunks appear by the fusion of the *sternal tracheæ* with each succeeding *ganglionic trachea*. This fusion is not completed in the abdomen. See Fig. 2.

In the thorax but two spiracles persist, the mesothoracic and the metathoracic. Of the prothoracic spiracle, some of the tracheal branches are present which would be expected with it but the spiracle itself has left no recognizable trace. The tracheal system of the metathorax is least modified. Here the spiracular trunk is still fully developed. In the mesothorax the spiracle has moved dorsad until the *spiracular trunk*, st, has been obliterated. It is also entirely lost for the prothorax.

The modification of the thorax due to the development of the wings has profoundly changed the proportions of the other thoracic branches also. In a later paper the writer will trace this change from the first instar where it is very similar to the abdominal tracheal system through its development to the extreme modification shown in Fig. 1 which is a tenth instar naiad.

The wings start as simple pleural folds no wise different from those of the abdomen. By the fourth instar those of the

thorax have moved dorsad and those of the mesothorax and metathorax have begun to take on the place and shape of wing pads. The simple *pleural trachea*, pt, tracheates them in the beginning and follows them as they pass from the lateral to their final dorsal position. The *pleural trachea* is the anterior or costal wing supply and is the original wing supply as this development shows. As the wing folds (later, pads) pass dorsad they pass the *tips* of an *anterior* and a *posterior dorsal connectives* in each segment and take on connections with these. Also the anal apex of each wing trachea (*pleural trachea*) connects also with the *anterior latero-tergal trachea* of the succeeding segment. Thus each wing in *Lestes* has four tracheal connections.

Several puzzling shifts and specializations have taken place. In segment 1 the leg branch is lost and the *anterior spiracular connective* has shifted from the spiracle down onto the *ganglionic trachea*. This has occurred also in the second and third thoracic segments so that the *posterior latero-tergal trachea* in each case has shifted to arise from near the spiracle.

In the metathorax the *metathoracic tip* of the *posterior dorsal connective* has shifted down onto the vertical *spiracular trunk*. This conclusion is arrived at by elimination of the other *tips*. This solution homologizes the tracheation of the hind wing with the tracheation of the front wing.

In the thorax the *ganglionic trachea* have shifted down onto the *leg trachea* in each segment, and in each segment a second or *accessory ganglionic trachea*, agt, has appeared.

The shortening of the *spiracular trunk* in the mesothorax has pulled the *leg trachea* of the prothorax out of shape and has greatly shortened the *anterior spiracular connective* of the mesothoracic spiracle so that the lateral trunk becomes a second dorsal trunk in the insect's neck.

This work in tracheation is very much confused by malformations and adventitious branches. Frequently there are two or even three *anterior* or *posterior latero-tergal trachea*, sometimes two *pleural trachea*, etc. One has to examine enough specimens that these abnormalities are recognized as such and no longer confuse. This readiness of the tracheal system to develop new branches has been one of the things which has made homologization of the branches seem a hopeless task.

The tracheation of the internal organs seems to be largely fortuitous except for two large trachea that run from the

metathoracic spiracular trunks to the region of the gut just back of the gizzard and two others that run from the *spiracular trunks* in abdominal segment 8 to the region of the intestine just back of the malpighian tubules. The tracheation of the head is very definite but so far has not been homologized with the parts of the system in the thorax and abdomen unless the tracheæ of the labium can be homologized with *leg tracheæ*.

This study supports the theory that the wings are developed from pleural folds as this feature can be positively homologized from the larval pleural fold stage to the adult winged stage.

The only other order the writer has examined is the Plecoptera. Here the tracheal system is greatly distorted by the thoracic gills and the depressed body. A pair of neural trunks are formed in the abdomen by the fusion of the *sternal tracheæ*. A lateral abdominal trunk is well developed which is probably homologous with the lateral trunk of the Zygoptera though this may be found to be homologous with the dorsal trunk of the Zygoptera. The thoracic trachea are less changed.

The writer believes that this reference of the tracheal branches back to those in a generalized abdominal segment will give a solution to the homologies of the tracheal systems in the various orders of insects. He hopes soon to carry the study farther.

EXPLANATION OF PLATE.

- Fig. 1. Lateral view of *Lestes* naiad, male, showing the homologies of the somatic tracheal branches.
- Fig. 2. Ventral view of *Lestes* naiad.
- Fig. 3. Hypothetical, primitive segmental tracheal organs. By the fusion of a series of such the *Lestes* trachial system may have been developed.

LIST OF ABBREVIATIONS USED IN THE ILLUSTRATIONS.

- sp.—spiracle.
spp.—spiracular pit.
spt.—spiracular trunk.
st.—sternal trachea.
dt.—dorsal trunk.
latt.—lateral trunk.
vt.—ventral trunk.
lt.—leg trachea.
pt.—pleural trachea.
gt.—ganglionic trachea.
agt.—accessory ganglionic trachea.
asc.—anterior spiracular connective.
adc.—anterior dorsal connective.
pdc.—posterior dorsal connective.
alt.—anterior latero-tergal trachea.
plt.—posterior latero-tergal trachea.
tadc.—tip of anterior dorsal connective.
tpdc.—tip of posterior dorsal connective.

