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THE RESPIRATORY SYSTEM OF MALLOPHAGA.

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Exhibition of 1851 Research Scholar of the University of Sydney.

(*From the Quick Laboratory, University of Cambridge.*)

(With 21 Text-figures.)

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INTRODUCTORY.

THE respiratory system in Mallophaga has not hitherto been described in detail. Kellogg (1896, p. 45) gives the disposition of the main trunks in *Tetrophthalmus*, together with a figure; Snodgrass (1899, p. 170) adds nothing to Kellogg's account; Fulmek (1907) dismisses the tracheal system with a paragraph; Shipley (1909) gives a detailed figure for *Goniodes tetraonis* which is neither complete nor altogether exact; and Mjöberg (1910), although devoting several pages of his morphological section to the respiratory system, is chiefly concerned with the occluding apparatus of the stigmata. He does, however, figure the main trunks in *Eutrichophilus*, and the occluding apparatus in *Gyropus ovalis*; and makes certain general statements which may be summarised as follows:

There are two main tracheal trunks, united behind by a bow-shaped transverse branch. Prothoracic stigmata have only been demonstrated in the Gyropidae, the Trichodectidae, and *Tetrophthalmus*. The abdominal stigmata are dorsal, and mostly in segments 2–7.

The value of this, the most recent statement of the tracheal condition in Mallophaga, may be gauged from the facts that I set out in detail below, namely that the two main trunks are only exceptionally united by a posterior transverse commissure; that prothoracic stigmata are universally present; and that the abdominal stigmata are in almost the whole of one sub-order found upon segments 3–8, that in at least one case they are all ventral, and that in two genera there are but five pairs in place of the usual six.

Possibly the difficulty of satisfactorily demonstrating the tracheal system has been the reason for the somewhat cursory treatment it has received. By the employment of suitable methods, however, I find that it is possible to trace the tracheal supply in great detail. As a superficial examination disclosed certain fundamental differences in the number and arrangement of the stigmata, and in the disposition of the tracheal trunks, I have thought it worth while to investigate the whole respiratory system as fully as the material available to me has allowed.

METHOD OF EXAMINATION.

Living material is essential if the best results are to be obtained. In some forms, where the main trunks are of fairly considerable size, and the taenidia of sufficient strength to resist collapse on treatment with reagents, specimens cleared in potash and mounted into balsam show the more important trunks and branches. *Heterodoxus*, *Tetrophthalmus*, and *Docophoroides* give good results with this treatment. I have seen some preparations of Mr B. F. Cummings in which acid fuchsin has been employed after potash with fair success. But for most genera, and for detail in any of them, live material is desirable. If the living insect be killed and dehydrated by immersion in absolute alcohol for about ten minutes, and then cleared and mounted, the tracheal tubes remain filled with air, and are very easily followed. Such a preparation is, however, not permanent, as balsam gradually replaces the air; but it will usually keep in good condition for several days. A still better method is to put the living insect direct into dilute glycerine under a coverslip, as the glycerine infiltrates the tracheae at a much slower rate, and has sufficient clearing action to render the smaller branches easily visible. Such a preparation will remain in good condition for several weeks. With pale forms, and with newly moulted individuals of darker species, good results may be obtained by examining the living insect under the pressure of a small cover-slip, without any mounting medium. *Menacanthus pallidulus* of the domestic fowl is a favourable species for examination in this way.

In addition to these methods for examination of the whole insect, I have made use of both dissections and serial sections in studying the stigmata, and the latter have also been used to verify certain other points, and for minute structure.

TRACHEAL SYSTEM OF *MYRSIDEA CUCULLARIS.*

As a basis for the comparisons which will follow, I give a detailed account of the distribution of tracheae in *Myrsidea cucullaris.* Figure 1 shows their general disposition in an immature individual of the second instar. The only difference between this stage and the adult is that in the latter the minor branches are more numerous, and their ramifications wider. The alimentary canal is indicated in light stippling, which has been varied sufficiently to differentiate the several regions.

It will be seen that the tracheae are disposed in two main longitudinal trunks; and that they open upon the surface by seven pairs of stigmata, one in the prothorax, and six in the abdomen. The prothoracic stigmata are ventral, behind the middle of the segment, at the junction of the lateral flange with the thicker median portion. The six pairs of abdominal spiracles pierce the pleura of segments 3–8, the first five pairs being dorsal, the sixth ventro-lateral.

The main trunks are not straight, but are bent outwards to form a sharp angle opposite each stigma, the two being connected by an irregularly sinuous stigmatic branch. Similar branches occur in the first and second abdominal segments, but end blindly. They evidently represent the stigmatic branches of these segments, the spiracles themselves having disappeared. On entering the thorax the main trunks converge on either side of the crop, then diverge sharply to the prothoracic stigmata. The trunks coming from the head meet those of the thorax and abdomen at a little distance from these stigmata, and the two sets are connected by short cross-pieces so as to form a complete triangle on either side. The tracheae forming these triangles are the largest in the body. The main trunks on entering the head diverge about the sides of the brain, coming together a little at the sides of the tentorium which is here present, and are continued forwards into the dorsal part of the frons, where they break up into many fine

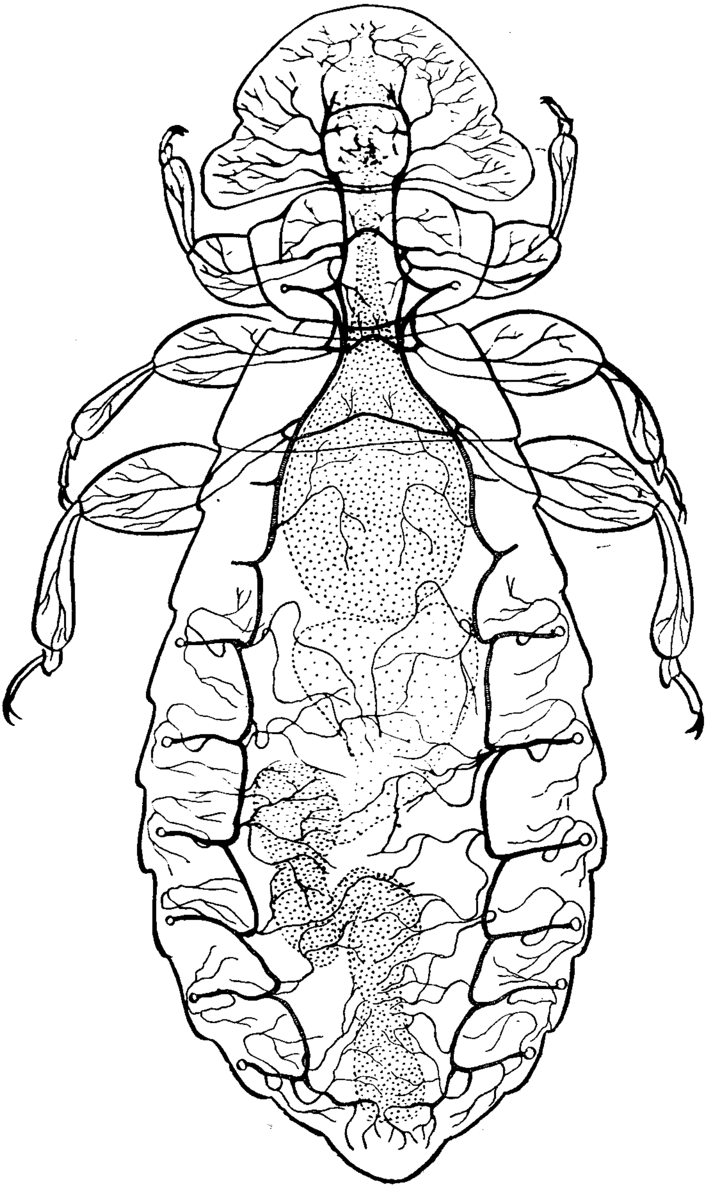


Fig. 1. Tracheal system of *Myrsidea cucullaris*.

twigs among the muscles. Similarly at the hind end of the abdomen the main trunks continue backwards beyond the last stigmatic branch, and break up into fine twigs dorsal to the rectum.

The tracheal branches of the head have the general arrangement shown in the figure. The most posterior pair of branches comes ventrally from the main trunks in the anterior part of the prothorax, and the branch of each side turns outwards and breaks up among the temporal muscles, both dorsal and ventral. Just within the head, small branches are given off internally to the oesophagus. Two large branches on either side run out to the lateral regions of the head. At the level of the anterior cornua of the brain each main trunk divides into dorsal and ventral branches. The dorsal gives off an internal branch which serves the pharynx and brain; and is continued forwards to the dorsal region of the forehead. The ventral gives off an internal branch which meets its fellow of the opposite side to form a commissure running along the anterior margin of the tentorium; and runs forwards and downwards itself to be distributed to the mouth-parts. Part of the internal dorsal branch of either side passes up through the gap between the cornua of the brain, dividing into two, so that four vessels run longitudinally backwards closely applied to the brain, giving off smaller branches which ramify over the surface.

In the prothorax a triangle is formed internal to each stigma, as already stated. The main trunks here lie nearer the dorsal than the ventral surface, and in front of the triangles a commissure descends ventrally so as to underlie the prothoracic ganglion, which is innervated by small branches from it, and gives off two branches to each prothoracic leg. The mesothoracic commissure comes off from the outer sides of the triangles, passing downwards and backwards, and exhibiting precisely the same relations towards the mesothoracic ganglion and legs. The metathoracic commissure lies at the back of the segment, passing below the crop, and innervates the corresponding ganglion and legs. I can find no indication whatever of the survival of any remnant of wing tracheae, unless the inner sides of the triangles can be looked upon as such. Nor is there any indication of stigmata, or of stigmatic branches, in either meso- or metathorax.

Metameric arrangement of the tracheae, which was not obvious in the head and fairly well marked in the thorax, becomes much more definite in the abdomen. The typical constituents on each side of any segment are (*a*) the portion of the longitudinal trunk contained within the segment; (*b*) the stigmatic branch; (*c*) the ventral branch; (*d*) the dorsal branch. A separate visceral element is not present. In the first and second segments the stigmatic branches are short, and end blindly, there being no corresponding stigmata. In the following six segments the typical arrangement is developed. The ventral branches arise in every case from the stigmatic branches, run towards the lateral margin of the abdomen, and turn ventrally, dividing into two main branches which are of much greater extent in the adult than in the young form figured. The dorsal branches arise from the main trunks in front of the corresponding stigmatic branches. These dorsal and ventral branches become greatly divided, and are distributed to all the body organs in an abundance of smaller branches, those of opposite sides freely mingling and crossing, but there is no anastomosis as far as visible branches are concerned, though a capillary anastomosis may be present.

General Account—Introductory.

For purposes of comparison I have examined species of the following genera:

Amblycera.	Ischnocera.
Ancistrona	*Akidoproctus*
Boopia	*Austrogoniodes*
Colpocephalum	*Degeeriella*
Eomenopon	*Docophoroides*
Eureum	*Giebelia*
Gliricola	*Goniocotes*
Gyropus	*Goniodes*
Heterodoxus	*Heteroproctus*
Laemobothrium	*Lipeurus*
Latumcephalum	*Nesiotinus*
Machaerilaemus	*Ornithobius*
Menacanthus	*Oxylipeurus*
Menopon	*Pectinopygus*
Myrsidea	*Philopterus*
Nitzschia	*Physconella*
Pseudomenopon	*Pseudonirmus*
Ricinus	*Psittaconirmus*
Somaphantus	*Rallicola*
Tetrophthalmus	*Trabeculus*
Trimenopon	*Trichodectes*
Trinoton	

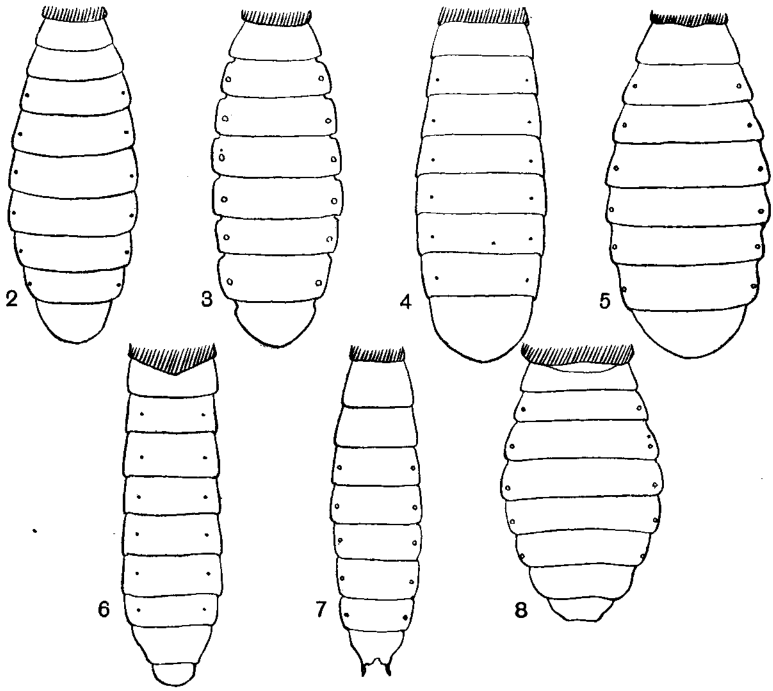
For opportunity to examine specimens of *Nitzschia*, *Trimenopon*, *Eureum*, *Physconella*, and *Nesiotinus* I am indebted to Messrs Gahan and Cummings of the Entomological Department, Natural History

Museum. Living material has, however, not been available in the majority of cases, but the forms which have been examined in detail show such a remarkable constancy in their tracheal arrangement that nothing of any great interest and importance is likely to result from further detailed comparisons. These forms include species of *Gliricola*, *Gyropus*, *Heterodoxus*, *Menopon*, *Menacanthus*, *Myrsidea*, *Ricinus*, *Degeeriella*, *Goniodes*, *Goniocotes*, *Lipeurus*, and *Philopterus*. The genera which I have not been able to examine are *Damalinia*, *Eutrichophilus*, *Trichophilopterus*, *Eurytrichodectes*, *Philoceanus*, *Kelloggia*, *Ornicholax*, *Bothriometopus*, *Trochiloecetes* and *Philandesia*. Of these the first four will certainly not differ very much from *Trichodectes*; the fifth, sixth and seventh, and eighth from other Giebeliidae, Goniodidae and Akidoproctidae respectively; and the ninth from *Ricinus*. *Philandesia* may prove on examination to present some features of interest, but it is the only distinctive genus excluded from my examination.

The generalisations which I shall proceed to make as to the number and disposition of the stigmata and main tracheal vessels are based, then, on observations of species belonging to forty-one genera in a total of fifty-one. The ten not examined are in the majority of cases monotypic; in seven cases only recent cleavages from larger genera with which they show a very close agreement; and number less than twenty species in a total of close upon two thousand.

THE STIGMATA.

In all Mallophaga except *Gliricola* and possibly *Trimenopon* there are seven pairs of stigmata, one prothoracic and six abdominal. *Gliricola* has but five pairs of abdominal stigmata. I have been able to examine only mounted specimens of *Trimenopon*, and in these I have not succeeded in demonstrating the existence of a sixth abdominal pair. I also find one species of *Trichodectes*, *T. divaricatus*, Neumann, with only five pairs of stigmata apparently present. I do not know of any other exception to this general statement, which, although several morphological accounts of the Mallophaga have been published, has not been made before. All that Snodgrass (1899, p. 170) says about the stigmata is: "Spiracles are situated laterally on the dorsal side of the abdominal segments, and *in some species*, as *Menopon titan*, there is a spiracle on each side of the prothorax." The italics are mine. Mjöberg (1910), as already stated, only demonstrated prothoracic stigmata in a few genera. Shipley (1909, p. 316) mentions that the prothoracic stigmata are difficult to see. It may be noted in passing that Kellogg (1903, p. 90) allows only five pairs of abdominal stigmata to *Nesiotinus*, but this is an error, as I have satisfied myself by personal examination, the six pairs being present in the usual position. (With the still more extraordinary error which has been made in describing the thorax of this insect I am not here concerned.)



Figs. 2–8. Abdomen, to show stigmata, of: (2) *Menopon*; (3) *Heterodoxus*; (4) *Ricinus*; (5) *Gyropus*; (6) *Lipeurus*; (7) *Gliricola*; (8) *Trimenopon*.

The abdominal stigmata are, with the exceptions mentioned above, constantly twelve in number. Their disposition differs in the two sub-orders. In the Amblycera (Fig. 2), with the exception of the Boopidae (including *Boopia*, *Heterodoxus*, and *Latumcephalum*) (Fig. 3), the Ricinidae (including *Ricinus* and *Trochiloecetes*) (Fig. 4), and *Gyropus* (Fig. 5), the abdominal stigmata open upon the third to the eighth segments. In the two families mentioned, in *Gyropus*, and in the whole of the Ischnocera (Fig. 6), the stigmata open upon the second to the seventh segments. In *Gliricola* (Fig. 7) and *Trimenopon* (Fig. 8), segments three to seven carry the spiracles; but in the latter, though the first pair is reckoned as occurring on the third segment, the first segment is so much incorporated with the thorax that only a small portion of the tergum, which does not reach to the sides of the abdomen, remains. In the Boopidae there is also a suggestion of the inclusion of an abdominal segment with the thorax, as a sternite quite distinct from that of the metathorax is visible on the under side, for which there is no corresponding tergum on the dorsal surface. It is reasonable to conclude that the same cause operates in the case of both Ricinidae and the ISCHNOCERA, and that the difference in stigmatal arrangement is due to the suppression of the first abdominal segment, or its incorporation with the thorax. This condition is strongly suggested in *Trichodectes*. The segments in front of those which bear the stigmata usually show

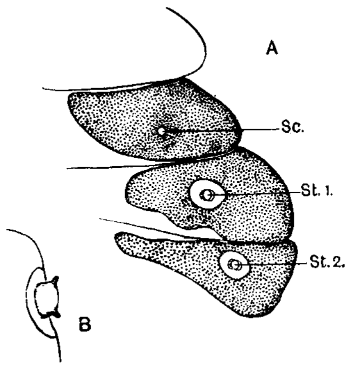


Fig. 9. *Philopterus brevicollis*; (*A*) Part of first three abdominal segments to show stigmata and stigmatal scar; (*B*) sixth abdominal stigma in profile.

small scars in the position which the spiracles would have had (Fig. 9), and indicate that the Mallophaga, or their ancestors, originally had two additional pairs of abdominal stigmata.

The abdominal stigmata open indifferently through terga, or pleura, or the softer integument separating the two. They are almost invariably dorsal, and usually perforate the terga in the ISCHNOCERA; but in the AMBLYCERA the more posterior tend to become lateral, or even ventral. In *Gliricola* all are ventral, piercing the pleura. In many species, more especially of ISCHNOCERA, each is surrounded by a clear pustule (Fig. 9). In others, as, for example, *Goniodes* and *Trinoton*, heavy pleural or tergal incrassations surround the stigmata. They are all alike in form, an external circular or ellipsoidal opening leading into a larger vestibule which in turn opens into a second chamber, or bulla, the latter receiving the narrow end of the stigmatic trachea.

The external aperture is usually circular, sometimes ellipsoid, in which case the long axis is usually transverse, or slightly oblique. Its size varies considerably, as the following table of measurements shows. Where the aperture is not circular, the longer axis has been measured.

DIAMETER OF ABDOMINAL SPIRACLES IN MILLIMETRES.

Lipeurus circumfasciatus	0·006	*Oxylipeurus sinuatus*	0·014
Giebelia hexakon	0·008	*Trabeculus heteracanthus*	0·014
Trichodectes appendiculatus	0·011	*Gyropus ovalis*	0·015
Goniodes curvicornis	0·011	*Lipeurus crassus*	0·015
Lipeurus mutabilis	0·011	*Ornithobius fuscus*	0·017
Lipeurus diversus	0·011	*Heteroproctus hilli*	0·017
Degeeriella cingulata	0·011	*Docophoroides brevis*	0·017
Rallicola bisetosa	0·011	*Pseudomenopon tridens*	0·017
Aptericola gadowi	0·012	*Trichodectes setosus*	0·028
Goniocotes fissus	0·012	*Lipeurus ferox*	0·033
Philopterus occidentalis	0·012	*Heterodoxus longitarsus*	0·039
Gliricola gracilis	0·013	*Philopterus brevicollis*	0·039
Latumcephalum macropus	0·014	*Tetrophthalmus titan*	0·047
Lipeurus asymmetricus	0·014	*Laemobothrium circi*	0·055

A study of this table shows that, in general, the stigmatic apertures of the ISCHNOCERA are considerably smaller than those of the AMBLYCERA. The exceptions which stand out prominently are *Trichodectes setosus*, which, in common with most species of the genus, possesses large stigmata; and *Philopterus brevicollis*, which belongs to a small group characterised, amongst other things, by the size of the stigmata. But it is not until after eight Ischnoceran genera are listed that the first Amblycera appear, and these are *Latumcephalum* and *Gliricola*, both very small forms. *Laemobothrium* caps the list, but in proportion to its size has small stigmata. The same may be said of *Ricinus*. Forms found upon mammals have, in both sub-orders, larger stigmata than those found upon birds. Seen in profile (Fig. 9, B) the stigma exhibits a rigid rim standing up from the general surface. The external opening is never protected by hairs, though in *Tetrophthalmus* (Fig. 10) certain bristles occur in close proximity.

The prothoracic stigmata differ, as a rule, in their larger size, and in having the actual external aperture slit-like rather than circular or ellipsoid. Several forms are shown in Figs. 11, 12, 13, 14. They are situated ventrally upon the prothorax, close to the postero-lateral angle in the ISCHNOCERA; and posteriorly where the wing joins the body in the AMBLYCERA. The Akidoproctidae and some species of *Trichodectes* have these stigmata lateral.

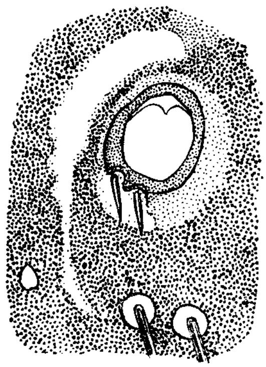
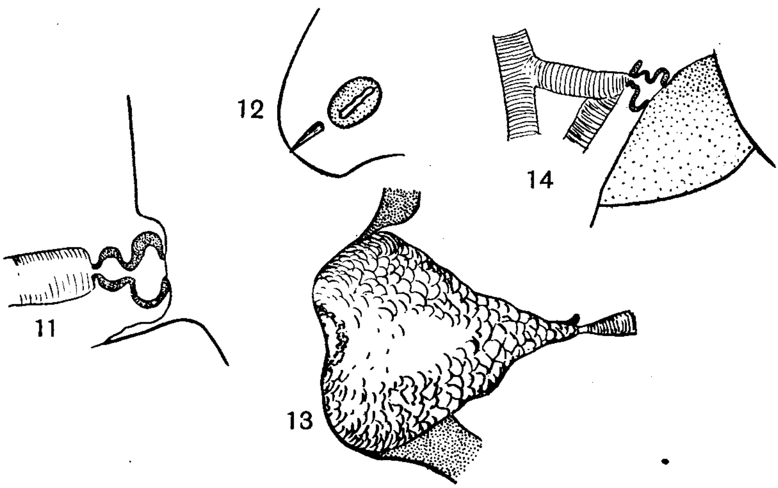


Fig. 10. Abdominal spiracle of *Tetrophthalmus titan.*



Figs. 11–14. Prothoracic stigmata of: (11) *Heteroproctus hilli*; (12) *Aptericola gadowi*; (13) *Trichodectes setosus*; (14) *Heterodoxus longitarsus* (11, 13, and 14 in optical section).

The vestibule, which lies below the external aperture, is very variable in shape and sculpture. The commonest form has the shape of a somewhat flattened sphere, sunk below the surface, with which it is continuous at the margin of the external aperture. Sometimes, as in *Tetrophthalmus*, the chamber projects above the surface as a hemispherical protuberance, on the summit of which is the spiracle. In *Gyropus* it has somewhat the shape of a kettledrum, the rim of which is flush with the surface, and the centre of the flat surface pierced by the spiracle. In *Trichodectes* the arrangement at the surface is the same, but the rim is thickened and sculptured, and the chamber the shape of an elongate cone. The prothoracic vestibules are often remarkably different from those of the abdomen. In *Trimenopon* a very long cylindrical vestibule with reticular pattern on its thick chitinous wall connects the external opening with the bulla. In *Trichodectes setosus* (Fig. 13) the vestibule is enormously enlarged, with scaly sculpture. Contrary to what is the case with the abdominal stigmata, the prothoracic vestibule is proportionately larger in the Ischnocera than in the Amblycera, as the following diametric measurements show.

MEASUREMENTS IN MILLIMETRES OF PROTHORACIC VESTIBULES.

Trichodectes setosus	0·075	*Goniodes curvicornis*	0·019
Heteroproctus hilli	0·039	*Gliricola gracilis*	0·019
Lipeurus asymmetricus	0·033	*Heterodoxus longitarsus*	0·019
Ornithobius fuscus	0·030	*Lipeurus fasciatus*	0·017
Aptericola gadowi	0·028	*Pseudomenopon tridens*	0·017
Docophoroides brevis	0·028	*Trabeculus heteracanthus*	0·014
Goniocotes gigas	0·028	*Latumcephalum macropus*	0·014
Oxylipeurus sinuatus	0·025	*Rallicola bisetosa*	0·013
Philopterus occidentalis	0·019	*Giebelia hexakon*	0·013

The sculpture of the vestibule differs considerably in different forms. A common type in the ISCHNOCERA is that in which the whole inner chitinous surface is raised into parallel ridges. In other genera the sculpture is reticulate, or scaly, the scales in some cases being so small and elongate as to look like hairs. This sculpture probably serves to hinder dust particles from entering the tracheae.

The term *bulla* I employ for what is usually a distinct chamber internal to the vestibule, which gives support to the occluding apparatus, and with which the stigmatic branch of the trachea actually connects. In some forms, e.g. *Heterodoxus*, there is little distinction between vestibule and bulla; in others, as *Trichodectes*, the bulla is reduced to a narrow chitinous tube. The precise relations of these parts will be seen in Figs. 16, 18 and 19.

The occluding apparatus has received attention only from Mjöberg. He has published (1910, p. 221) a diagrammatic figure of this apparatus in *Gyropus ovalis*, showing a chitinous tab resting upon an extremely narrow tracheal neck, and having attached to it distally a muscle, the other insertion of which is not indicated beyond a vague statement that it runs to the integument. Similar figures are given for various Anoplura. Mjöberg points out (*l.c.* p. 222) that his observations are confined to the AMBLYCERA, the opaque integument hindering them in the ISCHNOCERA. I was for some time at a loss to reconcile Mjöberg's statement and figure with my own observations in sections of Ischnoceran forms, or to understand exactly how occlusion was brought about. His figure affords no apparent fulcrum for the leverage exerted by the

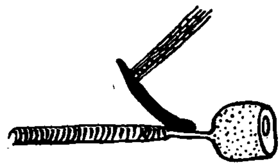


Fig. 15. Occluding apparatus of *Gyropus ovalis*, after Mjöberg.

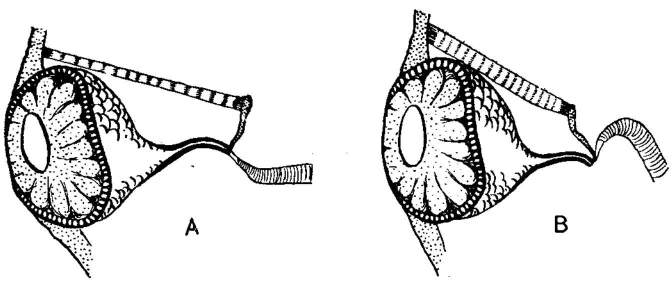


Fig. 16. Stigma and occluding apparatus of *Trichodectes longicornis*, semi-diagrammatic; (*A*) open; (*B*) closed.

tab. After some difficulties, due to the small size of the structures involved, and the very serious hindrance to the cutting of good sections which the thickness of the chitinous cuticle presents, I have succeeded in demonstrating at least two types of occluding apparatus, a simple and a more complex; with possibly some intermediate forms, but on these my observations are not complete.

The simple type is that figured by Mjöberg for *Gyropus ovalis*. I give his version in Fig. 15. Fig. 16 gives a diagrammatic view of the stigmatic apparatus open and closed in a species of *Trichodectes*. It will be seen that a long narrow rigidly chitinous bulla follows the wider vestibule, the inner narrow end of which is directly continuous with the extremely narrow initial portion of the stigmatic trachea. This inner end serves as a fulcrum for the closing lever, which in the open position stands at right angles to the trachea, closely apposed to the bulla. From the distal end of this tab a muscle runs to be inserted into the integument alongside the vestibular rim. On contraction of

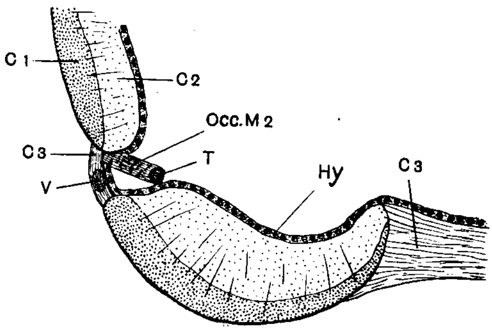


Fig. 17. Part of first of two consecutive sections through an abdominal stigma of *Philopterus bisignatus.*

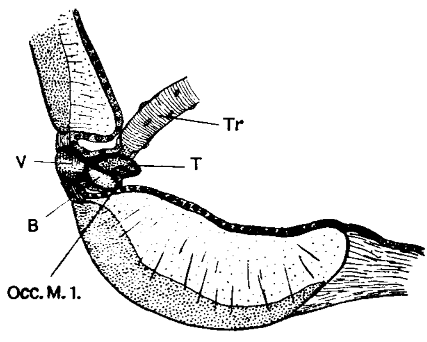


Fig. 18. Part of second of two consecutive sections through an abdominal stigma of *Philopterus bisignatus.*

this occluding muscle the tab is revolved through an angle of about 45°, and kinks the elastic trachea against the rigid inner end of the bulla, thus effectually cutting off the air. This form is best observed in the abdominal stigmata of *Trichodectes* and *Gyropus*, the prothoracic stigmata being more complex.

The second type is illustrated in Figs. 17 and 18, which represent a part of two successive transverse sections through the abdomen of

Philopterus bisignatus. Fig. 17 passes just in front of a stigmatic orifice. It will be seen that the pustulose area round the stigma is composed of a thin laminate cuticle (*C* 3) differing in structure from, and many times less thick than, the chitin immediately surrounding it. The latter is homogeneous, the outer part (*C* 1) deeply coloured, the inner (*C* 2) translucent. Within the pustulose area the section has just sliced the edge of the vestibule (*V*). It will be noticed that the hypodermis (*Hy*) is pushed out into a cylindrical pocket under the stigma. The apex of the chitinous tab (*T*) has been cut off by the section, and running from it to be inserted into the body wall on the inner circumference of the pustulose area is the *extrinsic occlusor muscle* (*Occ. M* 2). The next section (Fig. 18; the figure is slightly schematised, and shows more of the bulla than actually appears in the section) shows the continuation of the chitinous tab (*T*), which rests upon the heavily chitinised walls of both vestibule and bulla. The heavy framework shown on the upper side of the vestibule (*V*) is continued round the bulla (*B*) on the side opposite the tab. A short intrinsic muscle (*Occ. M* 1) runs from the tab to be inserted into this framework, which may be looked upon as the closing bow.

The actual closing of the trachea is brought about at the junction between the bulla and the narrow initial part of the stigmatic trachea. By the simultaneous contraction of both extrinsic and intrinsic occlusors the tab is rotated inwards and forwards so that the knob-like process on its proximal surface (which apparently represents the closing piece of the typical apparatus) is brought directly over the narrow tracheal channel, and is depressed so that the thin elastic dorsal wall is closely apposed to the more heavily chitinous ventral wall. This seems to me the most reasonable explanation of the observed facts; but they are, of course, capable of other interpretation. I assume that the trachea reopens of its own elasticity when the muscles are relaxed. It may be that occlusion is completely brought about by the intrinsic muscle, and that the extrinsic muscle reopens by exerting a leverage on the tab against the fulcrum afforded by the opposite end of the closing bow.

This type seems to be common to all ISCHNOCERA, and is, I believe, present in the same or a slightly modified form in many AMBLYCERA. An intermediate type seems to be present in *Heterodoxus* (Fig. 19), the figure being drawn from a potash-cleared mount; but I have been unable either by dissection or by the examination of several series of sections to convince myself as to the relations of the occluding muscle or muscles.

An examination of the literature concerning the occluding apparatus shows that the subject is still in a state of considerable confusion. Mjöberg (1910, p. 220) figures the occluding apparatus of *Phthirus pubis* (Anoplura) after Landois (1864), with a single extrinsic occlusor muscle; and gives original figures (*l.c.*, p. 221) of the same apparatus in *Haematopinus suis* (Anoplura) and *Gyropus ovalis* on the same plan. But Krancher (1881) had already figured *Haematopinus suis* with an intrinsic muscle only. Solowiow (1909), whose work I have only seen in summarised form, criticises the results of both Landois and Krancher; and finds, in lepidopterous forms, a third muscle present, the so-called *musculus Versoni* first indicated by Verson in *Bombyx mori*. This muscle I do not find in either Mallophaga or Anoplura. The remaining

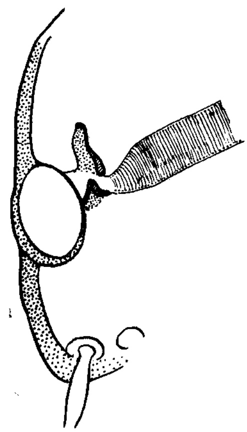


Fig. 19. Abdominal stigma of *Heterodoxus longitarsus* in optical section.

two, the *musculus constrictor* and *musculus tendinosus*, have somewhat similar relations to those which I describe, but I refrain from actually homologising them. Landois and Thelen (1867) figure an orthopterous stigma with an intrinsic occlusor, and with a second muscle arising from the point at which this is inserted into the closing bow, the other insertion not being given. This structure does not in any way resemble the arrangement found in Mallophaga. Finally Mammen (1912), after a detailed description of the stigmata in Heteroptera and Homoptera, summarises insect stigmata into four groups, according as they possess one extrinsic, one intrinsic, two, or three muscles concerned in closing the trachea. The simple type of Mallophagan apparatus would fall into the second division of his first group, that in which a single muscle passes from lever to integument; where it would find itself in company with *Geocores*, and the Homoptera. The more complex type, on the other hand, would be placed in the second division of his third group, forms with an extrinsic and an intrinsic muscle, including *Periplaneta* and *Chrysopa*. In the absence of sufficient data for sound comparative statement, the occluding apparatus in Mallophaga cannot at present be said to help towards establishing the affinities of the group.

THE TRACHEAE.

In all forms the main trunks are two in number, and run the full length of the insect, one on either side of the body, from head to hind abdomen. Usually each of these trunks lies about a fifth of the body width from the lateral margin, but in most Goniodidae and Trichodectidae they are much nearer to the mid-line. They may have the appearance of a series of loops between the abdominal stigmata, as in most AMBLYCERA; or they may form straight trunks as in *Tetrophthalmus*, *Heterodoxus*, and most Philopteridae and Lipeuridae. They vary considerably in diameter, as the following table shows.

GREATEST DIAMETER, IN MILLIMETRES, OF TRACHEAL TRUNKS.

Gliricola gracilis	0·005	*Lipeurus crassus*	0·011
Degeeriella cingulata	0·006	*Goniocotes gigas*	0·011
Philopterus occidentalis	0·006	*Trichodectes setosus*	0·014
Goniocotes fissus	0·007	*Docophoroides brevis*	0·017
Lipeurus absitus	0·007	*Lipeurus ferox*	0·030
Gyropus ovalis	0·008	*Heterodoxus longitarsus*	0·039
Aptericola gadowi	0·008	*Laemobothrium circi*	0·069
Lipeurus mutabilis	0·010	*Tetrophthalmus titan*	0·119

The most remarkable feature the table shows is the large size of the trunks in *Heterodoxus* and *Tetrophthalmus*. *Heterodoxus*, in common with other Boopidae, has large stigmata and tracheae, very like those of the Anoplura; and the main trunks are continuous as a posterior commissure, a characteristically Anopluran feature. This resemblance will be discussed further below. With regard to *Tetrophthalmus*, the enormous tracheae are probably a direct adaptation to the habits of the insect, which frequents the gular pouch of pelicans, where it must often be submerged for considerable periods while the host is feeding. Other than these enlarged trunks in *Tetrophthalmus*, no tracheal dilatations or air-sacs occur in any form which I have examined.

The posterior commissure described above for *Heterodoxus* is also present in *Trimenopon, Nesiotinus*, and some species of *Trichodectes*; and is figured by Mjöberg (1910, p. 218) for *Eutrichophilus*. It may be present in *Trichodectes setosus*, which Neumann (1913, p. 623) claims to be identical with Mjöberg's species of *Eutrichophilus*, but I have not been able to make it out in ordinary preparations. It is of the same diameter as the main trunks, thus differing from the neural commissures, which are distinctly narrower. Its presence in so many genera that otherwise exhibit primitive characters, as well as its universal occurrence in the Anoplura, leads me to look upon it as a primitive character also. It is not found in the more specialised genera.

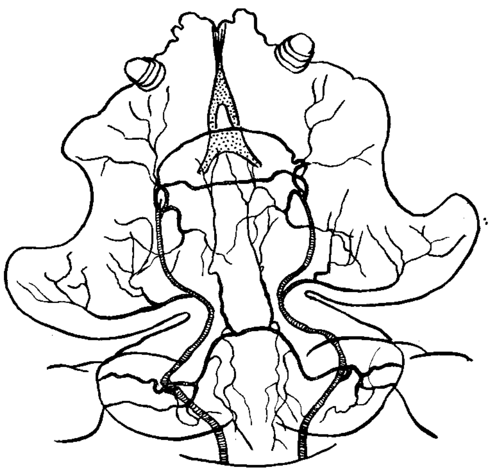


Fig. 20. Prothorax and head of *Gyropus ovalis*, to show superficial ventral tracheae.

Tetrophthalmus is remarkable for having a broad commissure in the fourth segment; but this is not worth stressing, as it is probably directly connected with the very extraordinary change in habit of the species of the genus.

In all species of which I have examined fresh material, I find a great constancy in the arrangement of the whole tracheal system. The four neural commissures are always present; as are the prothoracic triangles; and the chief variations are only in detail of the dorsal and ventral system of branches. *Gyropus* and *Gliricola* have alone afforded exceptions. Fig. 20 shows the ventral superficial tracheae of *G. ovalis*, from which it will be seen that there are two head commissures, and that two long branches run forwards from the prothoracic commissure into the head, extending beyond the brain. *Gliricola* also has two head commissures.

All parts of the body are profusely supplied with tracheal branches, which ramify through the fat-body and muscles, are thickly applied to the alimentary canal throughout its length, and to the internal genitalia, and which are especially abundant about the nerve ganglia. I cannot find in sections any trace of tracheal tubes actually entering into the ganglia, but they are closely and thickly applied to the whole surface. Fig. 21 is a *camera* drawing of the ventral surface of the metathoracic

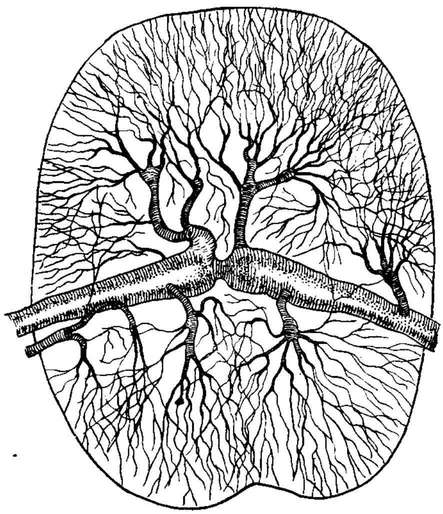


Fig. 21. Ventral view of metathoracic ganglion of *Goniodes piageti*, to show tracheal supply.

ganglion of *Goniodes piageti*, showing the neural commissure lying across it, and the extraordinary number of branches applied to the surface. These are not so numerous on the other ganglia, so I conclude that the metabolism must be more active here, as the ganglion innervates about three-quarters of the body, while the remaining quarter has four ganglia at its service.

The minute structure of the tracheal tubes agrees with that of insects in general. Each consists of a chitinous lining secreted by a cellular layer which is continuous with the reflected hypodermis. The nuclei of this layer can be seen (Fig. 18, *Tr*) easily enough, but I cannot make out any cell boundaries, and the membrane is of a thickness hardly measurable except where a nucleus occurs. In specimens that have been heated in potash till the soft parts were destroyed, and dehydrated in glacial acetic acid, the latter causes the taenidia to swell and burst the chitinous lining. They then tend to uncoil, and their arrangement may be observed. I have noticed in a dissected preparation of *Docophoroides* that the main trunk is composed, not of a single thread wound spirally, but of a band of five. The taenidia are continuous throughout several complete turns, but it is easy to observe their tapering ends in the larger forms.

I have made no mention of the mechanism of respiration, as I have not made any direct observations upon it. The usual dorsiventral depressor muscles exist, and it is probable that air is expelled from the tracheal system by the contraction of these, and re-enters on their relaxation.

Comparative Notes and Theoretical Considerations.

I have made some comparison of the respiratory system of Mallophaga with that of the Anoplura and the wingless Copeognatha, the two groups with which a gradually accumulating body of evidence indicates their close affinity. Mjöberg (1910, p. 222) has already pointed out the general agreement between Mallophaga and Anoplura. The latter have fourteen pairs of stigmata in all the forms I have examined. Of these the thoracic stigmata usually overlie the mesothoracic legs, but are often situated between the two anterior pairs. In any case the imperfectly divided thorax of the lice prevents much significance being attached to this difference, if difference it be. The abdominal stigmata are typically on segments 3–8, though in some cases reduction of the first segment makes it appear that the first abdominal spiracles open upon the second and not the third segment. The structure of the stigmata closely corresponds with that of the simpler Mallophagan type. The tracheal vessels show the same general distribution in two main trunks, with stigmatic branches, thoracic triangles, a posterior commissure, and in some cases at least (e.g. *Haematopinus equi* and *Polyplax*) with neural commissures anteriorly. This agreement is so strong that it is difficult to believe it can have any other cause than common derivation.

With regard to the Psocids, I have examined some undetermined wingless Atropidae, and find a broad agreement, though details differ.

There are seven pairs of stigmata, one thoracic, and six abdominal. Here again the reduction of the anterior segments of the abdomen is very marked. Two very short first segments each have well-marked stigmatic branches, but no stigmata, the latter lying, as in both the previous groups, typically in segments 3–8. The general arrangement of the main tracheal trunks, stigmatic branches and dorsal and ventral supply is on a similar plan to that of the Mallophaga; though the stigmatic branches usually form a plexus of two or three vessels with numerous anastomoses, in place of a single branch, and there are other differences in detail.

This brief statement is enough to justify the conclusion that the respiratory system in Mallophaga, Anoplura, and Copeognatha, exhibits a remarkable correspondence. In all three groups there are one pair of thoracic and six pairs of abdominal stigmata, the latter typically on segments 3–8. In all three groups there is evidence, in the shape of vestigial stigmatic branches, of the existence in past time of two additional pairs of abdominal stigmata; and in all three groups there is evidence pointing to the total or partial suppression of one or two of the anterior abdominal segments.

The comparative literature on the number and position of insect stigmata is not sufficiently definite to allow of any positive statement as to affinity indicated by this common possession of the three groups mentioned above. But I consider the relationship of Mallophaga and Anoplura to be definitely established; and as the latter are still usually included among the Hemiptera on account of their sucking mouthparts, and as we have a definite pronouncement on the number and position of the stigmata in this order, it may be useful to emphasise the essential difference between Hemiptera and Anoplura in this regard. Handlirsch (1899) gives the stigmata in Hemiptera as ten pairs, two thoracic on the two posterior segments, and eight abdominal on the first eight segments. He expressly points out that the Anoplura do not conform to this type. In his own words: "Nur die durche ihre eminent parasitische Lebensweise stark modifizierte, vollkommen flügellose Gruppe der Pediculiden (excl. Mallophaga) weicht stärker von dem Grundtypus ab indem bei ihr ausser den zwei ersten abdominalen Stigmenpaaren auch jenes des Metathorax verschwunden ist." As no reason is advanced to connect specialisation following on a parasitic mode of life with an alteration in the number and position of the stigmata which, though it may possess morphological significance, can make little practical difference to the respiration of the group, it seems more reasonable to conclude that this divergence implies a separate origin.

Packard (1874) gives the primitive number of spiracles in winged insects as twelve pairs. Neglecting the Anoplura and Copeognatha, although they are pretty certainly entitled to the same interpretation, it will be seen that seven of these survive in most Mallophaga, the posterior two pairs of the thorax and the anterior two pairs of the abdomen having disappeared, with, presumably, that of the ninth abdominal segment. This allows a generalisation which should be of frequent use in determining the number and disposition of the abdominal segments in Mallophaga, namely that the sixth pair of abdominal spiracles occurs on what is morphologically the eighth segment, though in the Boopidae, Ricinidae, and *Gyropus* of the AMBLYCERA, and in the whole of the ISCHNOCERA, this segment is apparently the seventh. Again certain post-embryonic stages in both ISCHNOCERA and AMBLYCERA show ten apparent abdominal segments, which become reduced to an apparent nine in the adult. In particular species of *Lipeurus* from petrels illustrate this condition. Kellogg (1896) has described as species two forms which he calls *L. diversus* and *L. limitatus*. The former has nine segments, the latter ten. But the latter is the young of the former. Similarly Taschenberg (1882) has described *L. fuliginosus* with nine segments, and *L. testaceus* with ten. The latter is not, in this case, the young of the former, but is the immature form of a species of the same type, for which the name will stand. In these, as in other examples that might be quoted, the last ecdysis changes the three terminal segments of the abdomen into an apparent two. The segments in question come after the last which bears spiracles, so we can thus state that the maximum number of segments in the abdomen of Mallophaga is eleven, though this number is not found in any adult. This statement, of course, involves the assumption that an anterior segment of the abdomen in the ISCHNOCERA has become incorporated with the thorax, or suppressed. We may assume this by analogy with what has been pointed out for the AMBLYCERA above; but, in addition, the condition in *Trichodectes* offers very strong support. In *T. longicornis*, for example, I find interpolated between metathorax and first abdominal tergite a rudimentary tergite which does not reach the lateral margins, but which bears a transverse band bordered posteriorly by a row of six hairs. In *T. divaricatus* a similar rudimentary tergite is very surely present, but is uncoloured and without hairs. In *T. setosus*, on the other hand, there is no trace of this tergite.

TAXONOMIC VALUE.

The general constancy of the respiratory system in Mallophaga seems to me a good argument for allowing a fair amount of importance to such differences as occur. The points on which I lay stress are primarily the number of pairs of stigmata in the abdomen, together with their distribution on the abdominal segments; and, in the second place, the presence or absence of a posterior commissure. This commissure when present is equal in calibre to the main trunks, and justifies the description of those forms which possess it as having a single continuous tracheal trunk, rather than two separate sub-parallel trunks.

On the basis of the respiratory system, the AMBLYCERA fall into seven groups:

A. With five pairs of abdominal stigmata (3–7) and a posterior commissure	*Trimenopon* (*Philandesia ?*)
B. With six pairs of abdominal stigmata (2–7) and a posterior commissure .	Fam. Boopidae
C. With five pairs of abdominal stigmata (3–7), no posterior commissure, and two head commissures . . .	*Gliricola*
D. With six pairs of abdominal stigmata (2–7), no posterior commissure, and two head commissures . .	Fam. Gyropidae (excl. *Gliricola*)
E. With six pairs of abdominal stigmata (2–7) and only the usual four neural commissures . . .	Fam. Ricinidae
F. With six pairs of abdominal stigmata (3–8) and only the usual four neural commissures	Fams. Menoponidae, Laemobothriidae, Ancistronidae
G. With six pairs of abdominal stigmata (3–8), the usual four neural commissures, and a transverse commissure in the fourth segment .	*Tetrophthalmus*

Of these Group A is undoubtedly of family rank, *Trimenopon* occupying a very isolated position. It shows a superficial resemblance to the Boopidae, but is without the accessory sac in the ♂ genitalia and the special sensory organs of the first three abdominal segments which characterise that family. In addition it exhibits a fusion of prothorax and mesothorax, a condition not seen elsewhere in the Mallophaga. *Trimenopon* must rank as the type genus of a family Trimenoponidae. *Philandesia*, which I have not had an opportunity to examine, probably belongs here also.

Group B has already been accorded family rank by Mjöberg (1910) on an examination of one species of *Boopia*. After examining a considerable number of species of *Boopia* and *Heterodoxus*, and two of *Latumcephalum*, I agree that the Boopidae hold a very distinct position.

Groups C and D, despite the difference in number of the stigmata, I leave for the present in the family Gyropidae, which was established by Kellogg (1896). But this difference further justifies Mjöberg (1910) in establishing a separate genus for *G. gracilis*; though this separation has not, apparently, been recognised by some later writers (Neumann, 1912; Kellogg and Nakayama, 1914). I have not handled sufficient material of this family to venture any interference; but I think it will possibly be found that there is less uniformity among the species than is commonly supposed.

Group E has already been accorded family rank by Mjöberg (1910) under the name of Physostomidae. As Neumann (1906) has pointed out that *Physostomum*, Nitzsch is a synonym of *Ricinus*, de Geer; and Johnston and myself (1911) that the family name Ricinidae must replace that of Liotheidae; it follows that this family, though now limited to two genera, must retain the name Ricinidae.

Group F includes most of the remaining AMBLYCERA. Mjöberg (1910) has established two families, Menoponidae, including a number of genera, and Laemobothriidae with a single genus. Of those genera not specifically mentioned by Mjöberg probably all may safely remain in the family Menoponidae with the exception of *Ancistrona*, which, on the structure of the lateral region of the head and antennary fossa, is quite as distinct as *Laemobothrium*, and is certainly entitled to family rank. There will thus be three families in the group, Menoponidae, Laemobothriidae, and Ancistronidae, towards the separation of which the respiratory system gives no help.

Finally Group G includes the single genus *Tetrophthalmus*, and is only distinguished from the last by the transverse commissure of the fourth segment. In view of the enormous development of the tracheal trunks in connection with a change of habit such as we have not previously had to take into account, this is best looked upon as a correlated adaptation. The presence of combs upon femora and abdomen shows that the affinities of the genus lie with *Colpocephalum* rather than with *Menopon*, with which it was for so long associated; but the genus may remain in the Menoponidae.

Turning to the ISCHNOCERA, we find the stigmata are uniform throughout the group, and the only difference of any importance is the occurrence of the posterior commissure in *Nesiotinus* and some species of *Trichodectes*.

Kellogg (1903) has already pointed to the fact that *Nesiotinus* possesses both Ischnoceran and Amblyceran characters. The additional evidence afforded by the primitive tracheal arrangement indicates that it must certainly be looked upon as a very primitive Ischnoceran form; and also that it must, as I have previously suggested (1915, p. 384), form the type genus of a family Nesiotinidae.

The Trichodectidae require further examination. Stobbe (1913, 1913*a*) has recently revised the family, and established two new genera, but on the same somewhat superficial grounds that have proved such a stumbling-block to a proper understanding of Mallophaga in the past. From the variations I have noticed in some twenty species which I have had under my eyes, variations which include the presence or absence of a vestigial segment in front of the abdomen, and of a posterior commissure; the possession of three, four, or five antennal joints; the presence, in one species at least, of only five pairs of abdominal stigmata; and the very variable structure of the hind-abdomen and ♂ genitalia, I am convinced that this apparently homogeneous group is capable of being split up upon sound lines, and that a comparative study of the tracheal and stigmatal arrangement will considerably assist such division. Such a task must, however, be left to some worker with a far more considerable material at his disposal than is available to me.

The remaining six families of the ISCHNOCERA (Lipeuridae, Docophoroididae, Goniodidae, Philopteridae, Giebeliidae, Akidoproctidae) show such uniformity in their tracheal systems that nothing of help in taxonomy can be gained from a study of the respiratory apparatus.

CONCLUSIONS.

The results of this study may be briefly summarised as follows:

The tracheal system of Mallophaga is disposed in two main trunks, with stigmatic, dorsal, and ventral branches, with four narrow commissures (*neural commissures*) in connection with the main nerve masses, and with, in primitive forms, a posterior abdominal commissure.

The stigmata are typically fourteen in number, one pair prothoracic, and six pairs abdominal, usually dorsal, typically on segments 3–8. At least two types of occluding apparatus are present.

In the structure and relations of the respiratory system the Mallophaga agree very closely with the Anoplura, and also, in a more general way, with the wingless Copeognatha.

As the respiratory system is very uniform, such variations as do occur have some taxonomic importance, and have served to emphasise some divisions already made, and to establish new divisions.

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THE RESPIRATORY SYSTEM OF MALLOPHAGA

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