On some Points in the Anatomy of the Mouth-parts of the Mallophaga. By Bruce F. Cummings *

(Text-figures 24–32.)

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The Mallophaga are for the most part such small parasites that the dissection of the mandibulate mouth is often a matter of considerable difficulty. It seems scarcely surprising, therefore, that a good deal of misunderstanding has arisen in regard to the mouth-parts, and in the literature which deals with this subject a variety of opinion will be found on such questions as the palpi, the esophageal sclerite, and so on.

The Palpi of the Ischnocera.

In a paper in the P.Z.S. 1909 (1), appear figures and descriptions of the Ischnoceran species Goniodes tetraonis Denny, from the Grouse, in which a pair of very minute one-jointed appendages is shown to exist on the labium below the paraglossae. In G. falcicornis N., I can find no trace of these minute appendages, which perhaps represent the palpi of the second maxilla. In the same place, the second maxillae of G. tetraonis are described as rounded with certain setæ or hairs, whence it appears that in this species they are less degenerate than in the other Ischnocera so far examined, where the second maxillæ are usually obsolete, flat lobes without palpi, thinly chitinized (or not chitinized at all), and situated within the mouth-cavity behind the mandibles. From the figures of both G. tetraonis and another Nirmus cameronus N. they are omitted, and instead, the paraglossæ of the labium are labelled first maxillæ and the minute appendages second maxillæ.

The Palpi of the Amblycera.

The other suborder, the Amblycera, is distinguished by the presence of a pair of jointed palpi absent from the Ischnocera. The view of Nitzsch, who first considered them in 1818 (2), may at length be considered as sound, namely, that they belong to the first maxilla and not to the labium. Grosse (1885) (3) assigned

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them to the labium. Snodgrass (1896) (4) followed suit, but in 1905 (5) retracted in favour of Nitzschia, as the result of examining preparations of Ancistroma gigas P. and Lœmobothrium gypsis Kell., in which the stipes of the palpus was seen to be separate from the labium. C. O. Waterhouse (1904) (6) had already illustrated the fact that in L. titan P., the palpus was connected with the maxilla by a delicate band of connective chitin. I have discovered similar slips not only in L. titan, but in Ancistroma procellaris Westwood (text-fig. 25, p. 132) and in Nitzschia pulicaris N.

The Œsophageal Sclerite and Lingual Glands.

These structures are unique in the comparative anatomy of the insect mouth. They occur in their typical form in the Ischnocera. In the other suborder it is customary to say that they are either modified or absent, but, as I show below, they are really present in all the Amblycera with the possible exception of Lataneophalium, which was not available for examination. The œsophageal sclerite and glands in the Mallophaga were first discovered by Snodgrass (4). They are unusually difficult of dissection in the Amblycera on account of their delicacy and minuteness and their position below the œsophagus, having regard to the flatness of the head in the Mallophaga as a whole.

The sclerite in the Ischnocera is of a densely chitinous character, usually quite visible through the integument lying in the lower wall of the œsophagus behind the labium. There are two anterior cornua and sometimes a posterior pair, but these are absent in L. ferox G. (text-fig. 24, p. 131). Lying longitudinally in the dorsal wall of the œsophagus immediately above the sclerite, I find in Goniodes falcicornis and in Lipeurus ferox a long, narrow chitinous splint. Towards this, the posterior cornua in G. falcicornis curl up the sides of the œsophagus.

The lingual glands are hard, flat, oval pieces of chitin in which no glandular structure can be detected, though they still await histological examination. In L. ferox and G. falcicornis, if not in most other Ischnocera, the anterior ends of the two glands are encompassed by a small compound plate of chitin (text-fig. 24, E), narrowing towards the edge of the labium. A curious duct, cross-barred like a trachea, arises from the sclerite and runs forward, where it bifurcates, one ramus (or "bronchus") entering each of the glands. My own dissections lead me to agree with Mjöberg (1910) (7) and Grosse (3), who regard the "glands" as chitinous and as part of the sclerite, the whole to be regarded as a compound hypopharynx*. Normally the hypopharynx lies

* A central canal is almost certainly present in the ducts of some, but its meaning remains problematical, unless we suppose that a kind of chitinous sclerosis has overtaken real glands and ducts, until finally, in such genera as Ancistroma and Trinopta (text-figs. 26 & 29), the original structures have become obliterated and replaced by chitin.
immediately above the labium in front of the mouth and not below the oesophagus, and on this account Snodgrass gives the term hypopharynx only to certain setose lobes he found in *Laemobothrium gypsis* which actually overlies the labium. A similar arrangement of lobes is seen in *L. titan*, where, as the anterior area of the hypopharynx, they are in close relation with the sclerite and "glands"—the elaborate posterior area. The Ischnocera possess an anterior area—the true hypopharynx of Snodgrass—in the small encompassing plate mentioned above, which is much reduced in correspondence with the fact that in the Ischnocera the whole labium has been shifted backwards so as to leave the large mandibles a free field. In some genera of the Amblycera such as *Boopia* or *Heterodoxus* the anterior area, in which, as in *Laemobothrium*, the "ducts" are incorporated, is so large as to extend not only as far as above the labium but even beyond it as two lobes protruding from the mouth (cf. Mjöberg (7), p. 22). The two areas run into each other without any dividing line.

**Varieties of Sclerite and Glands.**

I shall now discuss the various forms the hypopharynx assumes in the different genera of the Amblycera. Modification begins with *Laemobothrium* (see diagram, text-fig. 25, p. 132), in which the sclerite is elongated and the anterior cornua very long, extending almost up to the bifurcation of the "ducts." The "glands" are less developed. The posterior cornua are present. In *Gyropus* the main "nucleus" of the sclerite has disappeared, the anterior cornua are fused at the base, and the posterior cornua are longer and the "glands" very much reduced. In *Trinoton*, the "glands" as such have quite disappeared, but may here be represented by the lateral pieces, the bifurcating sclerite being the broadened "duct."* The anterior cornua are entirely fused together. In *Ancistrona procellaria* the anterior cornua are quite distinct but adpressed closely against the broad rami; each of the rami bears in front a rounded plate with a strongly serrate edge corresponding with the anterior area of the hypopharynx. The diagram is intended to show the probable evolution of the structure in the Ischnocera and Amblycera.

The presence of oesophageal sclerite and "glands" in the Psocidea as well as in the Malloplaga points to the antiquity of the structures. Several features in the anatomy of the Psocidea

* In *Dochrophorus sphenophorus* (text-fig. 27), an Ischnoceran, the ducts are so minute and delicate as to suggest atrophy. In front, they are accompanied and supported by a forked piece of chitin, and in other species and genera the duct is clearly seen to be accompanied along its course by chitin, so that in those forms where the ducts qua ducts are absent their former course along the bottom of the pharynx may be traced in the track of persisting chitin which they leave behind. It is this forked piece of chitin, rather than the duct itself perhaps, which is homologous with the bifurcating sclerite in *Trinoton* (text-fig. 29, B) and other genera.
and Mallophaga indicate their affinity, and a plausible theory has been suggested that the latter are Psocids which have undertaken a parasitic existence. In any case the "glands" and sclerite must be regarded as part either of their Psocid or pre-Psocid inheritance, so that the typical oesophageal sclerite and "glands" of the Ischnocera are older than the modifications

Text-fig. 24.

Hypopharynx and lingual glands of Lipurus ferox, × 186.
A, oesophageal sclerite; B, anterior cornu; C, duct; D, gland; E, anterior compound plate.

described in the Amblycera, in spite of the fact that the Amblycera by the possession of jointed palpi, by the form of the alimentary canal, by the position of the mouth-parts which have not shifted backwards, and in several other respects appear to be the less specialised of the two suborders.
Diagram to illustrate the evolution of the hypopharynx.

1. Ligeurus. 2. Lamobothrium. 3. Hypothetical. 4. Acantho...

A, edge of labium; B, anterior compound plate; C, osophageal sclerite; E, ramus; F, "glands" or lateral pieces; G, anterior corn...
### Distribution of the Sclerite and "Glands."

A revised list of the distribution of the sclerite and "glands" in the Mallophaga must now stand:

<table>
<thead>
<tr>
<th>Genera with sclerite and glands more or less typically developed</th>
<th>Genera with sclerite and glands modified</th>
<th>Genera with sclerite and glands absent</th>
<th>Genera with sclerite and glands present or absent</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Ischnocera.</strong></td>
<td><strong>Amblycera.</strong></td>
<td><strong>Ischnocera.</strong></td>
<td><strong>Dochophorus?</strong></td>
</tr>
<tr>
<td>Goniodes,</td>
<td>Boopia,</td>
<td>Ornithobius?</td>
<td>Lipeurus?</td>
</tr>
<tr>
<td>Goniocetes,</td>
<td>Nitzschiia,</td>
<td>Akidoproctus?</td>
<td>Menopon?</td>
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<tr>
<td>Onchophorus,</td>
<td>Heterodoxus,</td>
<td></td>
<td>Nirmus?</td>
</tr>
<tr>
<td>Trichodeetes,</td>
<td>Trinoton,</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Eutrichophillus,</td>
<td>†Trimenopon,</td>
<td></td>
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<tr>
<td>Eurymetopus,</td>
<td>Ancistriona,</td>
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<tr>
<td>Giebelia,</td>
<td>Latuncephalum?</td>
<td></td>
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<tr>
<td>*Ornicholax,</td>
<td>Gliricola?</td>
<td></td>
<td></td>
</tr>
<tr>
<td>*Kelloggia,</td>
<td></td>
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</tr>
<tr>
<td><strong>Amblycera.</strong></td>
<td><strong>Ischnocera.</strong></td>
<td><strong>Amblycera.</strong></td>
<td></td>
</tr>
<tr>
<td>Colpocephalum,</td>
<td>Dopchohorus</td>
<td>Eureum?</td>
<td></td>
</tr>
<tr>
<td>Laemodiothrium,</td>
<td>sphenophorus,</td>
<td></td>
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<tr>
<td>Physostomum,</td>
<td>Tetroptalmus,</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Gyropus,</td>
<td>Pseudomenopon,</td>
<td></td>
<td></td>
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</tbody>
</table>

All the species examined of *Nirmus*, *Menopon*, *Lipeurus*, and *Dochophorus* in the collection of the British Museum possess sclerite and glands. Snodgrass records them as absent from *N. signatus*, *L. picturatus*, and *L. longipilus*, *D. icterodes*, and the following species of *Menopon*—*distinctum, mallensis, persignatum, precursor, rediculosa, robustum, titan*, and *tridens*. The sclerite and glands are certainly present in *titan* and in *tridens*, though they are considerably modified and require careful dissection. They are described below. From a summary inspection of *Dochophorus sphenophorus* N. the structures appeared to be absent, but here again on dissection I found them present in a modified form (text-fig. 27, p. 135).

### Descriptions of Special Cases.

*Ancistriona procollarice* Westwood (from *Procollaria caepensis*).—The hypopharynx was incorrectly described and figured by Westwood (1874) (8) as a rod bifurcating in front. The lateral pieces (text-fig. 26, D) were omitted. In all probability the

* The typical sclerite and glands where they occur are plainly visible through the integument, and, according to figures of these two genera, are present in them. When modified, the sclerite and glands cannot be discovered without dissection, and this, perhaps, accounts for the third column being so long in the list given by Snodgrass.

† Gen. nov, about to be described in the Bulletin for Entomological Research.
lateral pieces became detached while the preparation was being made, as they are very delicately connected. Snodgrass in his account of *A. gigas*, a closely allied species, does not mention any lateral pieces, figures the hypopharynx as a bifurcated rod and calls it the epipharynx. But the presence of "maxillary forks" is recorded in *A. gigas*, and these I have been unable to find in *A. procellariae*. If they are absent, it might very well be that Snodgrass has mistaken the detached lateral pieces for maxillary forks. They are alike in shape. The maxillae are attached to the lateral pieces (text-fig. 26, E).

Text-fig. 26.


A, esophageal sclerite; B, ramus; C, anterior hypopharyngeal plate; D, lateral piece; E, 1st maxilla.

*Dochophorus sphenophorus* N. (from *Platalea leucorodia*).—This species presents an interesting transition between the glands and sclerite typical of the Ischnocera and the conditions found in the
Text-fig. 27.

Hypopharynx of *Doclrophorus sphenophorus*, × 300.

A, oesophageal sclerite; B, duct; C, bilid sclerite; D, lateral piece; E, anterior cornu; F, posterior cornu.

Text-fig. 28.

Hypopharynx of *Tetrophthalmus titan*, × 204.

A, oesophageal sclerite; B, the two rami; C, lateral piece; D, posterior cornu; E, maxillary fork.
Amblyceran genera *Trinoton*, *Aneistrona*, etc. The glands are almost completely transformed into lateral pieces (text-fig. 27, D), but may still be represented by an indistinct circular impression on each lateral piece in front where it is joined by the delicate ducts which are supported by a forked piece of chitin, homologous probably with the forked piece in *Trinoton* and others. The Òesophageal sclerite is of a peculiar form, quite different from that of other Dochenphori and Ischnocera. It is not visible without dissection.

*Tetroptalmus titan* Piag. (formerly *M. titan*) [from the Pelican].—The rami of the broad "duct" bifurcate far forward at the front margin of the labium. No traces of the "glands" (text-fig. 28, p. 135). In *Pseudomenopon tridens* (formerly *M. tridens*), the hypopharynx is very similar, but the lateral pieces are narrow in front where they run into the rami.

Text-fig. 29.

Hypopharynx of *Trinoton luridum*, X 245.

A, Òesophageal sclerite; B, fused rami; C, anterior lobes of hypopharynx; D, lateral piece; E, maxillary fork; F, posterior cornu.

*Trinoton luridum* N. (from the Duck).—The anterior cornua have disappeared—probably fused in the central rod, which is
unusually broad here. The anterior area of the hypopharynx contiguous with the curving rami of the "duct" consists of two lobes with a few minute hairs (text-fig. 29).

Text-fig. 30.

Hypopharynx of *Nitzschia pulicaris*, × 570.

A, oesophageal sclerite; B, lateral piece; C, posterior cornu.

*Nitzschia pulicaris* N. (from the Swift).—The lateral pieces are broad and thinly chitinized. The "ducts" are broad, and there are teeth on the anterior area (text-fig. 30).
*Heterodoxus macropus* Le Souëf (from the Wallaby)—Numerous setae on the anterior area. The lateral pieces exhibit no traces of glands. There is a projection on the inner side of each lateral

Text-fig. 31.

Hypopharynx of *Heterodoxus macropus*, $\times$ 500.

A, oesophageal sclerite; B, rami; C, anterior lobe of hypopharynx; D, lateral piece.

piece which almost meets its fellow from the other side (text-fig. 31). *Booplia* is similar, with an elegantly curved hypopharynx thickly clothed in front with setae.

[12]
Physostomum sp.? mystax.—The "glands" are present but appear to underlie the ducts, with which I cannot find their point of attachment. Only one rather poor specimen formed my available material for dissection in this species. The anterior cornua are very long and curl round in front (text-fig. 32).

Text-fig. 32.

Physostomum sp., × 210.
A, oesophageal sclerite; B, glands; C, rami; D, anterior cornu.

The Maxillary Forks.

These problematic "forks" are delicate chitinous rods unconnected with the rest of the mouth-parts, but lying within the mouth, one on either side of the hypopharynx. They have been recorded from A. gigas P., Goniodes dissimilis N., Lambothrium gypsis Kell. I find them present in Tetrophtalmus titan P. (text-fig. 28, E), Leem. titan P., Trinoton luridum N. (text-fig. 29, F). On account of their fragile nature they may easily be overlooked, and therefore perhaps exist in many other species. It is tempting to look upon these "forks" as the maxillule or super-linguae of the hypopharyngeal or fifth segment of the insect head. A third pair of maxillae are present and well developed in many Apterygota, and recently Prof. G. H. Carpenter and Miss Mabel MacDowell have made a further contribution to the question of the serial homologies of the insect head by a paper (1912) (10) on the mouth-parts of certain beetle larvae, where the maxillule are represented, it is suggested, by the side pieces of the hypopharynx. This question in the Mallophaga is worth investigation. An alternative suggestion is that the maxillary forks are the inner
lobes of the first maxillæ, the maxillulæ being the glands and rami (or the lateral pieces as the case may be). This view has been actually put forward on behalf of the "glands" by Dr. Günther Enderlein (1903) (11).

Conclusion.

Dissections of the head, particularly in those species of the large genus *Menopon* where the hypopharynx has been reported to be absent, ought to yield useful data for systematic work. It is curious that the case of *Dochophorus sphenophorus* from which, at first, the glands and sclerite appeared to be absent, should on careful examination be found to present a hypopharynx constituting so abrupt a deviation from the normal form in the Ischnocera, because this species is a typical *Dochophorus* differing in external character but little from the group to which it belongs. Now that schemes of classification, instead of being merely arbitrary modes of arrangement for the convenience of systematists, are expected to indicate phylogenetic relationships whenever possible, it becomes necessary to include in descriptive work internal as well as external characters. If the hypopharynx were an external character, its peculiar form in *D. sphenophorus* would, with some students of the order, be sufficient reason for instituting a new genus for its reception.

The oesophageal sclerite is probably present in all Mallophaga, and in breaking up many of the unwieldy genera such as *Dochophorus* and *Menopon*, it should prove to be of great assistance. Of the list of species of *Menopon* in which Snodgrass discovered no sclerite present, one, *M. tridens*, has already been separated out as *Pseudomenopon tridens*, and another, *M. titan*, as *Tetrophtalmus titan*. Both these new genera are now found to possess an oesophageal sclerite, though in a modified form. These facts are suggestive.

Literature.


(2) Nitzsch, C. L.—Der Familien und Gattungen der Thierinsekten (Insecta epizoica) als Prodromus einer Naturgeschichte derselben. German’s und Zincken’s Magazin für die Entomologie, Bd. iii. 1818, Halle.


[14]
Dr. W. T. Calman has kindly drawn my attention to a memoir in the ‘Bollettino della Società di Naturalisti in Napoli’ (vol. xxiv. ser. ii. vol. iv. anno xxiv.), published in 1911, and entitled “Contributo allo Studio dei Mallofagi, Observazione sul *Menopus pallidum*.” This paper unfortunately arrived in this country too late for consideration. The author, Euclide Armenante, investigates *M. pallidum* and finds that the “glands” and “ducts” are, as I suppose, chitinous. The hypopharynx is not typical in this species, but lends support to the homologies indicated above, and appears to stand somewhere between *Lamobothrium* and such forms as *Trinoton*, *Nitzschia*, etc.