

**A Revision of the Mouth-parts of the CORRODENTIA
and the MALLOPHAGA.**

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(With Plate VIII.)

I. Introduction.

The conclusion reached by the writer through a study of the material described in this paper is that the mouth-parts of the Corrodentia and the Mallophaga are morphologically identical in structure. Furthermore, it will be seen by anyone acquainted with the mouth-parts of biting insects in general that the two groups possess several highly specialized mouth structures that are peculiar to them. It is, thus, evident that the two orders are at least more nearly related to each other than to any other order of insects.

On account of the usual small size of the Corrodentia and the Mallophaga and the consequent difficulty in making dissections the mouth-parts of the two groups have been given various interpretations. The writer, however, has had the fortune to obtain through Professor V. L. Kellogg specimens of two unusually large Mallophagan species, viz.: *Ancistrona gigas* Piaget and *Læmobothrium gypsis* Kellogg, the latter a giant among bird lice measuring nearly 11 mm. in length. These two species are described and figured in this paper.

The writer is indebted to Mr. Nathan Banks for the identification of Corrodentian specimens.

The variety of opinion that has been published concerning the mouth-parts of the two orders in question can probably be best illustrated by a brief historical resumé. The number given in parentheses after an author's name refers to the number of the paper given in the bibliographical list.

The earlier entomologists of course confused the Mallophaga with the blood-sucking or true lice, but since the beginning of last century it has been known that they have biting mouth-parts and that they feed on the feathers or hairs of their hostes.

Nitzsch (1) in 1818 published the first account of the Mallophagan mouth-parts and described them correctly. He recognized the biting mandibles, he ascribed the palpi of the suborder Amblycera

to the maxillæ, and he described the labium as having small 1- or 2-jointed palpi. He did not, however, mention the œsophageal sclerite and lingual glands of the Ischnocera, nor did he perceive the maxillary forks which are present at least in some forms.

In 1870 Rudow (2) published detailed accounts of the mouth-parts of a large number of Mallophagan species. He makes, however, the curious and unaccountable error of ascribing to Ischnoceran forms a 5-8-segmented maxillary palpus and a 3 segmented labial palpus, and to Amblyceran forms a 5-segmented maxillary palpus and a 4-segmented labial palpus. One would suppose he had taken the antennæ for palpi, but the antennæ he describes also.

Giebel (3) in 1874, following Nitzsch's work, gives correct descriptions and figures of the mandibles, maxillæ and labium, showing the 4-jointed palpi of the Amblycera as appendages of the maxillæ.

In 1878 Burgess (4) gave the first good account of the Corrodentian mouth-parts. He described the large biting mandibles, the maxillæ bearing each a 4-segmented palpus and one weakly developed apical lobe, and the simple labium with small 1-segmented palpi. Furthermore, he described and figured the curious œsophageal sclerite (or "œsophageal bone"), the lingual glands and the maxillary forks. The latter he called simply the "forks" and regarded them as morphologically independent of the maxillæ. He described the muscles connecting them with the stipes and apical lobe of the maxilla, and an "elastic ligament" extending from the inner end of each to the wall of the head.

In 1885 Grosse (5) published a new opinion concerning the palpi of Mallophagan suborder Amblycera. He states that in dissections of the mouth parts the palpi always come away from the head with the labium. He consequently regarded them as labial palpi, and gives figures of the labium of two species, each bearing a pair of 4-jointed palpi. He of course, therefore, described the maxillæ as being always small and weakly developed and as never possessing palpi.

In 1887 Packard (6) made the first intelligent comparison between the Mallophaga and the Corrodentia. He based his comparisons on the anatomical work of Burgess and Grosse. But, since Grosse described the labium of the Mallophaga as bearing palpi and the maxillæ as lacking them, and since the œsophageal sclerite, lin-

gual glands and the maxillary forks were then known only in the Corrodentia, the similarity which Packard was able to point out between the two orders was not nearly as great as can be demonstrated at the present time.

Kellogg (7) in 1896 adopted Grosse's view of the mouth-parts.

In 1896 the present writer (8) prepared an account of the mouth-parts of two Amblyceran and two Ischnoceran species of the Mallophaga. It was found that the palpi of the Amblycera, as was stated by Grosse, come away from the head in dissections attached to the labium, and that in cleared specimens they appear to be attached to the corners of the labium. On this account the mouth-parts were given the same interpretation as had been given them by Grosse. In this paper, however, was given the first description of the œsophageal sclerite, the lingual glands and the maxillary forks in the Mallophaga. Kellogg (9) in the same paper was then able to carry the comparison between the two orders, Mallophaga and Corrodentia, much farther than Packard had done. The œsophageal sclerite is usually a conspicuous object near the centre of the head in cleared specimens on account of its dark brown color and its shield-like shape. For this reason it has been figured by nearly all systematic writers on the Mallophaga, but apparently its true nature had never before been understood, some authors referring to it as the "labium." In 1899 the writer (9) repeated the descriptions of the Mallophagan mouth parts and gave observations on the distribution of the œsophageal sclerite in the two suborders Amblycera and Ischnocera.

Ribaga (11) in 1901 gave a good description of the Corrodentian mouth parts. The maxillary rod he calls the styliform apophysis (*apofisi stiliforme*), and regards it as morphologically distinct from the maxilla.

Finally in 1903 Enderlein (13) discusses the Corrodentian mouth-parts and compares them with the mouth parts of the Mallophaga. He regards the palpi of the Amblycera as belonging to the maxillæ, but does not admit any correspondence between the mouth parts of the two orders. The maxillary rod he describes as the inner lobe, *i. e.*, lacinia of the maxilla. To the organs called "lingual glands" by Burgess, he gives the following very curious interpretation: The hypopharynx or "endolabium" is described as consisting of a median lobe or "glossa" (the hypopharynx proper), and of two lat-

eral parts, the "paraglossæ" ("morphologically a third pair of maxillæ"). Then he farther states that the paraglossæ are the organs that Burgess called the "lingual glands." The ducts from the latter are described as chitinous bands, which unite in the lower wall of the œsophagus. He must have simply looked through the head of cleared specimens and supposed that the lingual glands were free lobes lying above the labium, whereas they really lie within the head cavity.

In the present paper anatomical preparations are described and figured that show definitely that in both the Mallophaga and the Corrodentia the palpi, when present, belong to the maxillæ, and that the maxillary forks are independent structures having no relation to the maxillæ, except that of proximity and muscular attachment.

II. *The Mouth-parts of the Corrodentia.*

The mandibles (figs. 13 and 14) are of the ordinary, strong, heavy, biting type. They are usually two toothed and have a large lobe projecting mesad from the inner basal angle. In all species examined they lie in a horizontal plane, parallel with the head, as in the suborder Amblycera of the Mallophaga.

The maxillæ (figs. 10 and 12) consist each of a body piece (*mx.*), probably representing the stipes or stipes and cards, of a 4 jointed palpus (*pl.*), with sometimes a palpifer (*plf.*, fig. 10), and of one weakly chitinized terminal lobe (*l.*). This lobe is regarded by Enderlein (13, 14) as the outer lobe or galea of the maxilla—the furca maxillaris being regarded as the inner lobe or lacinia.

Figure 12 shows sufficiently the shape of the maxilla of *Troctes divinatorius*, and figure 10 that of *Peripsocus californicus*. In the former the stipes (*mx.*) is a long club-shaped plate lying at the side of the labium, much as does the stipes of the Mallophagan maxilla. In *Peripsocus californicus* the stipes (*mx.*) is a small ovate plate. The palpus is 4-jointed in each species; in *T. divinatorius* it is born directly by the stipes; in *P. californicus* it is supported on a palpifer (fig. 10, *plf.*). The terminal lobe (*l.*) is in each case simple and weakly chitinized.

The labium (figs. 9 and 11) consist of a large submentum and of a mentum bearing a pair of usually 1-segmented palpi and one pair of terminal lobes. According to Enderlein (13, 14) the palpi are sometimes 2 jointed. Enderlein describes also an "endolabium"

corresponding with the endolabium of the Colembolla, but what he thus refers to are the organs described by Burgess (4) as the "lingual glands," and which are described under the latter name in this paper.

The furcæ maxillares or maxillary forks (fig. 12, *f*, and fig. 15) are organs as yet discovered only in the Corrodentia and the Mallophaga. From their anatomy it would appear improbable that they have any morphological relation with the maxillæ, but on account of their close proximity to, and muscular connection with, the latter the name of maxillary forks may be appropriately given to them. Westwood referred to them as the "horny processes," and Burgess (4) described them as simply the "forks."

The organs in question are two chitinous rods protruding into the mouth from below the inner edges of the bases of the maxillary lobes. Each extends from the latter point into the head-cavity, posteriorly and slightly outward, dorsal to the stipes and about a third of its length beyond the latter (fig. 12, *f*.). The free tip is usually bifid (whence the name fork), but may present three or four terminal points (fig. 15). The part within the head is imbedded in a sheath of protractor muscles (fig. 12, *p. m.*), whose origin is upon the dorsal face of the stipes. The posterior tip is attached by two bands of retractor muscles (fig. 12, *r. m.*) to the posterior wall of the head. Burgess (4) describes these retractors as elastic ligaments and not as muscles, but they certainly have the appearance of muscles in the preparation from which figure 12 was drawn.

Enderlein (13, 14), as has already been stated, regards these maxillary forks as the inner lobes or laciniae of the maxillæ. Burgess (4) and Ribaga (11) regard them as independent organs since they have no articulation of any sort with the maxillæ, being connected with the latter simply by the protractor muscles. Their actual origin has never been investigated. If they are, as they appear to be, independent organs, then the part of each within the head is to be regarded as simply an apodeme of the free rod projecting into the mouth. The rods may, hence, be simply hypopharynged structures. They are termed the "apofisi stiliforme" by Ribaga (11).

The œsophageal sclerite and lingual glands (fig. 16) are curious organs described in the Corrodentia by Burgess (4). The œsopha-

geal sclerite is a thick, densely chitinized, cup shaped sclerite located in the ventral wall of the œsophagus a short distance back of the mouth opening. The cavity makes a depression in the floor of the œsophagus, and the sclerite is probably simply a thickening of the œsophageal intima. Its shape varies in different species, but viewed from above or below it is usually shield-shaped or oval, with two elongate anterior arms and a small median posterior projection. In *Peripsocus californicus* (fig. 16, *œ. scl.*) the anterior arms are short, but there are two wide, expanded, plate-like arms projecting posteriorly and outward.

From the anterior end of the cavity of the sclerite a duct extends forward, which soon divides into two. These ducts (fig. 16, *d.*) continue anteriorly within the hypopharynx and then diverge outward and turn posteriorly to become attached to the lingual glands (*gl.*) whose outer edges they traverse. The lingual glands are oval or elongate-oval organs, with a thick chitinous lining, lying within the base of the hypopharynx. They are the structures called by Enderlein (13, 14) the "paraglossæ" of the "endolabium." Each gland is supported on a chitinous peduncle (fig. 16, *ped.*), which projects posteriorly toward the caudal wall of the head to which it is connected by means of muscles.

III. *The Mouth-parts of the Mallophaga.*

The mandibles (figs. 4 and 8) are always large and strongly chitinized. In the Amblycera they are horizontal and parallel with the head; in the Ischnocera they hang downward sometimes perpendicular to the plane of the head. They are nearly always two-toothed distally and usually have some sort of mesad projection from the inner angle of the base.

The maxillæ (figs. 2 and 5) consist each of a rather large basal piece (*mx.*) representing the stipes or stipes and cards, which is always fused with the lateral edge of the labium, of a simple, small apical lobe, and in the Amblycera of a 4 segmented palpus. On account of the union between the stipes and the adjacent edge of the labium the palpi have the appearance of belonging to the labium, and when the mouth-parts are dissected away from the head the labium, stipes and palpi generally come off together. On account of this the labium has been described by Grosse (5), and the present writer (8 and 10) as possessing two 4-jointed palpi in

the Amblycera, while the maxilla was regarded as consisting of only the small terminal lobe. However, a closer examination of *Ancistrona gigas* shows a distinct line on each side separating the stipes from the labium (fig. 5), while in the very large *Læmobothrium gypsis* it is easy to dissect the stipes off from the head and free from the labium, and attached to it, are also removed the palpus (fig. 2, *pl.*) and the single apical maxillary lobe (*l.*). Hence, we will have to admit that the original description of the mouth parts by Nitzsch is most probably the correct interpretation. The apical lobe of the maxilla is always small and inconspicuous, it is often soft and fleshy (fig. 5, *l.*), but may be more or less chitinized and bear a row of teeth distally (fig. 2, *l.*).

In the Ischnocera the maxillæ never have any trace of palpi, but otherwise are like those of the Amblycera.

The labium (figs. 1 and 5, *lab.*) is large and is usually composed of a mentum and a submentum. The distal edge of the mentum is produced into several small lobes of which the outer ones are regarded by most authors as the rudimentary labial palpi. They vary much in shape and size in the Amblycera where the maxillary palpi are present, being sometimes inconspicuous as in *Ancistrona gigas* (fig. 5), or comparatively large articulated lobes as in *Læmobothrium gypsis* (fig. 1, *pl.*). In the Ischnocera they are always cylindrical in shape, and, although short, project prominently from the mentum. The margin of the labium between the palpi is sometimes entire (fig. 1, *lab.*), but is more frequently produced into two or more lobes. A pair of large, thick, biramous processes arises from the submentum of *Ancistrona gigas* and projects backward (not shown in figure).

The furcæ maxillares (fig. 1, *f.* and fig. 7) have been discovered by the writer in three Mallophagan species, viz.: *Goniodes cervinicornis*, *Ancistrona gigas* and *Læmobothrium gypsis*. Since, however, they are extremely small, the fact that they have not been found in other species does not prove their absence in them. These maxillary forks are two delicate bars of chitin embedded in the floor of the mouth. Their distal ends project free into the mouth cavity beyond the edge of the labium and above the hypopharynx (fig. 1, *f.*). The tip of each is bifid in *Ancistrona gigas* (fig. 7) and divided into three small lobes in *Læmobothrium gypsis* (fig. 1, *f.*).

Near the middle are inserted several protractor muscles (fig. 7, *p. m.*), which are attached to the maxilla. On the posterior end are inserted the retractor muscles (*r. m.*) whose origin is on the wall of the head.

The œsophageal sclerite and lingual glands (fig. 3) occur in typical form in nearly all the Ischnocera, but are absent in most of the Amblycera. In the latter group they are present in probably all the species of *Colpocephalum*, in most species of *Menopon* and in *Læmobothrium gypsis*, but in these forms the sclerite does not have the shape characteristic of it in the Ischnocera. In two previous papers (8 and 10) the writer has given detailed descriptions of these organs in several species.

In the Ischnocera the œsophageal sclerite is nearly always of a shield-shaped form when viewed from above or below, is very convex ventrally, has two wide antero-lateral arms and a small median posterior lobe, and has a chitinous band extending from each lateral dorsal rim upwards toward the roof of the head. From its anterior end a rather long duct runs forward which divides and goes posteriorly to the lingual glands, which latter do not differ from those of the Corrodentia.

The sclerite is a thickening of the intima of the œsophagus and is not a hypopharynx in the sense in which this term is used in insect anatomy. The true *pharynx* of insects is of course the anterior end of the œsophagus, but the word "hypopharynx" refers to the median lobe developed above the base of the labium in the cavity between the mouth parts, which is outside of the true mouth located in the peristomal membrane.

In those species of the Amblycera that possess an œsophageal sclerite, the anterior arms of the latter are usually greatly elongate and frequently there are postero-lateral lobes present. The body of the sclerite is also relatively smaller and usually of an oval outline, rather than shield-shaped. Such a sclerite is shown in figure 3 (*œ. scl.*), representing in ventral view that of *Læmobothrium gypsis*. In this species the anterior arms are long thin plates slightly expanding at the anterior ends. The lingual glands are proportionately small and are ovate in shape. (The left gland is removed to show the anterior end of the left arm of the sclerite).

The histology of the œsophageal sclerite and the lingual glands has never been investigated, and their function is yet to be explained.

A *hypopharynx* and an *epipharynx* are usually not conspicuously developed in the Mallophaga. In *Læmobothrium gypsis*, however, there is a large and complicated hypopharynx projecting above the labium (fig. 1, *hyp.*). It consists of six lobes, of which two are large, wide and median, two are lateral and more elongate, and the other two are club-shaped and are situated between the middle and outer one on each side.

Ancistrona gigas possesses a bilobed epipharynx supported internally by a minute rod,* bifid at each end (fig. 6). The anterior prongs of the rod lie in the two lobes of the epipharynx, while the rest of the rod and the two large posterior arms are imbedded in the roof of the mouth.

IV. Conclusions.

1. The *mandibles* of the Corrodentia and the Mallophaga are practically identical.

2. The *maxillæ* of the Corrodentia consist always of a stipes, a 4-jointed palpus and of one apical lobe; in the Mallophaga the suborder Amblycera have maxillæ identical in structure with those of the Corrodentia, but the Ischnocera lack maxillary palpi.

3. The *labium* is similar in the two orders, the palpi being rudimentary in each, being 1-jointed, except in a few Corrodentia where they are 2-jointed. The distal edge of the labium is generally lobed, but is entire in some Mallophaga.

4. The *furcæ maxillares* are identical in the two orders. Although they have been discovered in only a few Mallophagan species, this does not prove that they are not present in others. They are probably structures developed independently of the maxillæ.

5. The *oesophageal sclerite* and *lingual glands* are identical in the two orders. They are present in all the Corrodentia, and in the Mallophagan suborder Ischnocera and in many members of the Amblycera. The sclerite is a thickening of the intima of the floor of the oesophagus; the glands lie in the head between the oesophagus and the submentum.

* By a mistake the writer (8 and 10) first described this rod in *Ancistrona gigas* as a hypopharynx.

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EXPLANATION OF PLATE VIII.

(CAMERA LUCIDA DRAWINGS.)

- Fig. 1. *Læmobothrium gypsis* Kell.—Labium (*lab.*) with maxillary forks (*f.*) and hypopharynx (*hyp.*) projecting above it; *pl.*, labial palpus.
- Fig. 2. *Læmobothrium gypsis* Kell.—Maxilla; *l.* apical maxillary lobe; *mx.* body of maxilla (stipes); *pl.* maxillary palpus.
- Fig. 3. *Læmobothrium gypsis* Kell.—Oesophageal sclerite (*œ. scl.*) and lingual gland (*gl.*) of right side. (Left gland removed to show anterior end of left arm of sclerite); *d.* duct.
- Fig. 4. *Læmobothrium gypsis* Kell.—Mandibles, ventral view.
- Fig. 5. *Ancistrona gigas* Praget.—Labium and maxillæ, ventral view; *l.* apical lobe of maxilla; *lab.* labium; *mx.* body of maxilla fused with edge of labium; *pl.* maxillary palpus.
- Fig. 6. *Ancistrona gigas* Praget.—Epipharynx and its supporting fork.
- Fig. 7. *Ancistrona gigas* Praget.—Maxillary forks; *p. m.* protractor muscles; *r. m.* retractor muscle.
- Fig. 8. *Ancistrona gigas* Praget.—Mandibles, ventral view.
- Fig. 9. *Peripsocus californicus* Banks.—Labium, ventral view; *pl.* palpus.
- Fig. 10. *Peripsocus californicus* Banks.—Maxilla; *l.* apical maxillary lobe; *mx.* body of maxilla (stipes); *pl.* palpus; *plf.* palpifer.
- Fig. 11. *Troctes divinatorius* Müll.—Labium, ventral view; *pl.* palpus.
- Fig. 12. *Troctes divinatorius* Müll.—Maxilla and maxillary fork of right side, ventral view; *ep.* epicranium; *f.* maxillary fork; *l.* apical maxillary lobe; *mx.* body of maxilla; *pl.* maxillary palpus; *p. m.* protractor muscles; *r. m.* retractor muscles.
- Fig. 13. *Troctes divinatorius* Müll.—Mandibles, dorsal view.
- Fig. 14. *Peripsocus californicus* Banks.—Mandibles, ventral view.
- Fig. 15. *Peripsocus californicus* Banks.—Maxillary fork.
- Fig. 16. *Peripsocus californicus* Banks.—Oesophageal sclerite (*œ. scl.*) and lingual glands (*gl.*), ventral view; *d.* duct; *ped.* peduncle of gland.



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