BRITISH MUSEUM (NAT. HIST.) DEPARTMENT OF ENTOMOLOGY

On the Systematic Position of the Mallophaga. By A. S. Packard.

(*Read before the American Philosophical Society, September 2, 1887.*)

The true position of the bird-lice has been in debate for many years, and it is only recently that, in the excellent essay of Grosse,* we have such an exact account of the mouth-parts of these insects, as to enable us to perceive that they have been wrongly referred to the Hemiptera. With the new information afforded by Grosse, who does not himself add any general conclusions as to the systematic position of the Mallophaga, beyond stating that they are not Hemiptera, nor allied to the true lice, we have for our own satisfaction made some comparisons with the Psocidæ, to which, among winged insects, the parasites in question seem nearest allied.

The name *Mallophaga* was first proposed by Nitzsch in Germar's "Mag. der Entomologie," iii, 270, 1812.† In Gerstaecker's "Arthropoden" of Peters and Carus' "Handbuch der Zoologie" (1863), where this group is placed with the lice among the Hemiptera, it is stated that Burmeister regarded the Mallophaga as Orthoptera: "Zwischen welchen und den Hemipteren sie in Anbetracht ihrer Verwandtschaft mit den Läusen ein Uebergangsglied abgeben, ohne füglich einer von beiden Ordnungen direct zugewiesen werden zu können."

In our "Guide to the Study of Insects" (1868), and in subsequent editions, influenced by general usage and also by Melnikow's arguments, based on embryological studies, we placed the Mallophaga among the Hemiptera, next to the true lice. In most, if not all German, Dutch, and French, as well as English text-books, the Mallophaga, if referred to, are described with the true lice. But, in his article, "Insects," in the "Encyclo-

* Beiträge zur Kenntniss der Mallophagen. Von Dr. Franz Grosse. Zeits. für wissen. Zool., xlii, 1885, pp. 530-558. A lengthy illustrated abstract by Prof. G. McCloskey will be found in the American Naturalist, April, 1886, pp. 340-348.

† I am indebted to Dr. Hagen for this reference to Nitzsch's paper.

pædia Britannica," 9th edit., Mr. R. McLachlan claimed that these insects should be regarded as degraded Pseudoneuroptera. This view seems a natural one. Struck by this suggestion, and before reading Nitzsch's essay on the internal anatomy of Atropos, we had been led into comparisons with the Psocidæ, particularly the wingless form Atropos, to which, as we hope to show, with the aid of Grosse's results, the bird-lice are more closely allied than to any other group of insects. Grosse himself, unfortunately does not intimate what his views are as to the exact systematic position of the group under consideration, beyond affirming that they certainly are not Hemiptera.

We will now turn to the conclusions of Melnikow,* derived from a study of the embryology both of the Mallophaga and the true lice. In this essay the author thus sums up his views as to the affinities of the Mallophaga:

"The study of the embryology of the Pediculidæ and Mallophaga affords proof of a complete similarity in the mode of development of these two groups of animals. We are convinced that the similarity urged is seen not only in the identity of the formation of the primitive streak and the relations of the embryonal membranes, but also in other more subordinate features of the development. We have for example perceived that in the lice as well as the Mallophaga a provisional mass of cells is formed before the completion of the blastoderm; that both have the provisional membrane which the larva leaves behind it in the egg at the time of hatching. Finally we are in a position to state that the beaks of both groups of insects are independently formed of the appendages of the head-segments.

"These, though subordinate processes of development, appear to us to be of more value in the comparison of the insects under consideration than the relations of the mode of formation of the primitive streak and of the embryonal membranes, since the last without doubt is generally common to those insects with an internal primitive streak, but the former must be regarded as the distinctive feature of the insects under consideration.

"If we add to the results mentioned, the fact that the anatomical structure of the mouth-parts in the insects of the two groups agrees in all essential points; if we add the generally similar external form of these insects, finally their ectoparasitic mode of life, then we need not hesitate to recognize the close relationship of the lice and Mallophaga.

"This conviction is not insignificant, since it affords us the possibility of decisively answering the question as to the systematic position of these insects.

"After the researches of Burmeister it was generally considered that the Pediculidæ belonged to the Hemiptera. The structure of their mouth-parts and the incomplete metamorphosis they undergo are the reasons which confirm such a view.

* Beiträge zur embryonal Entwickelung der Insekten. Archiv f. Natur-Gesch., xxxv, 1869.

"But the Mallophaga were regarded by De Geer as a special group, and by Nitzsch and others they were generally referred to the Orthoptera. So far as I am aware, only Gerstaecker, in his "Handbuch der Zoologie," places the Mallophaga at the end of the Hemiptera; still he is inclined to consider the group as a special one, forming a sort of transition from the Hemiptera to the Orthoptera, but without forming a direct connecting link.

"Since until now, we knew only of the biting mouth-parts of the Mallophaga, so the view that they were entitled to be regarded as Orthoptera was completely founded. In the Orthoptera we place those insects with an incomplete metamorphosis and biting mouth-parts. But after the existence of a beak in the Mallophaga has been proved, it becomes evident that they should be regarded as Hemiptera or bugs.

"This conclusion is wholly indisputable when we recall the above mentioned similarity of the Mallophaga with the genuine lice. As to the completeness of this similarity, I will call attention again to the relations of the mouth-parts, which have been cleared up by our embryological studies. We are thereby brought to the conviction that in the lice as well as in the Mallophaga, in their adult condition, no underlip (labium) exists, while the mandibles and maxillæ are present. The only difference in the mouth-parts of the two groups is this: that in the Mallophaga these head-appendages are the functional parts of the mouth-apparatus, while in the Pediculidæ they become rudimentary.

"But such relative differences do not have so great systematic value as to lead us to place so nearly related animals in two different orders.

"From the reasons we have presented we adopt the Linnean view that the Mallophaga belong with the Pediculidæ; we think we are right in regarding both groups as families of the Rhynchota."

From the foregoing facts and conclusions of Melnikow, we felt convinced that he had demonstrated that the Mallophaga were Hemiptera and nearly related to the Pediculidæ. But after a careful reading of Grosse's memoir on the Mallophaga, translated by Prof. McCloskey, we think he is right in considering that these biting lice are not genuine Hemiptera. The very fact, admitted by Melnikow, that the mandibles and maxillæ retain their biting function and do not become rudimentary as in the Pediculidæ, and the fact pointed out by Grosse, that the second maxillæ do exist in the Mallophaga, leads us to regard their louse-like shape as simply adaptive, and that they belong to some other group than the Hemiptera.

If we examine Melnikow's excellent figures we see that after the mouth-parts of the embryo of both the genuine Pediculidæ and Mallophaga are developed, the embryos of the two groups follow different developmental paths. The large clypeal region of the Mallophaga becomes still larger and broader, overhanging and concealing from above the labrum, which is short and broad; on the other hand, in the Pediculus it becomes long, narrow and slender. The mandibles become true biting jaws, while in the Pediculus they become long and slender; the maxillæ become minute

and short, of the masticatory type in the Mallophaga, while in the Pediculus they remain large and long (Melnikow, Fig. 371) and of the size and shape of the mandibles; the second maxillæ in Pediculus are, in this stage, as large as in the first maxillæ, while in the Mallophaga they become minute. After the stage indicated by Melnikow's Fig. 37 (Pediculus) and Figs. 32, 33 and 34 (*Trichodectes canis*) the ordinal differences become more marked.

Among the Pseudoneuroptera of Erichson, a group which is so unnatural that it will have to be abandoned, we have after the elimination of the Odonata and the Plectoptera or Ephemeridæ, the families of Perlidæ, Psocidæ, Embidæ, and Termitidæ, which we have associated together in the order *Platyptera*. It is to the wingless Psocidæ that the Mallophaga appear to bear the closest resemblance. If we compare certain Mallophaga, especially those with a small prothorax, such as Goniocotes, Docophorus, etc., with the wingless Atropos, or the wingless young of Psocus, there is a general similarity to the latter in the small thorax, the large oval abdomen and the large head, with the small eyes. But these resemblances are superficial. But, however, with the aid of Grosse's figures of the mouth-parts of the Mallophaga and Mr. E. Burgess' excellent figures of the mouth-parts of the Psocidæ*, three of which we reproduce, we find an unexpected homology, which shows that the Mallophaga are, so to speak, degraded Psocidæ.

One characteristic of the Mallophaga, in general, is the greatly enlarged front or clypeal region of the head, which is vaulted and conceals from above the mouth-parts, and sometimes even the antennæ, with the occasional exception of the labial palpi. In the bird-lice, the lower, rounded edge of this circular clypeal region is applied to the surface on which the animal rests, as seen in Figs. 1 and 5, the labium and mouth-parts not being seen from above, except in some genera where the maxillary palpi project laterally.

In the Psocidæ the position of the head is vertical, as seen in Fig. 10, and the labrum is not covered by the clypeus; but the Mallophaga are unlike these and other insects in having the labrum covered by the clypeus.

In the shape of the mandibles the Mallophaga closely resemble the Psocidæ, at least as much so as perhaps any other of the biting insects.

Mr. Burgess has figured and described the first maxillæ of Psocus (Figs. 10 and 11) and Atropos (Fig. 12). The cardo and stipes are rudimentary; the latter bearing besides the four-jointed palpus a thick fleshy lobe homologous with the galea or outer maxillary lobe of other biting, ametabolous insects. He also describes at length the peculiar "fork," which has no homologue in the Mallophaga any more than other insects, Mr. Burgess inclining to the view that this is an independent organ. It is to be noticed that, with the exception of the palpi, the maxillæ of the Psocidæ are much atrophied.

* The Anatomy of the Head, and the Structure of the Maxilla in the Psocidæ. By Edward Burgess. Proc. Boston Soc. Nat. Hist., xix, 291-296, 1878.

In the Mallophaga they are excessively so, there being, if we accept Grosse's statement, apparently no palpi, and the maxilla being reduced to a pair of minute conical appendages, divided into two segments. After careful examination, Grosse says that he has never been able to find the palpi of the first maxillæ which Nitzsch ascribed to the Liotheidæ.*

The labium or second maxillæ of the Liotheidæ, as described and figured by Grosse (Fig. 8), consists of two parts united by a transverse fold. To the mentum are attached the four-jointed labial palpi. In front of the mentum is the ligula or glossa (*g*). In all Liotheidæ, the interna of the ventral end of the oral cavity forms a fold-like duplicature, forming the hypopharynx, Fig. 2 *hy*. In Læmobothrium and Tetrophthalmus this extends forward over the labium, and its lateral borders are strongly bent upwards (Figs. 1, 8 *hy*).

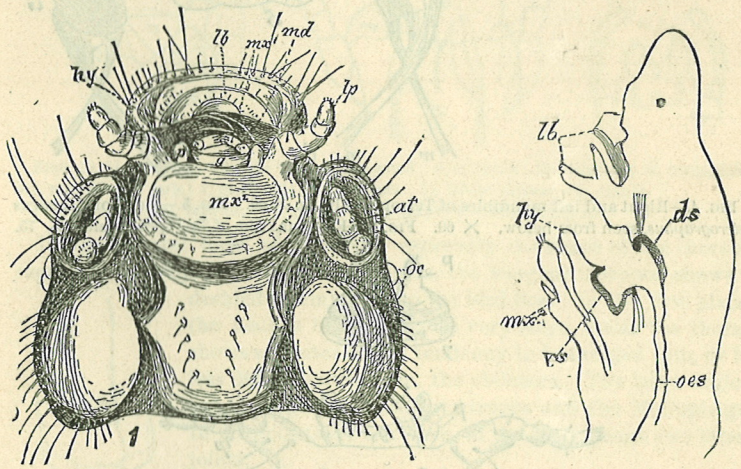


FIG. 1.—Under side of head of Læmobothrium. × 30.
FIG. 2.—Median section through head of *Goniodes dissimilis*. × 60.

The two-jointed organs on the sides of the tongue or ligula are called paraglossæ by Grosse (Figs. 7, 8, 9 *p*). In Nirmus and other Philopteridæ there are no labial palpi, the paraglossæ persisting (Fig. 7).

If we now compare the mouth-parts of the Mallophaga with those of the Platyptera we shall find a more or less close homology. In the first place the ligula appears as in the latter forms (Termes and Perlidæ), to be divided, as in Liotheidæ, into four lobes, while the outer pair of lobes, the paraglossæ, are usually, if not always, present, even when the labial

* Nitzsch figures them in *Trinotum conspurcatum*, but this can scarcely be correct, for he places the four-jointed papillæ on the blade near its anterior border. In Tetrophthalmus the palps belong, not to the first, but to the second maxillæ. The same is true of *Menopon pallidum*, *Colpocephalum zebra*, a Læmobothrium and a Trinotum, and probably is the case with all the genera and species. McCloskey's Transl.

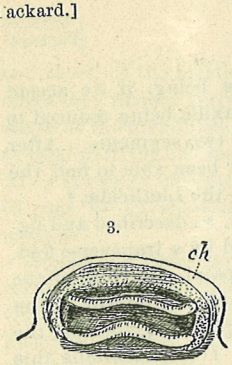


FIG. 3.—Labrum of *Goniodes dissimilis*. × 60.

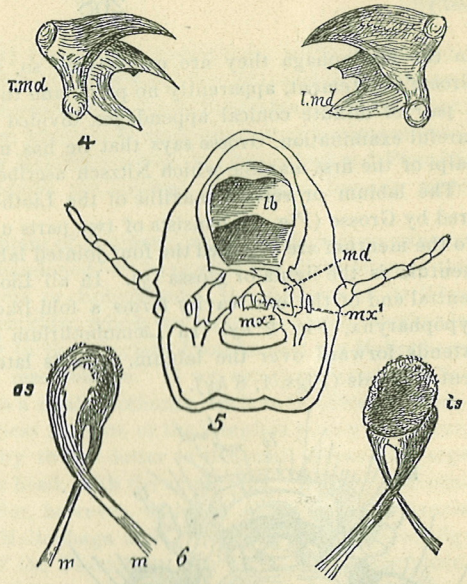
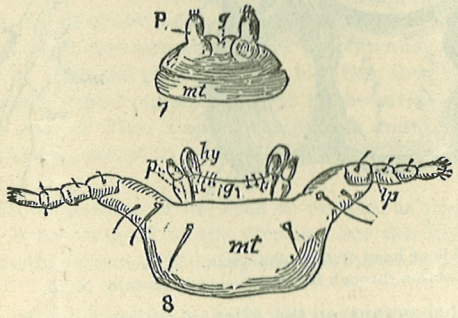


FIG. 4.—Right and left mandibles of Tetrophthalmus. × 60. FIG. 5.—Head of *Lipeurus heterographus*, seen from below. × 60. FIG. 6.—First maxillæ of Tetrophthalmus. × 75.



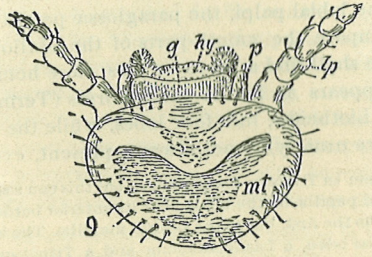
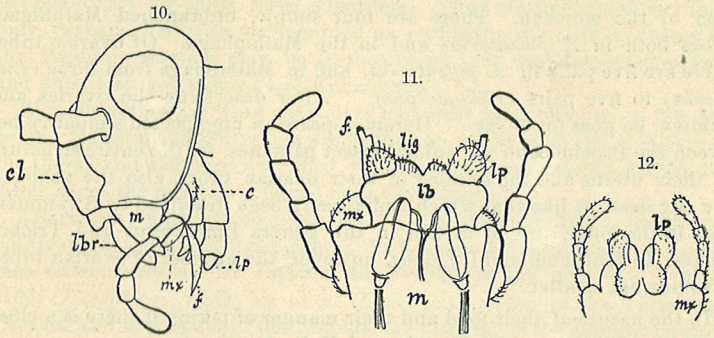


FIG. 7.—Second maxillæ of Nirmus. × 60. FIG. 8.—Second maxillæ of *Tetrophthalmus hil si* × 60. FIG. 9.—Second maxillæ of Læmobothrium. × 60.

palpi are atrophied. But while the second maxillæ of the Termitidæ and Perlidæ are well developed, the degraded condition of those of the Psocidæ affords a passage, though not a direct one to be sure (the labial palpi in Psocus and Atropos being simply one-jointed and there being no paraglossæ), to the Mallophaga. We copy, however, the accompanying sketches from Mr. Burgess' paper, so that the reader may compare the mouth-parts of the Psocidæ with those of the Mallophaga.



FIGS. 10, 11.—Psocus. 10, side view of the head; *cl*, clypeus; *lbr*, labrum; *m*, mandible; *mx*, maxilla; *f*, fork; *c*, cardo; 11, *m*, mentum; *lp*, labial palpus; *lig*, ligula.
FIG. 12.—Atropos, labium. *lp*, palpus; *mx*, maxilla.—After Burgess.

In the general form of the body, especially the shape of the thoracic segments as compared with the abdomen, the wingless Atropos shows a decided resemblance to the bird-lice. In the first place, the head is in both groups very large, while the thorax shows a greater or less tendency to be merged into, or be less differentiated from, the abdomen. The latter region has ten segments both in Atropos and the Mallophaga. In Atropos there are three, in the Mallophaga two tarsal joints.

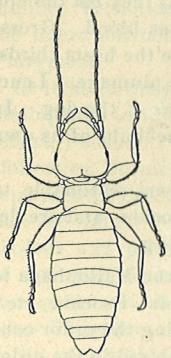


FIG. 13.—*Atropos pulsatorius*. Author del.

The eyes of Atropos are much reduced, there being from three* to seven simple ocelli on each side; in the Mallophaga the greatest number is two on each side.

After the foregoing portion of this paper was written, I read Nitzsch's paper (Germar's "Magazin der Entomologie," Bd. iv, 276–290, 1821) on the internal anatomy of *Atropos pulsatorius*, and found unexpected confirmation of the view we have taken as to the relationship of the Mallophaga to the Psocidæ. His observations, he says, were the result of researches carried on about the year 1814, at the time he was occupied with the study of the Mallophaga. "I undertook," he says, "the dissection of the Psocus, because this in-

* Scudder found but three simple eyes on a side in an Atropos he examined. Psyche, ii, 51.

sect has some external similarity with those parasites, and because I entertained the idea, that the internal structure of the same might offer some points which would be of value in throwing light on the natural affinity of the insect parasites, at least of the biting species." The following comparisons are taken from Nitzsch's memoir :—

"The digestive canal of *A. pulsatorius* differs from that of the Mallophaga only in the crop and the constantly present upper flap or diverticulum of the stomach. There are four simple, unbranched Malphigian tubes both in *A. pulsatorius* and in the Mallophaga. Of ovarian tubes there are five pairs in *A. pulsatorius*, and in Mallophaga from three (*Liotheidæ*) to five pairs (*Philopteridæ*)." After describing the ovaries and oviduct, he goes on to say : "Herein appears an unexpected similarity between the Psocidæ and the animal insect parasites, for the entire structure of their uterus and the number of their ovarian tubes, also the shape of the egg itself, is like that which had already been described by Swammerdam in the louse, and by myself in the genera Philopterus and Trichodectes. In Liotheum and Gyropus, however, the number of ovarian tubes is somewhat smaller."

In the nature of their food and their manner of taking it there is a close resemblance between the Psocidæ and Mallophaga.

As is well known, the Psocidæ occur on the trunks of trees, fences, old walls, etc., and feed on decaying vegetable matter. "Atropos, as is well known, lives on the paste in old books and boxes, as well as the specimens of entomological cabinets" (Burgess). While the food-habits of the Mallophaga are not fully known, Nitzsch stated that they eat the epidermal products of birds and mammals, and sometimes blood. Grosse found that blood is rarely taken, and only in cases where the hosts (birds) are so injured or diseased as to have blood among their plumage. Leuckart arrived at the same result as to *Trichodectes canis* of the dog. In Læmobothrium, Grosse found the intestine filled with the limbs of its own kind, as if it ate the product of its own moulting.

From the present state of our knowledge then, it seems reasonable to infer that the Mallophaga are nearest allied to the Psocidæ, and are degraded members of the order to which the Psocidæ belong.

It now remains to determine the exact relations of the Mallophaga to the order containing the families of Termitidæ, Embidæ, Psocidæ, etc., and here we are confronted with the difficulty of limiting the order containing these families, which were with other groups placed in the order of Pseudoneuroptera by Erichson. In my essay on "The Systematic Position of the Orthoptera in relation to other orders of Insects,"* I retained, though under protest, this order; at the same time stating, "It is difficult, if not impossible, to satisfactorily characterize by a sharp-cut definition this very elastic order. As regards the thorax, there is no uniformity in the structure that we have been able to discover, nor is there in

* Third Report U. S. Entomological Commission, 1883, pp. 286-345.

the structure of the wings, nor more than a general resemblance in the mouth-parts." I provisionally divided the group into three suborders :—

1. *Platyptera.* Termitidæ, Embidæ, Psocidæ, and Perlidæ (= Corrodentia and Orthoptera amphibiotica in part).
2. *Odonata* (Libellulidæ).
3. *Ephemerina* (Ephemeridæ).

I also added, "It is comparatively easy to give well grounded differential characters for these three suborders. They are so distinct that they may, perhaps, hereafter be regarded as entitled to the rank of orders, or the Pseudoneuroptera may be dismembered into the Pseudoneuroptera and Subulicornia (Odonata and Ephemerina)."

Without giving the wing characters and after describing on p. 291 the second maxillæ, the Platyptera are defined on p. 292, and the structure of the thorax and abdomen described in some detail on pp. 322-329 (in the latter pages the group is referred to as Corrodentia).

Afterwards, in his Systematisch-Zoologische Studien* (1885), Dr. Brauer boldly divides all the winged insects, the Synaptera (Thysanura) excepted, into sixteen orders. He regards the Perlidæ as the type of a distinct order (*Plecoptera*), while his order *Corrodentia* embraces the Termitidæ, Psocidæ and Mallophaga (the Embidæ are referred to the genuine Orthoptera).

In his description of the Corrodentia, Dr. Brauer frequently refers to the Mallophaga, especially referring to the similarity between the thorax of the Atropina and Mallophaga.

As will be remembered, Burmeister's order *Corrodentia* included the families Termitidæ, Embidæ, and Psocidæ. Under these circumstances the name Corrodentia should be restricted to a subdivision of the order Platyptera.

In 1886, in the fifth edition of our text-book on Zoölogy,† we added the Mallophaga to the Platyptera, which thus included the groups of Mallophaga, Perlidæ, Psocidæ, Embidæ, and Termitidæ. Although Dr. Brauer (following Burmeister who proposed the order Plecoptera for the Perlidæ) separates the Perlidæ from the Corrodentia as restricted by him for the reason that the former (Perlidæ) have numerous Malphigian tubes, are hemimetabolous and perennibranchiate, we are not yet prepared from a study of the trunk characters and of the shape of the second maxillæ, as well as the wings and their mode of folding, to separate the Perlidæ from the other Platyptera.

But once within the limits of the order, it is evident that the Mallophaga, even if degraded Platyptera, should occupy a space distinctly separate from the winged members of the group; in fine, they should be referred to a distinct suborder, equivalent to all the winged forms taken together. Hence the Platyptera may be divided into two suborders :—

I. Mallophaga.

II. Platyptera genuina : Superfamily 1, Plecoptera (Perlidæ) ; Superfamily 2, Corrodentia.

* Aus dem XCI. Bande der Sitzb. der Kais. Akad. der Wissensch. I. Abth., Mai-Heft, Jahrjang 1885.

† See also American Naturalist, Sept., 1886, p. 808.

MUSEUM (NAT. HIST.) DEPARTMENT OF ENTOMOLOGY