IV. *The Labial and Maxillary Palpi in Diptera.* By WALTER WESCHÉ, *F.R.M.S.*
(Communicated by G. MASSEE, *F.L.S.*)

(Plates 8–10.)

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HITHERTO only one pair of palpi have been known in Diptera, and these have generally been regarded as homologous throughout the order. They are described as maxillary by Savigny, and this nomenclature has been accepted and adopted by the large majority of morphologists.

The mouth-parts in the various families differ much in shape and armature: the *Œstridæ* have only a few tubercles, while the *Tabanidæ* have a nearly complete organ. The trophi of the *Muscidæ* are considered typical of the order, and *Calliphora*, on account of its large size and great abundance, has usually been selected for study; consequently, the rudiments of palpi, absent in *Calliphora*, but present in a very minute form in *Musca domestica* and many species related to it, have escaped notice. The second pair of palpi have been searched for, as Kirby and Spence * mention that Savigny thought he had seen the rudiments of the labial palpi in *Tabanus* †. Westwood gives as a character of the order, “always destitute of labial palpi” ‡. Later writers who have studied the proboscis in the *Muscidæ* hold similar views.

Dr. Benjamin T. Lowne worked at *Calliphora erythrocephala* in the larval, nymph, and imago stages. The subject has been most exhaustively treated, sections of the various parts having been largely used in his studies. He says § that the disc on the end of the proboscis (presumably the labella) is derived from the first pair of maxillæ, and the palpi present are, “without the slightest doubt, maxillary palpi.”

Kraepelin ||, Chatin ¶, and Macloskie ** are of opinion that the extremity of the proboscis is derived from a fusion of the labial palpi in the median line. Macloskie thus translates Kraepelin:—“The labella which Burmeister and Erichson have shown to be

* ‘Introduction to Entomology,’ Letter xxxv.

† Savigny, in the first part of his ‘Mémoires sur les Animaux sans Vertèbres,’ entitled “Théorie de la bouche,” gives a figure of the labium of *Tabanus italicus* (plate 4, pp. 51–53). A ventral view is given, and the rudiments consist of two minute tufts of hair, symmetrically placed on slight projections of the labium (“tiges”), immediately posterior to the labella. These he calls “vestiges des palpes?,” adding a note of interrogation. I have not seen any preparation of *T. italicus*, but I cannot find any similar structure in *Hæmatopata pluvialis*, or in any of the numerous drawings of *Tabanus* given in H. J. Hansen’s ‘Fabrica oris Dipteriorum.’ In *Tabanus bromius* and in *T. sudeticus* are tufts of hair on the ventral side of the labium, but no structures suggesting the rudiments of palpi.

‡ ‘Modern Classification of Insects,’ ii. p. 496.

§ ‘Anatomy and Physiology of the Blowfly,’ p. 131.

|| “Zur Anatomie und Physiologie des Rüssels von *Musca*,” in Zeitschr. wiss. Zool. xxxix. (1883) pp. 683–719, tt. 40, 41.

¶ ‘Mâchoires des Insectes’ (Paris, 1897, 8vo, pp. 202).

** Kraepelin’s ‘Proboscis of *Musca*.’

labial palps." Meinert *, of Copenhagen, has done much work on the trophi throughout the order. He has drawn, in a most admirable manner, the mouth-parts of the various families, but has passed over the large group of the Anthomyiidae, considering it typified by the Muscidae. According to Dr. Sharp †, Meinert (who writes in Danish) considers that not only the appendages to a head-segment, but also part of the body of the segment, may be used in the construction of the mouth-organs.

H. J. Hansen ‡, also of Copenhagen, has published beautiful drawings of the mouth-parts. His work is in Danish, with a Latin explanation of the plates. His studies were mostly confined to the Orthorrhapha, *Tabanus* being elaborately treated. A novel and unsatisfactory terminology is to be found both in this and in Meinert's work.

Fig. 1.

Trophs of *Blatta*.

The lettering as in Plates 8 and 9, as explained on page 229.

In the order Hemiptera the rostrum is considered homologous with the proboscis in Diptera. Those morphologists who have derived the labella in Diptera from the labial palpi have included the rostrum in their theory. In 1901, Dr. N. Leon §, a professor at the University of Jassy, in Roumania, found rudimentary labial palpi on the rostra of several aquatic Hemiptera.

I shall now endeavour to homologize the proboscis of *Musca* with the typical trophi of *Blatta*, as that has an intimate connection with the labial and maxillary palpi. The

* 'Trophs Dipterorum' (Kjöbenhavn, 1881, 4to).

† 'Cambridge Natural History,' Insects, part II. p. 444.

‡ 'Fabrica oris Dipterorum,' 1883.

§ 'Recherches morphologiques sur les pièces labiales des Hydrocores.'

observations I have made mostly confirm the ideas of Savigny. Speaking of the mouth-parts in Insecta he says: "the organ is the same, the use alone is modified or changed" *. His nomenclature of the palpi in the Muscidae must be excepted from this statement. Of all the morphologists known to me, Robineau-Desvoidy alone calls these labial. Dr. Lowne † thus quotes him:—The base of the labrum "is enveloped by the base of the labium, of which the palpi are always present."

Before proceeding further, it may be as well to say that I use the terminology, much the same as that of Kirby and Spence, given in C. O. Waterhouse's ‡ essay on the "Submentum," to which I wish to express my obligations.

In this investigation I have been guided by the following facts:—

1. *Mandibles*.—In the Tabanidae, which have all the mouth-parts present except the labial palpi, the proboscis or labium has tracheated labella, and is so like in appearance and position that there can be no doubt of its homology with the proboscis in the Muscidae. If a labium of *Hæmatopota pluvialis* has the soft parts dissolved away and is mounted with pressure (and I may remark, for the sake of brevity, that all the parts referred to later have been treated in this manner, unless expressly stated to the contrary), and is examined with the higher powers of the microscope, it will be seen that the *dorsal surface* has no chitinous structure, the necessary stiffening being afforded by a chitinous plate on the ventral side, the mentum (Pl. 8. fig. 1). I have examined *Tabanus sudeticus* and *T. bromius*, and have found the labium identical in this respect with *H. pluvialis*. It is, however, as well to mention that *Chrysops cæcutiens*, which has a very elongated labium, has chitinous structure on the dorsal side, while still retaining the mandibles. But this species, judging from the length of the labium, is a later and more specialized type than *Tabanus*, and the chitinous plate followed as a consequence of increased length requiring more "stiffening." It may generally be assumed, though not on conclusive evidence, that the archaic types in Diptera were furnished with a short labium and that extreme length is a case of specialization. A fairly obvious example is found in *Siphona*.

We may then say that *Tabanus*, having the mandibles present, has no chitinous structure on the dorsal side of the labium.

When we compare the corresponding parts in the Syrphidae and the Empidæ, families in which the mandibles have disappeared, though the maxillæ are present, we find well-marked chitinous rods on the dorsal side. We may reasonably presume that the mandibles are soldered into the dorsal surface of the labium. This view is held by Professor Packard, and has general acceptance with little or no opposition (Pl. 8. figs. 2, 3).

2. If we examine *Calliphora* we find a similar chitinous structure on the dorsal side of the labium. Dissection shows that the parts readily separate into two lateral rods with a broad central plate (Pl. 8. fig. 7).

In *Eristalis tenax*, *E. arbustorum*, and *Syrphus balteatus* these rods are different in

* 'Mémoires sur les Animaux sans Vertèbres,' Bouche, p. 11.

† 'Anatomy and Physiology of the Blowfly,' p. 130.

‡ 'The Labium and Submentum in certain Mandibulate Insects' (London, 1895, 8vo, pp. 12, 4 col. pls.).

shape and are continued along the sides of the main tracheæ. The central plate seems to be detached, but that the parts are homologous with those in *Calliphora* (Pl. 8. fig. 7) is evident.

3. *Maxillæ*.—Again examining *Calliphora* we find that, in addition to the mandibles, the maxillæ, which are present in the Syrphidæ and Empidæ, have disappeared. But if the base of the labium is dissected, the cardines of the maxillæ will be found embedded, and working the labrum as levers (Pl. 8. fig. 4). That these are cardines of the maxillæ may be proved by comparing the parts with those in *Eristalis* and *Helophilus* (Pl. 8. figs. 3, 5, & 6). A comparison with *Culex pipiens* only strengthens this proposition (Pl. 9. fig. 24) *.

We also find the palpi in a different position. In *Calliphora* they are above and posterior to the base of the labrum; in *Empis* and *Eristalis* they are in a more anterior position and firmly attached to the cardines of the maxillæ (Pl. 8. figs. 2, 3, & 4) †. A dissection of the maxillæ in *Helophilus pendulus* and *Eristalis tenax* shows the palpi attached to the maxillæ by a membrane, which has at its extremity a chitinous plate, which is probably the palpifer. The bases of the palpi connect with the maxillæ just before they emerge from the enclosing membrane of the labium. There are well-marked ridges halfway down the maxillæ that indicate the boundary of the cardo. The laciniae continue, the galæ having aborted. The palpifer shows only on the palpus, being pulled apart from the maxilla (Pl. 8. figs. 5 & 6). Further, I have dissected the maxillæ in *Culex pipiens*, ♀ (Pl. 9. fig. 24), in *Tabanus bromius*, *T. sudeticus*, *Chrysops cæcutiens*, *Asilus crabroniformis*, and a species of *Simulium*, all species with a nearly complete armature, and I find that invariably the palpus is firmly attached to the stipes and cardo of the maxilla.

4. *Labium*.—The palpi in the Muscidæ are in quite a different position, attached to the membrane of the labium; at their bases in *Calliphora* are plates of chitin and rows of two or three bristles. The palpi have no connection with the levers of the labrum, which, as we have seen, are the cardines of the maxillæ in *Eristalis*. They are therefore *labial* and not maxillary palpi, and have worked round from a lower part of the labium to the upper. The chitinous plates and rows of bristles in *Calliphora* have their analogies in a great number of related species. In some the chitin is evident, in others it has almost disappeared, but the row of bristles is very constant, and can be seen in all the species possessing labial palpi that I have examined. It is fairly obvious that these parts represent the palpiger.

5. A dissection of the trophi of *Culex pipiens* throws some light on the subject under discussion. In both sexes the labium is simply a chitinous sheath for the lancets. In its paired and segmented flaps may be seen the homologues of the labella.

The cardines and stipites of the maxillæ are present, having much the same appearance as in the Muscidæ, and a palpifer can be traced supporting the three-jointed palpus (Pl. 9. figs. 23 & 24).

* See note on page 229.

† The stipes and cardo are so soldered together that it is not possible, in the majority of cases, to define them. The palpifers are attached to the stipites and not the cardines.

In the female the maxillæ, mandibles, hypopharynx, and labrum are very beautiful weapons. In the male the lancets are obviously atrophying, and they can only with difficulty be dissected out from the enclosing labium. Here is seen the process, which has been completed in the Syrphidæ and Empidæ, actually proceeding, or suddenly halted in a stage of the process.

In the males the cardines of the maxillæ hinge on to the maxillary palpi, which, in this sex, are very long and highly developed (Pl. 9. figs. 25, 26, and text-fig. 2).

Summary.—In the Muscidæ the mandibles are embedded in the dorsal side of the labium. The maxillary palpi, galeæ, and lacinia are aborted, but the cardines remain. The palpi present are labial, and the palpifers are represented by chitinous plates with two or three setæ springing from or near them.

In the Syrphidæ and Empidæ the mandibles are similarly placed, but the maxillæ are represented by the lacinia, the palpi, cardines, stipites, and palpifers. The labial palpi are aborted.

Rule.—A rule can be formulated :—*The maxillary palpi when present in Diptera are always in contact with the upper part of the cardines, the stipites.*

Fig. 2.

Extremities of maxilla and mandible of *Culex pipiens*, ♀.

Rudimentary Maxillary Palpi.—I was fortunate in discovering a number of species, in the Anthomyiidæ, Muscidæ, and other families of the Cyclorrhapha, with four palpi which afford useful clues to the surrounding parts. They appear in different stages of atrophy, from a fairly developed organ to a rudiment of a few hairs. Some examples were described in a paper read at the meeting of the Royal Microscopical Society on June 18th, 1902, and since published in the Journal of that Society*. These palpi enable us to indicate the position of the maxillæ with certainty, and, by proving the other pair to be labial, establish the proposition that the whole organ is the labium.

We have now the mandibles, the maxillæ and palpi, the labium and palpi, and the mentum clearly defined.

Paraglossæ, Ligulæ.—We now come to the parts of the labium, the paraglossæ and

* Journ. Roy. Micr. Soc. 1902, p. 412. "Undescribed Palpi on the Proboscis of some Dipterous Flies, with Remarks on the Mouth-parts in several Families."

ligulæ. In the Muscidæ, Tabanidæ, Syrphidæ, and other families we find, at the extremity of the labium, two paired organs, the labella and the transverse chitinous levers that support them. They are in the situation where they might be expected to be found, and I have little doubt represent—the labella the paraglossæ, and the transverse levers the ligulæ (Pl. 8. figs. 4, 8 ; Pl. 9. fig. 17, &c.). In the paraglossæ of *Culex* (Pl. 9. fig. 23) I have seen two strengthening rods, which confirm me in the above homology. They only appear on dissection and are not shown in the figure. In species of *Empis*, such as *E. chioptera* (Pl. 8. fig. 2), and in *Siphona geniculata*, the ligulæ have aborted.

Teeth.—The large majority of species in the Muscidæ, from *Tachina* down to *Scatophaga*, have an armature of teeth at the bases of the false tracheæ. These may be traced through such specialized species as *Stomoxys* and *Glossina*, and may even be found in a most minute size in some of the species of the parasitic *Hippobosca*. They are arranged in symmetrical crescents, and are so close to both the mandibles and the ligulæ that they might possibly be parts of those organs ; but the simpler hypothesis that they are outgrowths from the paraglossæ is probably the correct one. Some light is thrown on this point by the very exceptional dentition shown in *Ephydra* (Pl. 9. fig. 21). Here each of the pseudotracheæ is furnished along its whole course with many short chitinous teeth disposed at regular intervals.

Labrum, Lingua, and Mentum.—All morphologists seem agreed that the lancet-case corresponds with the labrum, and the hypopharynx with the lingua. The homology of the ventral plate on the labium with the mentum is fairly clear (Pl. 8. fig. 4).

Submentum.—The submentum is possibly membranous, but it may be the “fulcrum.” This part is described as the chitinated walls of the pharynx, but a long tracheated tube is easily dissected out from the trophi of all the species I know, and seems to be the true pharynx. There is so little to guide that this point must remain doubtful ; allowing this, we thus have the parts complete.

Summary.—The proboscis in Diptera may be regarded as homologous with the trophi of the typical insect mouth. In the Muscidæ it has been modified into a rod-like organ, enclosed in a thin membrane, and capable of extension and retraction. It is mainly formed of the labium, and has the labial palpi well developed and placed near chitinous ridges, which are the palpigers. The palpi have worked round from the under to the upper side—or, taking the usual position of the labium into account, from a posterior to an anterior position, where it is obvious that they would be of greater service to the insect.

The proboscis has two symmetrical tracheated flaps at the extremity, which represent the paraglossæ. The teeth, which are often present, may be considered outgrowths of the paraglossæ. The transverse chitinous levers which expand the labella are the ligulæ. Mr. Waterhouse shows (‘Labium and Submentum’) that the paraglossæ have a tendency to enlarge at the expense of the ligulæ, and this has occurred in the Muscidæ.

The labium has absorbed into its structure the mandibles and maxillæ on the dorsal side, and the mentum, and possibly the submentum, on the ventral side.

The mandibles act as supports and assist in working the labella.

The upper parts of the maxillæ, which are present in *Syrphus*, have aborted, leaving the cardines and stipites, which find use as levers, acting on the labrum and hypopharynx. The maxillary palpi have mostly aborted, but in many species they are present in a more or less rudimentary state. When the maxillary palpi are present, they are based on structures homologous with the palpifers. These are attached to the stipites. The palpi are situated at proportionally the same distance from the bases of the cardines as the palpi in the Syrphidæ and the Empidæ (Pl. 8. figs. 3, 5, 6; & Pl. 9. fig. 17). The proboscis has, on its dorsal surface, a lancet-case, the labrum, which acts as a sheath for the hypopharynx, which homologizes with the lingua.

At the base of the hypopharynx, and continuing it, is a tube, the pharynx; this is sometimes tracheated, and is well marked in this state in *Calliphora* and *Stomoxys*. This tube curves upwards under the base of the labrum.

The proboscis in the Syrphidæ and the Empidæ corresponds with that in *Musca*, except that, in their case, the labial palpi have aborted, and the laciniae of the maxillæ and maxillary palpi are present.

Rudimentary Maxillary Palpi.—I shall now give a short description of the rudimentary maxillary palpi in a few species, figuring various forms.

Family ANTHOMYIIDÆ, subfamily *Mydæinæ*.—*Polietes lardaria*, Fabr. Palpi pyramidal in form, strongly haired, short pointed projection at extremity of stipes, palpifer marked; base $\frac{1}{275}$ in., length $\frac{1}{200}$ in. (Pl. 8. fig. 13.)

Same family and subfamily.—*Hyetodesia lucorum*, Zett. Very elongated, strongly haired, long blunt projection at extremity of stipes, palpifer marked; base $\frac{1}{1122}$ in., length $\frac{1}{257}$ in. (Pl. 8. fig. 16.)

Same family and subfamily.—*Hyetodesia perditæ*, Meig. Acutely conical, well haired, no projection, palpifer indistinct; base $\frac{1}{900}$ in., length $\frac{1}{300}$ in. (Pl. 8. fig. 10.)

Same family and subfamily.—*Myda impuncta*, Fallen. Broad at the base; base not haired; tapers off with a curve, where it is thickly haired; stipes broadens very much at end; palpifer indistinct; base $\frac{1}{600}$ in., length $\frac{1}{222}$ in. (Pl. 8. fig. 9.)

Same family and subfamily.—*Hydrotea dentipes*, Fabr. Short and thick; thickly haired, blunt projection of stipes; base $\frac{1}{600}$ in., length $\frac{1}{360}$ in. (Pl. 8. fig. 15.)

Same family and subfamily.—*Ophyra leucostoma*, Wied. Broad at the base, short and stout, thickly haired, palpifer distinct; base $\frac{1}{450}$ in., length $\frac{1}{400}$ in. The cardines are very strong in this species. (Pl. 8. fig. 14.)

Same family, subfamily *Homalomyiinae*.—*Homalomyia canicularis*, Linn. Very small, conical in shape; base $\frac{1}{1800}$ in., length $\frac{1}{838}$ in. (Pl. 9. fig. 28.)

Family MUSCIDÆ.—*Cyrtoneura stabulans*, Fallen. Tubular and short; stipes projects, well haired; palpifer fairly distinct; base $\frac{1}{600}$ in., length $\frac{1}{450}$ in. (Pl. 8. fig. 11.)

In a very rudimentary form I have found the palpi in a number of species. They have all very much the same appearance, so that a separate description would be superfluous. I have figured four species. In most cases only a few hairs remain, but in *Lasiops* I have found quite a tuft.

Family ANTHOMYIIDÆ.

Subfamily Anthomyiinae.

Hylemyia cardui, Meig. (Pl. 9. fig. 27).*H. pullula*, Zett. (very small).*Lasiops ctenoctema*, Kow.*Anthomyia radicum* (Linn.).*A. pluvialis* (Linn.).*A. sulciventris*, Zett.*Phorbia floccosa*?, Macq.*Pegomyia bicolor*, Wied. (Pl. 9. fig. 29).

Subfamily Homalomyiinae.

Azelia Macquarti, Stäg.

Family SARCOPHAGIDÆ.

Myiocera carinifrons, Fallen.

Family MUSCIDÆ.

Graphomyiamaculata, Scop. (Pl. 9. fig. 31).*Musca domestica*, Linn. (Pl. 8. fig. 12).*M. corvina*, Fabr.

Acalyptrate Muscidæ.—In a number of species in the Acalyptrate Muscidæ the palpi are quite fully developed, but, on account of the small size of the flies, are very difficult to make out. The maxillæ, when present in Diptera as hitherto observed, have only the lacinia and palpi present, the galæ having aborted. Such a state of things is seen in the Culicidæ, Simulidæ, Tabanidæ, and Asilidæ. In a small and common species of *Ephydra* (Pl. 9. figs. 21 & 22) I found a maxilla which has all the parts represented. This species has also the remarkable dentition previously alluded to.

In *Balioptera combinata*, Linn. (Pl. 9. fig. 18), an arrangement is seen differing from those already mentioned, but there are several species that follow this type. It is difficult to say whether the palpi or the lacinia are aborted. Comparing this species with the Syrphidæ one is inclined to think that the palpi are absent.

In *Nemopoda cylindrica*, Fabr. (Pl. 9. fig. 19), maxillary palpi can be made out, but the cardines are so faintly chitinized that their presence can only be suspected. In the nearly related *Sepsis cynipsea* the cardines and stipites are exceedingly short.

In *Sphærocera subsultans*, Fabr., the four palpi are found in a more developed state than any hitherto met with (Pl. 9. fig. 20.)

In the figure a dorsal view is given of the parts, showing the fulcrum, the mentum through the transparent membrane, and the labrum above it. I have examined several species of this family, but have only found similar palpi in *Borborus suillorum*, Hal. In *Limosina lugubris*, Hal., *L. sylvatica*, Meig., *L. fuscipennis*, Hal., and *Sphærocera denticulata*, Meig., the palpi were of much the same type as in *B. combinata* (Pl. 9. fig. 18).

Archaic Type.—The varying armature and shape of the trophi in Diptera suggest a speculation as to archaic types.

I. The labium was probably short as in *Tipula* and has gradually elongated. The labial palpi have remained at or near their original distance from the head, but have worked round to the upper part so as to be of service. Where this has not occurred (1) they have aborted as in the Syrphidæ, Empidæ, Bombylidæ, Asilidæ, Tabanidæ, and Culicidæ; (2) or they have followed the labella down, as in *Dilophus* (Pl. 8. fig. 8).

Siphona geniculata is an example of the extreme development caused by the advantages gained by elongation. In this species many parts usually present on the labella, teeth, and transverse expanding levers (ligulæ) have aborted, and no traces of the maxillary palpi are to be seen. From this we may infer that this type is more specialized,

and consequently less archaic, than *Ophyra leucostoma* (Pl. 9. fig. 17), which has an abnormally short labium, the maxillary palpi well marked, and the parts on the labella very evident.

II. *Pubescent Eyes*.—All the flies in the Cyclorrhapha with pubescent eyes that I have examined, either have the maxillary palpi only, or possess rudiments of them, *e. g.*, Syrphidæ, *Polietes*, *Hyetodesia*, *Hydrotea occulta*. Some species of Phoridae are apparently an exception; it is, however, very doubtful whether this family is in its proper division.

III. *Venation of Wings* (text-figs. 3 & 4).—The rudimentary palpi seem to follow the venation of the wings in a curious manner. The cell formed by the 3rd and 4th longitudinal veins (subapical or 1st posterior cell) is open in the Anthomyiidae, begins to close in *Cyrtoneura stabulans*, is nearly closed in *Musca domestica*, and is quite closed in *Phito melanocephala*. The palpi gradually diminish through these species till no sign is left in *P. melanocephala*.

Fig. 3.

Wing of *Polietes lardaria*.

Fig. 4.

Wing of *Phito melanocephala*.

IV. *Tegulæ*.—The tegulæ also seem correlated:—

- (1) When all the palpi are well developed, as in *Sphaerocera subsultans*, the subapical cell of the wing is open, the tegulæ are absent.
- (2) When the palpi are more or less rudimentary, as in the Anthomyiidae, the cell still remains open, but the tegulæ are well marked.
- (3) When the palpi are rudimentary, as in *Cyrtoneura stabulans*, the cell begins to close and the tegulæ increase in size.
- (4) When the palpi are very rudimentary, as in *Musca domestica*, the cell is still more closed, the tegulæ remain large.
- (5) When no trace of the palpi can be seen, as in *Calliphora*, the cell is still more closed, the tegulæ remain large.
- (6) In *Phito* and *Melanophora* the tegulæ are still more developed, no trace of palpi can be seen; the 4th longitudinal or median vein has closed the 1st posterior cell so much that it has left the margin.
- (7) In *Æstrus* the mouth-parts are rudimentary, the venation has left the lower part of the wing, and the tegulæ are at their largest development.

Working on the above data, a fly may be imagined with hairy eyes, a plumose arista, a venation approximating to that in the Anthomyiidae, mandibles fused into the labium, which would be short and stout; maxillæ also absorbed, but with both palpi well

developed, and the tegulæ small or absent. This might be an ancestral or primitive type of the Muscidæ.

Polietes and *Hyetodesia* would only differ from this insect by less developed maxillary palpi, a longer labium, and larger tegulæ. *Ophyra leucostoma*, while retaining the short labium, has lost the plumose arista, the hairy eyes, and retains fairly large rudiments of the palpi. *Cyrtoneura* has also lost the hairy eyes, developed a slightly longer labium, but retains the plumose arista and fairly large rudiments of the palpi.

In *Hydrotea* the palpi are present, but the plumose arista has gone. Some species retain the short labium, and others have lost the pubescence on the eyes. Finally, we come to the little *Lasiops*, with hairy eyes and only rudiments of the maxillary palpi.

My diagram is drawn up on this system—that is, as the species lose primitive characters they become more recent; and it would be tedious to trace the matter further, as a glance at the scheme will make my meaning clearer than any written explanation. (Plate 10.)

Classification.—It will be seen that this arrangement shows what excellent natural groups the species of the Anthomyiidæ and the Muscidæ have been divided into, and how one character more, the rudimentary palpi, follows the order in which the genera have been placed. It is well marked in the subfamily Mydæinæ, dwindles in the Anthomyiinæ and Homalomyiinæ, disappears in the Cænosiinæ, and no trace is found in the nearly related *Scatophaga*.

In this paper I have endeavoured to avoid a controversial attitude, but it must be obvious that if the conclusions I have arrived at are *correct*, the contrary must be the case with the works of several theorists, and that the generally accepted dogma that the palpi in Diptera are homologous and maxillary can no longer stand. Therefore it will probably be urged by some (and, looking at the subject from their point of view, I admit quite fairly) that my methods are out of date, and that comparative anatomy must give way to a minute sectional study of the insect from the ovum, through the metamorphoses, to the imago state. To this I answer that this method, so apparently promising and conclusive, when applied to the trophi of Diptera, is discounted by its results. Either it is a tool of such complexity and nicety that no observer has hitherto used it correctly, or the facts observed have not been properly weighed and understood.

Since the preceding pages were written, Professor V. L. Kellogg has published a paper which lends valuable aid to my contention as to comparative anatomy and ontogenetic study, when applied to the homologization of the mouth-parts of Diptera*.

If the presence of labial and maxillary palpi in Diptera is admitted, and I cannot see how, unless my facts are traversed, this can be denied, such speculations as the derivation of the labella from the fusion of the labial palpi or from the *first* maxillæ cannot be entertained, though my investigations quite agree with the theory that the labium is a modified double maxilla, derived from the second pair of jaws.

* "The Development and Homologies of the Mouth-parts of Insects," The American Naturalist, vol. xxxvi. (Sept. 1902), pp. 683-706.

NOTE.—*The Homology of the Cardines.*

It has been objected that the homology of the levers of the labrum in the Muscidae (the “apodemes” of Dr. Benjamin Lowne) with the cardines of the maxillæ is not quite clear. As this is of vital importance to my theory, I have enlarged my argument and summarized it as follows:—

1. In *Vespa* and *Apis* the cardines are on the same plan as in *Musca*. They are generally admitted to be the “hinges” of the “posts” supporting the palpifers and other parts. If these are cardines here, so must they be in Diptera.
2. It may be urged that the fact that the levers are enclosed is against the theory that they are cardines. This objection has no weight. The cardines being the lowest part, they would (if there were any tendency in that direction) be the first part to be embedded.
3. In *Culex*, ♀, the levers are undoubtedly cardines, the four-jointed palpi are affixed to them, and though the palpifer is differentiated, I have failed to see the point where the stipes and cardines fuse.
4. In *Eristalis* and *Helophilus* parts of the maxillæ are present with palpi. It is impossible to deny the homology of the posterior ends with the apodemes. Therefore as these parts bear the palpi, they must be in some part the stipites; and as similar parts in *Vespa* and *Apis* are admitted to be the cardines, in *Eristalis* and *Helophilus* they must be the fusion of the stipites and cardines, which applies equally to the Muscidae.
5. It may be suggested that in the Muscidae the levers are so obviously necessary to work the labrum and hypopharynx that they would specially evolve. To this it may be answered that the levers are present in *Culex*. In the female they hinge on to the blades of the maxillæ; in the male they work the long palpi characteristic of that sex. So in Diptera we know of three uses of the cardines, showing there exists a tendency to utilize this part.
6. In the small *Ephydra* figured (which, judging from a determination of Mr. Piffard, is *Hydrellia griseola*, Fallen), in the same places as the apodemes are also found complicated organs, which are evidently the complete maxillæ.
7. The negative proof—if they are not cardines, what are they?

EXPLANATION OF THE PLATES.

The lettering applies to all the figures.

<i>a</i> , labium.	<i>k</i> , stipes.
<i>b</i> , paraglossa.	<i>m</i> , cardo.
<i>c</i> , ligula.	<i>n</i> , maxillary palpus.
<i>d</i> , labial palpus.	<i>o</i> , palpifer.
<i>e</i> , palpiger.	<i>p</i> , mentum.
<i>f</i> , mandible.	<i>r</i> , submentum.
<i>g</i> , maxilla.	<i>s</i> , labrum.
<i>h</i> , galea.	<i>t</i> , hypopharynx or lingua.
<i>i</i> , lacinia.	

PLATE 8.

- Fig. 1. Labium of *Tabanus* (*Hæmatopota pluvialis*), lateral view. The remaining parts (the mandibles, maxillæ, max. palpi, labrum, and hypopharynx) have been removed.
2. Head of *Empis chioptera*.
3. Proboscis of *Eristalis tenax*, lateral view.
4. „ „ *Calliphora erythrocephala*, lateral view.
5. Dissection of the maxilla and palpus of *Helophilus pendulus*.
6. „ „ „ *Eristalis tenax*.
7. Dissection of the dorsal plate on the labium of *Calliphora erythrocephala*, showing the embedded mandibles. The lower end shows a portion of the pharynx, dorsal view.
8. Labium of *Dilophus albipennis*, ventral view.
9. Maxillary palpus of *Mydaa impuncta*. Only the anterior end of the stipes is shown, with a lateral view. This applies to all the figures of palpi on these Plates.
10. Maxillary palpus of *Hyetodesia perdita*.
11. „ „ *Cyrtoneura stabulans*.
12. Rudiment of maxillary palpus, *Musca domestica*.
13. Maxillary palpus of *Polietes lardaria*.
14. „ „ *Ophyra leucostoma*.
15. „ „ *Hydrotea dentipes*.
16. „ „ *Hyetodesia lucorum*.

PLATE 9.

- Fig. 17. Proboscis of *Ophyra leucostoma*, dorsal view.
18. „ „ *Balioptera combinata*, lateral view.
19. „ „ *Nemopoda cylindrica*, lateral view.
20. „ „ *Sphærocera subsultans*, dorsal view.
21. „ „ a species of *Ephydra* (*Hydrellia griseola*, Fallen?).
22. Maxilla of same, more highly magnified.
23. Part of the labium of *Culex pipiens*, ♀, showing the labella, dorsal view.
24. Dissection of the cardo, stipes, palpifer, and palpus of the maxilla of *Culex pipiens*, ♀.
25. Extremity of the labrum of *Culex pipiens*, ♂. This has affinities with the labrum in some species of the Syrphidæ.
26. Extremity of the labrum of *C. pipiens*, ♀, showing the higher organization of the female.
27. Rudiment of maxillary palpus, *Hylemyia cardui*.
28. „ „ „ *Homalomyia canicularis*.
29. „ „ „ *Pegomyia bicolor*.
30. End of stipes, *Phito melanocephala*.
31. Rudiment of maxillary palpus, *Graphomyia maculata*.

PLATE 10.

Diagram showing a speculative arrangement of genera and species, placed as they recede from a hypothetical primitive form.

West, Newman imp.

PALPI IN DIPTERA.

W. Wesché, del.

Collings, photoco.

HYPOTHETIC ARRANGEMENT OF GENERA OF MUSCIDÆ.