XI. The systematic affinities of the Phoridæ and of several Brachycerous families in Diptera. By W. Weschelé, F.R.M.S. Communicated by J. E. Collin, F.E.S.

[Read April 1st, 1908.]

Plate VII.

While making some dissections of the mouth and genitalia of Phora inerassata, Mg. (the comparatively large species common on our English hedgerows in August and September), I have met with many peculiarities, and have been struck with the position of the family in the systematic lists.

This position has often been debated, the last contribution being from Mr. Charles T. Brues of the Public Museum, Milwaukee, Wis., U.S.A. He considers that the Phoridæ and Lonchopteridæ are distinctly related, and that the former also have affinities with the Borboridæ and Hippoboscidæ, the wing venation being near that of Olfersia, but as a compromise is willing that they should be placed, as Dr. Williston placed them in 1896, in the Cyclorrapha, between the Platypezidæ and the Muscidae.

Since then Dr. Williston has found some "Nemocerous" characters, "the venation being quite identical with that of Aspistes of the Bibionidae," and considers that the antennæ do not offer "insuperable objections to the location of the family among the Nemocera." He attaches great importance to the fact that in several species the palpi are two-jointed.†

The publication of these views called forth Mr. Brues' essay, which contains a very able statement of the position, an exhaustive review of the literature, but, I regret to say, no convincing argument to support his views.

The late Baron von Osten-Sacken saw the affinities between the Phoridæ and the Lonchopteridæ and included

* The systematic affinities of the Dipterous family Phoridæ.—"Biological Bulletin," vol. xii, No. 6, May 1907.

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them both in a sub-family, "Energopoda," with the Asilidae and Empidæ, placing the group at the end of the Orthorrapha.* Herr Theo. Becker thinks that they are derived from Nematocerous forms allied to the Mycetophiliidae and notices the structure of the bristles found only in the Phoridae and Mycetophiliidae.†

Schiner in his "Fauna Austrica" placed them between the Bibionidae and the Borboridae, but whether for convenience, or on account of affinity is not clear.

Not one of these authors is sure whether this family belongs to the Orthorrapha or to the Cyclorrapha, and nothing definite seems known about the mechanism of the pupa-case.

The problem being so difficult of solution, Osten-Sacken even going so far as to say that "a real affinity with Phora does not exist anywhere," it may seem presumption in me to attempt to solve it, as I certainly have no pretensions to a comprehensive knowledge of exotic species of Diptera. But I am encouraged to present my views, as I attack from a new position, none of these writers with the possible exception of Becker having made much use of the microscope, while the great majority of the observations from which my conclusions have been arrived at, are founded on the anatomy and microscopic structure, the minute size of these insects mostly requiring a magnification of 250 diameters for a good view of such organs as mouth parts or genitalia.

After an examination and comparison of a number of preparations, and a study of the genitalia of several species of Phoridae, (I was already familiar with the Muscid forms), I came to the conclusion that they have no real affinities either to the Borboridae or the Hippoboscidæ, the families that are placed before and after them in Mr. Verrall's list of British Diptera. Further, they are sharply divided from any of the Muscidæ by the absence of the ptilinum, the membrane on the head, which being inflated, is used to push the cover off the pupa-case. The absence of this structure raises a very strong doubt as to whether the Phoridae have any place in the Cyclorrapha; a doubt that in my mind is a certainty that they have not.

It is not only (1) the absence of the pitilinum that separates this family from the Astiadeæ, or Borboridæ on one side, and the Hippoboscidæ on the other, but also (2) the venation, (3) the general morphology, particularly of the fore limbs, (4) the articulation of the antennæ, (5) the character of the anterior thoracic spiracles, (6) the structure of the eyes, (7) the peculiarity of the hair structure, (8) many characters of the mouth parts, (9) and the peculiarities of the genitalia.

2. The venation. This is so striking and so well known, that it needs no description, and the absence of true transverse veins, brings it far closer to such combinations as are found in the Simulidæ, the Mycetophilidæ, or even in some of the Dolichopodidæ than to the Muscid type.

In Trineira aterrima, F., is found a rudimentary vein, consisting of microscopic hairs, following the course of the wing-edge.* This probably shows that the lower thick vein which so abruptly stops, at one time continued to the end of the wing and is the second longitudinal; in comparing the venation with that mentioned above, this ought to be taken into consideration.

Becker has expressed very similar views to those announced earlier in this section, in his monograph already referred to. Brues, while holding to his opinion as regards Olfersia, admits that the affinity between the venation in Phora and Mycetophila, as analyzed by Girschner, and which is the source from which Becker's opinion is derived, is almost convincing.

It will thus be seen that the Phorid venation is but of small assistance to the systematist, as in spite of its being so simple, striking and peculiar, it has led to very divergent opinions, it having been claimed as identical with Aspistes, and near to Mycetophila and Olfersia!

3. Morphology. The general shape approximates more to that of the Pulicidæ at the other end of the scheme, than to the flattened Pupipara, and the long coxae and the legs are similar to those of the Mycetophilidæ, the Lonchopteridæ and the Dolichopodidæ.

4. The antennæ. The articulation of the third joint of the antennæ on to the second is very characteristic. I say the second joint as Brues has clearly shown in the paper already referred to, that what is usually called the first

* Indicated in Schiner's "Fauna Austria, Die Fliegen," Plate II, Fig. 4.
joint is a fusion of the first and second. Personally I am inclined to go further, and see more than two joints in the fused part, but for the present I will accept Brues' nomenclature.

The third joint when seen in microscopic section is found to be hollow, very neatly fitting round a bulb at the end of the second joint, which is articulated by a short process descending from the third joint. This is well seen in Coniceria atra, Mg., P. ruficornis, Mg. and indeed in every species I have examined; it appears to be a constant Phorid character.

In the Muscicic the third joint is slightly hollow at the base, and is penetrated by a cone-shaped process from the second joint which is in contact on all sides, there being no special articulating part. A similar arrangement to that found in the Phoridæ (as far as my observations go) is only found in a few genera in the Dolichopodidæ and in Lonchopetera flavicandula, Mg., and in these in a modified form. It will be found in most of the genus Dolichopus, and D. acuticornis, W., and Gymnopterus assimilis, Staeg., show it particularly well. This I consider a strong mark of affinity, which as I shall show later is only one among many.

5. The thoracic spiracles. The anterior thoracic spiracles are very constant in character in families, and show little or no variation in genera and species. In P. incrassata, P. concinna, Mg., T. aterrima, C., atra and Gymnophora arenata, Mg., they are circular, with chitinous rings or edges, and fringed with simple hairs.

In the Muscidæ and the Hippoboscicidæ they are oval and have branched hairs. In the Lonchopteridæ they are oval, but more rounded than in the Muscicidæ. In the Dolichopodidæ they resemble the conventional tear, rounded at one end, and gradually tapering to a point. In the Mycetophilidæ and the Leptidæ, the bordering ring is not so well defined and the shape is inclined to the oval. In the Empidæ they are circular, and as in the last four families, simply ciliated, and are very similar to the organs as they are found in the Phoridæ.

6. The structure of the compound eyes. In the Nematocera the compound eyes often consist of a chitinous plate, pierced with circular apertures for the lenses. When the eyes are pubescent, the sub-quadrate space between four lenses is occupied by a hair, the socket of which is very
marked, and relatively large; this condition is well seen in some Mycetophilidæ. A somewhat similar structure is found in some Dolichopodidæ, that in *Porphyrops gravipes*, Wlk., being a good example.

In *P. incrassata*, *P. rufipes* and *T. aterrima* and a number of other species this is so far modified that the plate has gone, but the eyes are bordered by chitinous bands, and in each junction of the bands is a socketed hair, very similar if not identical in structure with the hairs found in the Nematocera or Brachycera. The pubescence found on the eyes in the Muscidæ is of a different type, being transparent and weak, and not tapering, just the opposite being found in the Nematocera, where each hair tapers from a comparatively broad base to an exceedingly sharp point, while in the Muscidæ the socket is so minute as often to be scarcely visible, and the lenses are never separated by bands.

7. The structure of the hair and bristles. This is peculiar; it is as if each single bristle were made up of a number of fine hairs of various lengths, so that its point and edges appear almost plumose, certainly serrated. The hairs are numerous and strong, and so characteristic in appearance, that it is easy to recognise them as either from a Phorid, or as the apical bristles from the tibia of a Mycetophilid. The Mycetophilidæ are the only other family in which this structure is found, and in them only on the tibiae. It is figured in Becker's monograph already referred to; but will require a magnification of 250 diameters to see clearly on the actual insects. It is so characteristic, that even were other similarities absent, I should consider it a strong mark of relationship.

8. The mouth parts are difficult to study owing to smallness of size, but can easily be seen to have but little affinity with those of the Mycetophilidæ, and indeed might be thought to approximate (as they do in some characters) to the Muscid form, yet as I shall show later, can only be homologised by comparison with Nematocerous forms.

Except in *Gymnophora arcuata*, Mg., and here I am not quite certain owing to the imperfection of my preparation, the armature of the species examined is different in the sexes. Not in the manner found in *Tabanus* and *Culex*, where the males are without the mandibles, but in the structure of the labrum and the aculeations or teeth on the paraglossæ; the labrum has in the females of many
species, a frontal barb and lateral sharp processes, while in the male it is, though ample in size, quite unarmed, and the teeth on the paraglossæ are much less developed than those of the female.

The arrangement and number of parts are nearly similar to those in Bibio; but the paraglossæ are very large and bear rather widely separated, relatively narrow tracheæ; the cleft between the paired lobes is very deep and unlike Bibio has chitinised plates on the interior edges. The mandibles are soldered into the mentum in the median line, and consequently are as in Dolichopus as well as Bibio on the ventral side, opposed to the condition found in the Muscidæ, where they are invariably on the dorsal side.

The lacininæ of the maxillæ are fused at their points and form the curious triangular aculeation, at the base of the cleft of the paraglossæ characteristic of the Phorid trophi; the cardines are hard to differentiate and may have disappeared. The labrum has in addition to the armature already mentioned, in all the species I have examined, a minute pubescence on the anterior extremities, only to be seen with very high powers. The hypopharynx is strong, and deeply channelled and suggestive of a raptorial habit.

The paraglossæ carry a number of "taste hairs" which occupy two positions, as besides the usual solitary hair at the end of the trachea, there are a number of taste hairs on the edges of the paraglossæ, the ventral surfaces of which have a tendency to chitinise, and have an appearance similar to that found in Nematocerous forms.

This arrangement is peculiar, and a search through my collection has resulted in the finding of a striking similarity in the paraglossæ of Leptis scolopacea, L., not only in the position of the taste hairs at the edges, and the chitinous ventral membrane of the paraglossæ, but in the general appearance, in the narrow tracheæ, the tubes much separated from each other, and in the deep cleft, the edges chitinised between the two paraglossæ. The mandibles are also on the ventral side, but here the similarities end, as they are laterally placed and have not fused in the median line. Similar conditions are found on the labium of Lonchoptera flavicauda, Mg., together with an armature identical with L. scolopacea. The tracheæ are narrow, and spring from paired chitinous plates. The palpi are maxillary and not
labial, as I find atrophying blades of the maxillæ at their bases. In my paper on the mouth parts of the "Nemocera," published in the "Journal of the Royal Microscopical Society" in 1904, I described them as labial as my preparations showed no maxillæ, but my dissections lately made have been more successful, and enable me to say that the lacinia or blade of this insect is 85 μ. or \( \frac{3}{10} \) inch long, and I submit that it is as easy to overlook, as it is difficult to dissect, objects of this size.

It will thus be seen that I have found a striking affinity between these three families in the mouth parts, which show that the true place of Phora is among the older families of the Brachycera.

In the Phoridae the palpi in the limited number of species I have examined are labial. This point I very carefully studied, as the palpi being maxillary in Leptis and Lonchoptera made me suspect that I was wrong in describing them as labial, though perhaps this has little bearing on the matter, if it be remembered that Bibio and Chironomus differ in this respect.

The palpi are very large, and bear a number of the characteristic Phorid bristles; at their bases are many wrinkles, scarcely annulations, and in one preparation, Phora concinna, Mg., they are two-jointed. This is not, however, the only Nematocerous character; in T. aterrima the palpi bear the sense organ, found on the second joint in the Mycetophilidae, Bibionidae, Simulidae and Rhyphidae. This I have thought to be an olfactory organ and I have figured it as such, as it is found on the palpi of Bibio hortulanus, L.*

9. The genitalia (male). The hypopygium is free and is joined to the abdomen by a membrane; it is furnished with representatives of the usual paired organs. In P. incrassata these are hairy bulbs much closer in function and appearance to the cerci of Periplaneta than to the usual hooks or forceps of Diptera. In another species, P. concinna, Mg., only a single hairy organ with a transverse suture, placed on an asymmetrical platform, is present. In T. aterrima two minute hairy bulbs are present. The part that supports these organs and the anus, is in a more dorsal position and is separated by a suture from another lower part. This lower part seems to be formed of the


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forcipes interiores and palpi genitalium and contains the penis. Usually these organs are hidden in the cavity of the hypopygium. In *P. incrassata* are found paired hooks and plates, the latter covered with a minute sculpturing of the chitin identical with that found on parts of the genitalia of *Periplaneta*. These hooks and plates surround the penis, which is formed of a hyaline membrane based on a chitinous ring, and with some structure and tubercles on one side. The ejaculatory duct runs up through the chitinous ring, and opens on the side opposite the tubercles. The penis is asymmetrical, and is the simplest and rudest that I know in Diptera. The spinus (unless it has soldered into the back of the penis, and is present as the "structure" alluded to above), and the apodemes, appear to be absent. *P. convinna* has a more elaborate penis, and its base is fused with a lever which probably represents the great apodemes, and sensory structures represent the palpi genitalium and forcipes interiores, but this last portion of the genitalia is difficult to understand and requires more material for study. In *T. aterrina*, though the containing plates of the lower part are easily differentiated as forceps interiores and palpi genitalium, the penis is minute and unsymmetrical, and seems to be a membrane based on a ring as in *P. incrassata*, but the ejaculatory sac and apodeme are quite obvious.

A fourth species, *P. rufigipes*?, has the penis and surrounding parts of another type. The variations generally are much greater than usually found between species, or even genera in the Muscidae. One cannot but be struck by the extraordinary anomalies in the parts; all these insects have the organs representing the forcipes superiores and forcipes inferiores of a more archaic type than those found in the Mycetophilidae, together with (in *Trineura*) an ejaculatory apparatus such as is found in the highly specialised Muscidae.

In *Conicera atra*, Mg., the genitalia are far more symmetrical and appear to approximate to the form that is found in the Lonchopteridae, and both suggest a relationship to Dolichopus.

The genitalia (female). The ovipositor is fairly simple; it is similar in general plan to that found in the Dolichopodidae, that is to say it is moderately long, protrusile, and with distinct joints, but lacking the chitinous rods found in the Muscidae. At the distal extremity are
the usual sensory organs. The receptacula seminis are soluble in the process necessary for preparing the insect for high-power microscopic examination. This is never the case in the Muscidae, with the exception of the Chloropidae.

In the ovipositor of *P. curvimereis*, Becker, I found a single chitinous rod which appears to be homologous with the apodeme found in the ovipositor of *Simulium reptans*, L., and there are chitinous levers connected with the valves similar to those found in Chironomus, in *Gymnoptera arcuata*, Mg., *P. lutca*, Mg., and *P. ruficornis*, Mg.*

On the extremity of the ovipositor of *P. ruficornis* there is a chitinous serrated process, and the abdomens of two females contain larvae of an unfamiliar type, and I think that this species is viviparous.

Those who have had the patience to follow me through these details, necessary to prove my case, will see that in this family are preserved characters of very archaic type in the peculiar bristle structure, in the cerci, and in the Periplaneta-like structures in the male genitalia while other parts approximate to the Muscid type in the ejaculatory sac and apodeme. In the ovipositor of the female will be found similar anomalies. The ovipositor may be said to be nonexistent in the Nematocera, in the Phoridae it is well developed, yet in some species carries structures only found in the Simuliidae and Chironomiyidae.

In the trophi, the presence of two jointed palpi in at least two species, the sense organ in *Trincerva* and the very general situation of the embedded mandibles on the ventral side are distinctly Nematocerous characters; while the teeth on the paraglossae are a character only hitherto found in the Muscidae.

The labrum and hypopharynx are nearer the same parts in the Brachycerous Dolichopodidae and Empidae than to homologous structures in any other family, while the paraglossae and their tracheae are very similar to those of Lonchoptera and Leptis.

I have lately found in the heads of some Asilidae, Empidae and Dolichopodidae a chitinous bulb at the base of the hypopharynx, connected with that organ by a tube and having some contrivance resembling a valve. It is obviously homologous with the pharyngeal pump in *Culex,*

but differs in shape, in the valve, and in being more highly chitinised in the outer envelope. The appearance of this organ in *Asilus* and *Dolichopus* is so singular and so similar as to indicate a very near relationship between these three families. The *Asilidae* alone among the families of the Brachycera preserve the ciliated hypopharynx, which is so constant a character in the Nematocera.*

Weighing these facts, I must extend Becker's idea of relationship to the Mycetophilidae; I think that while the Mycetophilidae, Asilidae, Empidæ, Dolichopodidae, Lonchopteridae, Phoridae and Leptidae have had a common ancestry, the Dolichopodidae and the Phoridae have each inherited a more than normal tendency to vary, resulting in the curious contradictions in detail that are found in the Phoridae, and the wide departure of the Dolichopodidae from the usual type of mouth, the character of the tracheæ in most genera being unique.

It will be noticed in the families enumerated above, that the wing-venation is fairly complex in the larger insects, and simpler in proportion to the size of the others. Taking as an example the venation in *Hippobosca*, which we know by the character of the mouth, has degenerated from a Muscid form, we there see a tendency for the transverse veins to shorten or be lost, and for the veins to leave the lower part of the wing. This is what has also happened in the Phoridae and Simulidae, and all three groups appear to have undergone parallel degeneration. As the parasitic habit increased, or size decreased, the wings, being less used or having less weight to bear, became more simple as regards their venation. In the Lonchopteridae the mouth has closely preserved the characters found in *Leptis*, and except for the remarkable wings and their sexual differences, developed no striking peculiarities, and is probably a family much less liable to vary than *Phora*; so in the wings less simplification is seen though the transverse veins have disappeared. A parallel case appears to exist in the Psychodidae. The fact that apterous or semi-apterous species exist, belonging to the Phoridae, Dolichopodidae, and Hippoboscidae, bears on my argument, and demonstrates the superior value of the mouth parts as tests of affinity.

This being so the venation, invaluable as a generic character, must be a secondary consideration in grouping the families, for which characters derived from the mouth parts are of greater importance. It follows that drastic alterations are necessary not only in the group under discussion, but even in the Cyclorrhapha.

The families of the Brachyceorous Orthorrapha are arranged in Mr. G. H. Verrall's list of British Diptera in the order given below in the left column; in the right column as I propose to rearrange it.

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<th>Brachycerous Orthorrapha</th>
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<td>Stratiomyidæ</td>
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<td>Tabanidæ</td>
<td>Empidæ</td>
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<td>Leptidæ</td>
<td>Dolichopodidæ</td>
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<td>Asilidæ</td>
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<td>Therevidæ</td>
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<td>Scenopinidæ</td>
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<td>Lonchopteridæ</td>
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The Asilidæ are placed first on account of the Nematocerous hypopharynx and of the process in the pharynx homologous with the "pharyngeal pump" in the Culicidæ, and therefore also a Nematocerous character.

The Empidæ follow, as they have the same organ but in a modified form. It is well seen in E. livida, L. and in many of the minute Tachydromia.

The Dolichopodidæ must come next as the possession of a similar process shows a very close connection between these three families, while the arrangement of the mouth as regards the mandibles is also a Nematocerous character.

The Phoridæ follow, not only on account of their Nematocerous characters demanding an early place in the Brachyceera, but also from a number of characters which suggest an affinity with the Dolichopodidæ, and in a less degree with the Empidæ. I propose to state these at length at the end of the paper.

The Lonchopteridæ are placed next on account of similarities in the trophi and many other points, following Dr. Williston's and the late Baron von Osten-Sacken's
classification. The Leptidæ come next, as their mouth parts are nearly identical with those of the Lonchopteridæ.

Then come the Stratiomyidæ, Tabanidæ, Bombylidæ, Therevidæ and Scenopinidæ in their usual order, and the Cyrtidæ close the list in the Orthorrhapha, occupying a position where their very large tegulae do not seem at all out of place. It will be seen by this rearrangement that the first, second and third families possess the striking character of the process in the pharynx, the third, fourth and fifth, the equally striking character of the peculiar articulation of the antennæ, while the fourth, fifth, sixth and seventh have chitinous plates on the paraglossæ, and from the second to the seventh family (the Stratiomyidæ) all six have the mandibles embedded on the ventral side.

**Affinities between the Phoridæ and the Dolichopodidæ.**

1. **General morphology.**—The thorax and the coxae, particularly the fore coxae, are often similar, and the legs are sometimes much alike.

2. **Antennæ.**—The Dolichopodidæ, Phoridæ, and Lonchopteridæ have a common peculiar articulation of the third joint, discussed more at length in the earlier part of the paper.

3. **Characters in the mouth parts.**—(a) In Dolichopus the mandibles are also embedded on the ventral side, on the median line of the mentum. (b) What remains of the maxillæ instead of remaining in the base of the labium as is almost invariably the case, occupy a very anterior position, as far as my observations go—a unique position and a character confined to the two families. (c) There are only two other families in Diptera in which the labrum is armed, the Dolichopodidæ and the Empidæ. (d) On the labrum of many species of Phoridæ, high powers show a decided pubescence. The hairy nature of the labrum is a peculiar character of the Dolichopodidæ. (e) The hypopharynx is strong, deeply channelled, and viewed laterally is more like its homologue in Dolichopus than in any other family. (f) The palpi are large, and bear a number of bristles, and similar conditions exist in many Dolichopodidæ. (g) The taste hairs are similarly arranged, and are larger than in the Muscidae.
My study of the Phoridae is based on about a dozen species belonging to four, or if we admit Apiocheta of Brues, five genera, and in all the characters of the trophi, with the exception of the palpi, have been very constant, while in the Dolichopodidae they vary greatly. The short predaceous labium of Aphrosylus, Dolichopus or Medeterus, lengthens in some Gymnopterans (G. assimilis, Stag., for example), and is specialised for flower feeding in Orthochile, while Psilopus vielemannii, Fln., has lost the curious characteristic tracheae of the family. I therefore point out that the affinities pointed out are most readily seen and understood in the genera, Dolichopus, Aphrosylus and Medeterus.

4. The Structure of the Compound Eyes.—The character of the pubescence on the eyes is similar in some Dolichopodidae and Phoridae; it has been fully discussed in section 5.

5. Characters in the Male Genitalia.—The Dolichopodidae in the majority of species, have the hypopygium much developed, free, and attached to the abdomen by a membrane; the forcipes interiores and palpi genitalium are outside the cavity of the hypopygium. Similar conditions are only found in the Phoridae, the two families sharing these characters, though the armature is unlike in detail and general arrangement.

6. Characters in the Female Genitalia.—In the Dolichopodidae the ovipositor is similar in type, though with one joint more—all the Phoridae examined having six segments in the abdomen and three in the ovipositor, while D. griseipennis, Stan., has five in the abdomen and four in the ovipositor. The receptacula are also soluble in the preparation of the insect. This is common in the Nematocera, but quite rare in the Brachycera.

7. Predaceous Character.—This calls for evidence as it has not before been touched on. (a) The structure of the mouth parts in the hypopharynx and labrum suggests a raptorial habit. (b) The legs also. (c) A preparation of the female of P. rufipes shows in the contents of the abdomen, the appearance which I associate with the digested blood or juices of insects. (d) I have in my cabinet a small acalyptate Muscid which I took out of the grasp of P. concinna. Both are mounted on the same card, and till I examined them with a lens, I was under the impression that they were “in copula”; unfortunately the
head of the victim has been lost, but enough remains to take away the character, or to put it the other way, to establish the character of *P. concinna* as predaceous, but of course I do not commit myself to the statement that every species in the family is predaceous, probably like the Dolichopodidæ they will feed on any animal food. It is but fair to say, that so far nothing similar has been observed by collectors of Phoridæ.

In conclusion I must express my great obligations to Dr. J. H. Wood for the gift of named specimens, and to Mr. E. E. Austen for kind criticism and information on the literature of this subject.

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**Explanation of Plate VII.**

[See *Explanation facing the Plate*.]