

Preliminary notice of a subdivision
of the Suborder
Orthorrhapha Brachycera (Dipt.)
on chaetotactic principles,
by
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In adopting three (instead of two), Suborders of Diptera,¹⁾ I made at the same time an attempt at a subdivision of these Suborders into what I then called Divisions, but which, since the appearance of J. H. Comstock's „Manual“ etc. (1895), I prefer with him to call Superfamilies. I pointed out characters by means of which such Superfamilies could be defined, characters that, heretofore, had been entirely overlooked or neglected. The importance of the structure of the head of the male, for instance, which I called holoptic, had never been sufficiently appreciated, in so far even that there was no special term for it. The total absence of this character in my Superfamily *Nemocera vera*, and the presence of several other characters, borrowed from different parts of the body, as well as from the early stages of these insects, justify the separation of this Superfamily from a provisional division which I called *Nemocera anomala*. At the same time, there is no doubt that both Superfamilies belong to the same Suborder, *Orthorrhapha Nemocera*.

Within the Suborder *Orthorrhapha Brachycera*, for the families *Stratiomyidae*, *Tabanidae*, *Acanthomeridae* and *Leptidae* (including *Xylophagidae*), I formed the Superfamily *Eremochaeta* (the

¹⁾ In my paper: On the characters of the three Divisions of Diptera, in the Berl. Ent. Zeit. 1892. A preliminary notice of this paper: „Suggestions etc.“ appeared in the Entom. M. Mag. 1891, p. 35, and an „Explanatory notice etc.“ in the same periodical, 1893, p. 149.

derivation is analogous to that of the Greek word „ἐρημοζόμης“, deprived of hair), characterized by the absolute want of macrochaetae, by the predominance of holoptic heads in the male sex, by the presence, in most cases, of three pulvilli and of five posterior cells, by the more or less distinct development of the posterior squamae (which do not exist in the *Nemocera*), and by other characters. The larvae of this Superfamily belong to a peculiar type, called the long-headed larvae (Marno).¹⁾

After separating the *Eremochaeta* (1891), as a Superfamily, from the rest of the *Orthorrhapha Brachycera*, I attempted the grouping of the remaining families of this Suborder. All these families, with the exception of the *Mydaiidae*, *Cyrtidae* and *Nemestrinidae*, are chaetophora, as I called them in 1884, that is, macrochaetae-bearing. I found confirmed, in this case, some generalizations concerning the distribution of the macrochaetae, which I had foreshadowed in that same year (Essay of comparative Chaetotaxy, Trans. Ent. Soc. London, 1884, p. 500—501). Such generalizations are:

1) That among aërial Diptera, macrochaetae are scarce, while among the pedestrian Diptera they are abundant. 2) That the aërial Diptera show a distinct prevalence of holoptic heads, which is generally connected with power of hovering (in the Essay I called it poising). The pedestrian Diptera, on the contrary have, for the most part, dichoptic males, or, at least pseudo-holoptic ones, as I would call some of them (for instance those of some *Empidae*; the explanation will be given immediately). 3) That the aërial Diptera, in consequence of their mode of life, have weaker legs, of simple structure,²⁾ principally fit for alighting, and are usually provided with peculiar adaptations in the venation. The pedestrian Diptera use the legs not for alighting only, but for running,

¹⁾ My paper in the Berl. Ent. Z. 1892 has the words to be continued at the end (p. 466), because I intended to publish on the *Eremochaeta* as detailed a statement as I had done for the *Nemocera*. The paper was in an advanced state of preparation, but I postponed its publication for the purpose of a better study of the ancestral forms, so abundant in that Superfamily. I have not found in Museums as much as I expected, and so, from one postponement to the other, the paper remained unpublished to this day. I still hope to see its completion and publication.

²⁾ The use of the legs for cleansing (head, wings etc.) and the adaptations for that end, are, I suppose, common to all Diptera (small bristles, or spinules on the legs, especially the tibiae), and for this reason are taken for granted in my text.

and all kind of other work, seizing their prey, carrying it, climbing, digging etc.; their legs are provided not only with spines and bristles, but with still other appendages, which may be useful, or only ornamental, as secondary sexual characters.

I mentioned above the term pseudoholoptic head as distinct from a true holoptic one. In 1884, not having yet understood this difference, I did not make any mention of it; since then I learned to appreciate its importance. True, complete holopticism, as that in some male *Tabanidae*, *Bombylidae*, *Cyrtidae*, *Syrphidae* (among the *Cyclorrhapha*), is alone connected with the faculty of hovering in that particular fashion which distinguishes most genera of these families. Pseudoholoptic heads, more or less incompletely contiguous, occur in several pedestrian groups which, nevertheless, have aerial habits, and thus, by adaptation, acquire an incomplete degree of holopticism. They can swarm, soar, but they do not hover, like the males of the other group. Nobody will contest that *Empidæ*, in their organization, are truly pedestrian Diptera; at the same time it is their aerial habits that tend to develop their pseudoholoptic heads. The same is the case with *Homalomyiæ*, among the *Muscidae*, well-known for the aerial dances of their males; their eyes are more or less contiguous, but their heads are not truly holoptic, nor do such flies hover in the true sense of the word.

Among all the orders of Insects, the Diptera display the greatest variety in their modes of motion, and the greatest power of control over their motions. It seems, therefore, rational that, by means of the study of the motions in different groups of Diptera, we should, in this Order, more than in any other, find indications towards the discovery of corresponding differences in the organization, and hence a clue to a natural classification.

On the above-defined principles of subdivision, I now establish two new Superfamilies of the *Orthorrhapha Brachycera*:

1. The **Tromóptera** for the aerial families: *Nemestrinidae*, *Cyrtidae*, *Bombylidae* and *Therevidæ* (including the *Scenopinidae*).

The name is derived from the Greek substantive ὁ τρέμος, the act of trembling (from τρέμω, I tremble), in allusion to the characteristic faculty of hovering, which most of the Diptera of this family possess, a faculty that, as I have shown, seems to have some connection with true holopticism in the male.

2. The **Energópoda** for the pedestrian families: *Asilidae*, *Dolichopodidae*, *Empidæ* (in the widest sense), *Lonchopteridae* and probably *Phoridae*.

The name is derived from the Greek *ἐνεργός*, active, strong, in allusion to the development of the legs of the corresponding Diptera. (In composing these names I had the advice and assistance of the distinguished Greek scholar, Prof. Stadtmüller of Heidelberg.)

3. The **Mydaiidae** will form a Superfamily for themselves. In their peculiar structure they show no distinct relationship to any family; they have no trace of macrochaetae; they belong principally to the Southern hemisphere, where they seem to have originated, as they do not occur in the immense Eurasian continent, except along its extreme Southern outskirts. Among the families of Diptera, this is an exceptional case of isolation; the group seems to belong to an earlier geological horizon. I form a separate Superfamily for the *Mydaiidae*, coincident with the family, and do not, for the present, propose a new name for it. — The geographical distribution of the *Mydaiidae* shows a striking analogy with that of the *Parrots* (Order *Psittaci*). The latter also from a well marked and natural group, widely separated „from all other birds“ (Wallace); they abound in the warmer regions of the Southern hemisphere, and penetrate but little into the South-Eastern region of the Eurasian continent. They are a very antique race, „and not improbably date back beyond the dawn of the Tertiary period“ (Wallace). They are represented in the temperate climate of New-Zealand by most specialized and extraordinary forms: *Nestor* and the owl-like, nocturnal *Stringops*.

I shall now give some further explanations about the Superfamilies *Tromóptera* and *Energópoda*.

Tromóptera. The relationship of the *Nemestrinidae*, *Cyrtidae* and *Bombylidae* is obvious, and has been noticed by the earliest writers; it finds its confirmation in the history of the transformation of these families. They are all parasitic in their larval stages, and, as far as known, all show two stages of development of the larva, the mobile one after hatching, and the torpid, after reaching their intended host. The *Cyrtidae* and *Nemestrinidae*, both acheta¹) (that is without macrochaetae), are specialized types, the former, as far as known, are parasites of spiders; the *Nemestrinidae* are not universally distributed, but occur sporadically in disconnected, limited areas, far distant from each other, and characterized by a

¹) In my Essay etc. (1884) the term *eremochaeta* has not received an exact definition, and I have wrongly applied it to families like the *Syrphidae* (on p. 499) and *Bombylidae* (p. 501). The term must be restricted to the Superfamily of that name, and occasional cases of want of macrochaetae in other families, should be better called acheta, a term which has nothing to do with the latin Acheta, cricket.

warm, dry, almost rainless, climate. (Central Asia, South Eastern Europe, some parts of Africa, of Australia and the deserts of South America.) [Compare in Berghaus's Physic. Atlas, new edit.; the map Meteorologie, N^o. XI (1886) has areas tinted in the palest blue, indicating a minimum of rainfall; those are the regions of the *Nemestrinidae*.]

As I said above, the prevalence of holoptic heads in the male, connected with the power of hovering, and legs, fit principally for alighting, distinguish the *Tromóptera*. Dichoptic heads in the male occur only exceptionally. The number of posterior cells as a maximum is five in the *Cyrtidae* and *Nemestrinidae* and four in the *Bombyliidae*. But as the venation in all these families is very variable, and subject to degradation, this is not a very deep-seated character. The number of pulvilli is normally three in the *Cyrtidae* and *Nemestrinidae*, and in this, just as in the number of posterior cells, they approach the *Eremochaeta*. Whether this double coincidence is an index of some hidden relationship is as yet unknown.

The *Bombyliidae* are a much more numerous family than the two just mentioned ones, spread almost universally, but always seeking dry and sunny situations.¹⁾ The variety of forms in this family is unique among Diptera: *Bombylius*, *Anthrax*, *Lomatia* are the principal types, showing a more or less distinct system of macrochaetae, especially on the sides of the thorax (*Bombylius* on the abdomen, concealed within a dense clothing of fur). The extremes, as to form, are the slender *Systropus*, entirely bare of hairs or bristles, and the heavy *Toxophora*, with comparatively small wings, but stout legs, and showing an unusual development of stout macrochaetae on the thorax, and even a pair of ocellar bristles on the head (a unique case, I believe, among *Tromóptera*), almost a pedestrian among aerial Diptera! Among all this variety of forms, however, the parasitism of the larvae is a constant character.

I have no hesitation in placing the *Therevidae* among the *Tromóptera*, but I would consider them as an ancestral form. I derive this opinion from the fact that species of this family are apparently common in New-Zealand (which, as well known, abounds in non-evoluted forms, as Dr. D. Sharp calls them in his paper on N.-Z. Coleoptera). All collections from N.-Z. contain *Therevae*, and the earliest Dipteron described (1775) from these islands was *T. bilineata* Fab., collected by Sir J. Banks, companion of Capt. Cook.

¹⁾ The silvery hoariness which so often occurs on Diptera living in damp situations, like the *Dolichopodidae*, *Ephydriidae* etc. is never seen on *Bombyliidae*.

The greatest difference between the *Therevidae* and the three above-mentioned normal families of *Tromoptera* consists in their earlier stages; however the great mobility of the larva of *Thereva* in hunting for prey, favored by its serpentine shape and tough consistency, may be premonitory of the first, mobile stage of the larvae of the other groups. Besides the *Therevidae*, the *Cyrtidae* also seem to be comparatively frequent in N.-Z. Three species of *Cyrtidae*, representing as many genera, have been brought from that country. One of them, *Oncodes brunneus*, seems to be exceedingly common. Thus, of the four families of Diptera, composing the Superfamily *Tromoptera*, the *Therevidae* and *Cyrtidae* seem to be much more common in N.-Z. than in Europe or in North America. The *Bombylidae*, on the contrary, flourishing in the rest of the world, seem to be exceedingly rare in N.-Z. I have never seen a *Bombylid* (or still less a *Nemestrinid*) from N.-Z. in any collection, and none have been mentioned, as far as I know, in literature, except the two species of *Neuria*, in Schiner's Novara-work, quoted as coming from Auckland, N.-Z., but the origin of which still requires confirmation, as there is no other authority for the locality.¹⁾ Such a striking result, although based upon rather meagre data, has its significance, the more so as both *Bombylidae* and *Nemestrinidae* are very abundant in Australia. This result seems to me a potent argument for the opinion that the *Therevidae* are an ancestral form among the *Tromoptera*.

The *Scenopinidae*, according to the received opinion, may be placed alongside of the *Therevidae*, although they are glabrous and bristleless, while *Therevae* have a regular system of macrochaetae on the thorax.

The Superfamily **Energópoda**. The *raison d'être* of this group is easily found in the transitional forms interposed between its principal families. While the bulk of the *Empidae* (*Empis*, *Rhamphomyia* etc.), have aerial habits and therefore pseudoholoptic heads, the *Tachydromiidae*, *Hemerodromiidae*, *Clinoceridae* etc. are more decidedly pedestrian (some of them hardly fly at all) and therefore dichoptic heads begin to prevail among the males, and thus make an approach towards the *Dolichopodidae*, with whom they have many other characters in common.²⁾ Haliday very early

¹⁾ One of these *Neuriae* has been described by Macquart from Eastern Australia; the locality of the other is vaguely described by Fabricius as „the Islands of the Pacific Ocean“.

²⁾ Observe, for instance, that the eyes of the decidedly pedestrian genera of *Empidae* tend to greenish, like those of the *Dolichopodidae*, while aërial *Empidae* have more reddish and brownish eyes.

recognized the affinity between the *Empididae* and *Dolichopodidae*: compare in Curtis, Brit. Ent. Dipt. under *Opetia lonchopteroïdes* (1834), and later, the very instructive Introductions (due to Haliday) to the *Empididae* and *Dolichopodidae* in Walker's Ins. Brit. Dipt. Vol. I, p. 86—87 and p. 118 (1851). Just such transitional forms seem often to occur in New-Zealand. In my small collection of Diptera from that country, I have a series of *Phyllodromina* with enormously developed front coxae.

On the other hand, the *Asilidae* seem to be connected with the *Empididae* by means of the section *Apiocerina*, in which I persist in recognizing, not *Mydaïdae*, but *Asilidae*, „adapted to peculiar conditions of life" (O. S., Berl. Ent. Z. 1891, p. 314). These conditions of life became clear since the discovery of the habits of *Rhaphiomydas* „hovering over flowers like a humming-bird" (Coquillet, in the West. Am. Scientist, Jan. 1891, p. 85), which explains the elongation of their proboscis, and the strengthening of their venation along the posterior margin of the wing (not unlike the venation of the Cyrtids *Eulonchus* and *Lasia*, which likewise hum about flowers). „The change in the nature of the food has nothing to astonish us when we call to mind the *Tabanidae*, *Empididae* and other families, containing blood-sucking, predaceous and flower-sucking species at the same time" (O. S., Berl. Ent. Z. 1891, p. 314). *Rhaphiomydas* has the aspect of a large, flower-sucking *Empid.* *Apiocerina* have not been discovered in New-Zealand yet, but they occur in other countries which abound in ancestral forms, as Australia and the Western Coast of America (especially Chili and South California).

That the *Lonchopteridae* belong in the vicinity of the *Dolichopodidae* and *Empididae* will hardly be contested (compare again Curtis, l. c. under *Lonchoptera*, 1839; or still earlier, in his Guide etc. 1837). As to *Phora*, I cannot believe that it is well placed among the *Cyclorrhapha* (where they are placed by Becher, Wien. Ent. Z. 1882, p. 53). Its structural characters (head, legs, wings etc.) and some of its motions, are not those of a fly. I have seen *Phorae* move up and down, with the legs kept together and stretched straight down, as I have seen some *Hybotidae* and *Rhyphus*; but I have never seen a musciform Dipteron do this. The metamorphose of *Phora*, as described by Schnabl (Deutsche Ent. Z. 1876, p. 217) is more like that of the *Orthorrhapha*, and this author observes about the larva: „The first and second segments of its body seem to be much more like those of the long-headed larvae, as represented in Marno's schematic figure (Verh. Z. B. Ges. Vienna 1869), than like those of the *Cyclorrhapha*."

The position of the *Platypezidae* and *Pipunculidae* I leave entirely in abeyance. According to the recent arrangements (Becher, l. c.), they are placed with *Phora* and the *Syrphidae* among the *Cyclorrhapha Achiza*, and form with *Phora* a separate group, *Hypocera*. Here again, as in the case of *Phora*, I place a certain reliance on the observed motions of the flies. An agreement in peculiar motions, must, it seems to me, correspond to some deep-seated agreement in the organization. Schiner (Fauna I, p. 239) and quite independently of him, W. A. Snow (Kans. Univ. Quarterly 1894, p. 147) describe a manner of flying of *Platypezæ* similar to that which I have described above, as observed by me in *Phora*, *Rhyphus*, *Hybos*, but never in a cyclorrhaphe Dipteron.

There still exists an obscure borderland between the *Orthorrhapha* and *Cyclorrhapha* which, I suppose cannot be unravelled without resorting to anatomy.

The three Superfamilies *Tromóptera*, *Mydaiidae* and *Energópoda* must, according to my proposition, be added after the *Eremochaeta* in the concise tabular arrangement which I published in the Ent. M. Mag. 1893, p. 150. The last Suborder in that table, the *Cyclorrhapha Athericera*, is now under the care of MM. Th. Becker and E. Girschner, who may succeed in introducing a satisfactory distribution, based upon the new characters which they have recently discovered.

The tabular arrangement of 1893 would then appear as follows:

- Suborder I: **Orthorrhapha Nemocera.**
 Superfamily: *Nemocera vera.*
 " *Nemocera anomala.*
- Suborder II: **Orthorrhapha Brachycera.**
 Superfamily: *Eremochaeta.*
 " *Tromóptera.*
 " *Mydaiidae.*
 " *Energópoda.*
- Suborder III: **Cyclorrhapha Athericera.**

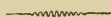
The sequence of the four Superfamilies of the *Orthorrhapha Brachycera* in this arrangement seems to me a matter of little moment. The *Eremochaeta* contain the greatest number of still surviving ancestral forms and may therefore represent an anterior, more ancient zoological horizon, involving covert affinities to more than one of the other Superfamilies of the same Suborder.

It is a matter of course, although too often forgotten, that, in

questions of the definition of zoological groups, there is no rule without exceptions. In the groups of a higher order especially exceptions are more frequent and more startling. But these exceptions themselves are subject to rules: if we have Diptera without wings, and even without halteres, we have none, and cannot have any, with four wings.

Ever since 1892, I have been engaged in the task of further developing the new arrangement which I introduced in that year. I have collected many facts and observations, of which my present communication is a mere outline. Still, it contains enough, I hope, to make my fundamental idea clear, and to enable others to follow it up, if they happen to agree with it. The standing difficulty I have encountered in all my entomological work, is want of scientific training, too late to mend at the rather advanced age when I began independent research. I often felt that the last word in certain questions was not for me, because it depended on anatomy. Of this limitation of my competence, I will give two instances. Having suggested the importance of the structure of the head, in matters of classification, I attempted a comparative study of heads and eyes in different families and in different genera of the same family, and accumulated enough material to furnish a theme for a publication (in fact, I promised such a publication in my paper of 1892, *Berl. Ent. Z.* p. 449, footnote). But I gave up my purpose, when I found that my results would remain unsatisfactory, unless accompanied by dissections, like those of Becher in his short, but very instructive paper, already quoted by me (*Wien. Ent. Z.* 1882). In the same paper of 1892, I tried to prove that each Superfamily may be expected to possess a characteristic type of structure for the antennae, and I even attempted to formulate a definition of such a type for the *Nemocera vera* and the *Eremochaeta*. A priori, I am convinced that the existence of such an antennal formula (more or less definable) for each Superfamily must underlie the importance of the antennae as organs of orientation, and I even feel that, in a certain measure, I could attempt such a definition for the antennae of the three Superfamilies which I introduce in the present paper. But I leave it for others to do, conscious as I am that such an attempt cannot prove satisfactory without the help of dissection.

My paper is, therefore, a *ballon d'essai* which I launch, attentive to the course it will follow!



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