

On the characters of the three divisions of Diptera: Nemocera vera, Nemocera anomala and Eremochaeta,

by

C. R. Osten Sacken.

Classes et genera naturalia, non sola instrumenta
cibaria, non solae alae, nec solae antennae con-
stituunt, sed structura totius, ac cujusque vel mi-
nimi discriminis diligentissima observatio.
Scopoli, Introd. ad Hist. Nat. 401. 1777.)

I. General survey of the subject.

In a short paper „Suggestions towards a better grouping of certain families of the order Diptera“ (Entomol. Monthly Magazine, February 1891) I have proposed an arrangement of a portion of the *Diptera Orthorrhapha* which I believe to be more natural than the groupings previously introduced for the same families. I said: „These attempts, first made by Schiner, and afterwards developed by Brauer²⁾ cannot be considered as successful. The reason is (as far as the families which I intend to discuss in this article are concerned) that these groupings were principally based upon a character of subordinate value, taken from the wings, and on another character of doubtful importance, borrowed from the larvae, without sufficient regard for the organization and the affinities of the imago. I believe

¹⁾ I found this in Kirby and Spence, Introduction etc., Vol. IV, p. 455. Compare the Additions to the present article.

²⁾ Schiner, in the Verh. Zool. Bot. Ges., 1864, p. 211; Brauer, in his Characteristic der Hauptgruppen, etc. (in the Denkschr. K. Akad. d. Wiss. Vienna, vol. xlii, pp. 105—216); a short synopsis of the same arrangement in l. c., vol. xlv, p. 43 (99); a modified system, l. c., xlvii, p. 11; further developments in his Systematisch-Zoologische Studien (Sitzungsber. d. K. Akad. d. Wiss. Vienna, 1885, pp. 237—413), and in the Verh. Zool. Bot. Ges., 1890, pp. 273—275).

Since 1880 Brauer published under the general heading: Die Zweiflügler des Kaiserlichen Museums zu Wien, five quarto volumes, each with a separate pagination. For brevity's sake I shall quote them thus: Z. K. M. I, 7; III, 10 etc. which refers to the volume and the separate pagination.

that a natural arrangement must be the result of the study of those organs of the imago which are necessary for the functions of external life, principally, therefore, of the organs of orientation connected with the head (eyes and antennae) and in the second line, of the organs of locomotion (legs and wings).¹ An arrangement of the imagos based upon such principles will of necessity be justified by a more or less tangible correspondence in the characters of their larvae. This structural correspondence, this parallelism, of larvae and imagos, among the *Nemocera*, suffers, as far as I know, but two exceptions: *Mycetobia pallipes* and *Rhyphus*; *Anopheles* and *Dixa*. In both cases almost identical larvae produce flies belonging to different families. This unsolved problem will be discussed by me in its place.

I shall endeavour in the present paper to give my „Suggestions“ a further development. I shall try to show how a number of useful distinctive characters have hitherto been overlooked; how others, although very well known, have not been sufficiently turned to account; and how a proper application of these characters easily brought about a subdivision which, I trust, will appear natural, and, I may say, self evident.

As very superficial and erroneous notions have prevailed for a long time about the true meaning of the subdivision of the Diptera into *Nemocera* and *Brachycera*, I shall begin with an historical sketch of its origin.

Linné, with his genus *Tipula*, foreshadowed more or less the present division of *Diptera Nemocera*, but his vague definitions (Syst. Nat. edit. X and XII) do not even mention the characteristic length and structure of the antennae.

In Fabricius' *Systema Antliatorum* 1805, under the heading: *Characteres generum* (pag. VII) the Diptera are divided into eight groups, characterized principally by the structure of the antennae. The first group is defined in three words: *Antennis porrectis articulatis*, and contains ten genera, all of which belong now to the *Nemocera* Latr. In the other groups the genera are arranged most unnaturally, and in the sequel of the book these groups are not mentioned again, and the genera are placed in a different order.

Latreille, in his „*Hist. Naturelle des Crustacés et des Insectes*“ Vol. III [1802]¹⁾ and Vol. XIV, p. 271 [1805], became the real founder of the division *Nemocera*. He called it: *Tipulaires*, and defined

¹⁾ It is in this volume that the Diptera are for the first time divided into families.

it: „Antennes ayant au moins sept pièces distinctes, le plus souvent de douze à seize (beaucoup plus longues que la tête pour la plupart); palpes placés en dehors et souvent de plusieurs articles.”

In his: „Genera Crustaceorum et Insectorum”, Vol. IV, p. 238 (1809) Latreille improved this definition thus: „Antennae (filiformes vel setaceae, saepissime capitis truncique longitudine), articulis sex et ultra (saepè 14—16) discretis. Palpi communiter elongati, sub-setacei, articulis quinque vel quatuor distinctis.” In 1817 Latreille gave this group of families the name *Nemocera*.¹⁾ Thus a rigorously defined division was established, separated from the bulk of the other Diptera by two characters taken from different parts of the body: the antennae and the palpi.

The first part of Macquart's „Diptères du Nord de la France” appeared in 1823—24, that is, before Latreille's „Familles naturelles etc.” (1825). Macquart, like Latreille, recognizes in the *Nemocera* one of the two great subdivisions of the Diptera, but he quite correctly points out that it is merely a division, containing various organizations, and not a homogeneous family like the *Tabanidae*, *Syrphidae* etc. At the same time, in advance, as we shall see, of other authors, he states distinctly that there is no transition between the *Nemocera* and the rest of the Diptera, but, on the contrary, that there is a discontinuity between them („une solution de continuité”). The whole passage is worth quoting: „En considérant les différences importantes par lesquelles les Tipulaires (in the sense of the *Nemocera* Latr.) se distinguent des autres Diptères, et l'espèce de solution de continuité qui les en sépare; en les voyant former une série considérable, très distincte de l'autre, et parcourant de même divers degrés de l'organisation, on pourrait les regarder comme constituant un ordre particulier, composé lui-même de plusieurs familles; et l'on trouverait peut-être autant de dissemblances entre elles et les autres Diptères, qu'entre les Hyménoptères par exemple, et les Névroptères.” For the second of these two great divisions of Diptera Macquart selected the name of *Brachocera* (Hist. Nat. Dipt. I, p. 14, 1834), although he fully recognized that this second division, like the first, consists of a miscellany of differently

1) This name, as I ascertained during my researches in the Library of the Academy of Natural Sciences in Philadelphia for my first Catalogue of the North-American Diptera (1857), appeared for the first time in the Nouveau Dictionnaire d'Histoire Naturelle (de Déterville) in 1817, under the headings of: Diptères and Entomologie.

organized families.¹⁾ On p. 24 of the same work he defines these two divisions, like Latreille, by the two characters borrowed from the antennae and palpi:

Antennae at least six-jointed; palpi four- or five-jointed.

Nemocera.

Antennae three-jointed; palpi one or two-jointed.

Brachycera.

For some unexplained reason later authors have neglected the character borrowed from the palpi, and have concentrated their attention on the antennae. None of them seem to have realized that we may separate the two divisions on account of the palpi alone, without regard to the antennae.²⁾

Meigen, in his definition of the *Nemocera* (his Tipulidae, Syst. Besch. Vol. I, p. XXIII, 1818) does not even state the number of the joints of the palpi („Taster vorstehend, gegliedert“). The other authors copy the statement about the palpi from Latreille and from each other in a sort of perfunctory³⁾ manner, without seeming to realize the importance of this character (Zetterstedt, Dipt. Scand. I, p. 68; Schiner, Fauna etc. I, p. XXXVII; Brauer, Z. K. M. I, p. 7 and 9). Haliday alone, in Walker's Ins. Brit. Dipt. I, p. 5 makes an independent statement, and comes nearer a true appreciation: „*Nemocera*, palpi plerumque deflexi, articulis pluribus exsertis; *Brachycera*, palpi porrecti, aut proboscidi incumbentes, quasi ex-articulati.“

The consequence of this neglect of the palpi was that when the genus *Rhachicerus* was discovered, this discovery induced entomologists to pay more attention to other forms of *Brachycera* with

¹⁾ For this reason the remark of Brauer (Z. K. M. II, p. 42, 1882): „Seit der verfehlten Eintheilung der Dipteren in *Nemocera* und *Brachycera* durch Macquart“ etc. is incorrect, and the failure is entirely on Brauer's side.

²⁾ It is strange that Latreille, in his later work: „Familles naturelles etc.“ (1825) for some reason did not use the character borrowed from the palpi; I mean to say that, in characterizing the two divisions, he has mentioned the antennae only (compare l. c. p. 482 and 486, both at the top). As this work of Latreille was the principal one used by later authors, it may be that the probably accidental omission of the palpi by Latreille himself has prevented his successors from grasping the importance of this character.

³⁾ Perfunctory in Webster's dictionary is defined: „Done without interest or zeal, and merely to get rid of a duty; performed mechanically, as a thing of rote.“ This is exactly the meaning I intended to convey.

multiarticulate antennae (*Xylophagus*, *Subula*, *Caenomyia* etc.) and to reach the conclusion that the pretended line of division between the two groups had no existence in reality.

In the chapter „On the terminology of Diptera“ (Monographs N. Am. Dipt. Vol. I, p. 2—4, 1862) Loew discusses the limits of the *Nemocera* and *Brachycera* and concludes by saying: „It is a fact, that some discoveries made in modern times have obliterated to a certain degree the sharpness of the limit which was considered to exist between the two sections etc. . . . All these facts however are not sufficient to oblige us at present to give up the separation of *Nemocera* and *Brachycera*“ etc. In other words, Loew seems to have felt that the subdivision is well founded in nature, although he was not able to define it; he did not know that, long before his time, a very good distinctive character had been found in the palpi. The same train of reasoning is maintained by Loew in his lecture „Ueber die Dipteren-Fauna des Bernsteins“, written in the same year 1860, which is the date of Loew's Preface in the Monographs etc. Vol. I; it does not contain a single allusion to the palpi (read, l. c. p. 7, column first, the passage which begins with: „Schon seit längerer Zeit“ etc. and ends in the next column.) Loew's conclusion in this instance is that the transitional forms between the two divisions exist now, just as they existed in the tertiary period, and that if they were noticed for the first time in the amber-fauna, is was because they are extinct in Europe, and were discovered only later in other continents.¹⁾ In this Loew was completely mistaken; transitional forms have not been discovered yet, neither in the living, nor in the fossil faunas. We do not know a single dipteran yet, whose position between the two divisions is doubtful.

The climax was reached in 1863, when Snellen van Vollenhoven discovered in the Museum in Leyden a fly that he called „*Antidoxion*“, which means: „against the doctrine“, and which afterwards was proved to be the same as *Rhachicerus*. In his article on this subject (Verslag en Mededeeling d. K. K. Ak. v. Wetensch. Vol. XV) van Vollenhoven discusses the two divisions proposed by Latreille, and accepted by later authors; he reproaches them with their inconsistency, in not at once rejecting these divisions, and especially takes to task Loew, „den grootsten Dipteroloog van onze dagen“ for the hesitation expressed by him in the passage already quoted „All these facts however etc.“ (see ante). Van Vollenhoven, in producing his

¹⁾ An earlier passage, in the same sense, will be found in Loew, Berl. Ent. Z. 1858, p. 102.

Antidorion concludes triumphantly: „It is my agreeable duty to bring before the Academy the proof that the subdivision in question is untenable in future"! About the palpi; not a word!

Brauer, in his writings since 1880, maintains the division *Ortorrhapha Nemocera*, but, like his predecessors he neglects the palpi in defining its character. In the dichotomic table (Z. K. M. I, p. 7, 1880) we find the usual perfunctory mention: „Taster selten kurz und drei-gliedrig, meistens lang, drei- bis fünf-gliedrig". But in the long discussion about the limits between *Nemocera* and *Brachycera* in Brauer's „Systematisch Zoologische Studien" (Sitzungsberichte d. K. Akad. d. Wiss. 1885, p. 406—416) the palpi are not mentioned at all. In the Z. K. M. III, p. 9 Brauer goes so far as to say: „Mögen die Dipterologen, der Bequemlichkeit wegen, auch heute noch von Nemoceren und Brachyceren sprechen, derlei natürliche Gruppen giebt es nicht, und man ist auch nicht im Stande, natürliche Charactere für sie aufzustellen" etc. (Compare the whole passage.)

That, in some earlier geological times there existed a connection between the two large groups of Diptera is very probable. But it is necessary to recognize and to maintain, as an important contribution, not only to the systematic arrangement of the Diptera, but also to their geological history, — that up to the present time, including even the accessible fossils, such transition-forms have not been discovered.

We may therefore safely use the following formulae for distinguishing the two divisions:

- I. Palpi generally four-, or five-jointed¹⁾, pendulous, and more or less filiform; antennae many-jointed (more than six-jointed), generally filiform (seldom pectinate), with the majority of the joints of the flagellum of a homologous structure.²⁾

Nemocera Latreille.

1) It is very probable that the palpi, in most cases, are only apparently five-jointed, the basal joint representing the maxilla, or a portion of it. Thus Westwood, *Introd.* II, p. 514, says: „It appears to me from a careful examination of the structure of these organs in *Tipula oleracea*, that the first, or basal joint is the analogue of the maxilla." Westwood adds, l. c., p. 525: „its texture is different from that of the palpus." Becher, *Mundtheile*, p. 9 calls it: Tasterschuppe. (See in the Additions.)

2) In this paper I have used the word homologous in its ordinary sense, as „having the same relative position, proportion, value, or structure" (Webster's Dictionary), and not in the narrower sense, used by zoologists: for instance that the hand of man and the fore-foot of a horse are homologous. — Observe that the joints of a flagellum, for being pectinate, do not cease to be homologous. —

- II. Palpi one or two-jointed, porrect (not pendulous), the second joint more or less clavate, larger than the first, which in this case appears like a handle to the second; the joints of the antennal flagellum, with rare exceptions, not homologous.¹⁾

All the other diptera.

After having thus vindicated the rights of the *Diptera Nemocera* Latreille, it remains for us to examine the contents of this division, and to ascertain whether it is homogeneous or not.

We soon perceive that some families in this division have, in most cases, holoptic heads in the male sex, while in the rest of the families, which form the bulk of the division, such heads never occur. After separating these two groups of families we easily discover that the larger one, whose males are never holoptic, is a very compact, homogeneous group, connected by several other characters besides that derived from the structure of the head. This large group (in my „Suggestions“) I called *Nemocera vera*. It contains the five largest families of the *Nemocera* Latreille, which are rather evenly distributed over the whole world: *Cecidomyiidae*, *Mycetophilidae*, *Culicidae*, *Chironomidae*, and *Tipulidae*. The *Psychodidae* form a sixth, smaller family. The still problematic *Dixa* may count for a seventh until further discoveries reveal its affinities.

The residuc of the *Nemocera* of Latreille consists of five small families, very peculiar in their organisation, but not showing any distinct relationship to each other. They seem to represent the remains of a more ancient fauna. I formed of them the artificial group: *Nemocera anomala*; the families which it contains are the *Bibionidae*, *Simulidae*, *Blepharoceridae*, *Rhyphidae*, and *Orphnephilidae*.

The *Nemocera vera* represent a natural, compact group, bound together by characters appearing in different parts of their organisation, as well as in their general aspect. They never have a holoptic head and hence, the differentiation of the sexes in the breadth of the front, and the size and shape of the eyes, if it exists at all, is reduced to a minimum. The eyes sometimes round or oval, but most often lunate, are placed on the sides of the comparatively very small head, and are separated by a more or less broad front; when lunate, their upper and lower ends are often approximate, but we never meet in this group with that broad contact of the eyes which constitutes a holoptic head. The ocelli are generally wanting, except

1) „Joints of the flagellum not homologous.“ I purposely use this, merely negative, definition, in order to leave room for the endless variety in shape of the third joint of the antennae of the *Brachycera*.

in the *Mycetophilidae* and their relatives, the section *Lestremina*. The development of the antennae is large, and, in comparison with the small head, sometimes, we may say, excessive (for instance in some male *Cecidomyiæ*); the contrast in this respect with *Bibio* and *Simulium*, with their large heads and small antennae, especially in the male sex, is striking. The distinctive character of the antennae of the *Nemocera vera* (in common with the *N. anomala*) consists in the homology of the majority of the joints of the flagellum. But the distinctive character of the antennae of the *Nemocera vera*, taken separately, is found in the large development of what we may call the sensitive hairs, which adorn the antennae, and are arranged, especially in the male sex, in the shape of verticils, peneils, and plumes (the *Mycetophilidae* form in this case an exception). The legs generally very long, but weak, are but little fitted for walking; structural peculiarities, useful for classification and description, occur only as exceptions (*Ceratopogon*; hairy fringes in *Chironomus* etc.). Empodia are sometimes present, sometimes not; but there are no pulvilli. In general aspect the true *Nemocera* are distinguished by their slenderness and lightness; the elongation of the abdomen in comparison with the thorax is especially noticeable (*Psychoda*, which is more thick-set, forms an exception). Their habits are rather crepuscular; they prefer shady places and evening hours.

The *Nemocera vera*, in accordance with the structure of their larvae, may be subdivided into two natural sections.

The *Cecidomyiidae* and *Mycetophilidae* have peripneustic and terrestrial larvae with eight or nine pairs of stigmata. The relationship of these two families is proved by the occurrence of intermediate forms: the *Lestremina* which, although usually referred to the *Cecidomyiidae*, are provided with ocelli like the *Mycetophilidae*; the genus *Sciara* which, although a *Mycetophilid*, has lunate eyes, contiguous above, like the *Cecidomyiidae*.

The second natural section of the *Nemocera vera* has amphipneustic or metapneustic larvae, usually aquatic or subaquatic, but sometimes terrestrial (principally in the *Tipulidae*, but also among the *Chironomidae*, for instance, some species of *Ceratopogon*). The affinity between the *Culicidae*, *Chironomidae* and *Psychodidae* is abundantly proved by the structure of their heads and antennae, their often lunate eyes, their venation and their sometimes bloodsucking habits. The *Tipulidae* agree in most respects with these families, although they never have lunate eyes, are never blood-suckers and have a more complete venation, including a discal cell.

The relationship of these two sections of the *Nem. vera* towards each other, the difference in the larvae notwithstanding, is well expressed in their general appearance, and in the analogous structure of their heads, eyes and antennae. (In the next chapter of this paper we shall have the opportunity to study these characters and affinities in greater detail.)

The *Nemocera anomala* are distinguished by some characters which never appear among the *Nemocera vera*. Thus holoptic heads occur here, not only in the male (*Bibio*, *Rhyphus*, *Simulium*), but also in both sexes (*Orphnephila* and some *Blepharoceridae*). The eyes are often bisected, the facets upon the upper side being larger; these two halves of the eyes are sometimes bicolored (*Simulium*), or they are separated by a distinct groove, or even by a transverse unfacetted stripe (*Blepharocera*, male *Bibio*). The antennae do not show, on the joints of the flagellum, those aggregations of hairs in verticils and pencils, which I have called sensitive hairs, and which are peculiar to the *Nemocera vera*. Three very distinct ocelli occur in the *Blepharoceridae*, *Bibionidae* and *Rhyphidae*; they are wanting in the *Simulidae* and *Orphnephilidae*. The empodia and pulvilli, in some genera, have an uncommon development; the legs are sometimes particularly strong (*Bibio*, *Dilophus*, *Simulium*); the sexes, in these same three genera, are remarkably differentiated in their whole appearance. The number of genera in these families is small (only a single one in the *Simulidae* and *Orphnephilidae*, three in the *Rhyphidae*, and about eight in each of the two other families); the number of species in these genera in most cases is likewise small (except in the *Bibionidae* and *Simulidae*). A certain monotony prevails, in forms and colours, within the same genus, notwithstanding an extensive, sometimes sporadic, geographical distribution; the metamorphoses are also peculiar. At the same time it is a significant fact that just like the *Limnobia anomala* among the *Tipulidae*, the *Nemocera anomala* seem to represent archaic forms, remains of bygone entomological horizons.

There must have been an age when the type of structure of the *Nemocera anomala*, combining filiform palpi and filiform antennae with holoptic heads and developed pulvilli, was more abundantly represented than it is now. What remains at present of that type are the cosmopolitan *Bibionidae*, *Simulidae* and *Rhyphus*; also *Orphnephila*, which may be considered as cosmopolitan, as it has been already found in different parts of Europe, as well as in North and South America. The only genera of this group which have a narrow geographical range are *Pachyneura* from Lapland, and the paradoxical

Lobogaster from Chili. In their originality these genera are probably the last remnants of long extinct local faunae, perhaps of the continents and islands which, in the tertiary period, have existed in the arctic and antarctic regions.

Latreille seems to have had a presentiment of my group *Nemocera anomala* when he established his division *Tipulae florales* (Genera etc. IV, p. 265) consisting of the *Bibionidae*, *Simulidae* and of the genus *Cordyla*. He has been misled about the location of *Cordyla* probably on account of the shortness and peculiar shape of its antennae. In placing *Rhyphus* among the *Mycetophilidae*, he overlooked its holoptic head which separates it from that family. *Orphnephila* and the *Blepharoceridae* were unknown at his time. But the characters he assigns to his *Tipulae florales* show that he was on the right track towards the isolation of the *Nemocera anomala* from the remainder of the division: Antennae ante oculos insertae. Caput . . . in masculis subglobosum et oculis penitus fere occupatum etc. Compare also Latreille's *Considérations* etc. p. 485 (1810).

A few words about the names I selected for these divisions will not be amiss here. As the author of this new grouping I would perhaps have had the right to invent new names for the two divisions. I prefer to retain the old and expressive name of *Nemocera* for both of them, and to establish a distinction by the addition of the adjectives *vera* and *anomala*. — Family-names in zoology must consist of one word only; but there is no inconvenience in using compound names for larger divisions. They are not exactly names, but designations; they must have something of the descriptive character in them (like *Orthorrhapha Nemocera* etc.). When the name *Linnobina anomala* was introduced by me, it was objected to by some writers. Verrall proposed *Rhamphidina* and van der Wulp: *Antochina*. But names ending in *idae* or *inae* imply a relationship between the genera of the group, which in this case does not exist. The addition of the word *anomala* describes the artificial character of the division, and is, in my opinion, preferable. — (I have expressed this opinion already in my „*Studies on Tipulidae*“ II, p. 183).

Having thus disposed of the division *Nemocera* Latreille, corresponding to the *Orthorrhapha Nemocera* of Brauer we reach now that of the *Orthorrhapha Brachycera*, and we meet at once with a group of families which have been for a long time converging towards each other during the successive changes in the systematic arrangement, but which found the keystone for their final association

only since the application to them of a chaetotactic character, the total absence of macrochaetae. This group consists of the families *Stratiomyidae*, *Tabanidae*, *Acanthomeridae*, and *Leptidae* (plus *Xylophagidae*). Among the *Orthorrhapha Brachycera* it represents the largest agglomeration of bristleless forms, and deserves for this reason the name *par excellence* of the Section *Eremochaeta*. Besides the chaetotactic character, these families are strongly bound together by other structural peculiarities, which naturally separate them from the *Nemocera*, as well as from the remainder of the *Brachycera*. 1. The heads (in the male) are predominantly holoptic; 2. bisected eyes, with larger facets above than below (in the male) are of very frequent occurrence; 3. eyes of variegated colour are more common in this Section than in any other of the whole Order of *Diptera*, principally in the *Stratiomyidae* and *Tabanidae*; 4. the antennae in the group *Eremochaeta* are characterized by what I should call a morphological restlessness; there is no other group of *Diptera* in which the structure of the antennae varies so much, even in closely related genera. These various forms offer a complete transition from the thread-like antennae of some *N. anomala* (*Rhyphidae*) to antennae like those of *Subula* and *Xylophagus*, among the *Brachycera*, ending in the disc-and-arista type, so common in the other great division the *Cyclorrhapha-Athericera*. This transition is effected by the joints of the proximal portion of the flagellum tending to coalesce and to form a compound joint in various shapes, while the joints of the distal portion gradually pass into the form of a simple bristle. 5. There are *three well-developed pulvilli*, which is one of the most characteristic features of the *Eremochaeta*; exceptions are rare. The legs are generally smooth, without those bristles and spines that distinguish the *Asilidae*, and, in a lesser degree, the *Bombyliidae* and *Therevidae*.

For the final adjustment of the families of the division *Eremochaeta* we must wait for more material. The original arrangement was principally based upon the common European forms; but this section, perhaps more than any other, is represented by very remarkable and often anomalous forms in the other continents, especially in the tropics; the anomalous forms that disturbed the old arrangements came especially from Chili (*Coenura*, *Heterostomus*,) and recently from North America (*Agnotomyia*, a Leptid, with only four posterior cells; *Arthroceras*, also a Leptid, but with the antennae of *Caenomyia*; the singular genus *Glutops*, etc.); about Australia and Africa we know almost nothing. Certain it is that the

very problematic family of *Xylophagidae* must be given up, and its contents, temporarily at least, united with the *Leptidae*.¹⁾

II. Tabular arrangement of the three groups, with their characters.

A. Palpi generally four-, or five-jointed, pendulous, and more or less filiform; antennae many-jointed (more than six-jointed), generally filiform (seldom pectinate), with the majority of the joints of the flagellum of a homologous structure. No macrochaetae; no tegulae, but the antitegula²⁾ is almost always distinct; the alula and the axillary excision are but little developed or entirely absent. No discal cell (exceptions: *Tipulidae*, *Rhyphidae*). Larvae with a distinct head in the shape of a horny shell, mandibles with a lateral mobility, opposed to each other like pincers; round-headed larvae, Rundköpfe of Marnó³⁾ (*Nemocera* Latreille; *Orthorrhapha nemocera* of Brauer).

I. *Nemocera vera*.

No holoptic heads in the male sex; no bisection or bicoloration of the eyes.

Antennae provided with sensitive hairs arranged symmetrically on the flagellum in verticils, or pencils of hair.

(Exception: *Mycetophilidae*.)

No ocelli (Exceptions: *Mycetophilidae*, *Lestremia*).

No pulvilli; empodia often, but not always, present.

A. Larvae peripneustic, always terrestrial.

B. Larvae meta-, or amphipneustic, aquatic, subaquatic, sometimes terrestrial.

Cecidomyiidae.

Culicidae.

Mycetophilidae.

Chironomidae.

Psychodidae.

(?) *Diixidae*.

Tipulidae.

1) A considerable portion of this last paragraph is a verbatim reproduction from my earlier article: „Suggestions“ etc.

2) I call antitegula what is usually called upper tegula, but which has no name and is generally overlooked, when there is no lower tegula present. It forms a more or less distinct lobe between the alula and the root of the wing and moves with the wing (different in that from the lower tegula).

3) Compare E. Marnó's useful little paper: Die Typen der Dipteren-Larven, Verh. Zool. Bot. Ges. 1869. Compare my Additions.

II. *Nemocera anomala*.

Diptera with homologous joints of the flagellum, usually four-jointed palpi, and besides with the following other characters, which exclude them from among the *Nemocera vera*:

Frequent occurrence of holoptic heads in the male sex (*Bibionidae*, *Simulidae*, *Rhyphidae*), or in both sexes (*Blepharoceridae* ex parte, *Orphnephilidae*).

Three distinct pulvilli (*Bibionidae*, Section I), or an enlarged, broad, pulvilliform empodium (*Bibionidae*, Section II, and *Rhyphus*). In the three other families the empodia or pulvilli are rudimentary (*Simulidae*, *Blepharoceridae*, *Orphnephilidae*).

Absence of sensitive hairs (in the shape of verticils) overtopping the usual hairy covering of the antennae.

Three large ocelli (*Bibionidae*, *Blepharoceridae*, *Rhyphidae*; no ocelli in *Simulium* and *Orphnephila*).

Anomalous larvae.

Bibionidae.

Simulidae.

Blepharoceridae.

Rhyphidae.

Orphnephilidae.

B. Palpi one or two-jointed, porrect, not pendulous, the second joint more or less clavate, larger than the first, which appears like a handle of the second; the joints of the antennal flagellum (with rare exceptions) not homologous (compare the explanation on p. 422, footnote 2).

III. *Eremochaeta*.

No macrochaetae; three well-developed pulvilli; heads in the male predominantly holoptic and eyes very often bisected, with larger facets above than below; the eyes in both sexes often variegated in different colors; the structure of the antennal flagellum polymorphous, more inconstant here than in any other group of diptera; tegulae undeveloped in the *Leptidae* and *Acanthomeridae*, very small in the *Stratiomyidae*, and in full development only in the *Tabanidae*. Axillary excision, alula and antitegula, in most cases, distinctly developed. Discal cell, as a rule, present; five posterior cells, sometimes four, through the partial or total obliteration of a vein. Legs rather smooth. Larvae with elongate heads, composed of horny plates; mandibles not opposed to each other, but moving with a more or less vertical mobility, and thus foreshadowing the hook-shaped mandibles of the larvae of the *Cyclorrhapha* (Long-headed larvae, Langköpfe of Marno).

Stratiomyidae.

Tabanidae.

Acanthomeridae.

Leptidae (plus *Xylophagidae*).

430 *Osten Sacken: on the characters of the three divisions of*

I have already stated (on p. 427) that the present arrangement of these four families must be considered as merely provisional, until we obtain further materials.

The aim of this tabular arrangement is to give a synopsis, a condensed view, of the characters of the three divisions. It is not intended for a dichotomic table for determining specimens; such tables must be arranged on a simpler plan.

In making use of this table as well as of the other generalizations which form the subject of this paper, it must be always borne in mind that the larger the group is which we are considering, the more we must look to the majority of the characters only, and the less be embarrassed by exceptions. The study of these exceptions affords a peculiar interest, because in some cases they probably represent the remains of a distant past, atavisms. All the *Tipulidae*, for instance, and especially the genus *Tipula*, have verticillate antennae; but, as an exception, the *Tipulae* from New-Zealand and also from the south end of South-America (especially from Chili), have no verticils (more detail will be given in the sequel). Among the *Nemocera vera* the *Mycetophilidae* are the only family which, as a rule, has no verticils on the antennae; but an exceptional *Platyura* from New-Zealand has them short, but quite distinct. The same *Platyura* has the eyes contiguous on the front, which is again an exception among the *Mycetophilidae*. We thus seem to witness the evolution of generic characters. It is well-known that New-Zealand and Chili abound in archaic forms of Diptera, and it is very much to be regretted that the materials which we have from those countries are so scanty.

The three large divisions of the Diptera which we are considering belong to those that are not provided with the protective system of macrochaetae described in my paper on that subject (Trans. Ent. Soc. London 1884). In some rare cases, among the genera of these divisions, stouter hairs occur, principally on the thorax, but their occurrence is merely sporadic; they do not represent a whole system, like the macrochaetae among the *Cyclorrhapha*, or in the families *Asilidae*, *Dolichopodidae* etc. They may have the same protective or sensitive functions; but they are conspicuous in one genus and wanting in the next; they cannot therefore, without further proof, be considered as homologous with the regular macrochaetae. The genus *Pachyneura* shows hairs of that kind, but they do not exist in its next relative, the genus *Bibio*. Some *Sciophilae* likewise possess such pseudo-macrochaetae. I leave the matter to the investigation by trained physiologists.

Hitherto I have been pointing out and defining the differences between the three groups of diptera which I propose to introduce. I shall attempt in the next paragraphs to take up each group separately and to prove the homogeneousness of the *Nemocera vera* and the *Eremochaeta* by the study of the detail of their characters. The *Nemocera anomala*, as I have already remarked, is an artificial subdivision.

III. Detailed characterization of the three divisions.

I. *Nemocera vera*.

The *Nemocera vera*, as I said above (p. 423) „never have a holoptic head, and hence, the differentiation of the sexes in the breadth of the front and in the size and shape of the eyes, if it exists at all, is reduced to a minimum“. As bisection and bicoloration of the eyes occur almost exclusively in connection with holopticism, they are never met with among the *Nemocera vera*. The relative size of the head is very small. The eyes, round, oval or lunate, are placed on the sides of the small head, and are separated in both sexes by a more or less broad front. The very frequently occurring lunate shape of the eyes is due to the smallness of the head, in order to leave room for the insertion of the antennae. When lunate, the eyes are often approximate or contiguous, sometimes even confluent without any distinct suture at their upper ends, and in some cases, at their lower ends also (below the antennae). When both eyes coalesce, above and below, the whole head looks almost like one eye. Such a structure (some instances of which will be given presently) must be looked upon merely as an exaggeration of the lunate eyes; it differs from true holopticism in that it occurs in both sexes, and often shows confluence and no suture between the eyes above the antennae.

Lunate eyes are found in all the families of the *Nemocera vera*, except in the Tipulidae; their frequent occurrence is characteristic of some families (*Cecidomyiidae*, *Chironomidae*, *Culicidae*, *Psychodidae*) although even in these families exceptions occur.

The *Cecidomyiidae*, as a rule, have lunate eyes, often confluent above the front in both sexes (compare the figures of *Cecid. pseudo-coccus* Rübsaamen, Verh. Z. B. Ges. 1890, Tab. VI, f. 8, and *C. pratensis* Kieff., W. E. Z. 1892, Tab. I, f. 9). Such eyes, confluent or, at least, without any visible suture, may be called cyclopic eyes.¹⁾ Some-

¹⁾ A case of coalescence of the eyes of the common bee, above the antennae and without suture, has been described by Lucas (in the Ann. Soc. Ent. Fr. 1868, p. 737, Tab. 12, f. 1—3) under the name of *cyclopia*; but this case is a monstrosity and not a normal occurrence.

times, as I said above, the development of the eyes is such that they invade nearly the whole head. I do not find such a conformation explicitly mentioned in any description; it is probably involved in such expressions as contiguous and broadly contiguous. I described such a development in *Diplosis resinicola* ♂ ♀, which I bred from accumulations of resin on pine-trees in the State of New-York (O. S. Trans. Am. Ent. Soc. Vol. III, p. 346, 1871). In this case the eyes, coalescent above and below the antennae, occupy in both sexes nearly the whole upper side of the head, without any suture, and leave only a small space for the insertion of the antennae. As exceptions among the *Cecidomyiæ* may be quoted *Heteropeza* and *Miastor* in which the slightly lunate eyes are separated by a broad front in both sexes (compare Winnertz Stett. Ent. Z. 1846, p. 13, Tab. I and N. Wagner's figures in his large folio on Paedogenesis, Kazan 1862). In a *Campylomyza* which I examined alive, the lunate eyes were in contact above the front, but a suture was distinctly visible.

The *Culicidæ* and *Chironomidæ* have lunate eyes, often in contact above the front and sometimes also below the antennae. The excessive development of the eyes, contiguous on the front and invading nearly the whole head, also occurs here; I have observed it especially among *Ceratopogons* with pubescent wings. I do not find such structures described by Winnertz, and the only published instance I can discover is the Cuban genus *Oecaeta*, described and figured by Poey, *Memorias etc.* 1851 I, p. 236, Tab. 27. This is the blood-thirsty midge, well known in tropical Spanish America under the dreaded name of „Jejen“. The coalescence of the eyes here is complete above and below the antennae, and the figure shows no trace of a suture („la cabeza esta cubierta casi del todo por los ojos“, says Poey). The question is whether this figure is correct. In the *Ceratopogons* with lunate, contiguous eyes I have been able to distinguish a slight suture.

In the *Mycetophilidæ* the eyes are generally separated by a broad front, and lunate eyes are rare. *Sciara* alone has deeply lunate eyes, the upper ends of which are either approximate, or even in complete contact above the antennae, but not confluent as in the *Cecidomyiæ*; in the cases observed by me I could see the suture. The group of *Diadocidia*, *Mycetobia* and *Plesiastina* have distinctly lunate eyes, approximate on the front; a large *Platyura* from New Zealand which I have examined has the upper end of each eye prolonged in a narrow strip, thus coming in contact with a similar prolongation of the opposite eye. In the Brazilian genus *Platyroptilon*

(allied to *Platyura*) as figured by Westwood in the Trans. Entom. Soc. V, p. 231, Tab. 23, f. 3, the eyes form a broad contact below the antennae; a New-Zealand species of the same genus has the same conformation.

The *Psychodidae* show lunate eyes in several genera (*Psychoda*, *Pericoma*).¹⁾

The eyes of the *Nemocera vera* (in life) are generally dark.²⁾ Variations occur, even in the same genus. *Culex* sometimes has bright-green eyes (*pipiens*), sometimes deep-black ones (*ornatus*): in the genus *Tipula*, the same colours occur. *Ctenophora pectinicornis* has deep-black eyes; the *Mycetophilidae* dark ones. I do not remember seeing red or reddish eyes among the *Nemocera vera*, except in *Tipula nigra* ♂ ♀, the eyes of which are bright purplish on the upper half and golden-yellow (♂) or reddish below. Among the *Nemocera anomala* which I observed alive (*Simulium*, *Blepharoceridae*) the eyes are reddish and purplish. Among the *Orthorrhapha Brachycera* the eyes of the *Asilidae* and *Dolichopodidae* are generally greenish, those of the *Empididae* red, except those of the *Tachydromiae*, which are olive-green. Among the *Cyclorrhapha* the red color largely prevails.

Finely pubescent eyes occur in the *Mycetophilidae* and in some *Tipulidae* (the section *Amalopina*, also in *Trichocera*). In this case the pubescence may serve as a protection against moisture, and not against an excess of sun-light, which seems to be its destination in some other families (*Syrphidae*). It is remarkable at the same time that some genera, the imago of which live near, or almost in

1) I have for a long time been puzzling about the position of the *Psychodidae* in the system. Latreille connected them with the *Cecidomyiidae*. In the introduction to my monograph of the *Tipulidae* (Monogr. N. A. Dipt. 1868, Vol. IV, p. 3) I said: „the connection between the *Psychodidae* and the *Eriopterina* is of a very obscure kind, and unless further developed by observation cannot have any scientific value". But why should not the *Psychodae* stand in a closer relationship to the *Culicidae*? Both have lunate eyes, a certain resemblance in the venation of the wings, an ambient vein, the veins clothed with hairs or scales; *Phlebotomus* draws blood like a *Culex*; finally, according to the anatomists, *Culex* and *Psychoda* (in the imago-state) have five Malpighian vessels, instead of four, the ordinary number among *Diptera*. The larvae may be different, but the larvae in the three families: *Culicidae*, *Chironomidae* and *Psychodidae* are inextinguishable in their capabilities of adaptation.

2) Dark eyes are not necessarily connected with crepuscular habits. Sun-loving species of *Anthrax* and *Syrphidae* have often nearly black eyes.

the water (*Elliptera*, *Antocha*) have glabrous eyes; the same is the case with *Simulium* among the *Nem. anomala*.

The majority of the *Nemocera vera* have no ocelli; these occur only in the *Mycetophilidae*, and in the smaller of the two groups of the *Cecidomyiidae*, the *Lestremiina*, which seems to be related to the *Mycetophilidae*. They also occur exceptionally in a single genus of the *Tipulidae*, *Trichocera*.¹⁾

As if in compensation for their small heads and eyes, the true *Nemocera* show a large development of the antennae. It is in this organ, and not in the eyes, as in many other Diptera, that the cephalic secondary sexual character of the family finds its expression. The antennae of the male are longer, often count more joints, and are more hairy than the antennae of the female. Other secondary sexual characters occur in the relative length of the palpi (*Culex*), in the size and shape of the wings (*Tipulidae*, *Chironomidae* etc.), the general shape of the body etc. But such characters are not characteristic of the *Nemocera* alone, and therefore do not require a particular notice here. The coriaceous pouch of the male *Ulomyia* (Walker, Ins. Brit. Dipt. III, p. 261, Tab. 26, f. 3a) reminds one of some formations on the wings in certain male *Dolichopodidae*.

In some groups the sexual character connected with the antennae is much more developed than in others. The *Culicidae* and *Chironomidae* in most cases have bushy antennae in the male, and not in the female. *Ctenophora* and *Rhipidia* have pectinate antennae in the male only. In some *Tipulidae*, like *Megistocera*, *Macromastix* and some *Erioceræ* the antennae of the male are enormously prolonged, while those of the female are short. Some *Cecidomyiæ* (*Diplosis*) have in the male twice as many joints of the flagellum as the female; in other cases the antennae are petiolate in the male and sessile in the female.

The size of the antennae in the true *Nemocera*, especially in the males, in comparison with their small heads, is worth noticing, and the contrast in this respect with other families of Diptera is striking. We have already mentioned above (p. 424) *Bibio* and *Simulium* with their large heads and small antennae. We may imagine how enormous the antennae of a *Tabanus* would be, if they stood in the same proportion to the head, as the antennae of some male *Cecidomyiæ*.

1) Schiner (Fauna II, p. XXVIII, footnote) observes that the microscope reveals traces of ocelli in some of the Chironomidae, especially of *Tanyptus*. About this compare the Additions.

In some genera of *Tipulidae*, for instance in *Megistocera*, the antennae of the female are very small in comparison not only with those of its male, but with the size of the insect in general. The antennae of *Amalopsis* and *Pedicia* are rather small in both sexes.

The distinctive character of the antennae of the *Nemocera* (in Latreille's sense) consists in the homology of the joints of the flagellum. In the *Nemocera vera*, in most cases, the flagellum counts between 11 and 14 joints; these joints are cylindrical, elliptic, or globular, and their juxtaposition produces the characteristic filiform appearance of the antenna. The basal, and one or several of the terminal flagellar joints differ slightly from the others, without interfering with the threadlike appearance of the whole. In the pectinate antennae occurring in several genera of the *Tipulidae* and *Mycetophilidae* the homology of the majority of the intermediate joints of the flagellum is likewise preserved.

In this homology of the joints of the flagellum the *Nemocera* (in the wider sense) differ from all the other *Diptera*, and the only approach to this form of antennae I am aware of is found in the family *Xylophagi* (*Xylophagus* proper, *Rhachicerus* and perhaps also the fossil amber-genera: *Chrysothemis* and *Electra*, the two latter with 23 and 13-jointed antennae respectively). Some species of the genus *Subula* also have antennae with almost homologous flagellar joints. All these genera undoubtedly are very old forms in the geological series. Their palpi however, two-jointed and generally club-shaped, easily distinguish them from the *Nemocera*.

Another distinctive character of the *Nemocera vera* consists in the presence of what I have called the „sensitive hairs“ on the antennae. They are arranged symmetrically in both sexes, but are especially conspicuous in male specimens, in the shape of verticils, pencils and plumes. In some cases, they are shorter than usual and difficult to discern among the general pubescence of the antennae (for instance in the antennae of *Spaniocera*, as represented in Winertz, Cecidom. Tab. 4, f. 7, a. b.).

The *Mycetophilidae* alone have no sensitive hairs in the above-described sense, except in the two genera *Zygoneura*¹⁾ and *Epidadus*. I have already mentioned (p. 430) a New-Zealand *Platyura* ♂ which

1) In my „Characters of the larvae of *Mycetophilidae* (Proc. Ent. Soc. Philad. 1862, republished by me in Heidelberg, 1886) I have described (p. 18) the metamorphosis of *Sciara toxoneura* O.S., which later, in my Catal. N. Am. Dipt. 1878 I placed in the genus *Zygoneura*, on account of its venation. Nevertheless, at is has no verticils on the antennae, it is a transitional form and not a true *Zygoneura*.

has little erect hairs in the middle of the joints of the flagellum that may be considered as „sensitive hairs“. Among the *Cecidomyiæ* such hairs are wanting in *Asphondylia*; among the *Tipulidæ* in *Phalacroceræ*. It is also worthy of notice that the *Tipulæ* from New-Zealand which I have seen, as well as several species from the southern end of South-America (Chili, Argentine) which I know either by sight, or from descriptions, have no verticillate hairs. Compare in Macquart D. E. I, 1, p. 55—56 the descriptions of *Tip. nubicornis*, *trimaculata*, *rufostigmata*, all of which speak of the antennæ as bare (nues); compare also the antenna of *Tip. trimaculata* figured in Gay's Chili, Dipt. Tab. I, f. 2a. A specimen of *Tip. decorata* Phil., with similar antennæ, I have before me. Such *Tipulæ* may perhaps represent one of those archaic types which occur so frequently in these faunæ.

The sensitive hairs of the *Nemocera vera* are usually inserted on a swelling at the base of the corresponding joints of the antennæ. Hence the tendency to the moniliform structure which characterizes the antennæ of this division. The greater the development which these hairs reach, the greater the swelling. It is at its maximum in the moniliform antennæ of *Cecidomyiæ*; at its minimum in the *Mycetophilidæ*, which have neither verticillate hairs, nor swelling. The chilian *Tipula decorata* which I have before me, and which, as I said above, has no verticillate hairs, has cylindrical joints of the antennæ, without the usual swelling at the base. On the contrary, in the exceptional *Platynura* from New-Zealand, which has short, incipient „sensitive hairs“, a slight swelling of the joints is also perceptible.

It will belong to a future micro-anatomist to investigate the structural and functional differences that exist between the different forms of bristles, hairs, pile, pubescence, down, and tomentum which occur on the different parts of the body of Diptera: on the antennal joints, the antennal arista, on different parts of head and face (mystax; frontal, vertical and orbital bristles), on the edges of the tegulæ, on legs and wings (surface, costa, veins etc.). The functions of most of these hairs are merely mechanical, as protective coverings, or tools for brushing, gathering, scraping or digging; but it is evident that some of them are organs of sense. There is not the slightest doubt that the peculiar, delicate, mostly erect and elastic hairs, arranged in regular whorls on the antennal joints of the *Nemocera vera* belong to the sensitive order of hairs, and, as they are much more developed in the male than in the female, that they have some part to play in the bringing together of the sexes. They are peculiar to

the *Nemocera vera*, and I am not aware of any structure that may be compared to them in other families. The erect hairs on the arista of some Diptera, as in *Ommatius*, *Sarcophaga*, *Drosophila* and some *Anthomyiæ* and *Ephydrina* stand perhaps nearest to the sensitive hairs of the *Nemocera vera*, but they differ from them in being inserted on the arista, and not on the joint itself; besides, the sexual differentiation in them is not apparent. They seem to come nearer to organs of smell (especially in *Drosophila* and *Sarcophaga*), while the verticillate hairs of *Culex* have been hitherto interpreted as organs of hearing (compare about the latter Chr. Johnson, Quart. Journ. Micr. Soc. 1855, p. 97—102, w. fig.; A. M. Mayer, Amer. Journ. of science, Vol. 108, p. 89—103). The functions of the sensitive hairs in the other families of *Nemocera* (*Chironomidae*, *Tipulidae*, *Cecidomyiidae*) have, to my knowledge, never been investigated.

It would perhaps be more rational to adopt in this connection a term that has been used by recent physiologists: the sense of „trepidation" or vibration. An instance of the effect of this sense was communicated to me by a naturalist in Cuba, and I published a brief account of it in the Stett. Ent. Zeit. 1861, p. 52: „when you stand in the midst of a swarm of gnats, and a musical instrument is sounded in the vicinity, you feel that a certain tremor pervades the swarm from time to time, so as to make a number of the insects to come in contact with your face; this happens every time the note A (1a) is sounded." I have not had occasion to verify this statement.

In my „Essay on Chaetotaxy" (Trans. Ent. Soc. London 1884, p. 500—502; also p. 517) I attempted to apply to the order Diptera the ideas suggested by Dr. A. Forel (Beitr. z. Kenntn. der Sinnesempfindungen d. Insecten, in the Mitth. Münch. Entom. Ver. II, 1878) to insects in general. I have shown the contrast between the pre-vaillingly aërial Diptera, with a holoptic head, weak legs, and a few, or no macrochaetae (*Tabanidae*, *Bombyliidae*, *Syrphidae* etc.) and what I called the pedestrian Diptera, the majority of which have a dichoptic head in the male, abundant macrochaetae, strong, well-developed legs, with which they run, climb, snatch their prey etc. (*Asilidae*, *Dolichopodidae*, most of the *Calypttrata* etc.). A third type, the antennal Diptera, I recognized in what I now call the *Nemocera vera*.

The legs of the *Nemocera vera*, sometimes very long, are weak in comparison to the legs of other families of *Diptera*; structural peculiarities, useful for the classification, are not abundant here. The genus *Ceratopogon* in its broadest sense forms an exception, and shows a great variety in the structure of the legs. Sometimes the

whole leg is stouter than usual; or the hind femora only; the tibiae are sometimes flattened; the relative length of the metatarsus is variable; the claws are large or small; equal, or unequal; simple, or bifid, or dentate; sometimes, there is a distinct empodium, or there are a few hairs instead; the underside of the femora and that of the metatarsi, especially of the last pair, are often beset with spines or short bristles.¹⁾ On the legs of other *Chironomidae* characteristic hairy fringes sometimes appear. In the *Tipulidae*, the presence or absence of spurs at the end of the tibiae, and the presence or absence of empodia, afford excellent characters for the definition of larger divisions only, not so much for genera and species. The same is the case with the spines and spurs used for the characterization of the groups of *Mycetophilidae*. The flies of the latter family are very active, with comparatively strong legs, especially the hind pair, with which, according to Westwood (Introd. II, p. 521) they are capable of leaping. The exceptional *Platyura* from New-Zealand, more than once mentioned in the present paper for its peculiarities, has very decidedly clavate hind femora, very much attenuate at the base; an unusual structure among *Nemocera*. *Cecidomyia* has a remarkable character in the brevity of the first tarsal joint; it was, I believe, first noticed by Meigen and published in 1818.

Tipulidae and *Culicidae* alight on their legs, but do not run much. Small *Chironomidae*, *Cecidomyiidae*, *Mycetophilidae* (especially *Sciara*) and *Psychodidae* run very well, but with a light tread, not with the slow gait of a *Bibio*, or the plantigrade one of a *Simulium*. The long legs of the large *Tipulae* serve them as balancers during their unsteady, headlong flight, and as buffers in case of contact; their prehensile tarsi as hooks for suspending themselves on trees, leaves and grasses.

Empodia occur among the true *Nemocera*, but never pulvilli. In some larger *Chironomi* (for instance *Chir. plumosus*) what I take to be merely a broad and bifid empodium assumes the appearance of a pair of pulvilli. —

The empodia of the *Nemocera vera* have been very much neglected by describers, and either entirely overlooked, or promiscuously called pulvilli. In Winnertz's papers on the *Mycetophilidae* and *Cecidomyiidae* I do not find anything about these organs. In his paper on *Ceratopogon* Winnertz calls *pulvilli*, what in reality are empodia. About *Chironomus* Schiner says: „pulvilli (Haft-

¹⁾ Compare also the statements of Loew, Bernstein u. Bernsteinfauna p. 30, about the curious *Ceratopogons* in amber.

läppchen) distinct" instead of empodia. The same in Loew, Bernstein und Bernsteinfauna, pag. 30 at the top.

The *Cecidomyiæ*, as far as I can see, have a pulvilliform empodium (Loew, Dipt. Beitr. IV, p. 16 says: Klauen schwach, zwischen ihnen ein Klauenpolster). N. Wagner in his work on Pädogenesis (1862) gives a very much magnified figure of the unguis of *Myastor* with a pulvilliform empodium. The *Tipulidæ*, as I have shown in my Monograph, sometimes have empodia, sometimes not; the same is the case with *Ceratopogon* (Loew makes the same remark about the *Ceratopogons* in amber). In *Diamesa* I perceive an empodium. In *Tanypus plumipes* Fallén I do not perceive anything between the claws of the front legs, and only a rudiment between the hind claws. *Culex* has empodia. Felix L. Arribalzaga, in his recent publication on the *Culicidæ* (Dipterologia argentina, La Plata 1891, p. 11 describes them as „little pillows, velvety on the underside, which enable the gnat to stand upon the surface of a liquid without drowning.“ *Mochlonyx* is represented by Meinert with a very minute empodium (compare the figure in Overs. K. D. Vidensk. Selsk. Forhandl. 1883).

The empodia of the *Nemocera vera* are not always pulvilliform. What Winnertz calls „haarige Pulvillen“ of the *Ceratopogons* and represents on Tab. I, f. 1 and 2 have a peculiar structure and may be an approach to the pectiniform empodium of that singular marine subapterous Chironomid *Psamathimyia pectinata* Deby, very distinctly figured in Journ. Micr. Soc. 1889, p. 180, Tab. 4, f. 9. The bristle-shaped empodium of the *Asilidæ* does not occur among the *Nemocera*.¹⁾

The *Nemocera vera* have no tegulae; these organs are merely represented by a rudimentary ligament between the root of the wings and the scutellum. The antitegula is almost always well developed; it is quite large in *Culex*, *Chironomus* and *Tanypus*.

1) Schiner, Fauna Austr. I, p. IX says about empodia and pulvilli: „Es sind in der Regel nur zwei Haftläppchen vorhanden, ist aber das Empodium so stark entwickelt, dass es die Form und Beschaffenheit der beiden Haftläppchen erreicht, so sagt man, dass drei Haftläppchen vorhanden seien.“ In the same sense Loew, Monogr. N. Am. Dipt. I, p. XXIII says: „Besides these appendages (pulvilli) many families have between them a third single appendage of similar structure, which is called empodium; in other families this organ is bristle-like, or altogether wanting.“ Is that really so? Is the bristle-like empodium of an *Asilus* really the homologue of the pulvilliform empodium of *Bibio* and of the *Eremochaeta*? Can a bristle be transformed into a pulvillus? It seems to me that the subject requires revision? A. Ockler's (Archiv f. Naturg. 1890; Separatum, p. 33) remarks on this subject are not quite satisfactory.

The alula, and the axillary excision near it, are either little developed, or rudimentary, or entirely absent. In *Culex*, *Chironomus*, *Tanytus* they are moderately developed; in *Ceratopogon* rudimentary or entirely absent. Their entire absence is especially noticeable in the *Tipulidae* where, owing to the usually small posterior angle of the wing, the interval between the last longitudinal vein and the margin is very narrow, sometimes a mere narrow strip, without any vestige of an axillary excision or an alula; the antitegula is nevertheless always present. The *Mycetophilidae* and *Cecidomyiidae* show no trace of an alula or an excision; only *Ceroplatus* and some *Sciophilae* have rudiments of them. — All these characters have been very little noticed in the existing descriptions.

All degrees of the development of the venation are found among the *Nemocera vera*, from the complete venation of the *Tipulidae* with seven longitudinal veins and a discal cell, to the degraded venation of *Heteropeza* and *Miastor*, which has but two longitudinal veins.

The so-called ambient vein is well-marked in the *Tipulidae*, *Culicidae* and *Psychodidae* (also in *Dixa*); it is weak or altogether wanting in the *Chironomidae*, *Mycetophilidae* and *Cecidomyiidae*. The contrast between stout veins near the anterior margin, and the evanescent ones of the remainder of the wing is strongly marked in the *Chironomidae* only; in this respect this family resembles the genera *Bibio*, *Simulium* and *Scatopse* among the *Nemocera anomala*.

The theory of the venation of the Diptera is not advanced enough to enable us to formulate a general character common to the *Nemocera vera*, and distinguishing their venation from that of the *Nemocera anomala*. Such a character may be in existence, but it has not been discovered yet.

The *Nemocera vera* in their imago-state are never predaceous, that is they never hunt for other insects, and it is probably for this reason that their faces and eyes never show the broad surface in front, which distinguishes the predaceous tribes (*Asilidae*, *Dolichopodidae*, *Empididae*), and their legs are not formed for seizing the prey. But there are some genera of *Nemocera*, which draw blood, and possess an apparatus for that purpose, while their next relatives are harmless. Thus we have as blood-suckers *Culex* and *Anopheles* (Culicidae), some species of *Ceratopogon* (Chironomidae) and *Phlebotomus* (Psychodidae). As a rule the female alone is a bloodsucker and has for this purpose mouth-organs of a peculiar structure, differing from those of the male (compare Dimmock, Anat. of the mouth-

parts etc. Boston, 1881, pp. 14, 15, 20). Dimmock tried experiments with the male *Culex* (l. c. p. 22) without success; he thinks that, on anatomical grounds, they cannot obtain food by piercing the skins of animals. Among the older authors J. H. Jördens (Entom. and Helminthol. d. menschl. Körpers, 1801, Vol. I, p. 165; quoted by Dimmock, l. c. p. 50) affirmed that male mosquitoes can bite; and more recently E. Ficalbi (Bullet. Soc. Ent. Ital. 1889, p. 25) asserted positively that he had observed two Italian species in which both sexes suck blood. He is probably right in asserting at the same time that originally all the species of *Culex* are suckers of vegetable matters („tutte le zanzare filogeneticamente dovevano esse fitofaghe“). I am not aware of the existence of any bloodsuckers among the *Tipulidae*, *Cecidomyiidae* and *Mycetophilidae*. Some genera of these three families sometimes show a remarkable development in length of their rostrum and mouthparts, probably intended for sucking moisture, or the sap of flowers. Such genera are *Geranomyia*, *Elephantomyia* and *Toxorrhina* (*Tipulidae*), *Clinorrhyncha* (*Cecidomyiidae*), *Gnoriste*, *Asyndulum*, and the Australian genera *Lygistorrhina* and *Antriodipila* (*Mycetophilidae*). (Compare the Additions.)

In their general aspect (as I have already stated on p. 424) the *Nemocera vera* are distinguished by slenderness and lightness; the elongation of the abdomen in comparison to the thorax is especially noticeable. The habits of the *Nemocera vera* are rather crepuscular (and also matutinal); they prefer shady places and cool evening hours. The crepuscular and nocturnal habits of the *Culicidae* and *Ceratopogons* (in comparison with the sun-loving Diptera, like the *Tabanidae*, *Bombyliidae*, *Syrphidae*) are well-known; also the shady abodes of the *Mycetophilidae* and *Psychodidae*, the evening dances of the *Chironomidae* and certain *Tipulidae* (*Trichocera*, *Limnobia chorea*, *Erioptera imbuta*), the dances in dark recesses of *Dolichopeza*. These evening-dancers form a contrast with the swarms of *Simulidae* (*Nem. anomala*) that disport themselves in the brightest sunshine; the difference is probably conditioned by the stouter integuments of the latter, which enable them better to resist dessication. The *Nemocera vera* dance, but never hover; hoyering, as I have shown elsewhere (Chaetotaxy, Trans. Ent. Soc. London, 1884, p. 501) is connected with holopticism.

It remains for me to say a few words about *Diwa*. This genus may be well placed among the *Nemocera vera* on account of its remote eyes in both sexes, the absence of pulvilli, and its general appearance, but it cannot be fitted into any of the established families. The *Tipulidae* seem to be the nearest to *Diwa*, but the latter differs

442 *Osten Sacken: on the characters of the three divisions of*

from them in the absence of the thoracic suture, of the „sensitive hairs“ on the antennae, in the small number of the abdominal segments (seven, according to the authors; I cannot count them on my dry specimens) and in the rudimentary condition of the seventh vein. The thorax resembles that of *Chironomus* in its shape. The larva has the most remarkable resemblance to that of *Anopheles* (compare the figures of Meinert); the pupa has the convoluted legs forming with thorax and wings a more or less uniform mass, a structure characteristic of the pupa of the *Culicidae* and *Chironomidae*. *Dixa* therefore must be placed, as a separate family, between the *Tipulidae* and the group *Culicidae* + *Chironomidae* + *Psychodidae*. (Compare the Additions.) About 27 species of this genus are known to exist: 15 in Europe, 8 in North-America, one in China, and three in New South-Wales. (The latter are not described yet, but merely mentioned by Mr. Skuse in the Trans. Austral. Ass. Adv. Sci. 1890, p. 350). Four species were found by Loew in amber.

The larvae of the *Nemocera vera*.

The *Nemocera vera* can be subdivided into two natural groups, in conformity not only to the structure of their imago, but also of their larvae (compare above, p. 428).

I. The *Mycetophilidae* and *Cecidomyiidae* have peripneustic larvae, the former with eight, the latter with nine pairs of spiracles¹⁾ The larvae are strictly terrestrial and have none of the numerous adaptations for aquatic life which distinguish the next group.

In my: Characters of the larvae of *Mycetophilidae* (Proc. Ent. Soc. Phil. 1862; also reprinted separately, with additions, in Heidelberg 1886) I have shown the perfect unity of type, prevailing among the larvae of the different genera of this family. There is one exception to this rule however, to which I have alluded in my paper, but which deserves a more detailed notice than it received at that time. It is the larva of *Mycetobia pallipes*, which is not peripneustic, like the larvae of the other *Mycetophilidae*, but amphipneustic; it shows

1) Stannius, as early as 1831, has noticed this relationship between the two families, which he connects with a character common to both, the faculty of spinning a cocoon for the pupa.

Stannius, Observationes etc. 1831, p. VIII:

Imo etiam contigit ut in *Cecidomyiarum* larvis stigmata observaverim lateralialia, quod memoratu dignissimum, quum haecce simili modo ac *Tipularium* fungicolarum larvae, antequam in nymphae statum abeant, contextum sibi parent sericeum. Singularis igitur nexus huic respirandi rationi cum tela conficiendi facultate interesse videtur!

My attention to this passage was drawn by Westwood, Introd. II, p. 519, footnote.

the most remarkable resemblance to the larva of *Rhyphus*, and often occurs together with it. Three trustworthy authors have described the larva as amphipneustic: Lyonet, Dufour and Perris. The two latter have found the larva together with that of *Rhyphus*, and were struck by their resemblance, although fully aware of the differences. Winnertz, who bred such larvae from the flowing sap of trees (see his Monogr. d. Pilzmücken, p. 668) did not notice their peculiar structure and says nothing about it. The pupae of *M. palipes* figured by Lyonet and Dufour and described by Perris have two rows of little spines on each of the abdominal segments; the pupae of all the other *Mycetophilidae*, as far as known, have no such spines. Pupae of *Rhyphus* have similar spines, but only a single row on each segment.¹⁾ If there is a real relationship between the larvae of *Mycetobia* and *Rhyphus*, we have a right to expect a corresponding relationship among the imago. But as this relationship does not exist, this is a problem yet to solve.²⁾ The larvae of the *Cecidomyiidae*, as far as known, are also remarkable for the unity of their type, which is different from that of the *Mycetophilidae*. Besides the nine pairs of spiracles, their peculiarity consists in the structure of the head, only a small portion of which is chitinized; the peculiar breast-bone (spatula sternalis); the shagreened surface of the skin, often provided with characteristic processes in the shape of warts, pseudopods, and anal projections etc. A remarkable instance of adaptation was described by me, in the larva of *Diplosis resinicola* (Trans. Amer. Ent. Soc. III, p. 345, 1871) the imago of which, judging by the structure of its antennae, must be closely related to *Diplosis pini* De Geer. The larva of the latter forms a cocoon of resin, while the larva of *D. resinicola* lives imbedded in a lump of resin, exuded on the smaller limbs of young scrub-pines (*Pinus inops*). I did not perceive any lateral spiracles on it; the two tracheal trunks end in a double tube at the end of the body, by means of which the larva breathes. It brings to mind a similar case among the Coleoptera, where the aquatic larva of *Dytiscus*, although peripneustic, absorbs the air through the last abdominal pair of spiracles.

1) Weyenbergh, in his *Varia Entomologica* (in 'Tijdschr. v. Ent. XVII, 1874, Tab. 9, fig. 10 gives a figure of the pupa of *Mycetobia* independently of other authors; but he represents it erroneously with a single row of spines.

2) And it is a very important physiological problem to solve for the right understanding of the metamorphoses of diptera; a fine opportunity for a physiologist, skilled in dissecting, to render a great service to science. It is astonishing that it has not been attempted before.

As the group *Lestremia* according to both Loew and Winertz forms the passage between the *Mycetophilidae* and *Cecidomyiidae*, it will be very interesting to discover the hitherto unknown larvae, and to ascertain towards which side their affinity is tending.

II. The larvae of the second division of the *Nemocera vera* (*Culicidae*, *Chironomidae*, *Psychodidae*, *Tipulidae*) belong to the amphi-, or metapneustic type with a great variety of adaptations to aquatic life. They illustrate a phenomenon which has also been observed in other groups of animals (for instance the *Crustacea*): the great divergence of younger forms produced by various requirements of adaptation, while the imago has a closer resemblance. We have here instances of a closed tracheal system (*Chironomus*, *Tanytus* and the aquatic larva of the *Ceratopogon*, according to Meinert). In *Chironomus*¹⁾ „the tracheal system is rudimentary and completely closed“, the larva living in the mud at the bottom of slow streams, quits its burrows from time to time, especially by night, and swims towards the well-aerated surface-water by means of looping the body to and fro, and thus procures a supply of oxygen. This oxygen, dissolved in the blood of the larva is apparently stored up in the „blood-red pigment, which is identical with the haemoglobin of the vertebrate animals“. Experiments proved that the larvae could survive a long time (forty-eight hours and longer) without a new supply of oxygen. Those larvae of *Chironomus* which live at, or near, the surface „have colorless blood, and a more complete, though still closed, tracheal system“. — *Corethra* likewise has no spiracles, and a very little developed inner tracheal system, probably supplemented by the respiration through the skin (Weismann); besides which there is a hydrostatic apparatus of tracheal bladders, enabling the larva to float motionless below the surface of the water. *Culex*, *Anopheles*, *Mochlonyx* have a pair of regular tracheal longitudinal trunks, inhaling the air through the spiracles. Besides the tracheae, the larvae and pupae of the *Culicidae* and *Chironomidae* are provided with different branchial appendages. The larvae of *Psychoda* are distinctly amphipneustic, but owing to the amphibious or subaquatic life of some of them they are also provided with branchiae in various shapes (Haliday, Fritz Müller). The majority of the larvae of the *Tipulidae* are metapneustic and terrestrial; many aquatic larvae of

1) I borrow these interesting facts about *Chironomus* from the excellent paper of Prof. Miall: „Some difficulties in the life of aquatic insects“ (Nature, Sept. 10, 1891). I strongly recommend the perusal of this most instructive and graphic account of the aquatic larvae of the *Nemocera*.

Limnobia breathe through the posterior spiracles; but many other larvae have tracheal branchiae. The retractile processes which I observed in an aquatic Tipulid larva in North-America I recognized as branchial (O. S. Studies etc. II, p. 166; Berl. Ent. Z. 1887); they resemble the processes figured by Réaumur IV, Tab. 14, f. 10. Similar processes are described by Beling on the larva of *Pedicia rivosa*, Verh. Zool. Bot. Ges. 1878, p. 45, and by Prof. Miall on that of *Dicranota* (Miall, in litt.). The plumed appendages at the end of *Elliptera omissa* (Mik, Wien. Entom. Zeitschr. 1886, p. 340) and those on the larva of *Limnophila fuscipennis* described by Beling and figured by Brauer (Vienna Denkschr. etc. Vol. 47, 1883, Tab. I, f. 6) are evidently branchiae. The two short projecting lobes at the base of the breathing-tube of *Ptychoptera* Grobben (Vienna, Sitzungsber. etc. 1875), calls branchial appendages. Such are also to all appearances the filaments issuing from different parts of De Geer's aquatic larva of *Phalacrocerca replicata*, the use of which has not been investigated yet.

In most of the larvae of the *Nemocera* the head is free, that is, not imbedded in the skin of the thorax; the *Tipulidae* alone have it imbedded. But among the *Tipulidae* the genus *Ptychoptera* forms an exception, and has a protruding head, like the other *Nemocera*. Being protruded, the head of *Ptychoptera* is provided with a chitinous covering of a stronger consistency than the heads of the other larvae of *Tipulidae*, which being imbedded, are protected by the thick larval skin. In other respects both kind of heads are homologous; the parts of the mouth have the same structure (compare the figure by Brauer in his Z. K. M. III, Tab. II, f. 19), and the dentate mentum, characteristic of the *Tipulidae*, is present in both. The separation of the *Ptychopterina* from the *Tipulidae* by Brauer has no foundation, neither in the structure of the larva, nor of the imago, as I have already shown in my „Studies on *Tipulidae*“ (Berl. Ent. Zeitschr. 1887, p. 227).

I may add that the general statement of Brauer about the position of the cephalic ganglion within the head of his *eucephalous* larvae, and outside of it in other larvae, as yet requires confirmation.¹⁾ Prof. Miall, in his recent article on the larvae of *Chironomus* (Nature, Sep. 10, 1891, p. 458) distinctly says that their larval head

1) „Der Bau der Cecidomyiden-Larven nähert sich nur dadurch mehr den Tipuliden (Polyneuren), weil bei beiden das Nervensystem hinter der Kieferkapsel beginnt, während die Eucephalen einen Kopf mit Ganglien zeigen.“ Brauer, Z. K. M. III, p. 10. — The same statement l. c. p. 1. — Compare the Postscript.

„contains no brain“, although, according to Brauer, they belong to his *eucephalous* larvae.

2. *Nemocera anomala*.

The group of *Nemocera anomala*, as I have already explained in the introductory chapter, is an artificial one, intended to receive for convenience's sake, those forms of Diptera with filiform antennae and filiform palpi which, on account of their aberrant characters, cannot be included within the homogeneous group of the true *Nemocera*. The principal aberrant characters of such forms, as we know them at present, consist: 1) In the frequent occurrence of holoptic heads in the male sex; 2) in the absence of the so-called „sensitive hairs“ on the antennae; 3) in the occasional presence of well-developed pulvilli; 4) in the presence of three distinct, rather large ocelli in the three principal families of this group: the *Bibionidae*, *Blepharoceridae* and *Rhyphidae*, while among the *Nemocera vera* ocelli occur in the family *Mycetophilidae* and in the *Lestremia* only; 5) in the abnormal character of the larvae.

All the five families now composing the group of *Nemocera anomala* contain a majority of forms with holoptic heads in the male sex. Exceptional cases, where the males are dichoptic, occur among the *Blepharoceridae* (*Liponeura*, *Paltostoma*, *Apistomyia*), the *Bibionidae* (narrow front *Spodius* ♂, *Pachyneura* ♂) and the *Rhyphidae* (narrow fronts in *Lobogaster* ♂ and *Olbiogaster* ♂); the close relationship however of these dichoptic genera to the holoptic ones, which are in the majority, cannot be contested.

It is possible, and even probable, that new forms will be discovered, aberrant from the *Nemocera vera* in yet other ways than those already known. It will be then found convenient to place them among the *Nemocera anomala*. The experience we had with the artificial group of *Limnobina anomala* has proved the usefulness of such temporary arrangements.

I have already spoken (p. 425) of the interest connected with the *Nemocera anomala* as representing the remains of long-extinct faunas and of past entomological horizons.

Bibionidae. The bulk of this family consists of the genera *Bibio* and *Dilophus* which in their structure offer a strong contrast to the *Nemocera vera*. The males have a holoptic head with a long line of contact of the eyes between the antennae (placed very low) and the ocelli; the lower part of the eyes in the male is cut off by a deep groove, at the bottom of which the facets are more or less

obliterated; the larger portion of the eye, above the groove, contains the larger facets; the lesser and lower portion much smaller facets. In the female the eyes are much smaller, separated by a broad front, and not bisected. This peculiarity of the eye of the male *Bibio* was described and figured by Lyonet (Recherches etc. 1834, p. 64, Tab. VII, f. 27—28), more than a hundred years ago, but since then, it has been entirely ignored in entomological literature. I alluded to this omission in the Berl. Ent. Zeit. 1878, p. 403 and find now that Carriere¹⁾ (Kurze Mittheil. üb. d. Sehorgane etc., Zool. Anz. 1886, p. 142), to whom Lyonet's description was not known, has also noticed the silence of entomological literature about this structure.

The legs of *Bibios* have nothing of the slenderness of the legs of the *Nemocera vera*; the femora, especially the front ones are incrassate and provided with characteristic longitudinal furrows; the front tibiae are incrassate and end in two spines, the outside one of which has no suture at its insertion, and therefore is not a spur, but a prolongation of the tibia. *Dilophus*, on the front tibiae has peculiar rows of spinules at the end and in the middle; similar rows of spinules exist on the front part of the thorax. The tarsi are strong, prehensile and provided with three well-developed pulvilli. Such legs are evidently not intended for alighting only, as most of the legs of the *Nemocera vera*, but for walking and perhaps for digging.²⁾ The sexes in the genera *Bibio* and *Dilophus* are strongly

¹⁾ I deem it useful to reproduce here the principal part of this statement. Carriere, Zoolog. Anzeiger 1886, p. 142, says:

„Dagegen glaube ich nach eingehenden Literaturstudien ein ähnliches Vorkommen (Doppelaugen) bei Dipteren als noch neu betrachten zu müssen, obwohl die Thiere selbst so auffallend als gemein sind. Von den Bibioniden hat das Weibchen einen kleinen Kopf, mit seitenständigen, kleinen, ovalen Augen, während der viel grössere Kopf des Männchens fast ganz von den Augen eingenommen wird Bis in die neueste Zeit scheint unerwähnt geblieben zu sein, dass sich ausser diesen grossen Augen ein Paar kleinere findet, welches nach Form, Lage und Farbe mit den Augen des ♀ übereinstimmt Die genaue Untersuchung zeigte, dass die kleinen Augen des ♂ mit denen des ♀ bis auf geringe Unterschiede in den grösseren Verhältnissen ihrer Elemente übereinstimmen; die accessorischen Augen des ♂ dagegen in Grösse und Ausbildung der Theile so sehr von dem ♀ abweichen, dass man auf den ersten Blick einen ganz anderen Typus des Insecten-Auges zu sehen glaubt. In der That aber gehören beide zu demselben Typus, dem „aconen Auge“, stellen aber verschiedene Stufen der Ausbildung derselben dar.

²⁾ Dr. F. Dahl (Wieg. Arch. Bd. 32, 1884) is probably right when he says: „In einem solchen Sinne (that is getting from underground) ist entschieden auch der Schienenfortsatz an den Vorderschienen von

448 *Osten Sacken: on the characters of the three divisions of*

differentiated, not only in their shape, but often in their color. I am not aware of such a difference between the sexes in any genus of *Nemocera vera*. It occurs again in *Simulium*.

The chitinous covering of *Bibio* is thicker than that of the *Nemocera vera* and therefore the whole body is heavier. Their wings are broad, and have a heavy armature of veins on the front part only; the posterior veins are weak and generally pellucid, and there is no ambient vein along the posterior margin. They fly well, but, as far as I have noticed, they do not direct their motions easily.

The next relatives of *Bibio* and *Dilophus* are *Plecia* (including *Penthetria*) and the genera *Spodius* and *Pachyneura*. They all have three well-developed pulvilli, three large ocelli, and the venation more or less like *Bibio*, only the veins on the front and hind part of the wings differ less in thickness. The head of the male shows a gradual passage from a long and complete contact of the eyes in several exotic *Pleciae* and in *Penthetria velutina* Loew, from Japan, to closely approximate eyes without actual contact, in the European *Penthetria* and to a distinct front between the eyes in *Spodius* and *Pachyneura*. Bisection, as observation teaches us, never occurs but with contiguous eyes¹⁾ (although contiguous eyes may occur without bisection). As *Spodius* ♂ and *Pachyneura* ♂ have a narrow front, separating the eyes, the latter, in accordance with the above rule, are not bisected. *Penthetria holosericea* represents a transitional case: its eyes are closely approximate, but not in actual contact; nevertheless bisection takes place here.²⁾ In *Plecia* the heads of the male are holoptic; bisection occurs in many cases, but not in all.

It is only recently that I became aware that holoptic male *Pleciae* occur in two different forms: with bisected, and with unbisected eyes. The European *Penthetria holosericea*, as well as the *Penthetria melanaspis* from Java, and its probable synonyms *P japonica* W., *ignicollis* Walk. and *Crapitula Motchulskii* Gimmerth. have each eye of the male divided by a more or less deep bisecting groove. In the Berlin Museum I saw many male specimens from South-America

Bibio zu erklären. Die Larve lebt nämlich in der Erde." According to Beling (Verh. Z. B. Ges. 1872, p. 646) the larvae, for the purpose of pupating, descend 7 or 8 centimeters below the surface of the soil, and form a round earthen cavity with smooth walls, in which they remain 8–14 days, awaiting transformation.

¹⁾ The only exceptions known to me from this general rule will be mentioned in the paragraph on the *Blepharoceridae*.

²⁾ Loew (Wien. Ent. Mon. 1858, p. 103) does not say whether the eyes of the male of his *Penthetria velutina* are bisected or not.

Diptera: Nemocera vera, N. anomala and Eremochaeta. 449

and Mexico with bisected eyes; among them *Plecia plagiata* Wied., also a *Plecia* from Sydney, Australia. At the same time the *Pleciae* from South-Eastern Asia, which I have seen, for instance *Plecia fulvicollis* Wied. and *P. forcipata* O. S. from Sumatra, do not show any trace of bisection.

This difference in the structure of the eyes in the genus *Plecia* was unknown to Loew when, in the Berl. Ent. Zeit. 1858, p. 116, he discussed the question of the fusion of *Penthetria* and *Plecia*. Does the presence or absence of bisection alone, without support of other characters, justify generic separation? We have many genera (to begin with *Tabanus*) in which bisection in holoptic heads often, but not always, occurs, without ever having been used for generic separation. I merely call attention to a character hitherto much neglected, without pretending at once to solve the involved questions.¹⁾

Bibio and *Dilophus* are distributed nearly all over the world, and are represented in each region by a considerable number of species. A centre for the genus *Dilophus* is Chili, from which twenty-five species have been described (including the genus *Acanthocnemis* which is but a slightly modified *Dilophus*). From Australia, on the contrary, we have but a single well-authenticated *Bibio*, four *Dilophus* and four or five *Pleciae*. *Plecia* is principally tropical. — The monotony in form and color among the multitude of species of *Bibionidae* from all parts of the world is remarkable: the colors are generally black and red, sometimes yellow. *Spodius* Lw. (*Hesperinus* Wk.) has been found in Hungary, in the British possessions of North-America, in the White-Mountains, New Hampshire, and on the heights of the Rocky Mountains in Colorado; I also saw a specimen brought by Whymper from the altitude of 11—13 000 feet in the Andes of Peru. The occurrence of *Hesperinus* in Brazil (Schiner's Novara, p. 23) requires confirmation. *Pachyneura* has been found in Swedish Lapland only. The abundance of the *Bibionidae* (*Bibio*²⁾, *Plecia*) in different geological strata is wellknown. Loew discovered two species of *Plecia* and a single specimen of *Dilophus*, but no *Bibio*, in the Prussian amber (Bernstein etc., p. 39).

The larvae of *Bibio* and *Dilophus* with their horny head, a complete set of mouth-organs, and the characteristic, symmetrically

1) I hope to find occasion, in a future publication, to enter with more detail into the question of the relation of holopticism with bisection, and into other questions connected with the eyes of Diptera.

2) Are the fossils described by Heer from the tertiary formations as belonging to the genus *Bibio* real *Bibios*? Compare Loew, Zeit. f. d. Ges. Naturw. 1868, vol. XXXII, p. 181, sqq.

arranged, spinelike processes on the segments of the body, have been often described. Lyonet, Bouché and Beling have stated correctly that they have ten pairs of spiracles, but none of them (nor even Brauer) seems to have noticed that this is a very extraordinary number, almost unique among insects. Nine pairs is the maximum number of spiracles for all the other peripneustic larvae of Diptera, and the occurrence of a supernumerary pair on the thoracic segments is a very exceptional character.¹⁾ Zeller, in describing the larvae of *Penthetria* does not mention the number of spiracles.

The second section of the family *Bibionidae* consists of the three related genera: *Scatopse*, *Aspistes* and *Corynoscelis*. (I do not know anything about *Penthera* Philippi, from Chili, which may belong to the *Bibionidae*.) In the general appearance of the body, the venation, the structure of the antennae and legs, and the presence of three ocelli they are allied to the genera of the first section. The points in which they differ are as follows: the palpi of *Scatopse* and *Aspistes* are apparently single-jointed and rather indistinct. *Corynoscelis* with its three-jointed palpi forms the transition (comp. Loew, Berl. Ent. Z. 1858, p. 103). The three pulvilli of the first section of the *Bibionidae* are replaced here by a broad empodium, which looks like the coalescence of the pulvilli („Haftläppchen in ein einziges verschmolzen“; Schiner). The eyes of *Scatopse* are lunate, contiguous in both sexes above the antennae (at least in those species which I have examined; *Scatopse biflata* Halid. ♂ in Walk. Ins. Brit. Dipt. III, Tab. 24, f. 5 is represented with a broad interval between the eyes). In this respect the head of *Scatopse* resembles that of some of the *Culicidae* and *Chironomidae*, where the antennae are also inserted within the excision of the lunate eyes, and where the eyes in both sexes are contiguous above the antennae, and

¹⁾ A parallel case occurred to Erichson among the Coleoptera and excited his astonishment. His remarks are worth repeating here (Erichson, Zur system. Kenntn. der Insecten-Larven, in Wieg. Arch. 1841, p. 92):

„Two larvae of Lampyridae from Java, recorded in Westwood's Introduction etc. I, p. 254, f. 1 and p. 259, f. 1, show a peculiarity which I never met with in any other coleopterous larva, and even among other larvae of Lampyridae. While the thorax usually bears a single spiracle on the mesothoracic, or more seldom on the prothoracic segment, or between both, in this case there is, besides the normal mesothoracic pair, a supernumerary one in the corresponding place of the metathoracic segment. If this latter pair is really the opening of a spiracle, and that should be ascertained by dissection, then these larvae would offer a remarkable anomaly in having ten pairs of spiracles.“

Diptera: Nemocera vera, N. anomala and Eremochaeta. 451

separated by a mere groove or suture, and not by any breadth of front. In the first section of the *Bibionidae* the eyes are contiguous in the male only, and the antennae are inserted, not in the middle, between the eyes, but below them, near the mouth. The eyes of *Scatopse* are therefore not truly holoptic, and this distinction between the two sections is an anomaly, which requires a further explanation. It has never been noticed in any of the existing descriptions. The eyes of *Corynoscelis*, judging by Boheman's description and figure, have the same structure as those of *Scatopse*; the eyes of *Aspistes* are slightly remote at the top (I have compared specimens, as well as the figures in Meigen, Loew and Westwood, in Walker's Vol. III).

There is the genus *Anarete* Hal. which Loew refers to the *Cecidomyiidae* (Section *Lestremia*) and Schiner to the *Scatopsina* (Fauna Austr. II, p. 353). The antennae of *Anarete* are without verticils, the venation is very like that of *Scatopse*, the eyes are reniform. but separate on the front; there are distinct ocelli. *Anarete* differs from *Scatopse* in its slender legs, with a very long metatarsus and in its four-jointed palpi. Loew would not admit the relationship of *Anarete*, with its four-jointed palpi, to *Scatopse*, whose palpi are almost abortive (Loew, Stett. Ent. Z. 1845). But at that time Loew did not know the genus *Corynoscelis*, which undoubtedly belongs to the *Scatopsina*, but nevertheless has three-jointed palpi, and thus forms the transition. In Loew's Dipter. Beitr. IV, *Cecidomyia*, p. 22 he mentions the very large pulvillus (should be empodium) of *Anarete*, which of itself speaks most decidedly in favor of the relationship with *Scatopse*. I have not seen *Anarete*, and therefore de visu have no opinion about it.¹⁾

Scatopse notata is cosmopolitan, probably imported in North-America, Australia and New-Zealand. The european *S. recurva* and *pulicaria* likewise occur in North-America (see my Catal. N. Am. Dipt. 1878, p. 17). A species is described by Wollaston from Madeira, half a dozen species from China and Argentina, and two from Australia. (The *Scatopse* from Java described by Doleschall is a *Sciara*.) *Aspistes* has been found in Europe and N.-America; *Corynoscelis* in the north of Europe only. Loew found several *Scatopse* in amber.

¹⁾ Since writing these lines I have received a specimen of *Anarete* through the kindness of my friend Mr. v. Röder, and I feel convinced now that Schiner was right, and that *Anarete* belongs to the *Scatopsina*. The legs, for a *Scatopse*, are remarkably long.

The larva of *Scatopse* has been described by Bouché, Dufour and Perris; the two latter took it for amphipneustic, but it is a question whether Bouché was not right in taking for spiracles the nine projections on the sides of the body, one on the thoracic segment and eight on the abdominal ones. The pupa does not shed the larva-skin, but remains in it, emerging with the front part only (some larvae of *Ceratopogon*, occurring under the bark of trees, do the same).

Simuliidae. The principal characters which exclude this family from the *Nemocera vera* are: the holoptic head of the male; the bisected and bicolored eyes of the same sex; the structure of the antennae, which are comparatively short, attenuated towards the tip, with short, transverse, closely compressed joints, clothed with an almost microscopic pubescence, without any verticillate hairs; the short, but strong and stout legs, with broad, flattened tibiae, and long, likewise broad and flattened, metatarsi, which are almost as long as the tibiae.¹⁾ Among other characters I shall notice very minute spurs on the four posterior tibiae (generally not mentioned in descriptions); the tarsal joints 2—5 which are very small in comparison with the very large first joint; the fourth tarsal joint bilobed as in *Orphnephila*, *Diamesa* and some species of *Chironomus* and *Ceratopogon*; the fifth joint generally at an angle to the fourth (even in living specimens); unguis very small in the male, a little longer in the female; empodia rudimentary; body thickset, comparable to *Psychoda* among the *Nemocera vera*; no ocelli; wings broad, iridescent, glabrous, with strong veins on the anterior, and evanescent ones on the posterior part; no ambient vein; anal angle large, axillary incision very little marked, but containing a chitinous knot, resembling that in the *Blepharoceridae*; alula small, antitegula rather large, both with long, delicate

¹⁾ With their long front metatarsi *Simulium* execute peculiar motions, for the first time described by Macquart, Dipt. du Nord, Vol. I: „Lorsqu'elles sont posées sur une feuille, leurs tarses antérieurs s'appuient dans toute leur longueur sur le plan de position; ils sont dans un mouvement continu de tâtonnement et paraissent servir très peu à marcher. C'est cette habitude qui a fait donner par Linné le nom de *Culex reptans* à l'espèce la plus connue. Comme ces insectes habitent ordinairement les buissons situés sous les arbres et qu'ils y recueillent avec la trompe les sucs répandus sur les plantes, et particulièrement ceux produits par les Pucerons, leurs tarses font les fonctions de palpes; ils servent à reconnaître cet aliment et on les croirait l'organe d'un sens supérieur au toucher."

I reproduce this passage because the observation about the food of *Simulium* seems to be new, and because Macquart's Dipt. du Nord etc. are not often consulted by dipterologists.

cilia; tegulae rudimentary. The color of the eyes in life is reddish. The female differs very much from the male in the color of the body and its pubescence; the eyes are reniform, or rather oval with an abrupt excision on the inner side, separated by a broad front.

The habits of *Simulium* (comp. p. 444) are the opposite of crepuscular; they love heat and strong light, and the males disport themselves high in the air in the sunshine. (I have often watched swarms of male *Simulium* dancing about the towers erected on the mountain-tops around Heidelberg; they occur on both sunny and clouded days. The females generally remain in the lower regions, and annoy men and horses.)

The metamorphoses of *Simulium* have been often described and are very peculiar. As larvae and pupae live in rapidly running waters, they cannot swim about freely, like most of the larvae of the *Nemocera vera*, for fear of being carried away; protection against this danger is therefore one of the conditions of their existence. Fastened by their tail-end to stones and aquatic plants, they move from place to place by means of a thoracic pseudopod, always followed by a thread of silk emitted from their mouth; these threads proved very destructive to young trout in the breeding ponds in the State of N. York (compare the Amer. Entomologist and Botanist, Vol. II, p. 227, 1870). The larvae require „a brisk flow of well-aerated water There are no externally visible organs of respiration, but the skin is supplied by an abundant network of fine tracheal branches which take up oxygen from the water They subsist entirely upon microscopic plants and animals. Among these are great numbers of Diatoms, and the stomach is usually half-full of the flinty valves of these microscopic plants." (Miall, Nature Feb. 1892.) The pupae are maintained in position by a semi-oval cocoon fastened under water to a stone or waterweed; the opening of the cocoon is always directed with, and not against the current;¹⁾ the pupae breathe by a number of respiratory filaments on each side of the thorax. The wonderful escape of the fly from under water is also described by Prof. Miall (Nature, May 5, 1892). According to Tömösvary the pupae spend the winter in a state of torpor and come out in the spring (l. c. p. 9).

This family contains but a single genus *Simulium*²⁾ represented by rather numerous species in Europe, North- and South-America;

¹⁾ Observation of Dr. Edmund Tömösvary in his pamphlet: Die Kolmbaczer Mücke; 1885.

²⁾ Latreille has it *Simulium*. Meigen, Syst. Besch., made it *Simulia* without giving any reason. Macquart, in the Dipt. du Nord,

it also occurs in New-Zealand and the Auckland Islands, and has been recorded from Assam and the Islands of Bourbon and Madeira. Two species are described from Australia. Wherever *Simulium* appears, it is in myriads of specimens; in Australia alone they seem to be „rare and local“ (Skuse). Loew discovered half a dozen species in amber.

Blepharoceridae. Although this family, by reason of its long legs and slender body, resembles the *Tipulidae*, it has many characters which distinguish it from the *Nemocera vera*, principally in the structure of the head and eyes. Holopticism and bisection of the eyes frequently occur here in both sexes.

The genus *Blepharocera* has contiguous eyes, bisected by an unfacetted crossband; the facets of the upper part of the eye are larger than the lower ones; these characters belong to both sexes. *Hammatorhina*, known in the male sex only, has a similar structure of the head. In *Blepharocera ancilla* O.S., California, the unfacetted crossband is replaced by a groove.

Bibiocephala and *Agathon* (both known in the male sex only) also have contiguous, bisected eyes, with larger facets above than below, but the unfacetted stripe is replaced here by a mere line.

In *Liponeura*, *Apistomyia* and *Paltostoma* the eyes are separated by a more or less broad front (in *Liponeura* in both sexes; the females of the two other genera are not known). In *Liponeura yosemite* ♂ the eyes are bisected by a line with larger facets above than below; about the female, as well as about the other species of *Liponeura*, observations are wanting. (My observation on *Lip. yosemite* I took from fresh specimens. I have a pair of *Lip. cinerascens* before me which I captured in the Pyrenees; but I cannot perceive the bisection in the dry specimens; comp. Berl. Ent. Z. 1878, p. 410). *Apistomyia* ♂ has, like *Blepharocera*, the eyes bisected by an unfacetted stripe, its broad front notwithstanding; this and *Liponeura yosemite* are the only known exceptional cases of bisection without holopticism.

Paltostoma ♂, which I saw in Turin (Berl. Ent. Z. 1878, p. 411), appeared to me as having facets of the same size all over the eyes, without any bisection. The *Paltostoma torrentium* (Müller) male, is represented with contiguous eyes, distinctly bisected; but I have shown in the Berl. Ent. Z. 1891, p. 409 that, on account of these characters, it cannot be a true *Paltostoma*.

follows Meigen, but returns to *Simulium* in his later publications. Schiner has *Simulia*.

Hapalothrix ♂ has contiguous eyes; I could not ascertain the existence of bisection in the dry specimens which I examined.

The color of the eyes of *Blepharocera capitata*, which I took down from living specimens was reddish-green on the upper half, and purple on the lower one.

The eyes of all the known species of the *Blepharoceridae* are finely pubescent, but some of them have a covering of longer hairs besides (*Hapalothrix* and the lower portion of the eyes of *Bibliocephala*). Three large ocelli are present (the majority of the *Nem. vera* have no ocelli). The antennae are comparatively short and without verticils. No pulvilli and a rudimentary empodium. In its pulvilliform unguis, *Hapalothrix* has a character unique among *Diptera*.

The wings of the known *Blepharoceridae* differ from the wings of all the other *Diptera* in the presence, besides the ordinary venation, of a net of crease-like lines which extend over the whole surface. The wings have moreover a peculiar iridescence (not unlike that of *Simulium*). The axillary excision is replaced here by a chitinous knot, which I have observed in all the species; the alula, antitegula and tegula are absent, or rudimentary. An interrupted longitudinal vein, between the fourth vein and the large fork of the fifth, distinguishes four among the eight genera of the family. The ground-pattern of the venation is more or less the same in all the genera, only the number of longitudinal veins between the first and the fourth vein is gradually diminishing from *Bibliocephala* and *Agathon*, which have three such veins, to *Liponeura* and *Blepharocera*, which have two, *Apistomyia* and *Paltostoma* one, and *Hammatorhina* — none.

The larvae of the *Blepharoceridae* (those of *Liponeura* and *Paltostoma* have been described in detail) are very aberrant, and cannot be compared to any other larvae of *Diptera*. They are subject to the same condition of life as those of *Simulium*, the life in rapidly running waters; from this condition arises the necessity of precautions against the danger of being carried away by the current, and in the present instance the problem is solved by adaptations quite different from those of the larvae of *Simuliidae*, and apparently capable of resisting a much stronger current. The larvae live in rapid mountain-streams, and are found on slimy stones under water, clinging to them by means of six suctional discs, one on the underside of the thorax, the others on the ventral segments; they move slowly on the stones by means of these discs, and find their food among the slimy matter (Dewitz, Berl. Ent. Z. 1881, p. 64, says

about *Liponeura*: „the digestive tube was filled with black matter, apparently nothing but mud and slime“). They breathe by means of bunches of tracheal branchiae on each side of the segments of the body. The larva of *Liponeura* is remarkable for its long antennae; that of *Paltostoma* has much shorter ones. The pupa is protected by a tortoise-like flat roof, fastened to the stone or weed; on the thorax it has a pair of perfoliate branchiae for breathing. According to Fritz Müller the larvae have five Malpighian vessels, like the larvae of *Culex*; not four, which is the usual number.¹⁾

Since 1840 when the first *Blepharocerid* was described, fifteen species have been discovered — six in Europe, one in Asia (Ceylon), six in the United States and Mexico and two in South-America. Their extraordinary characters, their graceful shape, their mode of life, almost exclusively among romantic mountain-scenery, the males dancing in the spray of picturesque waterfalls, all these anomalies and eccentricities lend to this family a peculiar charm.

Rhyphidae. *Rhyphus* is a singular genus, and Loew must have felt it, when he said (without giving any reason) that he considered it „as standing in a closer relation to the *Brachycera* than any other genus among the *Nemocera*“ (Loew, in Nat. Hist. Review, London 1856, p. 79). *Rhyphus* is a stranger among the *Nemocera vera* principally on account of its holoptic head in the male, and its largely developed empodia, which resemble those of *Scutopse*, and look as if the pulvilli were connate with them. There are three ocelli. The filiform antennae are clothed with hair, but have no distinct verticils. The wings have a discal cell (like the *Tipulidae* among the *Nem. vera*); the axillary excision is present, the alula moderately, the antitegula largely developed; no tegulae. The larva is amphipneustic, serpentineform.

The thoracic dorsum shows two rows of dorsocentral, weak, but distinct, little bristles, two abbreviated lateral rows of similar little bristles, some others on the post-alar calli, and two on the apex of the scutellum. These little bristles, in the regularity of their distribution, seem to foreshadow the macrochaetae of other families.

1) F. L. Arribalzaga, Dipterol. Argent. 1891, p. 13 and 17 found five Malpighian vessels in the pupa and imago of *Culex*, and six in the larva. Some *Psychodidae* (imago) likewise have five Malpighian vessels, but the usual number is four (compare Dufour, Rech. anat. Dipt. 1851, p. 213: „j'ai constaté l'existence de cinq vaisseaux hépatiques, comme chez les cousins, presque aussi souvent que celle de quatre, que je regarde comme le nombre normal“).

Half a dozen or so of *Rhyphus*, congregated together in a shady place, often near the trunk of a tree, may sometimes be seen flying slowly up and down, the legs stretched out perpendicularly downwards and kept close together. This genus occurs in almost every part of the world which has been explored: Europe, North-America, Colombia, Brazil, Chili, New-Guinea, Tasmania, New-South-Wales, New-Zealand; in all these countries it is represented by a small number of species; all these species are very nearly alike in structure and coloring. And yet, although represented everywhere, *Rhyphus* is everywhere a solitary genus. His only relatives, at present known, occur on the western coast of South-America, a coast which, with Australia and New-Zealand, harbours many primeval forms. The genera *Lobogaster* in Chili and *Olbiogaster* in Central-America and the West-Indies are undoubtedly *Rhyphidae*. The family must have been more abundant in the tertiary period, if Loew was right in distinguishing four or five species of *Rhyphus* among the amber-diptera.

That *Rhyphus*, „notwithstanding its many-jointed antennae possesses the venation and the shape of the body of a Leptid“ (Brauer, Verh. Z. B. Ges. 1890, p. 273; the same in Z. K. M. II, p. 4) I deny most emphatically. Anybody who has eyes can easily convince himself that the venation of *Rhyphus* shows several other differences besides the one mentioned by Brauer, and as to the shape of the body, one must be singularly wanting in appreciation of affinities to make such a comparison.

Remarks about the larva of *Rhyphus*.

Perris (Ann. Soc. Ent. Fr. 1870, p. 190) is the only author who describes the anterior spiracles of this larva: „deux très petits orifices sur les côtés du premier segment.“ I find in my notes about the american *Rhyphus punctatus* which I bred many years ago, „in front a pair of distinct elliptical three-creviced spiracles“. The larvae have five fleshy points or protuberances at the end of the body, as Perris, Beling and myself saw them. Brauer's statement (Z. K. M. III p. 20): „Aftersegment mit zwei kurzen Fleischspitzen“ is copied from Bouché, p. 43 and erroneous. Réaumur, Dufour and Walker, Dipt. Brit. III are also in error, when they speak of four protuberances.

Beling says (Wieg. Arch. 1872, p. 54): „Die Larven des *R. fenestralis* unterscheiden sich sogleich von denen des *R. punctatus* durch die bei Letzterem um drei grössere (it should be „kleinere“) Anzahl der Körperabschnitte etc.“ The following passage in Perris,

l. c. p. 101, about *fenestralis* explains this discrepancy: „Les deux derniers segments sont divisés chacun en deux parties presque égales, de sorte qu'on serait tenté de compter onze segments abdominaux.“ Beling counted eleven segments in the larva of *R. punctatus* and fourteen in *R. fenestralis*. I counted twelve segments in *R. punctatus*, taking the last segment for one; in adding to these twelve the two spurious segments observed by Perris in *R. fenestralis* we obtain for this species fourteen apparent segments, which is exactly the number counted by Beling.

Orphnephilidae. They are represented by a single genus *Orphnephila* which, with regard to its relationship, is perhaps the most refractory form among all Diptera. Hitherto four species have been found in Europe, one of which also occurs in North-America; one species has been mentioned by Mr. v. Roeder (Stett. Ent. Z. 1886, p. 261) as occurring in Equador at an altitude of 14,000 feet. The genus *Orphnephila* offers one of the rare instances of a holoptic head in both sexes¹⁾ (the eyes, which I observed in life, are dark, unicolored). The palpi are comparatively long, the antennae, on the contrary short, 11 (or 12?) jointed, nearly of the same structure in both sexes, with more or less homologous joints of the flagellum; they bear some scattered hairs, but none of those verticillate or bushy hairs that distinguish most of the true *Nemocera*. The venation cannot be compared to any other; the evanescence of the proximal section of the fourth vein is remarkable. The axillary excision and the alula are obsolete, the antitegula small, but distinct, the tegula rudimentary. The structure of the male forceps is also peculiar; the lamella supera forming a kind of covering for the forceps below it. The halteres (and especially the club) are rather large. Legs simple, bare, unarmed, of moderate and nearly equal length; tibiae without spines; tarsi rather long, metatarsi of the front legs nearly as long as the tibiae, those of the hind legs shorter; penultimate joint short, emarginate, obcordate; unguis very small, empodia rudimentary, beset with minute hairs (this is as I see it in my dry specimens; Haliday in his excellent description, in Walk. Ins. Brit. Dipt. III, p. 265 has: „*onychium dilated, empodium inconspicuous*“).

The early stages are unknown.

1) Besides *Orphnephila*, holoptic heads in both sexes occur, as far as I know, only in the following families and genera of Diptera: among the *Cyrtidae* and *Blepharoceridae*, in *Systropus* and in certain *Empidae* (*Hybos* and the related genera).

Additions.

p. 417. The motto borrowed from Scopoli. Fabricius (1745—1810) was not friendly to his predecessor Scopoli (1723—1788; both reached the same age: 65). The former seems to have been a sort of pedant; Scopoli was an enthusiastic friend of nature and knew how to use his eyes (although he lost them before his death). The following passage in the Preface of the „*Philosophia Entomologica*“ 1778 is evidently directed against the passage from Scopoli which I have prefixed as a motto to this paper: „*Entomologis veris strenue commendo: characteres omnes iisdem semper partibus desumendos. Regula enim hac haud observata chaos omnino erit res entomologica.*“ — In the letterpress of the „*Philosophia*“ there are many hits against Scopoli: pag. 124, § 5, 6; pag. 126, § 8, 9; pag. 128, § 12 (the latter is rather comical: „*Erroneae ideo sunt omnes differentiae, quae ab odore desumuntur: Cerambyx moschatus, elytra viridia; odor moschi, Scopoli; pag. 115, two generic names proposed by Scopoli are blamed: Anthrax Scop., Erax Scop. „nauseosa, quae nescio quid insueti produnt“.* P. 114: „*Scopoli mutavit Linnæi Asilus in Erax, Empis in Asilus, et Conops in Enpis, inde necessario oritur confusio, quum jam ideam aliorum insectorum cum his nominibus combinare soleamus*“. And in spite of this reproach, Fabricius allowed himself exactly similar changes, for instance when he called *Bibio* — *Hirtea*, while Scopoli had selected this name for a *Stratiomyia*. — Scopoli was decidedly the better head of the two. „*Scopoli's Arbeiten sind so vortrefflich, dass es nicht begreiflich ist, warum denselben von neueren Dipterologen (Linné, Fabricius, Rossi und die älteren Autoren berücksichtigten Scopoli, wenn auch nicht immer nach voller Gebühr) so wenig Aufmerksamkeit geschenkt worden ist Scopoli's Beschreibungen sind meistens sehr vollständig und genau, ja ohne Bedenken denen des Fabricius vorzuziehen*“ (Schiner, *Scriptores austriaci rerum dipterologiarum*; Verh. Zool. Bot. Ver. 1856). I am glad to take advantage of this opportunity to recall the name of Scopoli, who maintained against Fabricius the true principles of a natural classification.

p. 422. „Palpi generally 4-, or 5-jointed, pendulous etc.

The palpi of *Culex*, *Anopheles* and *Aedes*, even when long, are stout and stiff and therefore not pendulous. But the palpi of the very next genera (*Corethra*, *Mochlonyx*) are pendulous. Atrophied, short palpi like those of *Ceroplatus* (Winnertz, Tab. XIX, 7) and

Scatopse are, of course, not pendulous. However in the great majority of cases, the term pendulous is descriptive, and therefore useful.

About the basal (fifth) joint of the palpi, Becher, Mundth. p. 9 says: „In those cases where, as in most *Nemocera*, the palpi are apparently five-jointed, the first joint corresponds to the palpal scale" (Tasterschuppe).

p. 428 (footnote). Marno, Die Typen der Dipteren-Larven, Verh. Zool. Bot. Ges. 1869. In this paper Marno does me the honor to ascribe to me the first notice of the organ in the larvae of *Cecidomyia*, which I called breastbone. And indeed I remember distinctly that in preparing my paper: On the N. Am. Cecidomyidae for the Monogr. N. Am. Diptera Vol. I, 1862, I was astonished not to find any notice of this very conspicuous and important organ in either of the three monographs by Bremi, Winnertz and Loew.

Since that time I have discovered two much earlier descriptions of the breastbone. One is found in Ratzeburg's Ueber den Bau etc. zweier an der Kiefer lebenden Gallmücken-Larven (Wieg. Arch. 1841). On page 237 he says: „Eines merkwürdigen Theiles (Brustbein?) muss ich noch erwähnen etc." This organ is figured on the plate (Tab. X, f. 3, 4). The other description, with a figure, has been given by Dufour (Mém. de Lille 1845, p. 209—210, fig. 4) and concerns the larva of *Lasioptera*. Dufour says: „A la région inférieure et à la ligne médiane du corps, il y a constamment une lame allongée, cornée, brune, bifide à son bout antérieur. Quoique placée à une certaine distance du pseudocephale, je la considère comme un vestige intéressant de ces mandibules intérieures et rétractiles qui s'observent dans plusieurs larves dépourvues de véritable tête et dont j'ai exposé la composition et la structure dans un mémoire sur la *Piophila petasionis*. Réaumur a décrit et figuré cette lame sous le nom de trait brun corné etc."

Réaumur's statement refers to some larva of a Muscid, and not to that of a *Cecidomyia*.

The magnificent large in-folio of N. Wagner about Paedogenesis, appeared in the same year (1862) with my little essay on Cecidomyiae. It contains probably the most complete description of the larva of *Cecidomyia* in existence and, of course, gives a description and figures of the breastbone.

p. 434, at the top, about the ocelli. Schiner (Fauna II, p. XXVIII, footnote) says, referring to the *Chironomidae*: „Traces of ocelli may sometimes be discovered, under a magnifying power, especially in *Tanytus*". In MM. Miall's and Hammond's recent

paper (The devel. of the head of the imago of *Chironomus* p. 269, Tab. XXIX, fig. 14, c) I find the same observation: „On the vertex, and between the posterior angles of the eyes, are seen a pair of minute tegumentary processes, probably of little, if any, functional significance. We find, however, that in the pupa they are connected with the brain by a single median nerve. It may be of interest in this connection to recall a statement of Dufour (Rech. Anat. sur les Dipt. p. 178; 1851) that in *Tipula oleracea*, an insect belonging to a genus characterized by Meigen, Macquart etc. as devoid of ocelli, he found at the posterior border of each compound eye a minute ocellary nerve terminated by a subglobular violet-coloured retina. He further found behind the insertion of each antenna a minute sub-hemispherical tegumentary prominence. Although failing to trace with certainty the connection between the nervous and tegumentary structures so described, he hazards the conjecture that they are really associated, and regards them as the functionless vestigiary representatives of the ocelli of other Dipterous genera.”

In my Monograph of the N.-American Tipulidae (Monogr. of N. A. Dipt. IV, p. 234; 1869) I have mentioned that in that family the genus *Trichocera* alone has distinct ocelli on each side of a gibbosity immediately behind the antennae. I thought at that time that I could also see something like it in the genus *Pedicia*.

p. 441. *Campylomyza* sucking a caterpillar. J. G. Apetz in the Stett. Ent. Z. 1849, p. 62 records an observation of a *Campylomyza*, apparently sucking a caterpillar of *Smerinthus ocellatus*. I am not aware of another observation of this kind, although caterpillars are sucked by *Culex* and *Simulium*.

p. 442. *Diwa*. While reflecting about the location of *Diwa* in the system and searching the literature in the hope of discovering some ray of light about it, I happened to find a passage in Westwood (II, p. 515) which I had overlooked before: „these pupae“ (of *Chironomidae*) „offer a marked difference from those of the true incomplete pupae, their legs, from their great length, being partially convoluted, and forming, with the wings and thorax, an uniform mass, the limbs being less distinct even than in the obteated pupae of the Lepidoptera.“ This gave me the clue that I wanted. In the work of Meinert (De Enc. Mygg.) I compared the figures of the pupae of the *Chironomidae* and *Culicidae* (*Culex* Tab. I, f. 11, *Anopheles* I, 30, *Corethra* II, 54, *Mochlonyx* III, 74, *Chironomus* III, 84, 88, 91, *Tanyppus* III, 97, 101), and found that all these pupae have the structure described by Westwood. Those of the genus *Chironomus*

differ from the others in having the convoluted legs less closely soldered to the body of the thorax. But still more important for me was the fact that the pupa of *Diixa* (l. c. IV, 111) shows the same structure and comes nearest to the pupa of *Anopheles*. *Diixa* and *Anopheles*, which differ in the imago-shape so much, have therefore very closely resembling larvae and pupae.

Yet another important fact results from Westwood's observation. In this convolution of the legs of the *Culicidae*, *Chironomidae* and *Diixidae*, we seem to have a good character for distinguishing their pupae from those of the other families of *Nemocera vera*: *Tipulidae*, *Mycetophilidae* and *Cecidomyidae*. These have their pupal legs stretched out straight, appressed to each other, and extended over the abdominal segments. Even the aquatic Tipulid pupae share this character, for instance that of *Phalacroceraplata*, figured by De Geer, and that of *Ptychoptera*. And this character furnishes us a new proof that *Ptychoptera* is a true Tipulid and has nothing to do with *Culicidae*, as Brauer contended. In the *Cecidomyidae* the legs of the pupa stretch along the abdomen the farthest (compare the figures in Winnertz's monograph; or the pupa of *Cec. papaveris* Laboulb., or of *Lasioptera picta* Meig., figured by Dufour. Mém. de Lille 1845; in the two latter cases the legs nearly reach the tip of the abdomen.)

There is an exception however among the pupae of the *Chironomidae*. The genus *Ceratopogon*, aberrant in so many respects from the other genera of the family, has the legs of the pupa straight (perhaps because they are shorter?). The terrestrial pupae of this genus are so represented by Dufour, Perris, Heeger. Of the aquatic pupae of *Ceratopogon* we have that of Gerke, which is not quite distinct, but seems to have straight legs. The pupa figured by Meinert (l. c. Tab. IV, f. 136) is represented from the back, so that the legs are not visible. Comp. also Laboulbène, Ann. S. E. Fr. T. IX, Tab. VII, f. 7.

The pupae of the *Psychodidae* have straight legs. Compare the figures of Bouché, Curtis, Journ. Roy. Agric. Soc. Vol. X, 1850; p. 403, Tab. V, fig. 48—50 (excellent figures of the pupa in three positions); Perris, Ann. Sc. Nat. 1840, p. 346—48 (the pupa is that of *Psychoda*; but the larva that of some muscid!).

p. 442. Concerning the two groups of larvae of the *Nemocera vera*. That the metapneustic system of tracheal breathing is originally derived from the peripneustic is beautifully illustrated in Brauer's description of the metapneustic larva of *Chionea* (Verh. Z. B. Ver. 1854, p. 614). The longitudinal tracheal trunks emit lateral branches

which, as Brauer says: „probably reach a spiracle“. In the postscript to the same article (p. 616) Frauenfeld confirms Brauer's observation: „ich habe bei der Untersuchung der Larven nur mit „äusserster Mühe im wechselnden Lichte zu beiden Seiten rundliche „Flecken bemerkt, die ich ohne weiteres für Stigmenpunkte erklären „muss. Ob aber dieselben wirklich durchbohrt mit dem Inneren des „Leibes communiciren, oder nur jene Stellen andeuten, die beim vollkommnen Thiere diese Function erst übernehmen, möchte ich nicht „bestimmt entscheiden“. Such cases may occur quite often and have been overlooked. For instance the aquatic larva of *Simulium* has been generally figured with little dots on the sides, apparently foreshadowing lateral stigmata (compare the figures of Verdat and Meinert, l. c. Tab. IV, f. 5).

Postscript.

A paper by Professor L. C. Miall and A. R. Hammond recently published in the Transactions of the Linnean Society (Vol. V, Sept. 1892) reached me while my own paper was going through the press. This masterly paper is entitled: „The development of the head of the imago of *Chironomus*“, and contains some facts which I have foreshadowed in my „Suggestions“ (Ent. M. Mag. Febr. 1891), as well as in the present paper, but which, not being a trained zoologist, I could not prove. I am happy to have acquired, in my disagreement with Brauer, such powerful allies.

Brauer says (Z. K. M. III. p. 7, footnote; also in other places): „Ich nenne den ersten Segmentcomplex nur dann Kopf, wenn derselbe „eine Kapsel darstellt, welche die ersten Ganglien einschliesst. Liegen „die Ganglien hinter dem ersten Complex, so stellt derselbe nur eine „Kieferkapsel dar, die Muskel und den Schlund enthält. Einen wahren „Kopf scheinen nur die Eucephalen Larven zu besitzen.“ I do not find, in Brauer's writings, any explanation of the method, by means of which he reached this conclusion. Did he dissect the heads of all his so-called eucephalous larvae? If he dissected any of them why does he not give the names of the genera dissected, or not dissected, by him? -- *Chironomus*, according to Brauer, belongs to the group *Eucephala*. MM. Miall and Hammond show, by means of a most careful dissection and beautiful figures (l. c. Tab. 29, fig. 17, 21, 22) that the head of the larva of *Chironomus* contains no ganglion whatever, and that the first ganglion, or brain, is placed in the first thoracic segment. Therefore, in accordance with

Brauer's definition the head of the larva of *Chironomus* is merely what he calls a „Kieferkapsel“ and not a real head (Kopf). It follows further that *Chironomus* does not belong to Brauer's division *Eucephala*. If *Chironomi*, their exserted larval head notwithstanding, are not *Eucephala* Brauer, what are *Eucephala*? Is it probable that *Culicidae* are *Eucephala*, while *Chironomidae* are not? That *Culex*, *Corethra* and *Chironomus* are closely allied genera, nobody will deny; and yet, the mode of development of the imago within the larva, as MM. M. & H. have shown (l. c. p. 274—275) is quite different in each of these genera. Here therefore the relationship is patent in the imagos and disguised in the larvae. These authors further say (p. 276): „As a mere matter of dimensions such a head „as that of the male fly of *Chironomus* could not be developed „within the larval head. This explanation at once provokes a further „question: why should any such disproportion exist between the head „of the fly and that of the larva? We may say in reply that the fly „is a nimble aerial insect, requiring keen senses and some degree of „intelligence that it may escape danger, find a mate, and lay its eggs „in a suitable position. The larva (of *Chironomus*), on the contrary, „is an animal of very simple mode of life, feeding upon dead vegetable matter at the bottom of dark and slow streams. The abundance „of its food, and the ease with which it can be appropriated, have „led in this, as in many other cases, to some degree of degeneration, „which is particularly apparent in the larval limbs and head.“

These results tally exactly with what I asserted in my „Suggestions“ (l. c. p. 31): first, that the divisional character borrowed by Brauer from the head of the larva was an uncertain one, and second that better results might be obtained by beginning the inquiry with the imago, especially with the organs of orientation about the head. I said verbatim that Brauer's groupings did not succeed because they were „principally based upon a character of subordinate value, „taken from the wings, and on another character of doubtful importance, borrowed from the larvae, without sufficient regard for „the organization and the affinities of the imagos. I believe that a „natural arrangement must be the result of the study of those organs „of the imago, which are necessary for the functions of external life, „principally therefore of the organs of orientation connected with the „head (eyes and antennae), and in the second line, of the organs of „locomotion (legs and wings).“

In his reply to my „Suggestions“ (in the Sitzungsberichte of the Vienna Zool. Bot. Ges. 6 May 1891) Brauer deplores „den unglaublichen Irrthum einiger Entomographen, dass die Larven keine Be-

deutung für die Systematic hätten" etc. („the incredible error of some entomographers [sic!] who maintain that larvae have no importance in the classification" etc.). Such an assertion I never made anywhere. Further on, Brauer calls me an entomographer and catalogue-maker, people „who have no right to permit themselves, without „any foundation, changes in the system, and to thrust aside uncere- „moniously the opinions of entomologists of greater authority than they" („welche sich, ohne weitere Begründung, Aenderungen im System erlauben, und Ansichten gewiegter Entomologen bei Seite setzen").

Whenever vituperation begins, one may be sure that arguments are exhausted. I flatter myself that my arrangement of the *Nemocera* is quite satisfactory both as regards the imagos, and, as far as possible, the larvae. And I am convinced at the same time that Brauer's arrangement, and especially his „*Eucephala*" form an incredible („unglaublich" to use his own expression) and incongruous medley, so much as regards both the imagos and the larvae.

Larva, as a name of one of the early stages of insects, was introduced by Linné, and means a mask, as known to everybody. The name was very well chosen; the larva disguises the systematic position of its future imago; among the diptera it does more than that: by various adaptive contrivances it often disguises its own position among its congeners. In many cases we succeed in discovering generic characters even among larvae. Still there are cases, like *Mycetobia* and *Rhyphus*, *Anopheles* and *Dixa* (compare above, p. 418), where two almost similar larvae produce imagos belonging to entirely different families. Such cases are as yet unsolved problems. Brauer ignored them entirely. He, apparently, never saw the larva of *Rhyphus* (see above, p. 457); and the larva of *Anopheles* he mistook for that of *Dixa*, and was corrected by Meinert (*Eucephale* Myggellarver, p. 452).

For the sake of an easier comparison with my arrangement on p. 428—429 I reproduce here

Professor Brauer's System (Z. K. M. III, p. 11).

I. Diptera Orthorrhapha.

Section I. Orthorrhapha Nematocera.

Tribe I. Eucephala.

Families: Mycetophilidae, Bibionidae, Chironomidae, Culicidae, Blepharoceridae, Simuliidae, Psychodidae, Ptychopteridae, Rhyphidae.

Tribe II. Oligoneura.

Family: Cecidomyiidae.

Tribe III. Polyneura.

Families: Limnobiidae, Tipulidae.

Section II. Orthorrhapha Brachycera.

Tribe I. Acroptera.

Family: Lonchopteridae.

Tribe II. Platygenea.

I. Group: Homöodactyla.

a. Notacantha.

Families: Stratiomyidae, Xylophagidae.

b. Tanystoma.

Families: Tabanidae, Acanthomeridae, Leptidae
etc. etc.

(to be continued)

ZOBODAT - www.zobodat.at

Zoologisch-Botanische Datenbank/Zoological-Botanical Database

Digitale Literatur/Digital Literature

Zeitschrift/Journal: [Berliner Entomologische Zeitschrift](#)

Jahr/Year: 1892

Band/Volume: [37](#)

Autor(en)/Author(s): Sacken C. R. Osten

Artikel/Article: [On the characters of the three divisions of Diptera: Nemocera vera, Nemocera anomala and Eremochaeta. 417-466](#)