

On the atavic index-characters

with some remarks about the classification of the Diptera

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In a notice of Mr. H. Krauss on the recent work of Mr. Brunner von Wattenwyl: Révision du Système des Orthoptères etc. (Entom. Nachr. 1893, p. 237) I found the following passage:

„The perspicacity and talent for observation of the author have enabled him to discover and to make use of often very recondite and apparently insignificant characters, taking but a very subordinate part in the ordinary functions of the animal, and arrested in their development, but which, for these very reasons, have a great phylogenetic importance, as indications of descent and relationship. Such characters the author has used in defining the larger groups. The biological characters on the contrary, playing an important part in the life of the species, and variable in consequence of adaptation, were used by him for the characterization of the genera.“

I was greatly pleased with this passage, because it reminded me that I had arrived at exactly the same result in the classification of the Tipulidae which I published in 1859, and, in a more developed form, in 1869.¹⁾ Finding now that the very same method is equally useful in determining the classification of orders so widely different as the Orthoptera and Diptera, my confidence in its efficiency is naturally increased, and I feel impelled to give a somewhat detailed account of my experiences in working it.

The family Tipulidae, perhaps on account of the fragility of the specimens, has always found little favor with dipterologists, collectors

¹⁾ New genera and species of North-American Tipulidae with short palpi, with an attempt at a new classification of the tribe. — (In the Proc. Acad. Nat. Sc. Philad. August 1859; 60 pages and two plates.)

On the North-American Tipulidae Part first; *Tip. brevipalpi*. — (In the Monographs of the Diptera of N.-America. Part IV; XII and 346 pages and four plates.) — Washington, Smithsonian Institution, January 1869.

as well as describers. This was perhaps the very reason why I became interested in it, especially in the Tipulidae brevipalpi. Their classification was, forty years ago, at the beginning of my entomological career, in the most primitive condition. The following statement will give an idea of the state in which I found it. Two years before my earliest entomological publication (Stettiner Ent. Zeitung 1854) the tenth volume of Zetterstedt's „Diptera Scandinaviae" had appeared (in 1852), in which the author accepted the genus *Limnobia* in Meigen's sense, and distributed the species among eleven (unnamed) subdivisions. One of these subdivisions contained fourteen species. They were so ill-matched that in my classification they had to be distributed among six sections of the seven which I adopted for the Tipulidae brevipalpi (compare Mon. N.-A. Dipt. Vol. IV, p. 21). As I said above, my classification was published in 1859, and later, in a much enlarged edition, in 1869. These two works principally concerned the North-American fauna. Since then, up to 1887, I published several papers in which Tipulidae from other parts of the world were taken into consideration.

Thus my distribution, originally based upon a small North-American material, has been in operation now for thirty-five years, and has been found applicable in all parts of the world. Schiner adopted it in his Fauna Austriaca and, recently, Skuse for the Australian fauna. —

What struck me most, at that time, as well as some years later, when I came to apply this classification to abnormal tropical forms, or to anomalous native ones, was the great usefulness of the spurs at the end of the tibiae and of the empodia for the characterization of the larger divisions, which I called sections. I found them, whether present or absent, the most persistent of characters, in spite of great modifications, for adaptive purposes, of other organs. Reduced to the smallest proportions, and apparently as useless as the proverbial tail-buttons on our coats, they play their part as phylogenetic indexes of descent and affinity.

The three principal sections of the genuine brevipalpi, may be distinguished, in the great majority of cases, by the use of this simple formula (compare l. c. 1859, p. 199):

I. No distinct empodia, no spurs at the tip of the tibiae:

Limnobia.

II. Empodia distinct

}	Tibiae with spurs: . . .	Limnophilina.
}	Tibiae without spurs: . . .	Eriopterina.

The section *Limnobina* is a very compact group; I mean to say that the great variety of forms, which belong to it, are evidently adaptations to certain, as yet unknown, conditions of life; in the essential characters, on the contrary, there is a remarkable agreement. Often transitions may be found, or may be reasonably expected, between the normal type and the most aberrant forms. The normal types are *Dicranomyia* and *Limnobia* (sensu stricto), represented by numerous species in the temperate regions of the old and the new world, and also in Australia. *Rhipidia* is a *Dicranomyia*, but with pectinate antennae. Sometimes these antennae are, instead of pectinate, only moniliform in the female, sometimes even in both sexes, and thus come near the antennae of *Dicranomyia*. *Geranomyia* is likewise a *Dicranomyia* with the parts of the mouth elongated, and, as a consequence, with the palpi reduced in size. But there are gradations in the length of the proboscis, as well as in the size of the palpi. I possess a *Dicranomyia* from New Zealand, with a longer proboscis than usual; and Mr. Skuse has even established new genera on such variations of the proboscis and of the palpi of *Geranomyia* in Australia (Skuse, *Tip. brevipalpi* in Proc. Lin. Soc. N. S. W. Sept. 1889). — In other respects, the organization of these three genera is the same; the venation, and especially the characteristic male forceps, belong to the same type, and all these genera, in accordance with the formula of their section (compare above) have neither spurs, nor empodia.

In tropical countries the original type of the section *Limnobina* is sometimes modified in the most extraordinary manner, especially in the shape of the wings and the venation. It becomes almost unrecognizable and may deceive the most experienced eye. Here the index-characters, like sentinels, are invaluable. There is the South-American genus *Peripheroptera* Schiner, Novara, p. 47 (compare about it my Studies on Tipulidae, II, Berl. Ent. Zeitschr. 1887, p. 174). In this genus the proximal half of the wings becomes enormously developed, in consequence of which the whole wing assumes a different shape. Minute cells, near the root of the wing, which generally are not noticed at all, and have no name in the nomenclature, acquire here a great development; in *P. incommoda* O.S. (Vienna Mus.) they occupy the whole proximal half of the wing. But the degree of this development is variable; it differs in different species, and is less apparent in the female. In one case the diminution of such a development was so great that in a specimen before him Schiner did not recognise his own genus *Peripheroptera* and placed a female of

this genus (*P. aberrans*), as a doubtful form, a few pages off in the genus *Rhamphidia* (l. c. p. 43). All these variations notwithstanding the *Peripheropterae*, as belonging to the section *Limnobina*, have neither spurs, nor empodia.

Another tropical form of the section *Limnobina* has the wings developed just in the opposite direction; the distal half is very much enlarged, and the veins and cells in it are singularly elongated and curved. This is the genus *Libnotes* Westw. (Trans. Ent. Soc. London 1876, p. 505, Tab. III, fig. 6b) occurring in Ceylon, the Moluccas, the Philippines, New Guinea and Queensland. About the location of this genus two distinguished entomologists were doubtful. The author of the genus, Westwood, said: „It is not easy to speculate on the near affinities of so anomalous an insect.“ V. d. Wulp (Tijdschr. etc. XXI, p. 196, 1877) says: „It seems to me that the forked radial vein, the microscopic pubescence at the end of the longitudinal veins, and the absence of spurs on the tibiae prove conclusively that the place of this genus is among the *Eriopterina*, where, on account of its aberrant form, it should be placed either at the beginning, or the end of the series.“ The venation, in this case, has not been correctly interpreted: the radial (or second) vein is not forked, and therefore there is only one submarginal cell. But even without regard to the venation, if we simply refer to the formula which I have given above for spurs and empodia, we find at once the natural place of *Libnotes*: it has neither spurs, nor empodia, and therefore it belongs to the *Limnobina*. This location is fully justified by the other characters of *Libnotes*: it has but one submarginal cell, 14-jointed antennae, the unguis dentate on the underside, the forceps of the male has a structure characteristic of a true *Limnobia* etc. The *Eriopterina*, on the contrary, are provided with distinct empodia, have two submarginal cells, 16-jointed antennae etc. Thus we have in *Libnotes* a new proof of the efficacy of spurs and empodia as trustworthy index-characters. (In my *Studies* etc. II, p. 179—183, Berl. Ent. Z. 1887, I have published a detailed account of the genus *Libnotes*, with an analytical table for thirteen species.)

In Vienna I have seen a *Peripheroptera* which, in the elongation of the veins and cells of the distal half of the wings, shows some approach to *Libnotes* (*Studies*, l. c. p. 176).

The genus *Dapanoptera*, from New Guinea, with its peculiarities in the venation and its beautiful coloring, can, on the same principles, be easily proved to belong to the *Limnobina* (*Studies*, l. c. p. 178).

Many tropical forms of *Tipulidae* will be discovered yet, showing rather intricate venations, where contortions and coalescences of veins

and cells completely disguise the original type from which such venations were derived. The best course to pursue, in such cases, is first to determine the section to which the species belongs, by means of the formula of spurs and empodia. This being done, as every section has its own type of venation, the homologies between the typical and the intricate forms will, in most cases, be easily traced. Of course exceptions will occur here as anywhere else.

The crucial test, and at the same time the triumph, of the spurs and empodia as index-characters were reached when I received for the first time a specimen of *Chionea*, a two-winged insect without any wings, looking more like a spider, and which, for half a century, was a puzzle for classificators. Dalman, the discoverer (Act. Holm. 1816 and *Analecta* 1823) referred *Chionea* to the *Tipularia*e¹⁾, in the sense of Latreille (1809), Fallèn and Meigen, that is, of our *Nemocera* Latr. (1817). He did so, very probably, on account of the antennae, which are more or less filiform, although only 6-jointed. In the *Analecta* Dalman describes the ovipositor, the structure of which, if he had been aware of the value of this character, might have induced him to place *Chionea* among his *Tipularia terricola*. Latreille (*Fam. Natur.* 1825, p. 484) places *Chionea* among his *Tipularia terricola*; Macquart (*S. à B.* 1834) does the same, but both without giving any reason. Westwood (*Introd.* II, p. 525, 1840), always accurate, follows suit, placing it among the „*Tipulides* Macq. (*Terricoles* Latr.)“ and adds, in a foot-note: „My specimen is a female, with an ovipositor like a *Tipula*.“ Here, for the first time, the reason of the location among the *Tipulidae* is given. Zetterstedt (*Dipt. Sc.* XI, p. 4255, 1852) forms a family *Chioneidae*, and, as if to separate it as much as possible from the *Tipulidae*, places the *Mycetophilidae* between them. In Walker (*Ins. Brit.* *Dipt.* III, p. 268, 1856) *Chionea* is placed among the *Tipulidae*. Loew (*Monogr. N.-Am. Dipt.* I, p. 11, 1862) places it with *Dixa* among the anomalous *Tipulidae*. In Schiner (*Fauna etc.* II, p. 573, 1864) it is treated as an annex to the *Tipulidae* („als Anhang“).

Nobody has attempted to investigate the affinities of *Chionea* any further, although the decisive characters were already predetermined in my formula of 1859 (comp. above), long before I had examined any specimen of this genus. *Chionea* has no spurs at the tip of the tibiae: that restricts the choice between the sections *Limnobina* and *Eriopterina*. *Chionea* has very distinct pulvilli; this settles

1) The family-name *Tipulidae*, in our present sense, appears for the first time in Macq., *Dipt. Exot.* I, 1, p. 24 and 38 (1838). Until then, the family was called *Tipularia*e rostratae by Meigen and *Tipularia terricola* by Latreille and Macquart (in 1834).

its position among the Eriopterina. Having got so far, it was easy for me to discover the analogies between *Chionea* and *Trimicra* (in the incrassate male forceps, in the legs and the antennae), and thus, by dint of a correct method, to place a spider-like being alongside of a daddy-long-legs! (Compare Monogr. etc. IV, p. 136 and 168; Studies etc. II, p. 196). It seems doubtful whether, without those index-characters, the curious relationship between two so dissimilar forms would ever have been found out.

The genus *Dolichozeza* has been always described as having the tibiae unarmed, although, as belonging to the longipalpi, it should have spurs at the tip of the tibiae. I have shown (Studies etc. II, p. 157) that such spurs, although very minute, are really present.

Empodia and spurs on the tibiae are not the only characters that can be used as index-characters among the Tipulidae. One of my correspondents asked me why I did not place *Rhamphidia* somewhere near *Dicranomyia*, because it is so very like it, and has many characters with it in common. But *Rhamphidia*, besides its 16-jointed antennae (*Dicranomyia* has them 14-jointed), has another character which, insignificant as it looks, is very persistent. In both the european and the north-american species the marginal crossvein is wanting. In a brazilian species (Berlin Mus.), which I have described (Studies etc. II, p. 184), the same crossvein is also wanting. The same is the case with an australian species, described by Skuse. More than that: the genus *Elephantomyia* is nothing but a *Rhamphidia* with a prolonged proboscis and modified palpi; and the marginal crossvein is likewise wanting in *Elephantomyia*. Next comes *Toxorhina* evidently related to *Elephantomyia*, but distinguished by the venation in which the second vein appears suppressed, as if connate with the first vein and the costa, in consequence of which the submarginal cell has disappeared. It looks as if the absence of the marginal crossvein in the two other genera had foreshadowed the contact of the two veins which the crossvein, before its disappearance, had kept asunder. I have attempted an explanation of this anomaly in the Monogr. etc. IV, p. 112; the figures of the wings will also be found there (Tab. I, fig. 5 *Elephantomyia*; fig. 6 *Toxorhina*).

Thus these three genera form an inseparable group, which I could not place among my first section *Limnobina*, on account of the abnormal number of the joints of their antennae and other aberrant characters (as I explained above). I placed them therefore in a provisional section *Limnobina anomala*, which I had formed for a number of genera having a single submarginal cell, like the true

Limnobina, but, at the same time sixteen-, instead of fourteen-jointed, antennae. Such forms often showed other anomalies besides, such as the presence of empodia, some peculiarity in the pubescence of the wings (*Antocha*), an anomalous venation (*Antocha*, *Orimarga*, *Elliptera*) etc. As early as 1859 (l. c. p. 200) I have considered such intermediate, synthetic forms, combining the characters of two or more of the large, compact groups, as probable remains of some earlier palaeontological horizons, and I found it expedient to isolate them from the other groups; later experience has confirmed me in this opinion. Without entering into this interesting subject now, I will merely say, that if I had followed the advice of my correspondent, and placed *Rhamphidia* among the true Limnobina, I would have been obliged to drag together with it its congeners *Elephantomyia*, *Toxorrhina*, perhaps also *Styringomyia* (compare Monogr. etc. IV, p. 102), and thus I would have spoiled the homogeneousness of the section Limnobina, and lost the advantage of having the archaic forms grouped together. I gained that advantage by paying attention to apparently insignificant characters, as the exact number of the antennal joints²⁾ and the disappearance of the marginal crossvein, characters which in this case proved to be index-characters.

If index-characters have proved to be useful in the family Tipulidae there is no reason why they should not be equally efficient in other families of Diptera. In order to discover them, a more exact comparative study of the dipterological characters in general is necessary. Even in leaving aside anatomy, the external characters of the Diptera have, as yet, been very insufficiently studied. For instance, a complete comparative description of the structure of the external tegumentary skeleton in different families has never been given. When I attempted the study of chaetotaxy I did not find any sufficient nomenclature of the segments of the thorax, and had to begin with introducing one. The structure of the prothorax and metathorax, the connection between the latter and the base of the abdomen, the relation of the dorsal and ventral segments of the abdomen, the abdominal segments preceding, and those containing, the sexual organs, afford a multitude of characters which have never been sufficiently taken into account. But their study and description

1) I agree with Verrall (E. M. M. 1887, p. 205) in that there is only one well-ascertained species of *Rhamphidia* in Europe.

2) *Elephantomyia* has only 15 joints and *Toxorrhina*, stunted in its venation, has only 12 joints. Nevertheless there is not the slightest doubt about their relationship to *Rhamphidia*, which has 16 joints, the normal number for the Limnobina anomala.

requires a previous training, which every entomologist cannot be expected to possess, and which would be a task worthy for an expert to undertake.

The theory of the venation of the Diptera has not been worked out yet; so much of it as exists is merely hypothetical. The attachment of the wing to the thorax, and the structures connected with it, deserves, it seems to me, more attention than they have received.

The further development of chaetotaxy promises much for the classification; it may perhaps afford more atavic indexes, than any other set of characters.

In my „Essay on comparative Chaetotaxy“ (Trans. Ent. Soc. London, 1884, p. 510 „Sternopleural bristles“ and p. 512) I have called attention to the two or three sternopleural bristles „the position of which may afford valuable generic characters“. During a visit I paid several years ago to my respected friend v. d. Wulp he told me that he found just these bristles very useful for the classification of Anthomyiæ. And now I see in Mr. E. Girschner's paper Berl. Ent. Z. XXXVIII, p. 305, that in *Aricia* one of these bristles is inserted anteriorly (cephalad), and two posteriorly (caudad); while in *Lucilia* and *Echinomyia* just the reverse takes place, two bristles are situated anteriorly and one posteriorly. This, and similar characters so minute in appearance, may represent real indexes by means of which we may discover affinities by a short cut (if I may be allowed the expression), instead of a roundabout investigation. In this respect Mr. Girschner's paper is full of promise for the future.

P. S. ad p. 71, l. 17 from top.

The *Dicranomyia* from New Zealand (*D. monilicornis* O.S. Studies etc. II, p. 172) has, besides the elongated proboscis, distinctly moniliform antennae in the male (ordinary ones in the female) thus apparently forming a passage towards *Geranomyia* on one side and *Rhipidia* on the other. — In California, near S. Francisco I caught a *Geranomyia* with almost moniliform antennae and very small fleshy lobes of the forceps (l. c. p. 173).
