The Phylogeny of Nematocerous Diptera: a critical review of some recent suggestions.

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With 2 text-figures.

„Classes et genera naturalia, non sola instrumenta cibaria, non solae alae, nec solae antennae constituunt, sed structura totim, ac cujusque vel minimi discriminis diligentissima observatio." — Scopoli, Introd. ad Hist. Nat., 401 (1777).

With the above quotation from Scopoli as a motto, Osten-Sacken in 1892 published his paper „On the characters of the three divisions of Diptera, Nemocera vera, Nemocera anomala and Eremochaeta". The paper would seem to have been written largely as a polemic against Brauer, whose classification of Diptera, based almost entirely on larval and pupal characters, Osten-Sacken regarded as one-sided and unnatural. He therefore attempted to formulate a more balanced arrangement of Diptera which, while based mainly on the whole adult structure, should also take account of the early stages.

In this aim he can hardly have been said to have been conspicuously successful, as he was evidently overwhelmingly impressed by the importance of one character, the structure of the eyes, and was therefore hardly less biased than Brauer, who placed the strongest emphasis on the condition of the larval head.

In spite of Osten-Sacken's criticisms, many of which were perfectly just, Brauer's classification has until recently been generally adopted, but in the last decade several entomologists, chiefly in America, have put forward alternative suggestions. Some of these recent suggestions, however, are even more frankly based on a single structural feature than the systems of Brauer and Osten-Sacken.

The purpose of the present review is not so much to bring any new facts into the discussion, as to attempt to correlate those which are already known and to re-emphasise Scopoli's contention that, in order to arrive at a natural or phylogenetic classification of a group of animals, a close study of the whole structure of the species is essential. Nor must such a study be confined to the structures of the adult, since the early stages can often provide most valuable information.

Many writers appear to object to the use of larval characters in classification on the ground that different habits and surroundings produce their own special modifications independently of what may happen to the adults. Thus G. C. Crampton writes (in letter to the present author) „The adult form represents the end-result towards which evolution is aiming, rather than does the specialised larval form which is usually modified temporarily for a brief sojourn in fields aside from the travelled road, and in these fields convergence plays a much stronger role than in the adult, since the larval form is so much more plastic.“ An almost exactly opposite view has beeen expressed by Langeron: „The adult state is only a brief and temporary (passagère et très courte) period in the life of the insect: the greater part of its existence is passed in the larval state.... The term larva implies, in current language, the idea of something incomplete, imperfect, provisional. This conception is in my view entirely erroneous. The larva of a mosquito has its own degree of perfection.“ The present writer's view is rather that the individual insect should be regarded as a single entity from egg to imago, and that all the different external forms which it assumes should be recognised as equally important manifestations of its life. Appropriate modifications appear at different stages of the life of the individual in correlation with different external conditions, but whatever they may be they appear in an orderly sequence, and are conditioned by the past history of the species. It is inconceivable that, rightly understood, the evidence as to ancestry provided by the larvae should be in conflict with that given by the adult forms. Where such appears to be the case, it can only be due to a mis-reading of the facts.

A good illustration of this point may be taken from the history of the classification of the mosquitoes. These insects were formerly arranged according to the length and structure of the palpi, especially in the male sex. Later the larvae were studied and it was found impossible to form any grouping of them which would harmonise with that in vogue for the adults. This led again to a re-study of the adults, and it was soon found that small and largely overlooked characters existed by which they could be classified in perfect accord with the arrangement based on the more obvious characters of the larvae. Subsequent researches have all confirmed the conclusion that these characters are the ones of real phylogenetic importance.

Exactly the same has occurred in regard to two other instances mentioned by Osten-Sacken, those of *Anopheles* and *Dixa*, and of *Anisopus* (*Rhyphus*) and *Mycetobia*. In both these instances very similar larvae were found to give rise to very dissimilar adults, which were even classified in entirely different families. Attempts to show that the larvae were superficially similar through convergence only revealed the contrary, that the resemblances were fundamental and much greater even than had been imagined. The adults were then re-examined and it became clear that there were indeed many important points of resemblance between them which indicated a fairly close relationship, while the differences to which primary importance had formerly been attached could be regarded as superficial only. A converse case is perhaps that of *Anisopus* (*Rhyphus*) and *Trichocera*, in which practically no adult characters have yet been discovered confirmatory of the resemblance in the larvae, which must presumably be explained by the parallel rentention in this stage of numerous archaic features.

We must conclude therefore that larval and adult characters should be treated as complementary to one another, and the evidence derived from each stage considered together. Sometimes the adults and sometimes the larvae will furnish the crucial points of the summing up; when the latter is the case, it may often be due to the fact that the affinities of the adults are obscured in a confusing complexity of secondary adaptations.

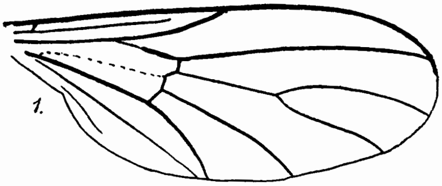
The value of embryology in affording evidence of phylogeny is well recognised among zoologists, and may yet furnish important clues in the case of the Diptera, although in its early stages it has as yet been but little studied. With holometabolic insects, however, where only a part of the development takes place within the egg, the rest is deferred to the larval or pupal stage, and these deferred stages of development may probably be the most valuable in indicating relationship within an order.

In order to arrive at a natural or phylogenetic classification it is of course essential to bear in mind that resemblances between species, even in striking features, are not necessarily indicative of a close relationship. There are in fact three distinct ways in which resemblance between somewhat distantly related species can come about:

1. By independent development of some special adaptation to their surroundings, e. g. the telescopic tail of the larva of *Ptychoptera* and *Eristalis*, or the raptorial legs which are independently developed in

several families of Diptera. Such cases are usually easily recognised for what they are.

2. By parallel reduction, e. g. by the independent loss of the wings or of some veins in the wings. These cases also are little liable to lead the systematist astray, so long as too great reliance has not been placed upon a single character. Thus there is a rather remarkable resemblance in venation, as shown in the accompanying figures, between the Mycetophilid *Diadocidia* (Textfig. 2) and a species of the Bombyliid (or Leptid) genus *Empidideicus* (Textfig. 1), although the species obviously belong to entirely unrelated families. The resemblance is merely due to the loss of two branches of the radius and one of the media, together with the discal cell. Similar cases of parallel reduction among less distantly related insects might easily be attributed to relationship.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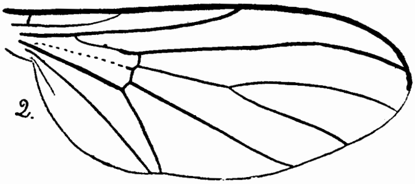
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3. By the retention from a remote common ancestor of certain archaic features, while in other respects the species have diverged. Although in a sense such archaic features do indeed indicate affinity, yet it may often happen that species which have lost these characters stand much closer to others which have retained them than some of the latter do to one another. Thus the *Tabanidae*, which have retained powerful mandibles, are obviously close to the *Rhagionidae* (*Leptidae*) which have lost them, and have only the remotest connection with the mandibulate Nematocera.

In estimating degrees of relationship therefore it is important, though not always easy, to distinguish between archaic or palingenetic and newer or coenogenetic characters; while among the latter we must further distinguish between those which are due to reduction and those which are accrescent or due to specialisation; and again among the accrescent features we must separate the adaptational, in the development of which environment as well as heredity has played a large part, from the non-adaptational, which are presumably due to the action of hereditary causes alone. It is the last class which offers us the most valuable evidence. This was well understood by Lameere, who suggested a new classification of Diptera based on such considerations. Consequently it is not surprising that some of his suggestions have been confirmed by later research, although many of his conclusions were completely vitiated by his obviously scanty knowledge of the order, while his uniformly dichotomous arrangement hardly seems the best method by which to express the facts of nature.

An extremely important principle from the point of view of the phylogenist is that of the irreversibility of evolution, that is to say that characters once lost can never be regained. There are many familiar instances of this in the morphology of adult insects, but it appears to be equally true of other stages as well. Keilin has done valuable service in pointing out the applicability of the law to Dipterous larvae. The larva of the common ancestor of all the Diptera seems to have lost its legs and replaced them by sensory bristles, and there is no single instance of the redevelopment of legs in the larval stages of any Dipteron, notwithstanding the fact that normal legs are present in the adults and even in the pupae; where the need of locomotory appendages arises, special pseudopods are developed to meet this need, or the mandibles may even be used for locomotion. Williston has pointed out what appear to be the main lines of evolution shown in the adult morphology of the Diptera, all of which he regards as irreversible, since they consist in the main in the reduction of various organs. All these types of reduction (in antennae, venation, spurs, etc.) may be regarded as evolutionary tendencies which are inherent in the original ancestors of the Diptera and may become apparent at different times and in different branches of the stock. This idea has been expressed by de Meijere in his paper on Dipterous larvae, and he also quotes Handlirsch to the same effect. The same may also be true of some of the specialised features of these insects, such as the great development of the eyes in the male sex.

Having now briefly considered the principles on which we should base our conclusions, let us examine some of the main characters which have been used or suggested as useful for arriving at a natural classification.

Eggs and oviposition.

Naturally the eggs alone can give us little assistance except in regard to smaller groups, such as genera. They may, however, sometimes afford confirmation of other evidence, as in the case of *Anisopus* and *Mycetobia*, which both deposit a whole batch of eggs in a mass of jelly, instead of scattering them dry as do all the *Mycetophilidae*. The habit of enclosing eggs in jelly is common to many aquatic Diptera, as well as other aquatic animals, and though the genera in question are not now truly aquatic, it may perhaps be supposed that their immediate ancestors were so.

Larvae.

It is only possible to mention here a few of the more important features round which discussion has centred, leaving aside the smaller details in structure of the mouthparts, etc., which may nevertheless be of great importance.

Habitat. — It has sometimes been suggested that the majority of families of Nematocera have arisen from ancestors whose early stages were spent in water, since even at the present day the aquatic habit is of such frequent occurrence. As regards several groups this is certainly true. In the case of the *Tipulidae*, however, the rather small number of aquatic forms mostly show signs of recent specialisation, while the more generalised types in the family breed either in rotten wood or rich humus. Again, none of the *Bibionidae, Mycetophilidae* or *Cecidomyiidae* are aquatic, or show any indication of ever having been so. It is probable therefore that the aquatic groups, though they may date from a remote past, have been derived originally from wood or humus feeding ancestors.

Number of larval stages. — A reduction in the primitive number of larval stages is a marked tendency in the Diptera, and the number is often constant through whole families or groups. Although no families of Nematocera are known to have reached the minimum of three stages (i. e. changing to pupa at the third moult) characteristic of the Cyclorrhapha, the *Culicidae* and *Chironomidae* have reduced the number to four. On the other hand, some of the other aquatic families (e. g. *Simuliidae*) retain a larger number. As regards many of the other families, however, we are still in ignorance.

Head capsule. — It is now generally recognised that the two groups of Nematocera in which reduction of the head capsule has taken place are not nearly related, and the reduction has evidently taken place independently, as it has again in the Brachycera.

Premandibles. — In a recent study Goetghebuer describes the various forms taken by the articulated appendages of the labrum in different families of Nematocera. He apparently concludes that toothed premandibles are a coenogenetic feature, and if this is really the case, the strikingly similar form of these organs in *Trichocera, Anisopus* and *Scatopse* is strong evidence of the relationship of these groups, since we can hardly suppose a rather complex specialised structure would be evolved three times independently in almost exactly the same form. But it is just as easy, and better fits in with other known facts, to suppose that premandibles are a primitive feature of Dipterous larvae and have been retained independently in a number of groups (*Scatopsidae, Anisopus, Trichocera, Psychodidae*) and lost independently in a number of others (*Bibionidae* [1]), *Tipulidae, Ptychoteridae, Thaumaleidae, Blepharoceridae*), while in a few their structure has been modified to suit special requirements. The similar and evidently specialised structure of the labrum in *Mycetophila* and *Sciara* clearly indicates that these genera belong to the same stock, and Goetghebuer may also be correct in assuming a relationship between the *Culicidae* and *Simulium* on account of the somewhat similar transformation of the premandibles into rotatory organs, though it is perhaps more likely that this is a case of convergence on account of the similar feeding habits. Further, there seems no reason why the peculiar premandibles of *Chironomus* could not have been derived from the brush-like Culicid type, while the absence of these organs in *Tanypus* need not be regarded as an archaic character of the *Chironomidae*, even if *Tanypus* is in many other respects the most archaic genus; possibly the loss of premandibles in *Tanypus* may be connected with the adoption of predaceous habits, as they are also absent in the predaceous *Culicidae Mochlonyx* and *Chaoborus*. In any case Goetghebuer's conclusion that the *Chironomidae* are related to the *Psychodidae* rather than to the *Culicidae* seems to be unwarranted.

Spiracles. — The presence of functional lateral abdominal spiracles was treated by Osten-Sacken as a fundamental character, on the basis of which he divided the Nematocera vera into two groups. Since the use of this character led to the association of the *Cecidomyiidae* with the *Mycetophilidae* rather than with the *Tipulidae*, an apparently much more natural grouping, its importance was evident, and it was therefore not surprising that Knab later on proposed to

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[1] **Goetghebuer assumed the presence of premandibles in the *Bibionidae* on account of the generally accepted relationship of this family with the *Scatopsidae*, but they are in fact absent.**

make it the main basis of a division of the whole of the Nematocera into two main groups, one containing all the peripneustic forms, including the Bibionidae, the other the amphipneustic and metapneustic forms. The value of this suggestion lay in emphasising the connection between the *Bibionidae* and *Mycetophilidae*, but in some respects Knab went astray. Thus he grouped the *Chironomidae* with his Oligoneura, believing that peripneustic larvae occurred within the family and that the apneustic forms had been derived directly from peripneustic ones. It now appears certain, however, that Chironomid larvae are without exception apneustic, and it is most probable that they have been derived from metapneustic forms such as those of the Culicidae. Malloch, in criticising Knabs view, has referred to the reported existence of lateral abdominal spiracles in the *Dolichopodidae*, but as these are not known in any other Brachycera it appears very doubtful if they really exist in this family. Minute nonfunctional lateral spiracles are traceable in most if not all the amphipneustic Dipterous larvae, and in some transparent forms (such as, perhaps, the Dolichopodid larvae in question) they are fairly easily seen in life. It does really seem to be the case therefore that all the truly peripneustic larvae can be formed into one natural group, though the character is an obviously primitive one and might have been retained independently in more than one family.

The majority of Dipterous larvae have lost the use of the lateral abdominal spiracles, and this may have happened more than once among the Nematocera. In no known case, however, do these spiracles reappear in a functional condition in a group which has once lost them, even when the conditions of life might be regarded as favourable to such a re-development. For example, amongst the *Chironomidae* there are a number of cases where the larvae have left the water for a terrestial habitat, but they always remain apneustic like the other members of the family. It is therefore certain that the suggestion recently made by Crampton that „the *Mycetophiloidea* may be the direct descendants of the *Anisopodidae*“ cannot be accepted, since the former have a more primitive larval tracheal system than the latter. On the other hand the absence of the last pair of spiracles in the *Sciarinae* and *Mycetophilidae* confirms the relationship of these groups and is not consonant with Enderlein's grouping of the former with the *Cecidomyiidae*.

Leg-bristles. — The minute sensory bristles which represent the vestiges of the legs in all Dipterous larvae may afford some clues to relationship, since they differ in form and number in different families, and are evidently little influenced by environmental conditions. Unfortunately they have not been examined in a sufficient number of forms for any general conclusion to be drawn. Keilin has however noted that *Anisopus* and *Mycetobia* both have two long and two short legbristles, while the *Mycetophilidae* have four long ones. It may be significant also that the *Culicidae* and *Chironomidae* which have been examined have three equal bristles; on the other hand *Thaumalea* has two long and two short like the *Rhyphidae*.

Pupae.

Not many characters of importance in classification have yet been derived from the pupae, but a number doubtless exist, of which the following are examples.

Respiratory system. — The peripneustic condition is no doubt primitive, and is retained by most of the terrestial forms, but the aquatic forms have mostly become propneustic. The absence of functional abdominal spiracles in all the *Ceratopogoninae* is evidence that the terrestial forms of this subfamily have been derived from the aquatic ones, while the presence of these spiracles in *Thaumalea* suggests that this genus may have adopted an aquatic life comparatively recently.

Leg-sheaths. — The arrangement of the leg-sheaths, particularly those of the hind tarsi, is very constant in some families. The primitive condition is for all the tarsal sheaths to be quite straight, even when the legs are long, and this is always the case in *Tipulidae*, *Mycetophilidae*, and most other families. In the case of several aquatio families however the hind tarsal sheaths are curved, so that they do not project beyond the end of the wing-pads. This may probably be regarded as an adaptation to the dorso-ventral movement of the whole abdomen largely used in swimming, instead of the usual lateral or rotary movement of the tip of the abdomen practised by most terrestial pupae. In all the *Culicidae*, including *Dixa* (as pointed out by Osten-Sacken, de Meijere and others) the hind tarsal sheaths make a double (s-shaped) curve, the tip lying along the margin of the wing-pad and ending just before the tip of the latter. *Chironominae* are similar, but the tips of the fore and mid tarsi are also recurved. In all *Ceratopogoninae* and in *Simulium*, also apparently in *Thaumalea*, the same result of freeing the basal abdominal segments is obtained in a slightly different way, the hind tarsus being first bent outwards and then at its tip curving inwards round the tip of the wing-pad and meeting the tip of the front or middle tarsus at right angles. This is one of the points which seems to indicate a connection between the last three groups mentioned.

Development of imaginal wings. — In most cases the wings of the imago are merely contracted and wrinkled within the pupal envelope, but as is well known, those of the *Blepharoceridae* attain almost their full size before the emergence of the adult, and are elaborately folded within the pupa. The same is also true of *Simulium* and *Deuterophlebia*, and it would appear to be an adaptation to life in swiftly running water, to enable the imago to take to the wing immediately on emergence. We can hardly therefore assume that this is any evidence of the relationship of these three groups. It is curious that folding of the imaginal wing also takes place in *Anisopus*, although this is a terrestial form.

The development of the venation, and especially the tracheation, in the wing-rudiments will probably provide valuable evidence when more fully studied, but as yet an insufficient number of types has been examined for any general conclusions to be drawn.

Adults.

Eyes. — The structure of the eyes of the male was regarded by Osten-Sacken and Lameere as of primary importance, and the latter author was doubtless largely correct in regarding the great development in the eyes of the males of some species as a compensation for the reduction in some other organs, such as antennae and legs. It has been noticed that the males with very large eyes usually dance in swarms, as do many longlegged *Tipulidae*, or the *Culicidae* and *Chironomidae* with feathery antennae. The large facets in the upper part of the eye may possibly serve to indicate the approach of enemies from above, the small ones on the lower part that of females from below. If we examine a large number of forms, however, we find it impossible to draw the sharp distinction between the „holoptic“ and „dichoptic“ types of eyes on which Osten-Sacken placed so much emphasis. Some forms have the eyes alike in the two sexes, and among these all gradations are found (e. g. in the family *Tipulidae*) between those with widely separated eyes and those which have them narrowly or broadly in contact. There are often, moreover, considerable differences among closely allied species, e. g. in the *Blepharoceridae* or even within the genus *Anisopus*, some species having separated and some contiguous eyes in the male, while among the latter some have differentiated large and small facets and others have not. In many *Culicidae* the eyes of the male are slightly larger than those of the female, while among families in which the eyes are normally all alike abnormal forms crop up in which the males are holoptic, with much larger eyes than those of the female (e. g. *Lygistorhina* among the *Mycetophilidae, Ectaetia lignicola* among the *Scatopsidae*). Probably the simple dichoptic eyes are to be regarded as primitive, but if so, the holoptic type appears in so many otherwise dissimilar forms that it seems reasonable to suppose it is an independent specialisation in each case, rendered possible by something inherent in the ancestral type of the order.

Another feature of the eyes, to which Enderlein has called attention, is the presence or absence and the width of the connecting bridge above the antennae. On the basis of similarity in this character he has proposed to unite the *Sciarinae* and the *Cecidomyiidae* into one group, but as shown elsewhere in this paper, the *Sciarinae* seem to have been derived directly from the *Mycetophilidae*, while the *Cecidomyiidae* belong to rather a different stock. If this isso, we have in the eyebridge another example of parallel accrescent development.

Ocelli. — The presence of three ocelli is evidently a primitive character. The ocelli have been preserved in a number of families, but lost in many others, e. g. a few *Mycetophilidae,* most *Cecidomyiidae,* all *Tipulidae* with the exception of *Trichocera* (which seems to be very near to the ancestral type of the *Tipulidae*) and all *Culicidae, Psychodidae* and other more or less related families. The presence or absence of these organs can therefore only be used with great caution, and in association with other characters, in formulating a classification.

Antennae. — Reduction of the antennae, both as regards length and number of segments, has evidently taken place along many different lines, e. g. in the *Tipulidae* (*Eriocera, Macromastix, Chionea*), *Mycetophilidae* (*Cordyla*), *Scatopsidae, Bibionidae, Chironomidae,* etc. The possesion of similar short and few-jointed antennae is therefore not a sufficient indication of relationship in such forms as the *Simuliidae* and *Bibionidae.*

The primitive antenna probably bore hairs of two kinds, longer and shorter. In some forms (e. g. *Tipula, Culicidae, Chironomidae, Cecidomyiidae*) the longer hairs are developed into regular whorls, while in others they are reduced or lost entirely. Here again we may find valuable clues to relationship, but both reduction and development of the longer hairs have clearly been polyphyletic. Osten-Sacken called attention to the value of these characters, but hardly appreciated their nature, since he cited *Zygoneura* as being very exceptional among *Mycetophilidae* in having „verticilate" antennae. If we examine this genus carefully, we find that the hairs on the antennae are really all of one kind, the stouter ones being absent (as in all other related genera) and the slender ones greatly lengthened to produce a verticilate appearance, which is enhanced by the elongation of the bare necks which are usually if not always present at the tips of the segments. This seems therefore to be another case of the „irreversibility of evolution". On the other hand the presence of stiff hairs on the antennae of the New Zealand *Nervijuncta* (also noted by Osten-Sacken) is clearly a primitive feature. The reduction of the first antennal segment and the enlargement of the second to contain a special sense-organ is a specialisation common to the *Culicidae* and *Chironomidae* and is one of several features indicating a close connection between these two families.

Mandibles. — These have been retained in the females of the blood-sucking groups, but seem to have been independently lost (in both sexes) in the *Tipulidae*, many *Psychodidae*, many *Chironomidae*, the Blepharocerid *Elporia*, also in the *Anisopodidae*, *Mycetophilidae*, *Cecidomyiidae*, etc. De Meijere regards the possession of „non-bloodsucking" mouth-parts as one of the primitive characters of the Nematocera, but it is much more probable that the original ancestor of the order possessed mouthparts which, by very slight modification, could be adapted to the blood-sucking habit.

Mesonotal Suture. — The presence of a complete suture dividing the main portion of the mesonotum into a praescutum and scutum is generally regarded as a primitive feature, but if it is so, it is remarkable that it is only clearly preserved in one family, the *Tipulidae* (including, for the moment, *Trichocera*). This would seem to indicate a very sharp demarcation of the *Tipulidae* from other Nematocerous families, a conclusion which is indeed supported by some other structures. The *Ptychopteridae* also possess the mesonotal suture fairly well preserved, but in the *Tanyderidae*, which in many other respects are more archaic than the *Ptychopteridae*, it is only feebly indicated.

Pleural sutures. — In his recent valuable study on the pleural structure of Nematocera, Crampton lays great stress on the importance of these structures from the point of view of phylogeny, on the ground that they are but little influenced by environmental conditions, and that experience with various groups has shown them to be among the most valuable characters for indicating affinities. Among the characters which he regards as primitive are (1) the straight suture between the anepisternite and sternopleurite on the one hand, and the epimerite on the other; and (2) the presence of a distinct meron of the middle coxae. The former is found only in the *Tipulidae, Ptychopteridae,* and related groups (which are segregated by the author as Tipuloids or „Pronematocera“), the remaining families having the suture more or less bent. The distinction, however, appears to be somewhat vague. The free meron is preserved in *Trichocera, Anisopus* and the Culicid group, but in most others has disappeared or is united with the epimeron, this process probably having taken place several times independently.

In discussing the affinities of *Mycetobia,* Crampton remarks on the numerous striking resemblances in pleural structure between this genus and *Anisopus*, but he disregards these, because in two points which he regards as fundamental — the small and incompletely separated meron and the rather narrow epimeron — *Mycetobia* apparently shows an approach to the *Mycetophilidae,* in which the meron is nearly always absent and the epimeron very much narrowed. However, it is not easy to see why these points should be regarded as more fundamental than the others referred to. In fact, an examination of the genus *Mesochria* clearly proves that thay are not so, since in this genus, which is indisputably a close ally of *Mycetobia,* the epimeron is rather broader, and the meron is large and separate, exactly as in *Anisopus.* Moreover, even in *Mycetobia* the epimeron, though indeed somewhat narrowed, resembles in shape that of *Anisopus* more than it does that of any *Mycetophilidae.* We may therefore conclude that the pleural structure bears out the evidence from other sources indicating that *Mycetobia* is an Anisopodid, and that any apparent resemblances to the *Mycetophilidae* are due to parallelism only. Crampton's opinion that „the *Mycetophiloidea* may be the direct descendants of the *Anisopodidae*“ is presumably based on his erroneous conclusion with regard to *Mycetobia,* and is negatived by the structure of the larvae in the two groups.

On the other hand there is much to recommend Crampton's suggestion that the large membranous cleft dividing the anepisternite which is seen in *Simulium, Ceratopogon*, and *Thaumalea* indicates some degree of relationship between these groups. Further, his conclusion that *Dixa* is a somewhat primitive branch of the Culicid stock is doubtless valid, as also is his conclusion of the rather near relationship between the *Culicidae* and the *Chironomidae,* and between the *Bibionidae* and *Mycetophilidae.* It is clear that the pleural structures can provide extremely important evidence in regard to phylogeny, but it is also clear that their very complexity renders them peculiarly liable to misinterpretation. The differences to be found within one family are often very great, and many more types must be studied before far-reaching conclusions based on these structures alone can be accepted.

Metanotum. — As pointed out by Crampton, the metanotum is well preserved only in the *Psychodidae* (including *Bruchomyia*), and on this account he would separate this family from the rest of the Nematocera.

Terminal abdominal structures. — The remarks made concerning the value of the pleural structures apply with at least equal force to the genital and anal chitinisations. It is possible to recognise a primitive type which is to be found in many different families, and also to trace the various modifications which this type has undergone within each family separately, but the comparative study of these organs in the suborder as a whole is but little advanced, though it should eventually yield important results.

Tibial spurs. — The tibial spurs, though variable in development, are normally present in most families. In some groups they have been entirely lost, including all *Cecidomyiidae* and *Scatopsidae*, a fact which confirms the evidence from other sources that these two groups have had a common origin, also that neither of them can be regarded as ancestral to the *Sciarinae*, which have retained tibial spurs.

Empodia and pulvilli. — Osten-Sacken in defining his groups Nematocera vera and Nemocera anomala stated, that the former had frequently a smooth empodium but no pulvilli, while the latter had either two pulvilli or a broad pulvilliform empodium. These statements, however, were based on incomplete observation, since pulvilli are present in many *Chironomidae*, some *Culicidae* and some *Mycetophilidae*. They occur in so many groups that their presence, as well as that of some sout of empodium, is probably a primitive feature. De Meijere is probably incorrect in listing the absence of empodia among the primitive characters of the Nematocera. The presence or absence or the form of these organs afford valuable means of tracing affinities among genera, as for example has been shown by Kieffer for the *Chironomidae*, but the characters are too uncertain to use in defining families.

Trichiation of the wings. — Tillyard has pointed out that in many of the more primitive Diptera, as well as in other related orders, the wing membrane and veins bear hairs of two different types, macrotrichia and microtrichia. The macrotrichia of the membrane have been lost in all Brachycera and Cyclorrhapha, but are preserved in at least some members of nearly every family of Nematocera. They are present in *Ptychopteridae*, but absent in *Tanyderidae,* showing that the former cannot have been derived directly from the latter. Similarly they are present in many *Chironomidae*, but lacking in all *Culicidae,* so that, although the latter family has retained a more primitive type of venation, it also cannot have given rise directly to the *Chironomidae*.

The veins all originally bore macrotrichia, with the exception of the cross-veins, which Tillyard distinguishes from the true (longitudinal) veins largely by this means. There are however many exceptions to the rule; when a section of a true longitudinal vein assumes a transverse position it is apt to lose its macrotrichia, and conversely, when a vein which is morphologically a cross-vein becomes more or less longitudinal, it may develop macrotrichia, as in *Sciara*. The occurrence of these hairs on the wing-veins is therefore a character of uncertain value. It is interesting to note, however, that the „great cross-vein" of *Tipulidae* sometimes bears macrotrichia on its lower portion only: this may perhaps mean that the lower part of the vein represents the remains of *Cu 1,* while the upper part is the true *m-cu.* Again, the presence of strong macrotrichia on the basal sections of *Cu 1* in the *Culicidae* (including *Dixa*) is some evidence that this section is not *m-cu* as suggested by Tillyard.

Venation. — No feature of the Diptera has been more used in classification than the wing-venation, and probably none can offer greater assistance in determining phylogeny, particularly as the wings are the only parts of fossil flies which are satisfactorily preserved. There are, however, serious difficulties of interpretation, and as shown by the example already quoted of *Diadocidia* and *Empidideicus*, an apparently identical venation may be arrived at independently in quite unrelated groups. **Tillyard** has endeavoured to deduce from morphological and palaeontological evidence the venation of the archetype of the Diptera, and concludes that it possessed a four-branched radial sector, a four-branched media, and a simple cubitus.

The radial veins. — Few forms have clearly preserved the four branches of the radial sector, the chief being the *Tanyderidae* and *Psychodidae*. In the other forms, which have lost one or more branches, it is often difficult, though obviously very important, to determine which are the lost branches. A useful criterion is that $R2+3$, when it is present, is a more or less concave vein occupying the furrow between *R 1* and *R 4+5*. Christophers and Barraud have pointed out that the second vein in the mosquitoes is a concave one, and it therefore seems safe to conclude that in this family it is *R 4+5* which has lost the fork. The same seems to be true of most other families, though in regard to the *Tipulidae* Alexander has recently suggested a different interpretation, assuming that *R 2* has been lost or modified into an apparent marginal cross-vein. If this is really the case, it would again indicate a rather sharp separation of the *Tipulidae* from most other groups, but except in a few genera, such as *Tricyphona* and *Molophilus,* the interpretation seems difficult to maintain, and it is hardly likely that there have been two radically different types of modification of the radius within the family.

In the families *Cecidomyiidae, Mycetophilidae* (sens. lat.), *Bibionidae* and *Scatopsidae* the vein *R 2+3* seems to have been entirely lost. A few forms, such as *Plecia, Hesperinus,* and the *Ditomyiinae* show a fairly long branch of the sector which might be interpreted as either *R 2+3* or *R 4,* but as it is distinctly a convex vein, and arises well beyond *r-m,* it is almost certainly to be regarded as *R 4.* As all the above-named families agree in having peripneustic larvae, and also in other respects (e. g. in the mouth parts, as shown by Frey), it would seem justifiable to regard them as constituting a rather sharply defined division of Nematocera, corresponding more or less to the Oligoneura in Knab's sense. There are a few other forms (e. g. *Simulium*) which have lost *R 2+3,* but these do not show resemblances in other respects to the Mycetophilid group. In a few others (*Mycetobia* and *Pachyneura*) which have often been included with the *Mycetophilidae,* the upper branch of the sector is concave and arises at or just before *r-m;* it is therefore certainly *R 2+3* and not *R 4,* and the two genera must be classed with *Anisopodidae* in regard to venation as well as in other respects.

The *Chironomidae* also do not belong to the *Mycetophilid* group, as they have mostly preserved *R2+3* and their venation is clearly derivable from the Culicid type. In the *Tanypodinae* the main difference from the *Culicidae* in the radial venation is that the fork of *R 2+3* has been shortened (it is already short in a few *Culicidae,* such as *Megarhinus*) and *R 2* has turned upwards and joins *R 1* instead of the costa, a not infrequent development in some other families. In the *Chironominae* matters have gone rather further, *R 2* being entirely lost and *R 2+3* often more or less evanescent. The *Ceratopogoninae* have taken rather a different line, but we may reasonably suppose that here *R 2+3* and *R 3* have been suppressed not by atrophy but by fusion with *R 4—5* throughout their whole length, while *R 2* remains (in most cases) as the „cross-vein" connecting the two main branches of the radius. The result may be a superficial resemblance to some of the *Mycetophilidae* such as *Tetragoneura* [1]), but it has almost certainly been brought about in an entirely different manner.

The media and cubitus. — The limits of these two veins are still not satisfactorily understood. Tillyard has endeavoured to show that the cubitus (*Cu 1*) is simple in the Dipterous archetype, not forked apically as it evidently is in some allied orders. This explanation fits in very well with the appearance of the venation in the *Tipulidae, Tanyderidae, Ptychopteridae* and *Psychodidae,* where the „great cross-vein" of Osten-Sacken may very well be regarded as *m-cu.* In regard to most of the other families, however, it is difficult to believe that *Cu* has not a true apical fork, especially for example in the *Culicidae,* where Christophers and Barraud have shown that this fork exists even in the developing wing in the larvae, each branch being provided with a distinct trachea. It seems therefore possible to suppose that the primitive Dipteron had both a four-branched media and an apically forked cubitus, and that some groups have lost *M 4* and others *Cu 1a.* If this is so, it should be of extreme value in the classification of the Nematocera, but unfortunately it may be very difficult to decide which vein has been lost. The fossil genus *Mesotipula* recently described by Handlirsch does appear to show the full number of veins postulated above.

Anal veins. — The only family which has preserved two well-marked anal veins, both reaching the margin, is the *Tipulidae* (including *Trichocera).*

In conclusion, it must be admitted that we have still a long way to go before we can reconstitute the true phylogenetic history of all the Nematocerous families. To do so we need the assistance of Palaeontology, and unfortunately little help seems likely to be forthcoming from this direction. The large number of amber forms which have been discovered and described do not reveal any important differences from genera and even species existing at the present day. Consequently we must conclude that our existing families have mostly or all had their origin in the Mesozoic period, perhaps in the Jurassic or even the Trias; and the available material from these earlier formations is scanty and mostly ill-preserved. We must therefore rely

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[1]) **Meunier has recently (1920) described as *Tetragoneura veterana* a fossil fly which appears from his photograph to be a species of *Palpomyia.***

mainly on morphological evidence, contradictory though it often appears to be. To the present writer the sum of this evidence appears to point to the following conclusions:

1. At a very early stage, probably about the beginning of the Jurassic period, if not earlier, the Diptera were already divided into three main stocks, the first being represented at the present day by the *Mycetophilidae, Bibionidae, Scatopsidae, Cecidomyiidae* and their allies; the second by the *Ptychopteridae, Psychodidae, Culicidae, Chironomidae,* etc.; and the third by the *Trichoceridae* and *Tipulidae.*

2. Among the families of the second group the *Psychodidae, Tanyderidae* and *Ptychopteridae* appear to belong to one stock, which shows many points of connection with the Tipulid series. The *Culicidae, Dixidae, Chironomidae* (with *Ceratopogoninae*) also form a single complex, within which the *Thaumaleidae* and *Simuliidae* may perhaps also be included. The *Anisopodidae* occupy a somewhat isolated position, though on the whole they appear to come nearest to the ancestral type of the whole group.

3. The specialised Brachycera and Cyclorrhapha arose somewhat later from a primitive member of this second group of families which was allied to the *Anisopodidae.*

4. The families whose affinities are still least certain are the *Blepharoceridae* (with *Deuterophlebiidae*), *Simuliidae* and *Thaumaleidae;* in regard to these we have not yet been able to make a much more satisfactory arrangement than did Osten-Sacken in describing them as Nemocera anomala.

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Discussion:

Im Anschluß an den Vortrag von Herrn Edwards stellt H. Schmitz eine Frage bezüglich der Literatur über vergleichende Morphologie des Pro- und Mesothorax, besonders der pleuralen Teile, bei Dipteren, welche vom Vortragenden beantwortet wird.

Postscript. — Since this paper was read Dr. G. C. Crampton has kindly allowed me to see an advance copy of his „Phylogenetic study of the thoracic sclerites of the Psychodoid Diptera, with remarks on the inter-relationship of the Nematocera“. The conclusions at which he arrives are in many respects remarkably similar to those we have reached in this paper; in particular the *Psychodidae* are no longer treated as an isolated group, but are recognized, as in this paper, as being in close relation with the *Tanyderidae* and *Ptychopteridae*, the thoracic characters evidently being in accordance with the venational ones on which my conclusion was mainly based. The main points of difference between Dr. Crampton's conclusions and those outlined above are in regard to some of the families of the second group, the *Anisopodidae* being placed with the Mycetophilid-Bibionid group and the Ptychopterid stock being grouped with the *Tipulidae*.