REMARKS ON THE PHYLOGENY AND INTERRELATIONSHIPS OF NEMATOCEROUS DIPTERA

By G. C. Crampton, Ph. D.

Massachusetts Agricultural College, Amherst, Mass.

During the course of an anatomical study of the Nematocerous Diptera, undertaken at the suggestion of Dr. C. P. Alexander, a number of interesting and important points concerning the interrelationships of these most primitive representatives of the order Diptera, were brought to light, and I would present herewith a brief resumé of the principal features suggested by this study. The accompanying diagram of the lines of

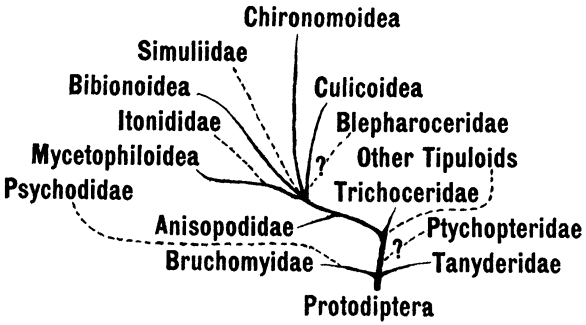

Fig. 1. Lines of descent of the Nematocerous Diptera.

descent of the Nematocerous Diptera will serve to illustrate the interrelationships here indicated.

Among the most primitive Diptera known, are the Tanyderidæ and Bruchomyidæ. Alexander, 1920, lists the Bruchomyidæ as a subfamily (Bruchomyinæ) of the Tipuloid family Tanyderidæ, but it seems preferable to raise them to family rank, since they differ from the Tanyderidæ in many important features.

The immediate ancestors of the Bruchomyidæ and Tanydreidæ evidently had a common origin—possibly in a Proto-

dipteran stem represented by such forms as *Austropsyche*, etc., described by Tillyard, 1919.

The Bruchomyidæ are very like the ancestors of the Psychodidæ, which branched off from the Bruchomyid stem to follow their own isolated path of development. On account of the isolated character of the Psychodidæ, which differ from both the Tipuloid Nematocera (Pronematocera) and non-Tipuloid Nematocera (Eunematocera) the Psychodidæ and their ancestral types, the Bruchomyidæ, might possibly be grouped together as Paranematocera, composed of the superfamily Psychodoidea but this point is of no particular importance in the present discussion.

The Tanyderidæ are among the most primitive of the Tipuloid Nematocera, and have departed but little from the ancestral Dipteran stock, but they have developed modifications of their own, and it would be impossible to derive the rest of the Tipuloid Nematocera from this family alone, although it is possible that the Tipuloid family Ptychopteridæ branched off from the ancestral Tanyderid stem, as shown in Fig. 1.

The Tipuloid subfamily Trichocerinæ of Alexander, is here raised to family rank, because the Trichoceridæ differ markedly from the Anisopodidæ (Rhyphidæ) in which family they have usually been placed. On the other hand, the Trichoceridæ are very like the ancestors of the Anisopodidæ, and apparently had a common origin with the Anisopodidæ, from which common origin they have departed less than the Anisopodidæ have. The ancestors of the Trichoceridæ arose from the common stem giving rise to the Bruchomyidæ and Tanyderidæ, and it would be impossible to derive the Trichocerids from any known Bruchomyid or Tanyderid. The rest of the Tipuloid Nematocera are of no particular interest in the study of the lines of development of the non-Tipuloid Nematocera, and need not be further considered here.

The Anisopodidæ (Ryphidæ) furnish the "key" group in tracing the phylogeny of the non-Tipuloid Nematocera, and it is a question as to whether the Anisopodidæ are still to be considered as true Tipuloid Nematocera, or whether they have progressed far enough toward the non-Tipuloid Nematocera

to be classed with the latter. At any rate, the Anisopodidæ are extremely close to the actual ancestors of the non-Tipuloid Nematocera, which were possibly of some "post-Anisopodid," but "pre-Mycetophilid" type intermediate between the Anisopodidæ and Mycetophilidæ.

The Mycetophiloidea (i. e. Mycetophilidæ, Mycetobiidæ, Sciaridæ, etc.) arose from the Anisopodidæ themselves, or from forms extremely like the Anisopodidæ, and it is extremely difficult to determine whether to group such annectant types as the Mycetobiidæ with the Mycetophilidæ, or with the Anisopodidæ. I have raised the subfamily Mycetobiinæ of Edwards, to the rank of a family, and have placed it among the Mycetophiloidea next to the Mycetophilidæ, rather than to include the Mycetobiinæ in the family Anisopodidæ as Edwards does.

The Sciaridæ are rather primitive Mycetophiloids worthy of family rank, but I do not think that Malloch is justified in raising the Mycetophilid subfamily Platyurinæ to family rank, and there is even some question of the advisability of raising the Bolitophilinæ to family rank.

The Itonididæ (Cecidomyidæ) might be included among the Mycetophiloidea. At any rate, they arose from the Anisopodid-like ancestors of the Mycetophiloids, and their line of development parallels that of the Mycetophiloidea remarkably closely, so that there can be no doubt that their closest relatives are the Mycetophiloids.

The Bibionoidea include the Bibionidæ, Scatopsidæ, etc., and the Simuliidæ may possibly be grouped in this superfamily also. The Bibionoidea are very closely related to the Mycetophiloidea, and apparently arose from the Anisopodid-like ancestors of the Mycetophiloidea.

The genus *Hesperinus* (and *Hesperodes* also) has been much shuffled about, having been placed in the family Bibionidæ by some, in the family Mycetophilidæ by others, and *Hesperinus* has even been placed in a separate family, the Pachyneuridæ, by certain European entomologists. *Hesperinus*, however, is so closely related to the Bibionid genus *Plecia*, that if *Plecia*

is retained in the family Bibionidæ, then *Hesperinus* must be retained in the Bibionidæ also.

The Simuliidæ are extremely closely related to the Chironomoid family Ceratopogonidæ, and apparently represent a connecting group annectant between the Chironomoidea and Bibionoidea, with some suggestions of affinities with the Culicoidea. The Simuliidæ apparently branched off at or near the base of the Bibionoid stem.

The Chironomoidea include the Chironomidæ and Ceratopogonidæ, and possibly the Thaumaleidæ (Orphnephilidæ) also. The Ceratopogonidæ branched off from the base of the Chironomoid stem, and have retained many characters suggestive of affinities with the Simuliidæ and with the Culicoidea also. The Chironomoidea are so closely related to the Culicoidea that it might be preferable to include them in the superfamily Culicoidea, but for the sake of convenience, the Chironomoidea have been treated as a distinct superfamily in the phylogenetic tree shown in Fig. 1.

The Culicoidea include the Dixidæ, Culicidæ, and Chaoboridæ, the latter being usually regarded as a Culicid subfamily, the Chaorborinæ (Corethrinæ). The Dixidæ appear to be very close to the ancestral stock from which the Culicidæ and Chaoboridæ were derived. The Culicoidea and their close relatives, the Chironomoidea, were apparently derived from ancestors very closely allied to the Anisopodid-like ancestors of the Bibionoidea and Mycetophiloidea, so that these Anisopodid-like forms were the types from which the Mycetophiloids, Bibionoids, Chironomoids and Culicoids were derived.

The Blepharoceroidea, containing the single family Blepharoceridæ, represent an extremely isolated "compact" group whose affinities are very difficult to determine. Of the three Blepharocerid subfamilies Edwardsininæ, Blepharocerinæ, and Deuterophlebinæ, the Edwardsininæ, represented by the genus *Edwardsina*, are the most primitive; but even with the help of *Edwardsina*, it is practically impossible to determine the closest affinities of the Blepharoceridæ, for despite *Edwardsina's* primitiveness, it is extremely isolated, and is not approached at all closely by any Nematocera I have seen. I find in the Blepha-

roceridæ some slight indications of affinities with the Bibionoidea, and also some slight suggestions of resemblances to the Chironomoidea and Culicoidea. The mouthparts of *Edwardsina* resemble those of the Tanyderidæ, and Dr. Alexander finds suggestions of affinities with the Tanyderids in the wings of *Edwardsina*; but the other structures of Edwardsina show no marked resemblance to the Tanyderids, so that it is preferable to group the Blepharocerids with the non-Tipuloid Nematocera provisionally, leaving the matter of their closer affinities until more data on the subject is available.

In brief, the Culicoidea, Chironomoidea, Bibionoidea and Mycetophiloidea were apparently descended from Anisopodid-like ancestors, which in turn lead to the ancestral Trichoceridæ. These were derived from ancestors like those of the Bruchomyidæ and Tanyderidæ, which sprang from the common Protodipteran stem, represented by such forms as the fossil Protodipteron *Austropsyche*. The latter is extremely Mecopteroid in nature, and beyond a doubt the Protodiptera arose from the Mecoptera themselves, or from the immediate ancestors of the Mecoptera, and the Trichoptera also arose from the same stock. These lines of development are joined by those of the Hymenoptera and Neuroptera as we trace them back to their ultimate source in the Protorthoptera, or in the common Protorthopteran-Protoblattid stem from which the insects above the Palædicyoptera (i. e., the "Neopterygota") were derived. These in turn lead to the Palæodictyoptera, and the Palæodictyoptera together with the Odonotoids and Ephemeroids (*i. e.*, the "Archipterygota"), were apparently derived from the Lepismatoid ancestors of the Pterygota in general.