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RECENT TRENDS IN THE TAXONOMY AND EVOLUTION OF MAYFLIES (EPHEMEROPTERA)

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ABSTRACT

The salient features of the different schemes of the classification of mayflies (Ephemeroptera) are outlined in the light of the evolutionary trends evident in the egg, larval and imaginal stages.

Mayflies are primitive insects with a prominent acquatic larval stage extending to several months or years whereas, as adults they live just for a day or two as indicated by the derivation of the order name, Ephemeroptera (ephemerous = living but a day). These primitive insects originally formed a section of the old Limnnaean Neuroptera but is now regarded as a distinct order. In recent classifications the Ephemeroptera are placed near the Odonata (Dragonflies), being considered more specialised than the Plecoptera (Stoneflies). The Ephemeroptera can reasonably be regarded as 'flying Thysanura' having been almost certainly derived from lepismatoid origins (Edmunds, 1972). They agree with the lapismatoids in having three caudal filaments and the wing venation pattern is very primitive (Edmunds and Traver, 1954). In all, there are 20 familes of recent Ephemeroptera, which include approximately 213 genera and 2139 valid species (Hubbard and Peters, 1976). Geological evidence indicates that they were once proportionately much more abundant in species and that they have steadily lost ground since the time of the earliest recognisable fossils found in the Permian shales of Kansas and Archangel (Kimmins, 1972).

The fossil record of Ephemeroptera is scanty and in most cases consists of wing prints or imperfect larval specimens. Apart from the Permian finds mentioned above, significant palaeontological discoveries include the Ural and Kansas findings. Jurassic finds from Solenhofen and Siberia and Tertiary finds from Baltic amber and the USA. Demoulin's (1958) classification is based to a great extent on palaeontological data, Recently Tshernova (1970) has established a new classificatory system based on the study of living and fossil families.

Although there has been general agreement at the family or subfamily level, there has been little agreement on the higher classification of the Ephemeroptera. Edmunds (1962) ably reviewed the earlier schemes (Needham, Traver and Hsu, 1935; Burks, 1953; Edmunds and Traver, 1954; Demoulin, 1958) and presented a concise outline of a new classification. But these earlier classifications tended to emphasize the structure, especially wing venation and tarsal segmentation of the adults.

Having studied the extensive material of imagos and nymphs. from the whole world, Edmunds, Allen and Peters have gained remarkable knowledge of the comparative anatomy of mayfly larvae and they have worked out a system of families and genera of this order, which is one of the best substantiated classifications of insects (Edmunds, Allen and Peters, 1963). Illies (1968) and Landa (1973) accepted this classification. A brief outline of the above scheme is presented below;

Order : Ephemeroptera

Super Family : Heptagenioidea	Family :	Siphlonuridae
		Siphlaenigmatidae
		Baetidae
		Oligoneuriidae
		Heptageniidae
		Ametropodidae
,, Leptophlebioidea	,,	Leptophlebiidae
		Ephemerellidae
		Tricorythidae
,, Ephemeroidea	,,	Behningiidae
		Potamanthidae
		Euthyplociidae
		Ephemeridae
		Polymitarcidae
		Palingeniidae

Super Family, Caenoidea	Family	Neoephemeridae Caenidae
Super Family : Prosopistomatoidea		Baetiscidae Prosopistomatidae

In the First International Conference on Ephemeroptera held in 1970, Riek emphasized that the nymphs offer a sounder basis for an outline of the higher classification of the order, although supporting evidence of the distinctiveness of some nymphal types is supplied by the adults (Riek, 1973). He agrees with Edmunds and Allen (1966) that a knowledge of the immature stages is essential to the task of reconstructing the probable phylogeny of the order. Landa (1959) has shown that the internal anatomy of the nymph is also significant in this respect.

Riek (1973) considered that the shrimp - like actively swimming type of nymph that is of general occurrence in Siphlonuridae and Baetidae (Baetoidea) is the basic form of mayfly nymph and that all other nymphal types have been derived from it. The first recorded mayfly nymphs, from the Lower Permian, are of the generalized siphlonurid type with short Caudal filaments bearing only lateral hair fringes (Riek, 1973).

Riek's classification differs from that of Edmunds, Allen and Peters (1963) mainly in separation of the Heptageniidae from the Baetoidea and elevation to superfamily status equivalent to the Leptophlebioidea. He is also of opinion that the Heptagenioidea, Leptophlebioidea and Ephemeroidea are all derivatives of a Siphlonurid - like ancestor along independant lines, and that there is as much justification for recognizing the superfamiiy Heptagenioidea as there is for recognizing the Leptophlebioidea and Ephemeroidea (Riek, 1973).

It cannot be gainsaid that a proper understanding of the evolutionary trends within a group is vital for establishing the evolutionary classification of that group. The correct application of the phylogenetic approach to the natural system of classification requires that the taxa should follow, step by step and in correct sequence, the actual events of diversification which took place in evolutionary history (Henning, 1966). Evolutionary taxonomy differs from empiricism by demanding an explanation for the existence of such groupings and by using the answer to this question for the improvement of classification (Mayr, 1969). The taxonomist no longer 'makes' taxa, he becomes a 'discoverer' of groups made by evolution (Darwin 1859).

This idea has led Vladimir Landa to scrutinize the existing classification of the Ephemeroptera, by studying the trends appearing in evolutionary lines of individual organs and the knowledge of ontogeny i. e., the knowledge of the larvae. For example, in the development of wings of mayfiles there is a marked tendency towards the reduction of the second pair of wings to their absence and irregularities in the venation and its simplification. Another tendency is the decrease in the number of movable tarsal segments. reduction of the median filament, conspicuous specialization of eyes, forelegs, external genitalia of males and females etc. In larvae there is an evolutionary tendency to the reduction of the number of tracheal gills and specialization of their shape (Landa, 1973.)

Based on the study of 127 species and 94 genera of mayfly mymphs, Landa (1969) has found that the comparative anatomy of the tracheal system, malpighian tubules and the nerve band provide new very important criteria for specification of the evolution of mayflies.

1. In the tracheal system, the tendency of evolution leads from a simple regular scheme to a complex and functionally more efficient system through the formation of anastomoses.

2. The malpighian tubes, originally numerous simple tubles. have been concentrated in a decreasing number of variously arranged trunks.

3. The last nerve ganglion has shifted into segment VII or fuses there with the previous one; the originally loose connections fuse in a band.

Another landmark in mayfly taxonomy and phylogeny is the contribution of Koss. Through a study of the eggs of approximately 100 of the known mayfly genera, he is convinced that the egg stage in this group of insects can provide valuable data for taxonomic and phylogenetic studies of the order.

Mayflies have a unique way of laying eggs freely on the surface of water rather than personally attaching them to fixed objects. To ensure survival and aid dispersal, the egg itself must have some means of attachment to submerged objects. For this purpose many elaborate chorionic structures have evolved which enable mayfly eggs to adhere to submerged surfaces. Such 'attachment structures' have evolved in different ways. The micropyle is the structure which allows sperm to enter the eggs and it is also useful in systematic studies of the Ephemeroptera. In addition to attachment structures and micropyles, chorionic sculpturing is a feature which varies at one taxonomic level or another. The small ridges, tubercles and other ornamentation found on the surface of the chorion are known as chorionic sculpturing and they can be quite useful for taxonomic purposes or in generic and specific level phylogenetic studies. Koss (1973) feels that chorionic sculpturing arose independently in nearly every family and sub-family, and therefore it is useless as a tool for reconstructing ephemeropteran phylogeny at the family level.

Total egg data collected by Koss (1973) suggests a classification which is similar to those published by Edmunds and co-workers since 1954 and entirely unlike those proposed by Demoulin since 1958. The classification proposed by Koss, however. makes a few changes over the earlier classifications. He places the Ephemerellidae and Tricorythidae in a super family (Ephemerelloidea) distinct from the Leptophlebioidea and that they are considered possibly having been derived from the Potamanthidae.

The latest taxonomic studies of the Ephemeroptera, as in other groups are beginning to employ the techniques of cytotaxonomy, chemotaxonomy and numerical taxonomy which will try to solve the problems of the status and the inter-relationships of the higher taxa of the order.

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