

PROBLEMS OF INTERNAL ANATOMY OF EPHEMEROP-  
TERA AND THEIR RELATION TO THE PHYLOGENY AND  
SYSTEMATICS OF THEIR ORDER

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THEORIES concerning the relations of recent may-flies to the phylo-  
genetic development of the Order, as well as the evaluation of higher  
systematic units, have been based up to the present time mainly on the  
external morphology of the imagines (wings, eyes, cerci etc.). I have  
studied the anatomy of more than 60 species of Middle-European larvae  
belonging to different genera and families. Interesting differences of  
phylogenetic value were revealed in the structure of various organs.  
These differences can be followed most conveniently in the tracheal  
system; see Landa, 1948, *Věst. Čsl. spol. zool.*, 12: 25-82).

Different tracheal systems in the abdomen of various larvae are seen  
in following examples:

(1) Tracheal system very similar to the original schema; free dorsal,  
visceral and ventral branches from the tracheal stems exist in every  
segment; anastomoses can be found occasionally in segments VIII and  
IX only, where they are formed in later larval stages (*Oligoneuriella*,  
*Ecdyonurus*).

(2) Strong anastomoses in the segments III-VIII on dorsal and still  
more on ventral branches; some of them develop in later larval stages;  
visceral branches of the segments I and II absent (*Leptophlebia*,  
*Ephemerella*).

(3) Ventral anastomoses in segments II-IX developed very early;  
visceral branches of segments I, II, III, absent, so that the branch of  
segment IV reaches the head.

The tracheal system also shows variations in the head and thorax.  
The formation of the tracheal system corresponds to the shape and  
development of gill plates. Differences can be noticed also in the dis-  
tribution of neuro-ganglia, in the digestive tube and particularly in the  
formation of the Malpighian tubes. Originally the last fused ganglion is  
situated in segment VIII (e.g. *Siphonurus*); this ganglion occasionally  
may be shifted into segment VII (e.g. *Ecdyonurus*) and sometimes fused  
with the existing one (e.g. *Baetis*); or all abdominal ganglia are shifted  
in the first six segments (e.g. *Caenis*); in an extreme case all the thoracic  
and abdominal ganglia are fused (*Prosopistoma*).

Malpighian glands consist originally of many tubes opening separ-  
ately into the digestive tract (e.g. *Siphonurus*); in a more progressive  
stage their system is alternated forming 8 main stems (*Ecdyonurus*), some-

times only 2 long stems (*Caenis*); in highly specialized young species the individual tubes are T-shaped.

Considering the above-mentioned anatomical data as well as results of morphological research, the species of to-day do not seem to form a phylogenetic series, but appear to be remnants of various phylogenetic age and position. According to the investigated species the probable development of the order Ephemeroptera would be as follows:

In early stages of evolution a branch was separated from the original type with simple interior organization, in which the tracheal system and its functions were subject to a higher development. This branch gave rise first to the families of the super-family Leptophlebioidea Edmunds (tracheal system type 2), and later to the families of the super-family Ephemeroidea Edmunds (tracheal system type 3). In this group belong for the most part the ancient species with wide ecological valence and a rather small number of species. The original type with a primitive tracheation continued its progress. The families of the super-family Heptagenioidea Edmunds are derived from it. The development went on towards the family Baetidae with many young, little differentiated and highly specialized species, separating besides just at the beginning the family Siphonuridae, with many archaic characters and towards the family Heptageniidae Edmunds. The families Oligoneuriidae and Isonychiidae possessing classic archaic characters took their origin in the time when the development of both branches went parallel. The super-family Caenoidea Edmunds shows certain relations to the group Leptophlebioidea; the characteristic formation of Malpighian glands, shift of ganglia forward and some other facts, however, point to a different origin.

The results obtained by the study of larval anatomy can be used in the evaluation of the existing Ephemerid system. They show that the present classification of Ulmer, Needham and others is incorrect as it brings together quite unlike groups. According to the results of this study the most appropriate classification seems to be that of Edmunds, with one reservation: in my opinion the super-family Prosopistomatoidea should be abolished and its families added to the super-family Caenoidea Edmunds. This conclusion is based on the similarity of their tracheal systems, their ganglia, the formation of the Malpighian tubes and the fact that the posterior part of the gut possesses caeca.

Even though the present investigations are based on only a part of the known species, it is evident that the study of anatomy can contribute substantially to the knowledge of the phylogeny of the Ephemeroptera and to a natural systematic classification.