A CONTRIBUTION TO THE EVOLUTION OF THE ORDER EPHEMEROPTERA BASED ON COMPARATIVE ANATOMY

VLADIMIR LANDA

Department of Developmental Morphology, Institute of Entomology, Czechoslovak Academy of Sciences, Praha, C.S.S.R.

The study of the evolution of mayflies has received much attention partly in connection with the evolution of insects in general, and partly for the endeavour to establish a classification based on phylogenetic relationships for this particular order.

Our knowledge of the evolution of mayflies as well as of the other orders relies on direct and indirect information. The direct information comes from palaeontological discoveries. Among the most important discoveries are the Permian finds from Archangelsk, the Ural and Kansas (CARPENTER, MARTINOV, TILLYARD, and TSHERNOVA), Jurassic finds from Solenhofen and Siberia (CARPENTER, MARTINOV, DEMOULIN, TSHERNOVA), and Tertiary finds from Baltic amber and the USA. DEMOULIN's (1958) classification is based to a great extent on palaeontological data.

Of course the palaeontological information by itself is not sufficient for the reconstruction of evolution, be it because of its incompleteness particularly in the key points of the evolution, or because of the limitation of characters retained. Therefore the study and reconstruction of evolution depend on indirect information - comparative morphology of recent forms. Trends appearing in evolutionary lines of individual organs and the knowledge of ontogeny, i.e. the knowledge of the larvae, form the basis of this study. For example, in the development of wings of mayflies (as of insects in general) 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 tail filament, conspicuous specialisation of eyes, fore legs, external genitalia of males and females, etc. In larvae there is an evolutionary tendency to the reduction of the number of tracheal gills and specialisation of their shape.

Having studied extensive material of imagos and larvae from the whole world, G.E. EDMUNDS, R.K. ALLEN and W.L. PETERS have achieved remarkable knowledge of the comparative anatomy of mayfly larvae, and they have worked out a system of families and genera of this order, which in my opinion is one of the best substantiated classifications of insects (EDMUNDS, ALLEN, PETERS, 1963).

In the past years I studied in two stages, 1945 to 1948 and 1964 to 1968, the comparative anatomy of mayfly larvae. The results obtained from the study of 127 species and 94 genera (more by today) are presented in the paper, LANDA (1969). The comparative anatomy of the tracheal system, Malpighian tubes and the nerve band provided new, very important criteria for specification of the evolution of mayflies. 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. The Malpighian tubes, originally numerous simple tubules, have been concentrated in a decreasing number of variously arranged trunks. The last nerve ganglion has shifted into segment VII, or fuses there with the previous one; the originally loose connections fuse in a band. Studies have shown that all these cases represent true evolutionary lines.

Making use of findings from the comparative anatomy and taking into consideration information from the external comparative morphology of imagos and larvae, as well as palaeontological discoveries, we arrive at the following hypothetical scheme of the evolution of mayflies (Fig. 1).

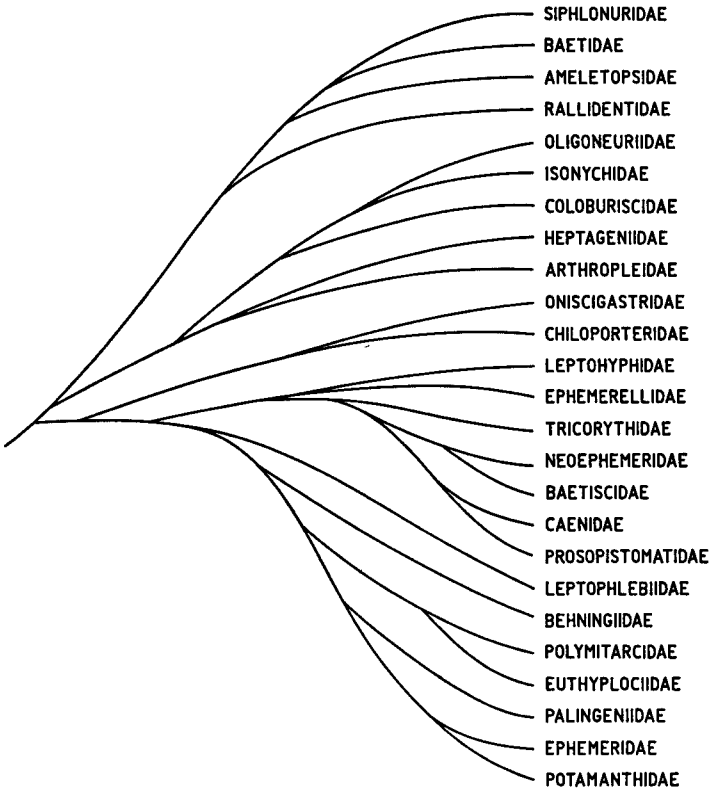

FIG. 1. Hypothetical scheme of the evolution of Ephemeroptera.

It follows from the scheme that there are two main lines in the evolution of mayflies.

The first evolutionary line is characterised by a very simple tracheal system without anastomoses, or with them in segments IX of VIII-IX only. The evolutionary line has two distinct branches.

The first branch links up with the most primitive species and goes in the direction of the first line. There are no anastomoses in the tracheal system. Gills, originally situated on 9 segments (e.g. the Permian larva of *Phthartus rossicus* is of this type), have no bundle of filaments and their function is not so much respiration as rather the supply of water. The Malpighian tubules individually open into the digestive system, without forming trunks. The family Siphlonuridae, represented today by very ancient species, stems from the base of this branch. The families Rallidentidae, Ameletopsidae and Baetidae gradually deviate from the main direction of the branch. They possess some related characters, e.g. straight Malpighian tubes, and arrangement of the nerve band. The genera of the family Baetidae undergo at present a rapid development and are represented by derivative, very variable species. Despite the

extreme specialisation of larvae as well as adults the members of this family have retained the above mentioned primitive characters of this branch and original line. The family Rallidentidae separated from the branch as early as at its base and has certain relations (gills with a primitive filamentous part) to the following branch.

The second branch of the first line separated very early from the first one. The tracheal system remains in the original simple form, but in segment IX, and sometimes VIII, too, there appear 1 to 2 simple anastomoses, arising only in the course of larval development. Bundles of respiratory filaments appear on the mouthparts, thorax, near the legs and on the abdominal segments where they are covered by gills. The tubules of the Malpighian tubes lead into trunks. The families Oligoneuriidae, Isonychidae and Coloburiscidae with bundles of respiratory filaments on the head and thorax, and represented by rather plesiomorphic genera and species, belong to the more primitive sub-branch of this branch. At the present time the second sub-branch of this branch, leading to the family Heptageniidae, undergoes a remarkable development. There are no more auxiliary gills on the head and thorax, and tracheal gills on the abdomen consist of the gill and a bundle of filaments. This sub-branch comprises primitive genera *Cinygmula*, *Rhithrogena* and *Epeorus* in which the last ganglion occurs in segment VIII, and trunks of the Malpighian tubes are not ramified. Also included are the derivative genera *Ecdyonurus*, *Heptagenia*, *Stenonema*, and *Thalerosphyrus* in which the last ganglion has shifted into segment VII, and trunks of the Malpighian tubes are not ramified. The family Arthropleidae is close to Heptageniidae, but it is more specialised (secondary loss of the bundle of filaments, formation of maxillary palps in larvae, and fusion of the connections between gangiia).

The second evolutionary line shows profound changes in the tracheal system. Numerous strong anastomoses appear on the ventral side of abdominal segments, and the number of regular visceral tracheae decreases. The remaining ones form strong branches. Four branches issue from this line of evolution.

The first, most specialised, branch has strong anastomoses from the first or third abdominal segment, strong visceral branches, feather-like ramified gills and bush-like trunks of the Malpighian tubes. One sub-branch is formed by the closely related families Polymitarcidae (primitive) and Euthyplociidae (derivative) and by the families Palingeniidae, Ephemeridae and Potamanthidae. The family Ephemeridae has more primitive genera (*Ephemera* and *Ichthybotus*) through which it is close to the family Palingeniidae; the genus *Hexagenia* is more specialised.

The second branch consists of the family Leptophlebiidae, which abounds in genera and in recent times has been distributed all over the world. It requires further study. Meanwhile the genera belonging there can be divided into two groups according to the tracheal system (the number of anastomoses, which on the whole are weaker and less numerous than in the preceding group) and formation of the Malpighian tubes. In the first, most primitive, group the Malpighian tubes lead into eight short or longer nonramified trunks (*Paraleptophlebia*, *Habroleptoides*, and others). In the second group the number of trunks of the Malpighian tubes is reduced to 6 of the same length (*Thraulus* and *Indialis*), or 6 of various lengths in which 2 lateral ones are long (*Choroterpes* and *Choroterpides*). In one of the most specialised genera of this group (*Hagenulus*) the number of trunks of the Malpighian tubes is reduced to two long lateral ones.

The family Behningiidae has a certain relationship to both these branches and therefore is placed between them in the scheme.

The third branch stems from the base of the second line, where an improved tracheal system

begins to appear. Anastomoses are either missing, or in the process of formation (be it their number or shape), or fully developed. Visceral tracheae are very variable. The branch is considerably heterogeneous and recently has been represented mostly by specialised derivative species. The first, more primitive sub-branch of this branch leads to the families Leptohyphidae and Ephemerellidae. The family Ephemerellidae is now intensively evolving. The more ancient group of the Ephemerellidae still possesses numerous visceral branches and the original arrangement of the Malpighian tubes, which individually lead into a band on the digestive tube or into eight low buds (*Attenuatella* and *Timpanoga*). The second group has a more specialised visceral tracheal system, the Malpighian tubes lead into eight longer trunks. The second sub-branch progresses to a marked specialisation, above all in the Malpighian tubes. It begins with the family Tricorythidae, where four of eight trunks are extended up to the base of the abdomen. In the other families there are two trunks only. In the family Neoephemeridae these trunks form one process on each segment; these processes are missing in the other families. The families Neoephemeridae and Baetiscidae seem to be closely related, as well as Caenidae and Prosopistomatidae. There are no anastomoses in the families Baetiscidae, Caenidae and Prosopistomatidae. Of course this may be a secondary simplification. In these three families the nerve ganglia are shifted forward, in Baetiscidae and Prosopistomatidae they are fused in a mass.

The fourth branch, comprising the modern families Oniscigastridae and Chiloporteridae, can be derived from a place still nearer to the original first line.

The family Ametropodidae has not been included in the scheme owing to the scarcity of the material studied. However, according to available information it seems to have stemmed from the boundary between the two lines.

In my comment on the scheme of evolution I have used only anatomical characters, because this is the first time these characters are being used in this connection. Of course I know that an evolutionary line cannot be constructed solely according to a few characters, however carefully studied. Therefore all information provided by the comparative morphology of adults and larvae was used for comparison when the hypothesis of evolution was created. In my opinion it does not contradict the present scheme.

Other systems will have to be studied if we are to obtain a more profound knowledge of the comparative anatomy. The study of the endocrines (neurosecretory cells and the corpus allatum), haemolymph and chromosomes is under way. Preliminary results promise useful new information.

Résumé

Une contribution à l'évolution de l'ordre Ephemeroptera basée sur l'anatomie comparative

Cette étude porte sur l'anatomie comparée interne des larves d'éphémères et l'utilisation de telles données pour la compréhension de l'évolution des familles d'éphémères. Ces résultats sont basés sur l'étude de 127 espèces et de 94 genres. Les systèmes étudiés comportent le système trachéal, les tubes de Malpighi et le tronc nerveux. Le système trachéal a tendance à évoluer par la formation d'anastomoses d'un système simple vers un système complexe et plus efficace du point de vue fonctionnel. Les tubes de Malpighi constitués à l'origine par de nombreux tubes simples ont évolué vers un nombre décroissant de troncs disposés de façons diverses. Le dernier ganglion nerveux a migré dans le segment abdominal VII ou a fusionné avec le gan-

glion précédent dans ce segment. Les ganglions, faiblement reliés entre eux à l'origine, fusionnent pour former un tronc. Basé sur cette étude d'anatomie interne et à partir des données de morphologie comparative externe des larves et des adultes ainsi que des découvertes paléontologiques, une phylogénie hypothétique des familles d'éphémères est présentée dans la Figure 1.

Zusammenfassung

Ein Beitrag zu der Evolution von der Ordnung Ephemeroptera, auf vergleichende Anatomie aufgebaut

Dieses Studium beschäftigt sich mit der vergleichenden inneren Anatomie von den Nymphen der Ephemeroptera, und dem Gebrauch von solchen Data für das Verstehen der Evolution der Eintagsfliegen-Familien. Resultate sind auf das Studium von 127 Arten und 94 Gattungen aufgebaut. Diese studierten Systeme umfassen das Tracheensystem, die Malpighigefässe, und das Nervenband. Die evolutive Tendenz des Tracheensystems geht von einem einfachen zu einem komplizierten und wirksamer funktionierenden System durch die Formung von Anastomosen über. Die ursprüngliche Beschaffenheit der Malpighigefässe ist die von vielen einfachen Röhrchen, welche sich zu verminderten Zahlen von verschieden arrangierter Stämme entwickelt haben. Der letzte Nervenganglion hat sich in das Abdomensegment VII verschoben oder ist mit dem vorhergehenden Ganglion verschmolzen. Die ursprünglich losen Verbindungen zwischen diesen Ganglien verschmelzen zu einem Band. Aufgebaut auf diese innere Anatomiestudie und in Verbindung mit Data von äusserer vergleichender Morphologie von Nymphen und Erwachsenen und palaeontologischen Entdeckungen, ist eine hypothetische Phylogenie von den Eintagsfliegen-Familien in Figur 1 präsentiert.

REFERENCES

Demoulin, G. (1958). Nouveau schéma de classification des Archodonates et des Éphéméroptères. *Bull. Inst. Roy. Sci. Nat. Belg.* **34**(27) : 1-19.

Edmunds, G.F., Jr., R.K. Allen and W.L. Peters. (1963). An annotated key to the families and subfamilies of mayflies (Ephemeroptera). *Univ. Utah Biol. Sci. Ser.* **13**(1) : 1-55.

Landa, V. (1969). Comparative anatomy of mayfly larvae (Ephemeroptera). *Acta entomol. bohemoslov.* **66** : 289-316.