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Vladimír Landa and Tomáš Soldán

Phylogeny and higher classification of the order *Ephemeroptera*: a discussion from the comparative anatomical point of view

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Introduction

There are three distinct periods traceable in the history of insect comparative anatomy and morphology in general. The first period, approximately up to the the 1850´s, gave the very basic data concerning the arrangement of some internal organs of the insect body.As far as the mayflies are concerned the first mention of internal organs appeared in the famous Schwammerdam´s Ephemeri vita (1675). Apart from some other organs,the gonads of *Palingenia longicauda* were described and illustrated in this remarkable work. Although this work had appeared even a century before the establishment of zoological nomenclature, it represented the only serious anatomical study of mayflies until the middle of the nineteenth century.

The second period in the development of insect comparative anatomy lasted approximately from 1850 to the end of the 1930´s. It is characterized by the large number of data concerning anatomical arrangement of individual organ systems. Not only the structure, but also the function of some organs started to be investigated. In the *Ephemeroptera* research there are, first of all, two classical studies by Palmén (1877, 1884) referring to the anatomical arrangement of the tracheal system and gonads. He described these organ systems in European species of the genera *Ecdyonurus, Rhithrogena, Oligoneuriella, Caenis, Potamanthus* and *Ephoron*. Earlier authors (e.g. N. Joly, E.Joly, Brandt, Wheeler and others) who studied anatomy of both larvae and adults,dealt with further European genera. In a series of papers, Vayssière (1882, 1890, 1934, 1937) described the anatomy of some genera not investigated earlier (*Prosopistoma, Baetisca, Proboscidoplocia*) in detail. The first papers referring exclusively to the anatomical arrangement of internal organs of mayflies appeared at the beginning of our century (Drenkelfort, 1910; Heiner,1914). Both "skeletal" and "soft" morphology was given by Needham et al. (1935) in their extensive monography on Nearctic mayflies. Chapters on anatomy in this excellent study are based mainly on original investigation of several Nearctic genera (*Stenonema, Hexagenia*). This study also summarised all previously published data concerning mayfly morphology.

A weak point of these anatomical studies is the insufficiency of comprehensive data concerning the whole order *Ephemeroptera* or at least larger taxonomic groups. Moreover, some of the studies dealt with the anatomical arrangement of individual organs only from the descriptive anatomical point of view mostly ignoring high comparative value of characters investigated. The comparative studies,which started to appear after 1950, represented the beginning of the last period in the history of mayfly comparative anatomy. Landa (1959, 1973) showed that the comparative anatomy of the tracheal system could give valuable data not only for morphology itself but also for phylogeny and higher classification. Based on world-wide material, we know the arrangement of the nerve cord, alimentary canal, Malpighian tubules, and gonads in most recent genera (Landa, 1969; Landa et al., 1980, 1982; Soldán, 1981). Also the investigation of the egg chorion (Koss & Edmunds, 1974) and some endoskeletal characters (Tsui & Peters, 1975) bring valuable data for study of phylogeny and higher classification. On the other hand, despite detailed knowledge of some other organ systems in European species (Grandi,1947, 1962 - abdominal and thoracic muscles; Eastham,1958 - gill muscles, Mayer, 1931 - circulatory system, Grimm, 1977 - muscles of male genitalia and others) we lack comparative data concerning extralimital material from remaining regions. Especially the study of endocrines, chromosomes and hemolymph promises useful new information.

Since last larval instar of all known species of mayflies possess, besides all other organ systems found in adults, also fully developed gonads,the comparative anatomy actually can acquire a complex background for the study of mayfly phylogeny.Based on both published and unpublished results obtained during the past 30 years by dissection of larvae of about 170 recent genera (most results have not been yet published) we feel that it is necessary to summarize the result obtained.

The objective of this study is to outline the anagenesis of the above mentioned organ systems and to discuss the phylogeny and higher classification of the order *Ephemeroptera* from the comparative anatomical point of view.

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Rewiev of higher classification of the *Ephemeroptera*

First authors considering mayflies as a well defined insect group classified *Ephemeroptera* as a part of the *Neuroptera*-like insect groups based mainly on wing venation similarities and some aspects of their biology. Although these groups are clearly unrelated, similar opinions survived even up to the beginning of our century. Some authors placed mayflies into a mostly unnatural group of insects called *Pseudoneuroptera*. For a list of the names applied to mayflies by earlier authors see "Higher classification of the *Ephemeroptera*" (p.85).

The first serious attempt to classify the order *Ephemeroptera* was made by Eaton (1883-1888). Before this classification, earlier authors had classified mayflies into a single family. Eaton´s classification divides the only family *Ephemeridae* into three groups containing 9 series and 14 sections.Some sections are divided into subsections.Groups and sections are arranged as follows: Group I: Section 1 - *Palingenia*, Section 2 - *Ephoron* (as *Polymitarcys*), Section 3 - *Ephemera*. Group II: Section 4 - *Potamanthus*, Section 5 - *Leptophlebia*, Section 6 - *Ephemerella*, Section 7 - *Caenis*, Section 8 - *Prosopistoma*, Section 9 - *Baetis*. Group III: Section 10 - *Siphlonurus* (as *Siphlurus*),Section 11 - *Baetisca* (adult), Section 12 - reserved for still unnamed larva of the genus *Baetisca*, Section 13 - *Atopopus*, Section 14 - *Ecdyonurus* (as *Ecdyurus*).

Eaton´s sections actually represent a very progressive step in the higher classification of mayflies. The sections mostly reflect even phylogenetic relationships between individual families as defined today. Some of them were later used to define families in the modern sense (e.g. Section 10 - *Siphlonuridae*, Section 14 - *Heptageniidae*, and others) or even superfamilies (e.g. Group I resembles in many respects the superfamily *Ephemeroidea*) and this classification served as a basis for following systems. On the other hand, there is a very extensive grouping in other sections, e.g. Section 1 - *Palingenia* includes subsection B - *Oligoneuriella* (as *Oligoneuria*) and Section 11 and 12 refer to different stages of species of the same genus.

Banks (1900) classified the mayflies in the single family *Ephemeridae* into seven tribes: *Baetiscini*, *Polymitarcini*, *Leptophlebini*, *Siphlurini*, *Ephemerini*, *Baetini*, and *Caenini*. These tribes mostly agree with modern families but they also resemble Eaton´s sections. The tribe *Poly-*

Tab. I

Comparison of higher classification of the order *Ephemeroptera* by Ulmer (1920), Handlirsch (1925) (only extant taxons included here), and Needham et al. (1935)

Ulmer (1920)		Handlirsch (1926)		Needham et al. (1935)	
suborder:	*Ephemeroidea*	family :	*Ephemeridae*	family :	*Ephemeridae*
family:	*Palingeniidae*	subfamily:	*Siphlurinae*	subfamily:	*Palingeniinae*
	Polymitarcyidae	tribe:	*Siphlurini*		*Ephoroninae*
	Ephemeridae		*Ametropodini*		*Ephemerinae*
	Potamanthidae		*Ecdyurini*		*Potamanthinae*
suborder:	*Baetoidea*	subfamily:	*Baetiscinae*		*Campsurinae*
family:	*Leptophlebiidae*		*Prosopistomatinae*		*Neoephemerinae*
	Ephemerellidae		*Baetidinae*	family :	*Heptageniidae*
	Caenidae		*Caenidinae*	subfamily:	*Heptageniinae*
	Baetidae		*Leptophlebiinae*	family :	*Baetidae*
	Oligoneuriidae	tribe:	*Ephemerellini*	subfamily:	*Oligoneurinae*
	Prosopistomatidae		*Leptophlebiini*		*Ametropinae*
suborder:	*Heptagenioidea*	subfamily:	*Ephemerinae*		*Metretopinae*
family	*Baetiscidae*	tribe:	*Ephemerini*		*Siphlonurinae*
	Siphlonuridae		*Potamanthini*		*Baetiscinae*
	Ametropodidae		*Polymitarcini*		*Ephemerellinae*
	Ecdyonuridae	subfamily:	*Oligoneuriinae*		*Caeninae*
					Baetinae
					Prosopistomatinae

mitarcini includes nearly the whole recent superfamily *Ephemeroidea*, the tribes *Leptophlebini* and *Siphlurini* are approximately identical with the *Leptophlebiidae* and *Siphlonuridae* as defined today.

Needham 1901 divided the former family *Ephemeridae* (in Banks´ sense) into three families (*Ephemeridae*, *Heptageniidae* and *Baetidae*). This classification became widely used in North America and have appeared in several textbooks or respective chapters of some compendia.Needham et al. (1935) undertook this classification (Tab. I) practically without any changes although relatively progressive systems by Klapálek (1909), Ulmer (1920) and Schoenemund (1930) were available. The family *Heptageniidae*, first defined in Needham´s classification represents a natural group as does the family *Ephemeridae*, except for the *Neoephemerinae* (closely related to the *Caenidae*) classified here in the family *Ephemeridae* while the subfamily *Caeninae* falls into *Baetidae*. The last group, family *Baetidae*, is a collection of remaining genera, although most of its subfamilies agree with families as considered recently.

Berner (1950) used the unmodified system of Needham et al. (1935) when publishing a monograph on the mayflies of Florida. Some aspects of this classification are reflected also in the system by Burks (1953). He presented 11 families of recent mayflies. Of these, the family *Ephemeridae* includes al groups of later superfamily *Ephemeroidea* and the family *Baetidae* contains also *Siphlonuridae* and *Isonychiinae* (as subfamilies).

Klapálek (1909) outlined the basic classification of recent mayflies into 10 families: *Palingeniidae*, *Polymitarcyidae*,*Ephemeridae*, *Potamanthidae*, *Leptophlebiidae*, *Ephemerellidae*, *Caenidae*, *Baetidae*, *Siphluridae*, *Ecdyuridae*. This author first recognized the position of mayflies as an independent insect order and separated this group from former heterogeneous and provisional group called "*Pseudoneuroptera*".

This system,fully accepted in Europe, and approximately corresponding to sections by Eaton reresents a schema used by all later workers in higher classification of the order. Only four European genera were misplaced or missing in this classification - *Ametropus*, *Metretopus*,*Oligoneuriella*,and *Prosopistoma*. *Oligoneuriella* (as *Oligoneuria*) were classified in *Palingeniidae*,*Isonychia* (as *Chirotonetes*) in *Siphluridae*. Respective families were established during the following ten years (*Ametropodidae*, *Oligoneuriidae* and *Prosopistomatidae*) although the family *Ametropodidae* (Bengtsson, 1913) originally contained diverse genera.

Schoenemund (1930) constructed his classification mainly on the system of Klapálek, not accepting suborders as established by Ulmer (1920) (see Tab. I). These suborder (in fact only major family groups or superfamilies) are clearly paraphyletic in origin, with the exception of the first suborder *Ephemeroidea* resembling the recently accepted superfamily. The remaining suborders *Baetoidea* and *Heptagenioidea* contain a mixture of the recently established suborders *Schistonota* and *Pannota*. For instance,the closely related families *Prosopistomatidae* and *Baetiscidae* (first established in this classification) were classified in different suborders.

Also the systems by Lamėere (1917) and Lestage (1917) brought certain confusion into classification of European families. On the basis of detailed study of larvae of most European genera Lestage (1917) reduced the number of families to five: *Ephemeridae, Heptageniidae, Baetidae, Oligoneuriidae*, and *Prosopistomatidae*. Lamėere (1917) established nine tribes into five subfamilies and only two recent families. In this classification, some influence of Needham´s (1901) opinion is recognizable but the tribes themself are mostly less inclusive than those by Banks (1900). Lamėere (1917) first included fossil genera into higher classification of mayflies and correctly recognized the proper taxonomic value of many extinct taxa (*Prothemeroptera, Hexagenitidae*).

Spieth (1933) recognized that the present systems did not satisfactorily reflect the phylogenetic relationships of major stem-groups. In his classification (only North American species considered), he redefined former superfamilies as follows: superfamily *Siphlonuroidea* including *Siphlonuriidae, Baetidae* and *Heptageniidae*, superfamily *Ephemeroidea* including *Ephemeridae, Leptophlebiidae* and *Ephemerellidae* and superfamilies *Caenoidea* and *Baetiscoidea* including the families *Caenidae* and *Baetiscidae* respectively.

Handlirsch (1925) using the results of study of very extensive fossil material (Handlirsch, 1906-1908) established the superorder *Ephemeroidea* to include the order *Protephemeroidea* (Carboniferous) and the order *Ephemerida* (recent and fossil forms from Permian period). The latter order including only the recent family *Ephemeridae* is divided into 8 subfamilies which contain 9 tribes (Tab. I). Most of these subfamilies are very inclusive evolutionarily related genera. For instance, the subfamily *Siphlurinae* resembles the superfamily *Siphlonuroidea* as now accepted by many authors and the subfamily *Ephemerinae* is identical with the superfamily *Ephemeroidea*. Handlirsch´s subfamily *Leptophlebiidae* combines primitive *Pannota* (Ephemerellidae) with advanced *Schistonota* (*Leptophlebiidae*).

While at the beginning of our century only approximately 50 genera of mayflies were known in the world fauna, (Ulmer´s (1933) key includes 115 genera, some of them later not accepted). This number has increased nearly three or four times by 1950. Several new families (*Behningiidae, Euthyplociidae* and *Tricorythidae*) have been established. It became clear that the need of a new modern classification was urgent and that this classification had to include genera from all the biogeographic regions. Based on study of extensive material Edmunds & Traver (1954) proposed a new higher classification of mayflies (Tab. II) consisting of 5 superfamilies and 19 families. This system excludes the genera *Isonychia, Coloburiscus, Coloburiscoides,* and *Murphyella* into a separate family *Isonychiidae,*based mainly on some common larval characters. The family *Neoephemeridae* is accepted in the original sense of Burks (1953) as well as the family *Ametropodidae,* here considered to include two subfamilies *Ametropodinae* and *Metretopodinae.* Lestage´s (1938) subfamily *Siphloplectoninae* is correctly fused with the *Metretopodidae* established by Needham et al. (1935) (as *Metretopinae*). Edmunds & Traver (1954) first defined the phylogenetic relationships of the following groups establishing them as subfamilies: *Oniscigastrinae* (*Siphlonuridae*), *Pseudironinae* (*Heptageniidae*), *Leptohyphinae* and *Dicercomyzinae* (*Tricorythidae*), *Astenopodinae* (*Polymitarcyidae*). Of the four superfamilies in this classification, three undoubtedly represent natural groups. The superfamily *Ephemeroidea* is nearly identical with one of the Ulmer´s (1920) suborders. The superfamily *Leptophlebioidea,* although homogeneous from the developmental point of view, actually includes families from both suborders *Schistonota* and *Pannota* as presently defined (McCafferty & Edmunds, 1979).

Demoulin (1958) presented a classification which included all known fossil taxa. With the exception of the extinct family *Triplosobidae* (one Carboniferous species included in the suborder *Protephemeroptera*) all known fossil and recent taxa were classified in suborder *Plectoptera* (Tab. II). The recent families were all identical with those outlined by Edmunds & Traver (1954) except for the newly established monotypic family *Ichthybotidae* (1 genus in New Zealand) which was originally included in the *Ephemeridae.* Later authors do not accept this family. Fossil taxa are included either in separate families of extinct (*Protereismatidae, Misthodotidae, Eudoteridae*) and recent (*Mesephemeridae,Paedephemeridae*) superfamilies or recent families (mostly terciary genera). Of the six superfamilies established by Demoulin (1958) no superfamily is identical with those of Edmunds & Traver (1954).The superfamily *Ephemeroidea* is divided into two superfamilies of which newly established *Palingenioidea* includes *Behningiidae* and *Palingeniidae.* Later (Demoulin, 1961) also the families *Euthyplociidae* and *Polymitarcyidae* were also included in the *Palingenioidea.* The families *Isonychiidae* and *Ametropodidae* were accepted in the original sense of Edmunds & Traver (1954). Demoulin´s (1958) system is based mainly on adult characters since the larvae of fossil forms are mostly unknown.

Tab. II
Comparison of higher classification of the order *Ephemeroptera* by Edmunds & Traver (1954) (only recent taxons included), Demoulin (1958) and Tshernova (1970) (extinct taxons marked +)

Edmunds & Traver (1954)		Demoulin (1958)		Tshernova (1970)	
superfamily	*Heptagenioidea*	suborder	*Protephemeroptera*	suborder	*Protephemeroptera*
family	*Siphlonuridae*	superfamily	*Triplosoboidea*	superfamily	*Triplosoboidea*
subfamily	*Siphlonurinae*	+ family	*Triplosobidae*	+ family	*Triplosobidae*
	Oniscigastrinae	suborder	*Plectoptera*	suborder	*Plectoptera*
family	*Isonychiidae*	superfamily	*Protereismatoidea*	superfamily	*Protereismatoidea*
	Oligoneuriidae	+ family	*Protereismatidae*	+ family	*Protereismatidae*
subfamily	*Pseudoligoneuriinae*		*Misthodotidae*		*Misthodotidae*
	Oligoneuriinae		*Eudoteridae*		*Eudoteridae*
family	*Heptageniidae*	superfamily	*Palingenioidea*	superfamily	*Mesephemeroidea*
subfamily	*Heptageniinae*	+ family	*Mesephemeridae*	+ family	*Mesephemeridae*
	Pseudironinae	family	*Palingeniidae*	superfamily	*Hexagenitoidea*
family	*Ametropodidae*		*Behningiidae*	+ family	*Aenigmephemeridae*
subfamily	*Ametropodinae*	superfamily	*Ephemeroidea*		*Hexagenitidae*
	Metretopodinae	family	*Ichthybotidae*	superfamily	*Ephemeroidea*
family	*Baetidae*		*Potamanthidae*	family	*Potamanthidae*
superfamily	*Leptophlebioidea*		*Euthyplociidae*		*Ephemeridae*
family	*Leptophlebiidae*		*Polymitarcidae*		*Ichtybotidae*
	Ephemerellidae		*Ephemeridae*		*Euthyplociidae*
	Tricorythidae		*Neoephemeridae*		*Polymitarcyidae*
subfamily	*Tricorythinae*	superfamily	*Siphlonuroidea*		*Palingeniidae*
	Leptohyphinae	family	*Siphlonuridae*		*Behningiidae*
	Dicercomyzinae		*Baetidae*	superfamily	*Heptagenioidea*
superfamily	*Caenoidea*	superfamily	*Oligoneurioidea*	+ family	*Epeoromimidae*
family	*Caenidae*	family	*Isonychiidae*	family	*Heptageniidae*
	Neoephemeridae	+ family	*Hexagenitidae*	superfamily	*Siphlonurioidea*

Tab. II. (continued)

superfamily : *Ephemeroidea*
family : *Behningiidae*
Potamanthidae
Euthyplociidae
Ephemeridae
Polymitarcyidae
subfamily: *Polymitarcyinae*
Campsurinae
subfamily: *Asthenopodinae*
family : *Palingenidae*
superfamily : *Prosopistomatoidea*
family : *Prosopistomatidae*

family : *Oligoneuriidae*
Baetiscidae
superfamily: *Heptagenioidea*
family : *Ametropodidae*
Heptageniidae
Leptophlebiidae
superfamily: *Ephemerelloidea*
family : *Ephemerellidae*
family : *Tricorythidae*
Prosopistomatidae
Caenidae

family : *Metretopodidae*
Ametropodidae
Leptophlebiidae
Isonychiidae
Siphlonuridae
Baetidae
Siphlaenigmatidae
superfamily: *Oligoneurioidea*
\+ family : *Mesonetidae*
family : *Chromarcyidae*
Oligoneuriidae
superfamily: *Ephemerelloidea*
family : *Baetiscidae*
Tricorythidae
Ephemerellidae
superfamily: *Neoephemeroidea*
family : *Neoephemeridae*
superfamily: *Caenoidea*
family : *Prosopistomatidae*
Caenidae

Edmund (1962), when discussing the general principles of the higher classification of mayflies,presented a diagram of the probable phylogeny of the families.The grouping of families according to phyletic relationships corresponds to that of his earlier system (Edmunds & Traver,1954), except for the *Isonychiidae* being a subfamily of the *Siphlonuridae*. In this paper the family level is defined as follows: "For application of the family level of the hierarchy, I have chosen a level in which the gaps within the family are small enough so that the relationships are readily evident, but the gaps between families are so large that the relationships can be discerned only by detailed study."

When keying the families of the *Ephemeroptera* according to larvae Edmunds et al. (1963) published a reworked system based mainly on larval characters.The most important changes were made within the *Siphlonuridae* (*Acanthametropodinae* and *Coloburiscinae* were newly established). This system also includes some recently discovered taxa - *Siphlaenigmatidae, Ephemerythinae* and *Machadorythinae*. Taking into account both fossil records and historical biogeography this system is later discussed in detail from the phylogenetic point of view by Edmunds (1972).

Tshernova (1970) presented a higher classification of extinct and recent mayflies based on two suborders, 11 superfamilies and 32 families (Tab. II). Classification of the fossil taxa mostly corresponds to that of Demoulin (1958), the families *Aenigmepheridae, Hexagenitidae, Epeoromimidae,* and *Mesonetidae* were newly established, based on detailed study of fossil material from the Palaearctic region. Suborders fully corresponded to those of Demoulin (1958). With the exception of the superfamily *Ephemeroidea* corresponding to that of earlier systems, all remaining superfamilies were newly established resembling neither those of Edmunds & Traver (1954) nor those of Demoulin (1958). The families *Isonychidae* and *Ichthybotidae* were fully accepted here, and the subfamilies *Chomarcyinae, Ametropodinae* and *Metretopodinae* were presented as families.

A slightly modified Tshernova´s classification was published in the extensive study of fossil insects (Tshernova,1980). Two suborders, *Ephemerida* and *Triplosobina* (one extinct species) were accepted and relationships of the extinct families *Eudoteridae, Misthodotidae, Mesoplectopteridae, Jarmiliidae, Kukaloviidae, Protereismatidae, Mesephemeridae, Epeoromimidae, Hexagenitidae* and *Aenigmepheridae* were discussed in a hypothetical phylogenetic diagram. In this paper, offering a quite new reclassification of insects, the order *Ephemeroptera* is included in the cohort *Ephemeropteriformes* Latreille and in the infraclass *Scarabaeones* Laicharting.

Landa (1969a) divided the order into 4 superfamilies and 20 families. This classification is based mostly on detailed study of the larval tracheal system. The families *Arthropleidae* and *Isonychiidae* accepted here mostly corresponded to subfamilies in the earlier system. Superfamilies are,except for the *Ephemeroidea*,different again.The superfamilies *Siphlonuroidea* and *Heptagenioidea* corresponded to *Siphlonuroidea* by Edmunds & Traver (1954) and the superfamily *Leptophlebioidea* corresponded to *Leptophlebioidea*,*Caenoidea* and *Prosopistomatoidea* of the latter authors. As Landa (1969b, 1973) pointed out the superfamilies, owing to chaotic application of names in earlier systems, would be considered rather as provisional than strictly taxonomic categories. Taking into account the anatomical arrangement of internal organs and their anagenesis, Landa (1973) presented the *Coloburiscinae*, *Ameletopsinae*, *Oniscigastrinae*, *Rallidentinae* and *Leptohyphinae* as separate and well defined families.

Riek (1973) published a classification based on study of external morphological characters of both the larvae and adults. This classification based primarily on larval gills, body form, development of hairs on the caudal filaments and adult wing venation included all recent taxa except of *Polymitarcyidae*, *Euthyplociidae*, *Potamanthidae* and *Palingeniidae*. In comparison with systems by Edmunds et al. (1963), Demoulin (1958) and Tshernova (1970) there were some considerable changes in the Riek system (Tab. III). Within the *Siphlonuridae*, the subfamily *Neameletinae* having certain relationships to the *Rallidentinae* was newly established, the subfamilies *Coloburiscinae* and *Isonychinae* were transferred into the *Oligoneuriidae* and the subfamilies *Ametropodinae*, *Metretopodinae* and *Pseudironinae* (formerly *Ametropodidae* and *Heptageniidae*) were incorporated into the *Siphlonuridae*. The family *Baetidae* consisted of three subfamilies (*Baetinae*, *Callibaetinae*, and *Siphlaenigmatinae*). The superfamilies roughly corresponded to those by Edmunds & Traver (1954).

The most recent suggestion concerning the higher classification of mayflies was published by McCafferty & Edmunds (1979). They divided the recent *Ephemeroptera* into two suborders according to the arrangement of the larval mesonotum,wing pads and several other characters.The suborder *Schistonota* (3 superfamilies) is characterized by larvae with free wing pads and unspecialized gills, while the larvae of *Pannota* (3 superfamilies) show conspicuous notal fusion and specialization of gill pairs. They also noted imaginal characters distinguishing these suborders,too. Based on the study of *Ephemeroptera* lineages from siphlonurid ancestors, some of the former superfamilies are reclassified. The superfamily *Leptophlebioinea* now contains only the *Leptophlebiidae* while

Tab. III

Comparison of higher classification of the order *Ephemeroptera* by Landa (1969), Riek (1973) and McCafferty & Edmunds (1979) (only extant taxons classified)

Landa (1969)		Riek (1973)		McCafferty & Edmunds (1979)	
				suborder:	*Schistonota*
superfamily:	*Siphlonuroidea*	superfamily:	*Ephemeroidea*	superfamily:	*Baetoidea*
family:	*Siphlonuridae*	family:	*Behningiidae*	family:	*Siphlonuridae*
	Baetidae		*Ephemeridae*	subfamily:	*Oniscigastrinae*
	Ametropodidae	superfamily:	*Prosopistomatoidea*		*Ameletopsinae*
superfamily:	*Heptagenioidea*	family:	*Baetiscidae*		*Siphlonurinae*
family:	*Oligoneuriidae*		*Prosopistomatidae*		*Rallidentinae*
	Isonychiidae	superfamily:	*Caenoidea*		*Acanthametropodinae*
	Arthropleidae	family:	*Neoephemeridae*	family:	*Ametropodidae*
	Heptageniidae		*Caenidae*		*Baetidae*
superfamily:	*Leptophlebioidea*	superfamily:	*Baetoidea*	subfamily:	*Siphlaenigmatinae*
	Ephemerellidae	family:	*Siphlonuridae*		*Baetinae*
	Tricorythidae	subfamily:	*Oniscigastrinae*	family:	*Metretopodidae*
	Neoephemeridae		*Rallidentinae*		*Oligoneuriidae*
	Caenidae		*Nesameletinae*	subfamily:	*Isonychiinae*
	Baetiscidae		*Siphlonurinae*		*Chromarcyinae*
	Prosopistomatidae		*Metretopodinae*		*Coloburiscinae*
	Leptophlebiidae		*Acanthametropodinae*		*Oligoneuriinae*
superfamily:	*Ephemeroidea*		*Ametropodinae*	family:	*Heptageniidae*
family:	*Behningiidae*		*Pseudironinae*	subfamily:	*Arthropleinae*
	Palingeniidae	family:	*Baetidae*		*Pseudironinae*
	Polymitarcyidae	subfamily:	*Callibaetinae*		*Heptageniinae*
	Ethyplociidae		*Baetinae*		*Anepeorinae*
	Ephemeridae		*Siphlaenigmatinae*		*Spinadinae*
	Potamanthidae	family:	*Ameletopsidae*	superfamily:	*Leptophlebioidea*

Tab. III (continued)

subfamily:	*Ameletopsinae*
family:	*Oligoneuriidae*
subfamily:	*Oligoneuriinae*
	Chromarcyinae
	Isonychiinae
	Coloburiscinae
superfamily:	*Heptagenioidea*
family:	*Heptageniidae*
superfamily:	*Leptophlebioidea*
family:	*Leptophlebiidae*
	Ephemerellidae
	Tricorythidae
family:	*Leptophlebiidae*
superfamily:	*Ephemeroidea*
family:	*Behningiidae*
	Potamanthidae
	Euthyplociidae
	Polymitarcyidae
subfamily:	*Polymitarcyinae*
	Campsurinae
	Asthenopodinae
family:	*Ephemeridae*
	Palingeniidae
subfamily:	*Pentageniinae*
	Palingeniinae
suborder:	*Pannota*
superfamily:	*Ephemerelloidea*
family:	*Ephemerellidae*
subfamily:	*Teloganodinae*
	Ephemerellinae
	Melanemerellinae
family:	*Tricorythidae*
subfamily:	*Leptohyphinae*
	Ephemerythinae
	Tricorythinae
	Dicercomyzinae
	Machadorythinae
superfamily:	*Caenoidea*
family:	*Neoephemeridae*
	Caenidae
superfamily:	*Prosopistomatoidea*
family:	*Baetiscidae*
	Prosopistomatidae

Tab. IV

Higher classification of the order *Ephemeroptera* accepted in the present monograph (extinct taxons marked +)

suborder:	*Protephemeroptera*
superfamily:	*Triplosoboidea*
+family:	*Triplosobidae*
suborder:	*Schistonota*
superfamily:	*Protereismatoidea*
+family:	*Misthodotidae*
	Protereismatidae
	Jarmilidae
	Oboriphlebiidae
	Mesoplectopteridae
superfamily:	*Mesephemeroidea*
family:	Mesephemeridae
superfamily:	Litophlebioidea
+family:	*Litophlebiidae*
superfamily:	*Baetoidea*
family:	*Siphlonuridae*
subfamily:	*Siphlonurinae*
	Acanthametropodinae
	Metretopodinae
	Pseudironinae
	Rallidentinae
superfamily:	*Ephemeroidea*
family:	*Behningiidae*
	Potamanthidae
	Euthyplociidae
subfamily:	*Euthyplociinae*
	Exeuthyplociinae
family:	*Polymitarcyidae*
subfamily:	*Polymitarcyinae*
	Campsurinae
	Asthenopodinae
family:	*Ephemeridae*
	Palingeniidae
superfamily:	*Hexagenitoidea*
+family:	*Hexagenitidae*
	Aenigmephemeridae
	Aphelophlebodidae
suborder:	Pannota
superfamily:	*Ephemerelloidea*

Tab. IV. (continued)

family: *Baetidae*
subfamily: *Siphlaenigmatidae*
Baetinae
Cloeoninae
family: *Oniscigastridae*
Ameletopsidae
Ameletopsinae
Chiloporterinae
family: *Ametropodidae*
superfamily: *Heptagenioidea*
+family: *Epeoromimidae*
family: *Oligoneuriidae*
subfamily: *Isonychiinae*
Colcburiscinae
Chromarcyinae
Oligoneuriinae
family: *Heptageniidae*
Arthropleinae
Heptageniinae
Anepeorinae
Spinadinae

superfamily: *Leptophlebioidea*
family: *Leptophlebiidae*
+subfamily: *Mesonetinae*
subfamily: *Leptophlebiinae*
Atalophlebiinae

family: *Ephemerellidae*
subfamily: *Teloganodinae*
Ephemerellinae
Melanemerellinae
family: *Leptohyphidae*
subfamily: *Leptohyphinae*
Dicercomyzinae
family: *Tricorythidae*
subfamily: *Tricorythinae*
Machadorythinae
Ephemerythinae
superfamily: *Caenoidea*
family: *Neoephemeridae*
Baetiscidae
Caenidae
Prosopistomatidae

the *Ephemerellidae* and *Tricorythidae* are contained in newly constituted superfamily *Ephemerelloidea* in the *Pannota.*Based on previously suggested rules (McCafferty & Edmunds, 1976) concerning the position of evolutionary intermediate lineages (such lineages would be associated with derived ones), some of Riek's (1973) conclusions were accepted: the positions of *Coloburiscinae, Isonychiinae* and *Siphlaenigmatinae* in the *Oligoneuriidae* and *Baetidae*. Because of insufficient knowledge of their larvae, the fossil taxa are not included in this classification. It was supposed that most of them would fall into the two suborders. In order to classify both fossil and recent mayfly forms we incorporated, mostly on published literary data basis, also fossil taxons in our classification (see Tab. IV). This classification is accepted also in descriptions of individual organ systems anagenesis.

Material and methods

During the past 30 years we have dissected larvae of the following genera (subgenera) and families (for authors of genera see p.85-107, for species dissected and localities see Landa, 1969b; Landa et al., 1980; Soldán, 1981):

Siphlonuridae: Ameletoides, Ameletus, Metamonius, Metreletus, Nesameletus, Parameletus, Siphlonurus, Metretopus, Siphloplecton, Rallidens, Acanthametropus, Analetris, Pseudiron.

Ametropodidae: Ametropus.

Oniscigastridae:Oniscigaster, Siphlonella, Tasmanophlebia.

Ameletopsidae:Ameletopsis, Mirawara, Chaquihua, Chiloporter.

Baetidae:Afrobaetodes, Baetiella, Baetis, Baetodes, Baetopus, Callibaetis, Centroptiloides, Centroptilum, Cloeodes, Cloeon,Dactylobaetis, Heterocloeon, Nesoptiloides, Procloeon, Pseudocloeon, undescribed genus A of Edmunds (New Guinea), undescribed genus B of Edmunds (New Guinea).

Oligoneuriidae:Isonychia, Coloburiscus, Coloburiscoides, Murphyella, Chromarcys, Elassoneuria, Macedoneuria, Homoeoneuria, Lachlania,Oligoneuriella, Oligoneurisca, Oligoneuriopsis, Spaniophlebia.

Heptageniidae: Arthroplea, Anepeorus, Afronurus, Cinygma Cinygmula, Cinygmina, Compsoneuriella, Ecdyonurus, Epeorus, Iron, Ironopsis, Ironodes, Heptagenia, Rhithrogena, Stenonema, Stenacron, Thalerosphyrus.

Leptophlebiidae: Adenophlebia, Adenophlebiodes, Aprionyx, Askola, Atalomicria, Atalonella, Atalophlebia, Atalophlebioides, Austroclima,Borinquena, Castanophlebia, Celephlebia, Choroterpes, C. (Euthraulus), C. (Neochoroterpes), Choroterpides, Dactylophlebia,Deleatidium, Demoulinellus, Farrodes, Habroleptoides, Habrophlebia, Habrophlebiodes, Hagenulodes, Hagenulus, Hagenulopsis, Hapsiphlebia, Hermanella, Homothraulus, Indialis, Isca, (Minyphlebia), Jappa, Kimminsula, Kirrara, Lepeorus, Leptophlebia, Massartella, Massartellopsis, Megaglena, Meridialaris, Miroculis, Paraleptophlebia, Penaphlebia, Petersophlebia, Polythelais,Terpides, Thraulodes, Thraulus, Traverella, Tenagophila, Ulmeritus, Ulmerophlebia, Zephlebia, Neozephlebia.

Behningiidae:Behningia, Dolania.

Potamanthidae:Potamanthodes, Potamanthus, Rhoenanthus.

Euthyplociidae:Campylocia, Euthyplocia, Afroplocia.

Ephemeridae: Ephemera, Dicremera, Eatonigenia, Hexagenia, Ichthybotus, Litobrancha.

Polymitarcyidae, Ephoron, Campsurus, Tortopus, Asthenopus, Povilla.

Palingeniidae:Pentagenia, Anagenesia, Palingenia.

Ephemerellidae:Attenella, Dannella, Drunella, Eatonella, Tribrochella, Caudatella, Cincticostella, Crinitella, Ephemerella, Eurylophella, Serratella, Torleya, Timpanoga, Teloganopsis, Ephemerellina, Teloganodes.

Tricorythidae:Tricorythus, Neurocaenis,Ephemerythus, Dicercomyzon, Leptohyphes, Leptohyphodes, Tricorythodes.

Neoephemeridae:Neoephemera, Neoephemerophis, Potamanthellus.

Caenidae:Austrocaenis, Brachycercus, Cercobrachys, Caenis, Caenomedea, Pseudocaenis, Tasmanocoenis.

Baetiscidae: Baetisca.

Prosopistomatidae: Prosopistoma.

Older larvae, i.e. those with fully developed larval characters (from about 10th instar to the last instar) were studied. The material studied was fixed with Carnoy, Bouin, AGA fixation (alcohol, glycerin, acetic acid) or alcohol-formalin fixation. Preferably fresh material was used for study of the tracheal system. Larvae were dissected on a Petri dish of paraffin stained with some contrast staining (Sudan III and others). They were opened mostly dorsally (species with gonads in dorsal position laterally) and edges were pinned with minutiae. Internal organs were loosened with a thin trickle of water. Pringle physiological saline or alcohol. Permanent mounts were prepared by transferring individual organs or their important parts directly into Canada balsam with Cellosolve (ethylenglycolmonoethylether). Preparations were observed under interference phase microscope,after staining light green. Clearing of subjects by glycerine was used before the study of the tracheal system. The methods with injection of some substances into the tracheal system by a vacuum pump (paraffin,asphalt - Lehman, Berlin blue - Tichomirov, olive oil with Sudan III - Gaebler) were not useful in this tracheal system study. The tracheal system is closed by gills preventing the injection and after gill removial the distal parts of the tracheae are mostly collapsed with closely adjacent walls. Injected solutions are not able to penetrate this collapsed portions. In some cases, the tracheization of the thorax and abdomen was studied by means of old intima before moulting of larva. Old intima can be easily pulled out after removing of tracheal gills through the places of future imaginal spiracles. Otherwise the fresh larvae were kept in warm water (30-40 °C) before dissection in order to disintegrated other internal organs. Injection of pepsin were also used.

Arrangement and anagenesis of organ systems studied

The results of anatomical examinations of larvae of individual families and subfamilies of the order are presented in this chapter.

Ventral nerve cord

The central nervous system of the *Ephemeroptera* consists of the following parts: brain (supraoesophageal ganglion), suboesophageal ganglion, 3 thoracic ganglia and 7-8 distinct abdominal ganglia. Brain cylindrical, situated between alimentary canal (pharynx) and dorsal or fore head integument (frons). All brain parts (proto-,deuto-, and tritocerebrum) completely fused but sometimes distinguishable or distinguishable only by means of nerve bases. Brain never fuses with other parts of central nerve system,circumoesophageal connective stout, situated around pharynx or oesophagus if pharynx not differentiated. Comparative anatomy of brain nerves and associated ganglia (frontal ganglion, suboesophageal ganglion, corpora allata etc.) unknown because of complicated dissection and need of fresh material. Preliminary results promise to provide us with very valuable data (cf. Arvy & Gabe,1952).Brain itself is relatively uniform within the mayflies - elongated with stout optical lobes, lobes of ocelli usually cylindrical or ocelli directly connected with brain. The shape of brain (as well as the arrangement of brain nerves as seen in some European genera) roughly follows the shape and position (pro- or hypognathous) of head.

Suboesophageal ganglion usually rectangular, situated between head or thorax (cervical region) or in head, below alimentary canal. It is mostly separated although the connectives between suboesophageal and prothoracic ganglion can be indistinguishable (e.g. *Dolania* - Soldán, 1979 and others).Connectives are nearly indistinguishable in *Prosopistomatidae* and *Baetiscidae* (Fig. IV/23,24).

Except for the latter two families, thoracic ganglia (pro-, meso- and metathoracic) are mostly well separated and equal in shape. Only metathoracic ganglion in fact represents a true ganglionic center (cf.

Bazyukina & Brodsky,1975) being composed of metathoracic ganglion itself and first abdominal ganglion in most recent mayflies. The metathoracic ganglion can be different in shape from pro- and mesothoracic ganglia. Three pairs of nerves emerge from pro- and mesothoracic ganglion, second (hind) pair branched near the base. Metathoracic ganglion with three pairs of nerves emerging from the anterior portion and with two other pairs of nerves from posterior portion (one of them are nerves of original first abdominal ganglion).

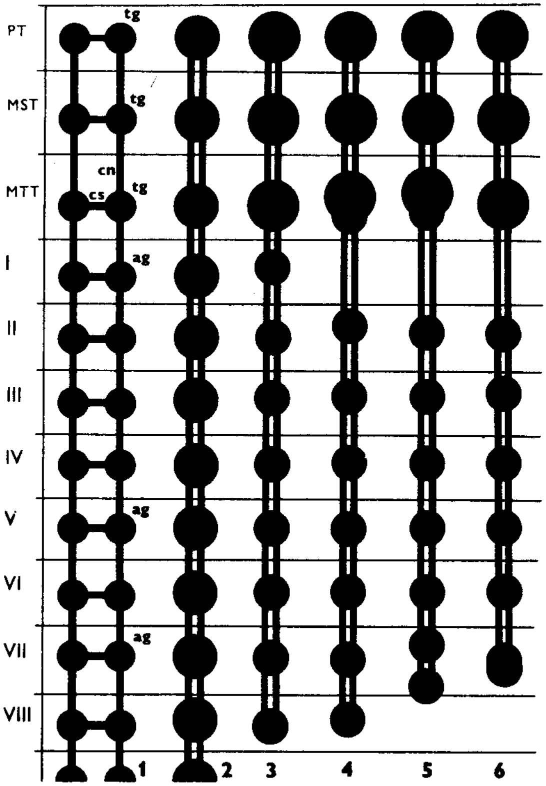

Fig. I. Comparative anatomy of ventral nerve cord of mayflies. 1 - hypothetical insect ancestor. 2 - hypothetical mayfly ancestor. 3 - *Ametropus*. 4 - *Siphlonurus*. 5 - *Tasmanophlebia*. 6 - *Rhoenanthus*. Sketch, relative length of body segments not followed. tg - thoracic ganglion, cn - connectives, cs - comissures, ag - abdominal ganglia, PT - prothorax, MST - mesothorax, MTT - metathorax, I-VIII - abdominal segments.

Of the abdominal ganglia, only the last one is a true ganglionic center (originally two neuromeres); remaining ganglia are simple, usual equal in shape,connected with doubled or fused connectives. If we do not consider the perisympathic nervous system only a single pair of nerve arises from abdominal ganglia (several pairs from last ganglion). No differences between the CNS of larvae and that of subimagoes and adult were found. The ventral nerve cord (thoracic and abdominal ganglia) provide us with valuable data as far as the comparative anatomy of nervous system is concerned. The following characters were investigated:

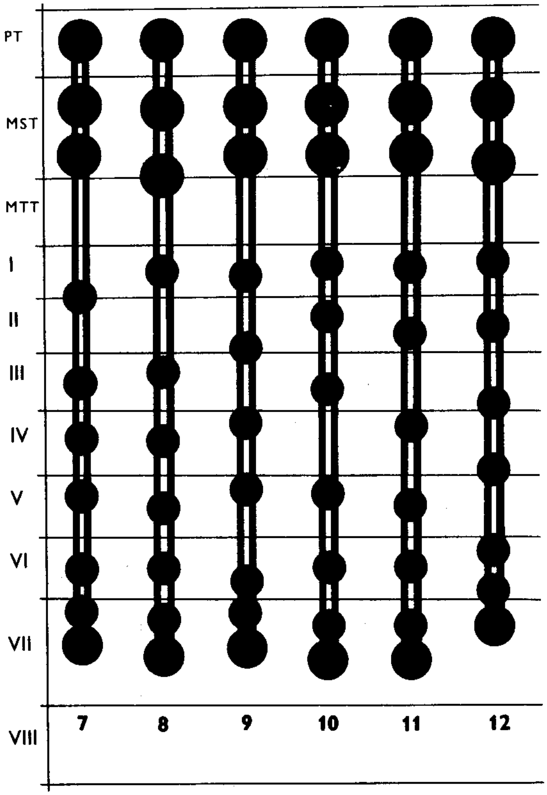

Fig. II. **Comparative anatomy** of ventral nerve cord of mayflies. 7 - *Zephlebia*. 8 - *Timpanoga*. 9 - *Kimminsula*. 10 - *Farrodes*. 11 - *Traverella*. 12 - *Dannella*. For explanations see Fig. I.

(A) position of metathoracic ganglion and relative length of connectives of thoracic ganglia:(Aa) metathoracic ganglion in metathorax (Fig. I/3-6); connectives of thoracic ganglia equal in length - some *Siphlonuridae*, *Oligoneuriinae*, *Ametropodidae*, some *Heptageniidae*, *Ephemeridae*, *Polymitarcyidae*, *Palingeniidae* and others, (Ab) metathoracic ganglion near the anterior margin of metathorax, meta - mesothoracic connectives slightly or apparently shorter than meso - prothoracic connectives. Two subgroups can be distinguished here: Ab_1 - metathoracic ganglion at the anterior margin of metathorax and Ab_2 - metathoracic ganglion between mesothorax and metathorax (Figs II/8,III/18). The group A_6 comprises advanced *Schistonota* (some *Leptophlebiidae* and *Baetidae*) and primitive *Pannota* (some *Ephemerellidae* and *Tricorythidae*); (Ac) metathoracic ganglion in mesothorax,no ganglion in metathorax or all thoracic ganglia fused (some *Baetidae*, some *Leptophlebiidae* and *Ephemerellidae*, *Neoephemeridae*, *Caenidae*, *Prosopistomatidae*, *Baetiscidae*) (Figs II/9-11; IV/19, 20,22).

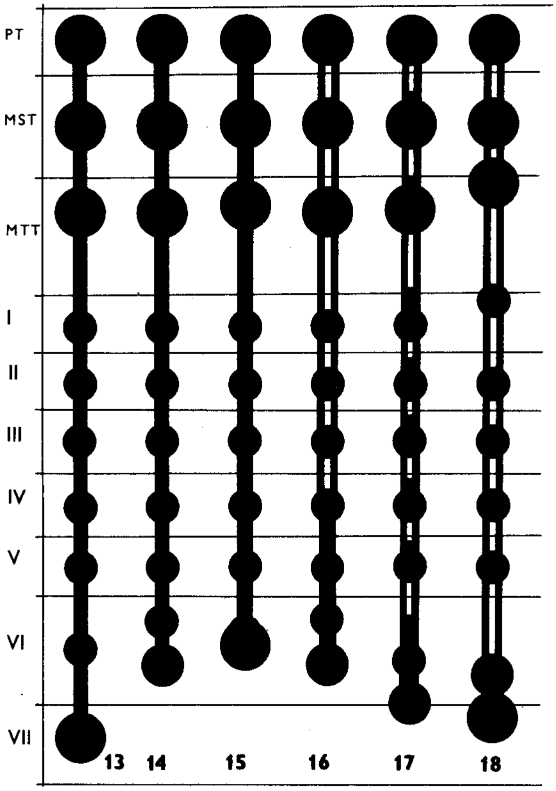

Fig. III. Comparative anatomy of ventral nerve cord of mayflies. 13 - *Rallidens*. 14 - *Coloburiscoides*. 15 - *Baetis*. 16 - *Afronurus*. 17 - *Massartella*. 18 - *Choroterpes* (*Neochoroterpes*).For explanations see Fig. I.

(B) Position of anterior abdominal ganglia (ganglia 1-5 in abdominal segments I-V): (Ba) abdominal ganglion 1 present in I and well developed (*Ametropus*) (Fig. I/3) or connectives in segment I (from metathoracic to abdominal ganglion 2 expanded, forming "ganglion" in some specimens (*Leptophlebiidae: Aprionyx, Jappa, Ulmerophlebia*). (Bb) no ganglion in segment I, connectives from metathoracic to abdominal ganglion 2 not expanded, ganglia 2-5 more or less in respective segments (*Acanthametropodinae, Ameletopsidae,* some *Heptageniidae* and *Leptophlebiidae,Oniscigastridae, Coloburiscinae, Neoephemeridae*) (Fig. I/3-6). (Bc) Abdominal ganglion 2 shifted anteriorly entirely (Bc_2) or partially (Bc_1) into segment 1; ganglia 3-5 situated irregularly in segments III-V (no ganglion either in segment III or IV) - some *Leptophlebiidae, Ephemerellidae, Tricorythidae, Caenidae* (Figs II/7-12, III/13-17).

(C) Arrangement of posterior abdominal ganglionic centres (abdominal ganglia 7 and 8). (Ca) Abdominal ganglia 7 and 8 in respective abdominal segments (VII and VIII) usually partially fused or well separated or ganglion VIII partially shifted anteriorly (between segments VII and VIII) - most *Siphlonuridae,Isonychiinae,* some *Oligoneuriinae,* some *Heptagennidae, Leptophlebiidae* and *Ephemeridae, Polymitarcyinae* (Fig. I/3,4) (Cb) Abdominal ganglia 7 and 8 in segment VII (two ganglia, fused or separated in one segment) - *Baetidae, Ameletopsinae,* some *Leptophlebiidae, Behningiidae, Potamanthidae, Euthyplociidae,* some *Ephemerellidae* (Figs I/6,II/7-12).(Cc) Abdominal ganglia 7 and 8 (mostly entirely fused together and partially or entirely fused with ganglion 6) shifted anteriorly into segment VI - some *Leptophlebiidae* and *Ephemerellidae, Caenidae.* (Fig. III/14-16). (Cd) Ganglia 2-8 not distinguishable, shifted into thorax and entirely fused with thoracic ganglia (*Baetiscidae, Prosopistomatidae*) (Fig. IV/23, 24).

(D) Arrangement of connectives of abdominal ganglia. (Da) Connectives of abdominal ganglia (except 7 and 8) doubled and well separated or contiguous but never fused (*Acanthametropodinae, Ameletopsidae,* some *Heptageniidae* and *Oligoneuriinae,Potamanthidae, Euthyplociidae,* some *Leptophlebiidae,Ephemerellidae, Tricorythidae, Neoephemeridae, Caenidae* (Figs I/3-6,II/7-12). (Db) Some of connectives (mostly those of ganglia 5-6) or all connectives partially fused - some *Leptophlebiidae* (*Massartella, Kirrara, Lepeorus, Kimminsula*) (Fig. III/16, 17). (Dc) All connectives entirely fused, forming a shallow band connecting abdominal ganglia (*Oniscigastridae, Coloburiscinae, Arthropleinae,*some *Heptageniinae,Anepeorinae, Baetidae, Behningia*)(Fig. III/13-15). (Dd) Connectives of both thoracic and abdominal ganglia not distinguishable, entirely fused together with ganglia (*Prosopistomatidae,Baetiscidae*) (Fig. IV/23, 24).

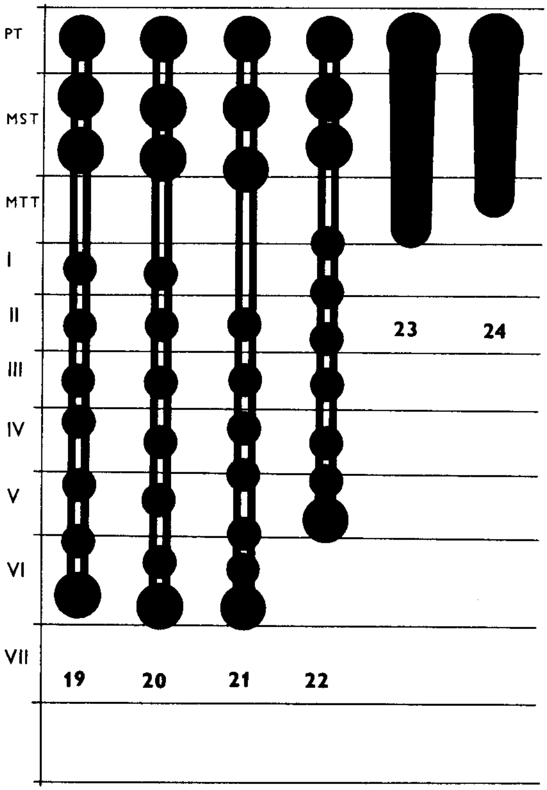

Fig. IV. Comparative anatomy of ventral nerve cord of mayflies. 19 - *Caenis*. 20 - *Dicercomyzon*. 21 - *Miroculis*. 22 - *Hyrtanella*. 23 - *Baetisca*. 24 - *Prosopistoma*. For explanations see Fig. I.

The anagenesis of the ventral nerve cord of mayfly larvae is relatively well understood based on comparative anatomy of recent genera.Nerve cord consisting of three thoracic and 8 abdominal ganglia which are deposited in respective body segments could be easily derived from nerve cord of an insect ancestor (Fig.I/1). It possesses a pair of nerve ganglia in each body segment either well separated and connected by transversal comissures or partially fused. The first step in the central nervous system association is complete fusion of ganglionic pairs in all segments into one ganglion communicating with the preceeding and following one (Fig. I/2). This fusion is phylogenetically very old, separated ganglia in the same segment are not known within recent insects. On the contrary, the connectives are more conservative in their development and remaine doubled in a large number of recent mayflies.Doubled connectives represent an evidence of originally doubled ganglia, one connective belong to one ganglion.

Further association of ventral nerve cord have been achieved by emerging of two ganglionic centers. First center appear in the abdominal segment VIII - a large ganglion actually representing fused 4-5 ganglia of last abdominal segments. This ganglionic center is well apparent in all genera investigated and the number of ganglia contained is not recognizable. This character is synapomorphic within the order. Second ganglionic center is represented by metathoracic ganglion which contains, in all recent genera except for *Ametropus*, first abdominal ganglion. This fusion is easily recognisable according to the inervation of abdominal segment I from metathoracic ganglion. The most primitive arrangement of ventral nerve cord was found in the genus *Ametropus* (*Ametropodidae*): three thoracic and 8 abdominal ganglia in segments I-VIII, connectives doubled. The following major anagenetic trends leading to further association of central nervous system can be recognized:shifting of metathoracic ganglion containing first abdominal ganglion to mesothorax, furher shifting and fusion of last ganglion (ganglionic center) to thorax and fusion of originally separated connectives to form a shallow band.

The shifting of metathoracic ganglion into mesothorax is undoubtedly connected with the reduction of hind wings and the metathorax as a whole. In the genera with well developed hind wings and relatively long metathorax is metathoracic ganglion usually in metathorax (*Ephemeroidea*,most *Siphlonuridae* and *Heptageniidae*). Metathoracic ganglion completely shifted into mesothorax is found in families where reduction or even loss of hind wing pair occur (*Baetidae*, some *Leptophlebiidae* and *Ephemerellidae*, *Caenidae*, *Tricorythidae*). However, as it has been shown by Landa et al. (1980) the shifting of metathoracic ganglion need not be strictly correlated with external degree of metathorax reduction (some genera of the *Leptophlebiidae*). Both meso- and metathoracic ganglia are shifted even into prothorax and fused with remaining abdominal ganglia in highly derived *Prosopistomatidae* and *Baetiscidae* (original ganglia are recognizable only on histological section or by means of emerging nerves).

The tendency to shifting of abdominal ganglia to thorax tending to further association of CNS i well apparent also on position of ganglia 2-5 and last ganglionic center. In more than a half of recent genera abdominal ganglia 2-5 are not deposited in respective segments although there are mostly no characters in external morphology of abdomen indicating this change in the arrangement of ventral nerve cord. Abdominal ganglion 1 is contained (except for *Ametropus*) in metathoracic ganglion. Primitively,no ganglion is in segment I. In some *Leptophlebii-*

dae (Aprionyx, Jappa, Ulmerophlebia) peculiar extensions of connective were observed in this segment (Landa et al., 1980) but they undoubtedly do not represent true ganglion. In more derived groups ganglion 2 is shifted to segment I (no ganglion in segment II) or ganglia 2,3 and 4 are shifted together (no ganglion in segment III or IV respectively). Various intermediate types are well apparent within the families *Leptophlebiidae* and *Ephemerellidae* (see Landa et. al., 1980,1982). Inervation of abdominal segments in never changed,however the ganglia move. In *Caenidae* or *Tricorythidae,* for instance, segment I is inervated from metathorax,segment II from segment I etc. Last ganglionic center follows the changes of remaining abdominal ganglia according to the following scheme: one ganglion in segment VII and one in VIII - two separated ganglia in VII - fused ganglia in VII - fused ganglia in VI or V - fused ganglia in thorax. As far as last abdominal ganglia are concerned, their fusion is always connected with shortening and gradual elimination of the former respective connectives. On the other hand, there are several examples of mosaic-like distribution of these characters. In *Choroterpidae,* despite the apparent shifting of ganglia 1-3, the last ganglionic center remains in segment VIII and in many genera of the *Ephemeroidea* (e.g. *Dolania* - see Soldán, 1979), despite deposition of ganglia 2-5 in the respective segments,last ganglionic center is in segment VII or even VI.

Taking into account the arrangement of insect ancestor nerve cord, the fusion of connectives is anagenticly much younger than that of ganglia.Within the *Ephemeroptera,*the gradual fusion of connectives seems to be more or less independent on fusion of ganglia, with the exception of connectives in segments VII and VIII. The doubled and well separated connectives of all thoracic and abdominal ganglia as found in *Ametropodidae* and some *Siphlonuridae* and *Heptageniidae* represent the most primitive situation. Partially fused connectives have been found only in some *Leptophlebiidae* of which e.g. *Massartella* otherwise possesses relatively primitive nerve cord. Connectives forming a shallow band probably arised more or less independently several times, in several lineages of nerve cord anagenesis (*Oniscigastridae,Arthropleinae,Behningia*).Extreme type of connectives elimination is again represented by the *Prosopistomatidae* and *Baetiscidae.* These families possess the most derived arrangement of ventral nerve cord - ganglionic mass in thorax, without any connectives or discernable ganglia.

Tracheal system

Since the tracheal system of mayfly larvae has been described in detail by Landa (1948) only the basic data and data important from the comparative anatomical point of view are mentioned here. The tracheization of the head, although useful for comparative anatomical purposes, is very complicated and its study requires mostly fresh material. That is why we have used mostly characters provided by study of thoracic and abdominal tracheization.

Head is supplied by two strong head trunks - dorsal and ventral which are branched near the head basis or even in cervical region into strong transversal anastomoses fusing in head Palmen organ. Anastomoses send several tracheae cranially and caudally; these tracheae supply muscles and internal organs in epicranium. Terminal branch of dorsal trunk leads to clypeus and labrum. At the place of branching of dorsal trunk and visceral (pharyngeal) trachea the trunk is conspicuously bent and anastomosed with mandibular trachea of ventral trunk. This anastomosis is very important for development of head tracheization in general representing probably the anastomosis between original head segments. Ventral trunk sends tracheae to mandibular muscles, brain and adjacent ganglia, hypopharynx, and labrum. Alimentary canal in head is tracheized from anastomoses of ventral trunk leading to the Palmen organ.Within the individual families there are some departures in the above basic arrangement e.g. in *Ephemeridae*, *Palingeniidae*,and *Potamanthidae*.Larvae of the family *Polymitarcyidae* possess 10 air sacks with thin tracheal epithelium and modified tenidium in head. Some modifications connected with the shortening of head capsula were observed in the *Behningiidae* (Soldán,1979). The larvae of *Siphlonuridae*, *Baetidae* and *Leptophlebiidae* lack longitudinal head anastomoses between ventral and dorsal trunks. Tracheae supplying epicranium are very well developed. Clypeum is richly tracheized from longitudinal anastomoses in *Heptageniidae* and *Oligoneuriidae* where main branch of ventral trunk leads directly into labium instead of maxillae (maxillar trachea is relatively weak). Special trachea leading from main trunks or anastomoses to accessoric gills on head are developed in the *Oligoneuriidae*.

In thorax of larvae, there are two pairs of future adult stigmas, now closed. Except for some *Baetidae* and *Oligoneuriidae* where special tracheae directly connecting trunks with accessory gills are present,the thorax is supplied with oxygen solely from abdomen (abdominal gills). Head trunks originate from the first (metathoracic) stigmatic plexus supplying prothorax and fore legs (pedal tracheae).No branches of dorsal trunk are developed in *Siphlonuridae, Baetidae, Heptageniidae*, and *Oligoneuriidae*. Tracheae supplying pro- and mesosternal muscles and integument (muscular and paratergal tracheae) and middle gut originate directly in first stigmatal plexus. Wing pads (and wings of imago and subimago) are tracheized, contrary to other insects, by the only trachea leaving mesothoracic pedal trachea near its base. Prothoracic and mesothoracic ganglion are mostly tracheized from head trunks.The arrangement of tracheae originating in metathoracic (second) stigmatic plexus is similar to those of mesothoracic one. Alimentary canal in thorax is tracheized by visceral trachea originating in metathorax,sometimes (*Oligoneuriella, Ephoron*) also by visceral trachea from dorsal head trunk in prothorax. Visceral branch from future stigma in metathorax is not developed in some *Caenoidea* (*Caenidae, Tricorythidae*).

A pair of strong longitudinal tracheal trunks is developed in the abdomen of mayfly larvae. Lateral trunks are connected with now closed future adult spiracles by narrow tracheae in segments I-VIII. The moulting of old tracheal intima is realised through these places (Landa, 1949). Longitudinal trunks are connected also with tracheal abdominal gills (primitively on segments I-VII in *Schistonota*). In the cases of gill reduction (*Pannota*) these tracheae are either reduced or lacking. Tracheae of lateral trunks in abdominal segments are inserted mostly at two places. Near the base of closed tracheae of future spiracles the dorsal branch,ventral branch (supplying nerve ganglion) visceral branch, and gonadal branch (supplying gonads) are inserted. This scheme is, usually is somewhat reduced arrangement of branches, repeated near the bases of gill tracheae (trachea branchialis). As far as the tracheal system of adults is concerned, there are no conspicuous changes in its arrangement. Spiracles open after subimaginal moulting and gill tracheae became non-function after loss of larval gills. They are reduced but usually present also in cases of larval gill persistence in subimagoes and adults (cf. Štys & Soldán, 1980). Some visceral tracheae are reduced as well, in connection with degenerative changes of alimentary canal and Malpighian tubules. The arrangement of ventral tracheal anastomoses connecting lateral trunks and of visceral tracheae in thorax and abdomen is the main character used in tracheal system comparative anatomy (Landa 1967, 1969b). We found the following cases of arrangement of these tracheae:

(E) Ventral anastomoses connecting abdominal trunks are lacking (Ea) (Fig. V/25) or abdominal trunks are connected only by thin branches of neural tracheae (Fig. V/26). The former case was found in the genera *Ametropus* (*Ametropodidae*),*Metretopus* (*Metretopodinae*) and *Mirawara* (*Ameletopsidae*), the latter arrangement occurs in the *Caenidae* and probably

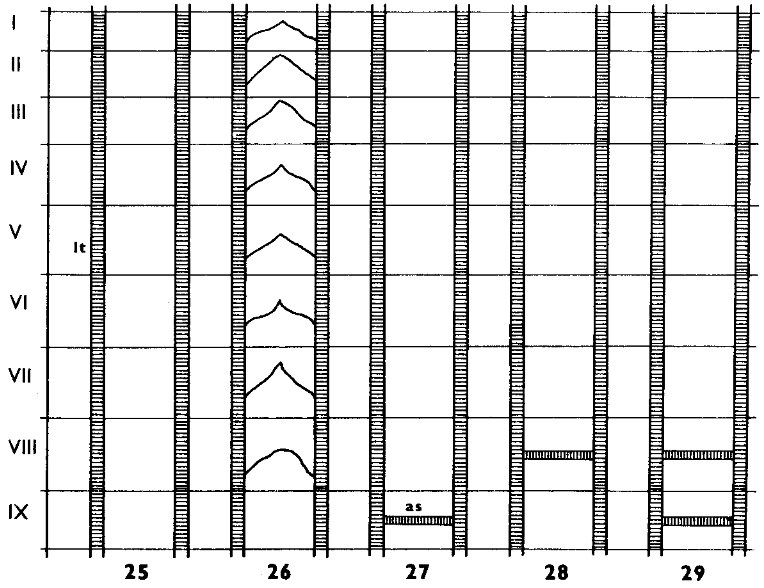

Fig. V. Comparative anatomy of tracheal system of mayflies, arrangement of ventral anastomoses. 25 - *Ametropus*. 26 - *Caenis* (neural tracheae in the abdominal segments I - VIII). 27 - *Siphlonurus*.28 - *Ameletopsis*. 29 - *Ecdyonurus*. lt - lateral tracheal trunk,as - anastomosis, I - IX - abdominal segments.Sketch,relative length of abdominal segments not followed, future adult spiracles marked with a blackened circle.

also in the genus *Baetisca* where weak anastomoses TAV7-10 cannot be excluded.

(F) Ventral anastomoses present only in abdominal segments VIII and IX or in one of these segments. (Fa) Single anastomosis in segment IX-TAV 10, IX in Landa´s (1967,1969b) classification. This case is possible only in genera possessing last nerve ganglion in segment VIII - *Siphlonurinae, Isonychiinae, Oligoneuriinae* and some *Heptageniidae* (*Anepeorus, Cinygmula, Rhithrogena*) (Fig. V/28). (Fb) Anastomosis only in segment VIII - TAV 10, VIII in Landa´s (1967, 1969b) classifications. This case occurs mostly in genera possessing last nerve ganglion in segment VII. Found only in *Ameletopsinae* (*Ameletopsis, Claquihua*). (Fc) Both anastomoses (in abdominal segments VIII and IX) are well developed - TAV 10,VIII; TAV 10, IX. This case was observed mostly in genera having last nerve ganglion in segment VII: *Coloburiscinae, Baetinae, Siphlaenigmatinae, Arthropleinae* and some *Heptageniinae* (*Ecdyonurus, Heptagenia, Stenonema, Stenacron, Thalerosphyrus*) (Fig. V/29).

(G) Ventral tracheal anastomoses occur also in other abdominal segments. (Ga) Anastomoses in segments IV-VIII (Fig. VI/30) or IV-IX (TAV 6,TAV 7, TAV 8, TAV 9, TAV 10, VIII; TAV 10, IX) - found in *Onisci-*

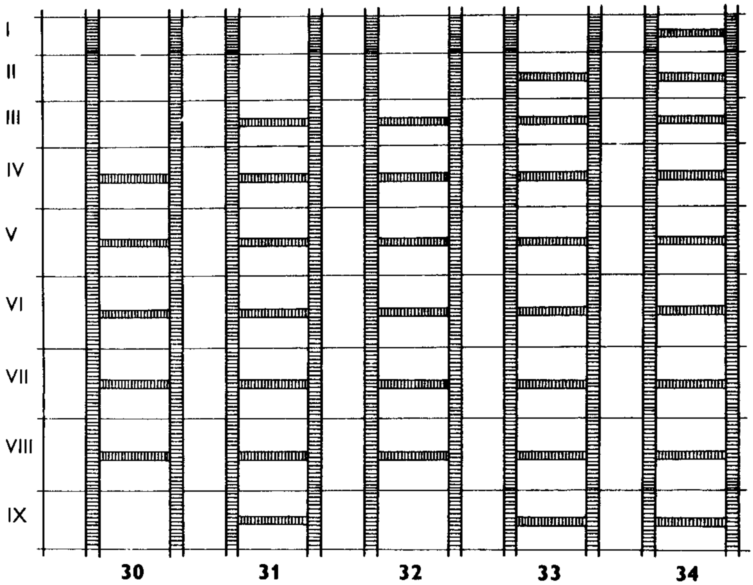

Fig. VI. Comparative anatomy of tracheal system of mayflies, arrangement of ventral anastomoses. 30 - *Attenella*. 31 - *Ephemera*. 32 - *Leptophlebia*. 33 - *Chiloporter*. 34 - *Hexagenia*. For explanations see Fig. V.

gastridae, some *Leptophlebiidae* (e.g. *Massartellopsis*, *Hagenulus*, *Paraleptophlebia*), some *Ephemerellidae* (e.g. *Drunella*, *Timpanoga*, *Ephemerellina*), *Tricorythinae* and *Dicercomyzinae*. (Gb) Anastomoses present also in anterior abdominal segments (II-III): they occur in III-VIII or III-IX, II-VIII or II-IX. TAV 5 - TAV 10, IX were found in some (*Ephemerellidae* (*Ephemerella*, *Torleya*) and *Leptophlebiidae* (*Adenophlebia*), *Ephemeridae* (*Ephemera*, *Ichthybotus*) (Fig. VI/31, 32), *Polymitarcyidae* (*Asthenopus*, *Povilla*) and in *Potamanthidae*; TAV 5 - TAV 10, VIII in some *Leptophlebiidae* (*Leptophlebia*) and *Tricorythidae* (*Tricorithodes*). Anastomoses in segment II (TAV 4 - TAV 10,IX) are in *Chiloporterinae* (Fig. VI/33), some *Ephemerellidae* (*Eurylophella*), *Ephemeridae* (*Ephemera*), *Polymitarcyidae* (*Ephoron*, *Tortopus*, *Campsurus*), and in *Palingeniinae*, *Neoephemeridae*, and *Prosopistomatidae*. (Gc) anastomoses present in all abdominal segments (TAV 3, TAV 4, TAV 5, TAV 6, TAV 7, TAV 8, TAV 9, TAV 10, VIII, TAV 10, IX - in Landa´s 1969b classification). These arrangement of anastomoses occurs in some genera of the families *Ephemeridae* (*Hexagenia*) and *Palingeniidae* (*Pentagenia*) (Fig. VI/34).

(H) visceral tracheae in mesothorax, metathorax, and in abdominal segments I-VIII (last visceral trachea may be in segment IX); visceral tracheae in all segments bearing future spiracles of imago: *Oligoneurii-*

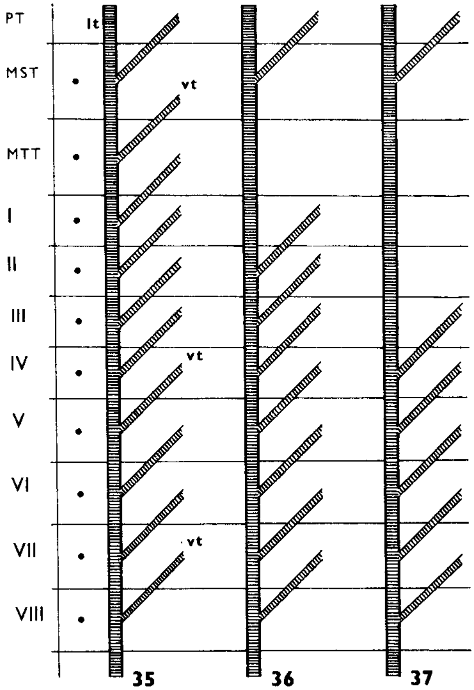

Fig. VII. **Comparative anatomy of treacheal system of mayflies**, arrangement of visceral tracheae. 35 - *Isonychia*. 36 - *Murphyella*, 37 - *Euthyplocia*. Sketch, relative lenght of segments not followed. lt - lateral tracheal trunk, vt - visceral trachea, PT - prothorax, MST - mesothorax, MTT - metathorax.

nae, *Isonychiinae*. (TV 1, TV 2, TV 3, TV 4, TV 5, TV 6, TV 7, TV 8, TV 9, TV 10) (Fig. VII/35).

(I) Visceral tracheae developed in mesothorax and in some of abdominal segments (Ia) Visceral trachea in mesothorax and abdominal segments II-VIII (TV 1, TV 4, TV 5, TV 6, TV 7, TV 8, TV 9, TV 10): *Coloburiscinae* (*Murphyella*), *Baetiscidae*, *Prosopistomatinae*. (Ib) Visceral tracheae in mesothorax and abdominal segments IV-VIII (TV 1, TV 6, TV 7, TV 8, TV 9, TV 10): *Euthyplociidae*, *Polymitarcyidae* (Fig. VII/36, 37).

(J) Visceral tracheae developed in metathorax and in some abdominal segments.(Ja) Visceral tracheae in metathorax and segments I-VIII (TV 2, TV 3, TV 4, TV 5, TV 6, TV 7, TV 8, TV 9, TV 10) (Fig. VIII/38).Tracheae in segments III-V (TV 5 - TV 7) may be sometimes very weak or even lacking in some species (e.g. *Ephemerellidae*).This arrangement was found in some *Ephemerellidae*, *Oniscigastrinae*, *Ametropodidae* and *Baetidae* (except for *Callibaetis* and some species of *Centroptilum*). (Jb) Visceral trachea in metathorax and abdominal segments II-VIII (TV 2, TV 4, TV 5, TV 6, TV 7, TV 8, TV 9, TV 10) (Fig. VIII/39) - some tracheae TV 6,TV 7,

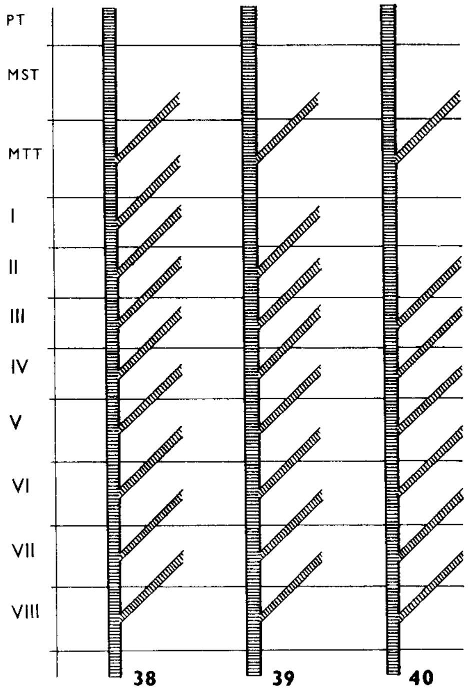

Fig. VIII. Comparative anatomy of tracheal system of mayflies, arrangement of visceral tracheae. 38 - *Nesameletus*. 39 - *Callibaetis*. 40 - *Hapsiphlebia*. For explanations see Fig. VII.

TV 8, (in segments IV-VI) can be weak or reduced in some genera. This arrangement found in *Siphlonurinae*, *Ameletopsidae* (*Chaquihua*), *Baetinae* (*Callibaetis*, *Centroptilum*), *Heptageniidae*, some *Ephemerellidae* (*Eurylophella*, *Timpanoga*), and *Metretopodinae*. (Jc) Visceral tracheae in metathorax and abdominal segments III-VIII (e.g. *Adenophlebia*, *Hapsiphlebia*, *Leptophlebia*,*Massartella*), and some *Ephemerellidae* (*Ephemerellina*) (Fig. VIII/4). (Jd) Visceral tracheae in metathorax and abdominal segments IV-VIII TV 2,TV 6, TV 7, TV 8, TV 9, TV 10): some *Leptophlebiidae* (*Choroterpes*, *Choroterpides*, *Kimminsula*, *Lepeorus*, *Traverella*), *Tricorythinae*, *Behningiidae* (*Behningia*), *Potamanthidae*, *Ephemeridae*, *Palingeniidae* and some *Ephemerellinae* (*Torleya*, *Drunella*, *Ephemerella* - some species) (Fig. IX/41).

(K) Visceral tracheae are not developed in thorax at all, they are present only in some of abdominal segments. (Ka) Visceral tracheae in segments II-VIII (TV 4,TV 5, TV 6, TV 7,TV 8, TV 9, TV 10) (Fig. IX/42): *Ameletopsidae* (except for *Mirawara*), *Coloburiscinae* (except for *Murphyella*). (Kb) Visceral tracheae present in abdominal segments IV-VIII (TV 6, TV 7, TV 8, TV 9, TV 10): *Neoephemeridae*, *Caenidae* (Fig. X/43).

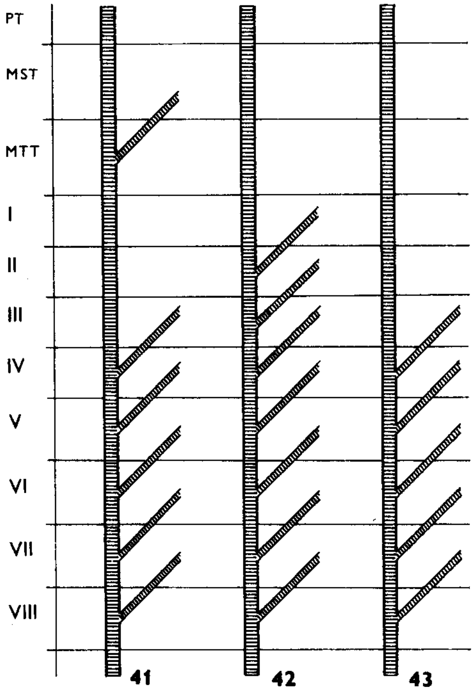

Fig. IX. Comparative anatomy of tracheal system of mayflies, arrangement of visceral tracheae. 41 - *Palingenia*. 42 - *Coloburiscoides*. 43 - *Potamanthellus*. For explanations see Fig. VII.

The tracheal system of thorax and abdomen in mayfly larvae is relatively simple. As has been pointed out above, we do not consider complicated head tracheization in the following paragraph. The arising of two pairs of main head trunks (ventral and dorsal ones) indicated important improvement of tracheization. Moreover, there are numerous specialized branches and anastomoses. This type of tracheization (anastomosed dorsal and ventral trunks) appears in the orthopteroid insects for the first time also in thorax and abdomen. Within the *Ephemeroptera*, there are several tendencies to improve head tracheization such as arising of air sacks in the *Polymitarcyidae* (Landa, 1948,1969b), shortening of common head trachea and shifting of some head tracheae into prothorax connected with shortening of head capsula in *Dolania* (Soldán, 1979), different branching of tracheae of clypeal region in the *Heptageniidae* and others. However, we lack comparative data concerning most of the world genera.

Apart from head and some prothoracic tracheae, the tracheization of thorax and abdomen in mayflies can be easily derived from hypothetical

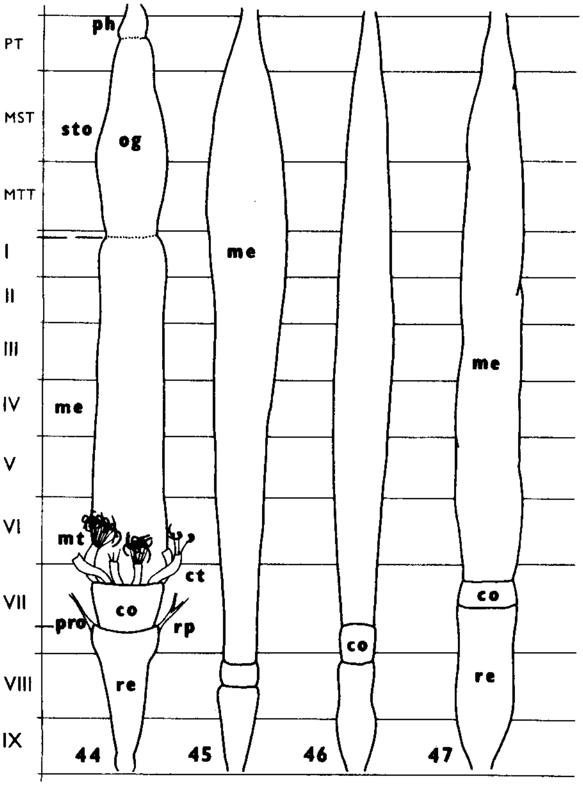

Fig. X. Comparative anatomy of alimentary canal of mayflies. 44 - sketch showing all existing structures. 45 - *Ameletoides*. 46 - *Baetis*. 47 - *Ametropus*. Sketch, relative length of body segments not followed. ph - pharynx, sto - stomodaeum,og-oesophagus,me - mesenteron, cr - crop, mt - malpighian tubules, ct - common trunks of malpighian tubules, co - colon, pro - proctodaeum, rp - rectal projections, re - rectum.

body tracheization of insect body originally consisted of tracheal clusters of spiracles on all thoracic (3 spiracles) and all abdominal (at least 10 spiracles) segments. The clusters were undoubtedly autonomous, not communicating each other and branched into several somatic and visceral plexi supplying muscles and internal organs in respective segments. These clusters were serial, tending to clear metamerical arrangement. Such tracheization can be found in some recent *Apterygota* (*Thysanura*).After comparison of mayfly thoracic and abdominal tracheization with this ancestral type certain important improvements of their arrangement of tracheae became apparent. The loss of original nearly metamerical autonomy of original stigmatic clusters is emphasized by arising of a pair of longitudinal anastomoses - ventral trunks.

Ventral trunks are well developed in all recent forms (synapomorphic character within the *Ephemeroptera*). The trunks enable oxygen supplying of the same body parts from different spiracles. Some of spiracles (most anterior and most posterior ones) become therefore supernumerary and gradually disappear. In mayflies, there are only two pairs of thoracic spiracles (on meso- and metathorax - contrary to three pairs in some *Apterygota*) and seven pairs of abdominal spiracles. The reduction of spiracles undoubtedly follows the reduction of tracheal gills from original 9 pairs (as documented in fossil material) to recent seven pairs or less. On the other hand, the alternating of different habitat during mayfly ontogeny represents a necessity of further tracheal system adaptation. That is achieved by duplification of basic set of tracheal branching (dorsal, ventral, visceral and gonadal branches) in each segment. This double set of branches usually remains unmodified even after a loss of gill pair or spiracle.

Within the recent genera, we can observe three main anagenetic trends concerning the tracheal system:(i) a trend to increase the number of ventral tracheal anastomoses between lateral trunks; (ii) a trend to decrease the number of visceral tracheae of ventral lateral trunks and (iii) a trend to unit the basis of visceral tracheae or even anastomoses with the basis of neural tracheae. The situation of a pair of not communicating lateral trunks is clearly most primitive, conserving the original autonomy of spiracle series. This arrangement was found in the primitive genus *Ametropus* and some other genera. The association of series of spiracles can be achieved either by ventral anastomoses (most recent *Ephemeroptera*) or by connection of neural tracheae at the midline, below the ventral nerve cord (*Caenidae*). The former way is much more common within recent genera. We can find gradual interstages (1 anastomosis in segment VIII or IX, 2 anastomoses in VIII and IX, 5-6 anastomoses in segment IV-VIII or IV-IX, 7-8 anastomoses in segments III-VIII or III-IX, 9 anastomoses in segments I-IX) to the most derived types with anastomoses in all the abdominal segments (*Hexagenia, Pentagenia*). Visceral tracheae present in each abdominal and thoracic segment with future spiracle represents undoubtedly the most primitive situation (*Oligoneuriinae, Isonychiinae*). This arrangement resembles the original autonomy of spiracles each of them being provided with then own visceral trachea. The situation where visceral trachea from one spiracle supplies the internal organs in preceding segments is clearly derived. Gradual reduction of visceral tracheae begins in thorax and in most derived genera (*Neoephemeridae, Caenidae*) we found only 5 visceral tracheae in abdominal segments IV-VIII. Various interstages are well traceable again

(10-9 visceral tracheae - in thorax and abdomen - 7 visceral tracheae in thorax and abdomen - 7 visceral tracheae in abdomen - 5 visceral tracheae in abdomen). In some families,the visceral tracheae in segments IV-VI (TV 6-8) are reduced earlier than those in segments II-III (TV 4-5) - this phenomenon may be connected with gill reduction (*Ephemerellidae* - cf. Landa et al. 1982). The tendency to fusion of basis of anastomoses and visceral tracheae is clearly connected with a tendency to shorten body segment. It becomes well pronounced especially within the suborder *Pannota*, e.g. in the *Ephemerellidae* (cf. Landa et al. 1981) and *Tricorythidae*. On the other hand, some of the *Pannota* families conserve very primitive arrangement of ventral anastomoses (*Caenidae*, *Baetiscidae*).

Alimentary canal

Alimentary canal of mayfly larvae consists of the stomodaeum, mesenteron and proctodaeum (Fig. X/44). Stomodaeum is a simple tube extending posteriorly. Pharynx and oesophagus is hardly, if any, distinguishable or slightly differentiated by mean of cardiac valve constriction. The anterior part of mesenteron is weakly differentiated from the posterior part of stomodaeum (pharynx) in most mayfly larvae. This differentiation is apparent only in predaceous larvae. Also it is lacking in some species which are supposed to prey on living animals (e.g. some *Siphlonurinae* and *Drunella doddsi* of the *Ephemerellidae* - cf. Landa et al., 1982). Posterior portion of stomodaeum is bulbous forming crop or ingluvies (Fig. XI/48, 50). This structure is not the proventriculus found in other insects because neither strong musculature nor inner chitinous elements occur here at all. It is usually unpigmented or slightly milky in fixed material undoubtedly with very elastic walls.The empty crop is about twice broader than stomodaeum, a crop full of food about 3-5 times broader. The crop is probably used for storing ingested food to the mesenteron (we have found small stonefly larvae and chironomids in the crop of larvae of *Ameletopsis* and *Chiloporter*). This modification of stomodaeum is mostly correlated with mouthpart modification - with occurrence of "carnivorous" mandibles (hypertrophied canine parts with heavily sclerotized teeth and reduced molar mandible part). On the other hand, it occurs also in *Behningiidae* with nearly unmodified mouthparts with normal orthopteroid mandibles of "chewing" type (Soldán, 1979).

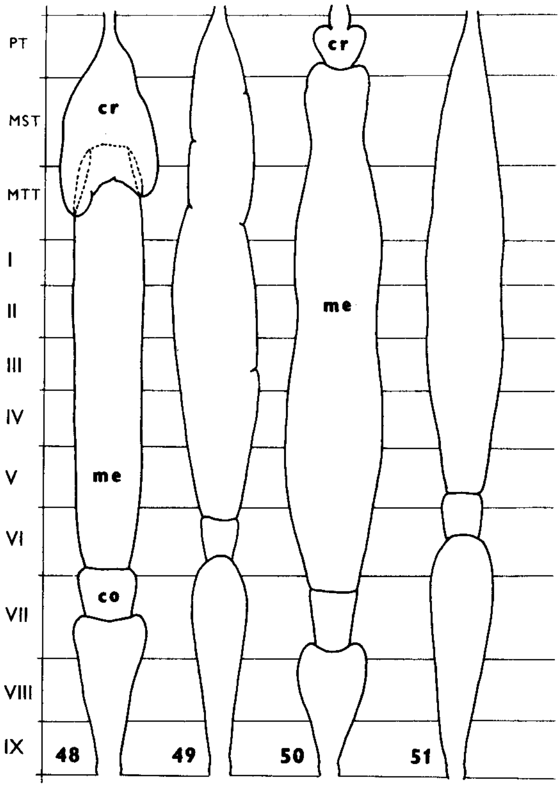

Fig. XI. Comparative anatomy of alimentary canal of mayflies. 48 - *Ameletopsis*. 49 - *Attenella*. 50 - *Dolania*. 51 *Eurylophella*.For explanations see Fig. X.

Mesenteron is a cylindrical or spindle shaped simple tube about 2-3 times broader than posterior part of stomodaeum. Although its width and shape usually depend on amount of food it is mostly tapered in abdominal segments VI-VIII and constricted at Malpighian tubules. The surface of mesenteron smooth, without any enterogastric coeca, only with surface folding in some families (e.g. *Ephemerellidae*). Mesenteron often with dark brownish or black stippling, apparent through dorsal integument in living larvae.

Proctodaeum always well differentiated into colon and rectum, the Malpighian tubules mostly inserted between colon and mesenteron.Colon is mostly narrower and much shorter than rectum, its length only exceptionally exceeds the length of abdominal segment VII. The shape of colon variable: colon usually cylindrical or subcylindrical but also pear-shaped, spindle-shaped or conical (cf. Landa et al., 1980), sometimes

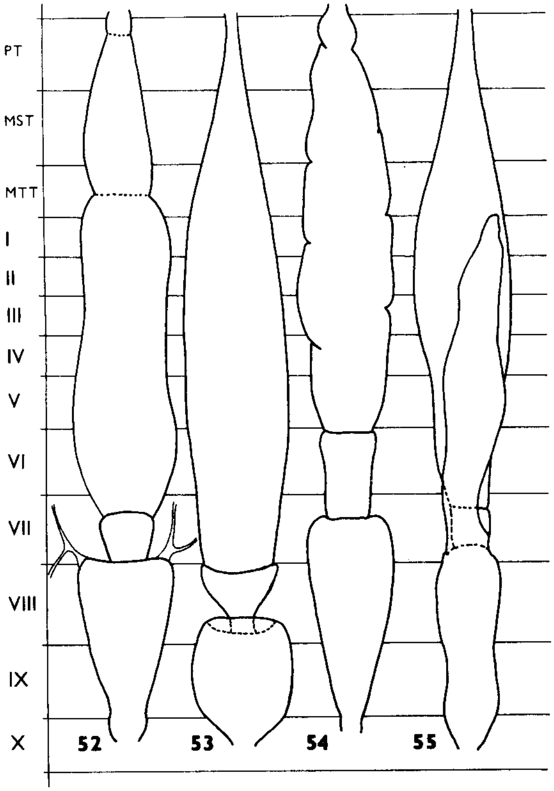

Fig. XII. Comparative anatomy of alimentary canal of mayflies. 52 - Kirrara. 53 - Hermanella. 54 - Neurocaenis. 55 - Baetisca.

tescopically connected with rectum. Colon shape is definitive, not depending on amount of food. Colon always without appendages or foldings and mostly hyaline whitish, unpigmented. Rectum cylindrical or subcylindrical, broad in abdominal segments VII or VIII and constricted in segment IX, extended again near the posterior margin of segment IX forming anal papillae. Anterior portion of rectum rounded and smooth, egg-shaped or bearing rectal projections. In some genera, only antero-lateral portions of rectum produced cranially,in many genera of the *Leptophlebiidae* and *Ephemerellidae* rectal projections hollow at base and extended into lumen of rectum connected with membraneous tissues extended distally. These membraneous tissues attach rectum to the abdominal integument. In some *Ephemerellidae* (e.g. *Timpanoga*), similar attachment tissues are well apparent also on mesenteron. Well apparent pair elongated cyllindrical projections are developed in *Caenoidea*.These projections not connected with connective tissues are directed forewards and can reach even to anterior abdominal segments.Only one unpaired long projection reaching the abdominal segments II-III is developed in some *Caenidae* (*Brachycercus,Cercobrachys*). It has a very wide base aring from bulbous anterior part of rectum and covering the colon and part of Malpighian tubules from above. The function of this rectal projection remains unclear. Dissection showed that their content was not different from content of rectum in abdominal segments VIII and IX (Figs. XII/55, XIII/57, 58).

There are considerable developmental changes during the larval - subimaginal moulting as far as the alimentary canal is concerned. Alimentary canal of mature larvae becomes filled with air bubbles and the stomodaeum and mesenteron are hardly distinguishable.Also alimentary tissues are gradually degenerating (cf. Pickles, 1931; Grandi, 1950). Stomodaeum and mesenteron disappear in subimagoes. In imagos only membraneous remnants of alimentary canal remain; the posterior part (mesenteron in abdominal segments and proctodaeum bearing Malpighian tubules) are mostly well distinguishable.

We found the following characters of the mayfly alimentary canal to be of comparative value. There are following cases of arrangement of these characters:

(L) Degree of apparent macroscopic differentiation of stomodaeum. (La) Stomodaeum not distinguishable from mesenteron, mesenteron and the posterior part of oesophagus about equal in width (Fig. X/45-47);cardiac valve probably absent or very weakly indicated: *Siphlonuridae*, some *Baetidae*, *Heptageniinae*, *Ametropodidae*, *Oligoneuriinae*, some *Ephemeroidea* (except for *Behningiidae*), some *Leptophlebiidae* and *Ephemerellidae*. (Lb) Stomodaeum differentiated from mesenteron; mesenteron (anterior portion) usually broader than posterior part of oesophagus;cardiac valve presented by constiction in thorax (this constriction can be well indicated); sometimes further constriction in cervical region representing differentiation of pharynx from oesophagus well apparent (Fig.XII/52): some *Leptophlebiidae* and *Ephemerellidae*, *Tricorythidae*, *Caenoidea*,some *Heptageniidae* and *Oligoneuriidae*;(Lc) Posterior portion of stomodaeum bulbous and membraneous forming crop or ingluvies; this part much broader than the anterior portion of mesenteron: *Acanthametropodinae*, *Ameletopsidae*, some *Baetidae* (new genus A of Edmunds, *Centroptiloides*, *Nesoptiloides*), *Anepeorinae*, *Pseudironinae*, and *Behningiidae*.

(M) Position of pyloric valve and colon to body segmentation. (Ma) Colon in the abdominal segment VII or even extended to segment VIII, pyloric valve in VII or in posterior portion of VI (Figs XII/52, 55, XIII/56): *Siphlonuridae*, some *Baetidae*, *Ameletopsidae*, *Ametropodidae*, *Oniscigastridae*, *Heptageniidae*, *Oligoneuriidae*, some *Leptophlebiidae*,and *Ephemerellidae*, *Ephemeroidea*. (Mb) Colon shifted partially or entirely

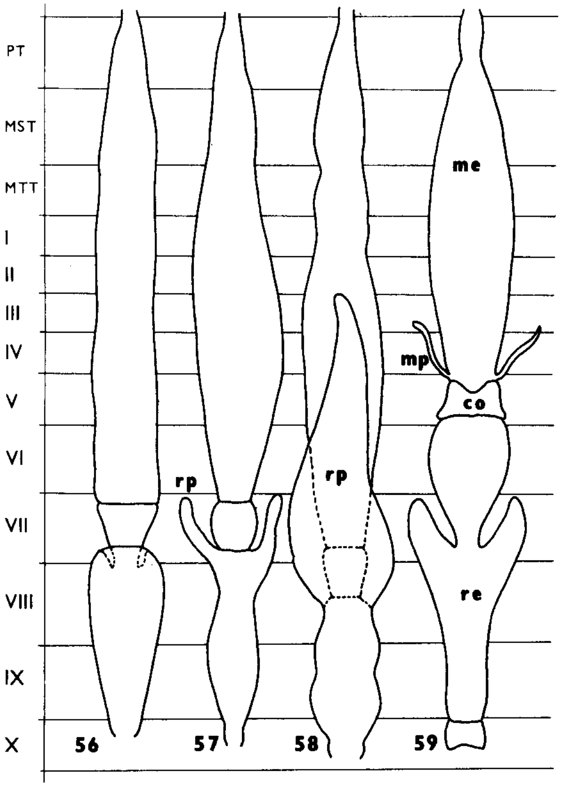

Fig. XIII. Comparative anatomy of alimentary canal of mayflies. 56 - *Neoephemera*. 57 - *Caenis*. 48 - *Brachycercus*. 59 - *Prosopistoma*. For explanations see Fig. X.

to abdominal segment VI,pyloric valve always in VI: some *Leptophlebiidae* and *Ephemerellidae*, *Tricorythidae* and *Caenoidea* (except some genera of *Caenidae*, e.g. *Brachycercus*) (Figs XI/49,51; XII/54).

(N) Arrangement of anterior part of rectum. (Na) Anterior portion of rectum smooth and oval telescopically or widely connected with colon: *Siphlonuridae*, *Ameletopsidae*, *Oniscigastridae*, *Heptageniidae*, *Ametropodidae*, *Oligoneuriidae*, *Ephemeroidea*, some *Leptophlebiidae*, *Ephemerellidae* and *Tricorythidae* (Figs X/45-47, XI/48-51). (Nb) Anterior portion of rectum with a pair of rectal projections of triangular shape connected with connective tissues: some *Leptophlebiidae* (Fig. XII/52) and *Ephemerellidae*.The rectal projections or at least their connective tissue part shows clear tendency to branching in some genera of the *Leptophlebiidae* (cf. Landa et al., 1980). (Nc) Rectal projection large, cylindrical and well differentiated; they are paired or only one dorsal projection above the alimentary canal (*Brachycercus,Baetisca*): *Caenidae*, *Baetiscidae*, and *Prosopistomatidae* (Figs. XII/55, XIII/57, 59).

Compared with other organ systems investigated,the alimentary canal provides relatively very small number of comparative character since it is relatively primitive in structure. Our knowledge of the alimentary canal of the ancestral *Ephemeroptera* is very fragmentary. In this case, no metamery in original arrangement can be taken into consideration. Ancestral alimentary canal probably consisted of a simple tube without any differentiation and any projections, with similar arrangement of inner epithelial and muscle cells along all its length. Gradual specialisation of internal structures at cell level was undoubtedly connected with specialization and differentiation of simple alimentary tube in head, thorax, abdomen. It can be supposed that this specialization proceeded from terminal portion to the middle. This presumption explains the presence of relatively long and not specialized portion of alimentary canal in the middle of its length - mesenteron.

The following anagenetic trends in the arrangement of alimentary canal within the mayflies were recognized (i) gradual differentiation of stomodaeum, extension of mesenteron and elongation of oesophagus tending to forming a crop; (ii) gradual emergence of rectal projections and tendency to their branching and elongation to the anterior abdominal segments; (iii) shortening of colon and rectum and their shifting cranially. Since the primitive *Ephemeroptera* are not specialized as far as the food is concerned also the fore portion of alimentary canal is not specialized remaining nearly in ancestral condition. In species collecting detritus, mostly not only pharynx from oesophagus but also even stomodaeum from mesenteron are not differentiated macroscopically. Of course, there are differences in internal arrangement of tissues as seen after histological treatment (cf. Csoknya & Halasz,1973). As far as the arrangement of stomodaeum is concerned, most genera show primitive situation (synplesiomorphic within some families). Emergence of crop (extended oesophagus) is undoubtedly derived, connected with predatory habits of larvae but not unconditionally. Little can be said about the original position of cardiac valve; its shifting caudally into thorax probably represents a more derived situation. Because of its weak macroscopical differentiation, this character was not investigated in detail.

The original position of colon and rectum remains also unknown. Contrary to cardiac valve, we believe that more posterior position (in abdominal segment VII) is more primitive and that the shifting of colon and proctodaeum in some genera into segments VI or V is secondary. This shifting (often occurring in derived *Schistonota* and *Pannota*) is most probably connected with shortening of posterior abdominal segments. This tendency is clearly accompanied by tendency of colon length reduction or at least by emergence of its telescopical connection with rectum. Contrary to stomodeum, the proctodaeum is always well differentiated (synapomorphic character within the *Ephemeroptera*) and thus much more derived in structure than stomodaeum.

The emergence of rectal projections undoubtedly represents derived situation tending to further specialization and branching of alimentary canal. In *Ephemeroptera*, contrary to some other insect orders, this tendency is pronounced on proctodaeum and not on mesenteron where active secretion and resorption take place.The physiological function of rectal projection remains unclear but they may serve only as a reservoirs of gut content. There are various interstages in anagenesis of this character from slightly produced anterolateral projections of proctodaeum to extremely long unpaired dorsal projection extended to anterior abdominal segments. Initial stages of emergence of rectal projection are well apparent within the family *Leptophlebiidae*.There are genera without any projections (*Adenophlebia*, *Paraleptophlebia*, *Hagenulus*), genera with small projections (*Atalophlebioides*, *Deleatidium*) and genera with well developed projection (*Kimminsula*, *Kirrara*, *Lepeorus*). Projections in *Caenoidea* have lost the connection with connective tissues; unpaired projection found in some *Caenidae* and in *Baetistidae* probably arises by fusion of originally paired projections. This fusion might be documented by extremely extended anterior portion of rectum (fused basis of projections).

Malpighian tubules

Malpighian tubules are attached to mesenteron or anterior portion of colon so that their position to abdominal segmentation depends on position of the colon. Tubules usually in segments VII-VIII but may extend to segments II-III or even partially to thorax in some genera of the *Caenoidea*. Tubules of all the genera investigated apparently differentiated into proximal and distal portions. Proximal portion tubular, hair-like and very narrow, sometimes slightly extended at base, directly connected with buds, trunks or band on alimentary canal. Proximal portion may be slightly bent but never coiled. Distal portion tubular either coiled or uncoiled but usually extended at base or slightly bent (Fig. XVII/78-81). Distal portion at least 3-5 times broader than proximal one and always at least slightly longer. Proximal

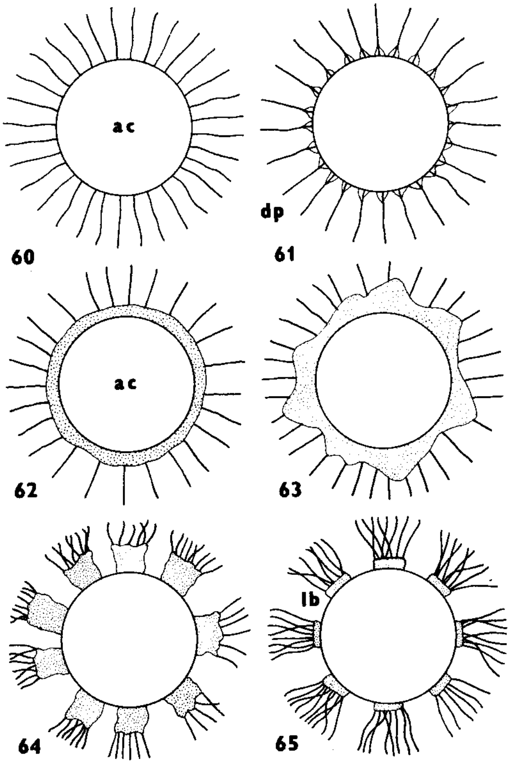

Fig. XIV. Comparative anatomy of Malpighian tubules of mayflies 60 - hypothetical ancestral situation. 61 - *Siphlonurus*. 62 - *Rallidens*. 63 - *Ephemerellina*. 64 - *Drunella* (*D.grangis*). 65 - *Paraleptophlebia*. Sketch, common trunks and buds dotted. ac - alimentary canal, dp - proximal portion of a tubule, lb - lower buds, ct - common trunks,dt - dorsal trunk pair, 1 - dorsolateral trunk pair, lt - lateral trunk pair, 1 - ventrolateral trunk pair.

portion most probably do not possess any excretory function; large excretory cells are contained in distal portion. In some genera of the family *Polymitarcyidae* (*Asthenopus, Povilla*) also secretory function has been discovered (cf. Sattler, 1967). The number of Malpighian tubules varies from species to species mostly apparently correlated with size of specimen. We found 53-92 (average 75) tubules in *Dolania* (*Behningiidae*) (Soldán, 1979). Within the *Leptophlebiidae* there are 40-70 tubules in *Isca* (body length 4 mm) and 200-300 tubules in *Massartella* (body length 30 mm) (Landa et al., 1980). Although additional study of distal portion of tubules (using specialized methods of staining) may yield other characters for comparative anatomy at present we use only two characters: degree of coiling of distal portion and the arrangement of Malpighian tubules bases:

(O) Arrangement of distal portion. (Oa) Tubules straight or slightly bent at most club-like extended at bases of distal portion:*Ameletopsidae (Ameletopsis, Chaquihua, Chiloporter), Baetidae.* (Ob) Distal portions of tubules spirally coiled at base and at the apex (*Siphlonurinae, Oniscigastridae, Ameletopsidae: Mirawara*) or coiled only at apex (remaining families).There are some isolated genera within some families (e.g. *Aprionyx* within the *Leptophlebiidae*) where distal portion can be only bent or slightly coiled.

(P) Malpighian tubules entering the alimentary canal in a narrow band or in lower buds, common trunks of tubules bases are not developed. (Pa) Tubules entering a narrow band on colon or between colon and mesenteron: *Siphlonurinae, Acanthametropodinae, Rallidentinae, Ametropodidae, Ameletopsidae, Oniscigastridae (Oniscigaster), Baetidae,* some *Coloburiscinae (Coloburiscus, Coloburiscoides),* some *Ephemerellidae* and *Tricorythidae.*In some genera of the *Ephemerellidae* (e.g. *Attenella* there is a narrow band with several triangular projections on alimentary canal

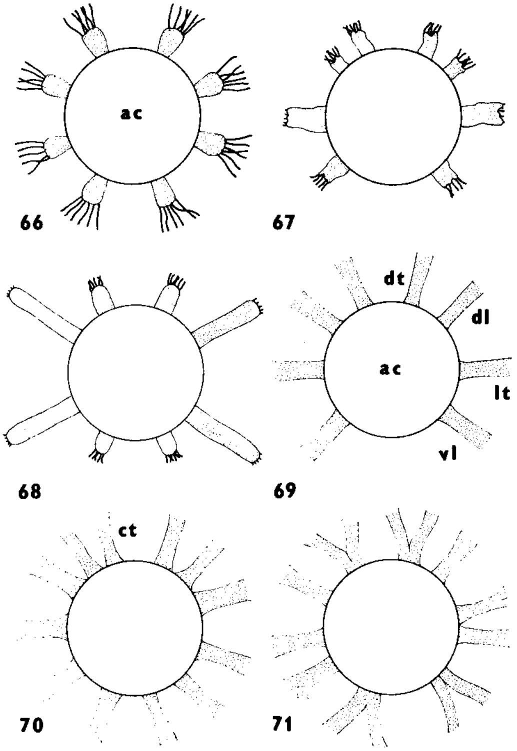

Fig. XV. Comparative anatomy of Malpighian tubules of mayflies. 66 - *Attenella*. 67 - *Hyrtanella*. 68 - *Acerella*. 69 - *Jappa*. 70 - *Ulmeritus*. 71 - *Massartella*. For explanations see Fig. XIV.

but tubules enter both the band and projections (Fig. XIV/63). (Pb) Tubules enter 8 (4 pairs) of lower buds on the alimentary canal, equally spread round the colon. All buds equal in length and size: *Oniscigastridae* (*Siphlonella*, *Tasmanophlebia*), *Coloburiscinae* (*Murphyella*), some *Leptophlebiidae* (*Leptophlebia*, *Paraleptophlebia*, *Penaphlebia*), most *Ephemerellidae*, *Behningiidae* and some *Heptageniidae* (e.g. *Cinygmula*, *Arthroplea*), *Metretopodinae*. Tubules singly entering a band on the alimentary canal occur also in *Leptophyphinae* and *Dicercomyzinae* (Figs. XIV/61-63, 65; XV/66).

(Q) Malpighian tubules entering the alimentary canal as common trunks consisting of fused bases of proximal portions of individual tubules. (Qa) Number of common trunks is not constant, fluctuating between 8-9, trunks do not possess typical dorsal, dorsolateral, lateral and ventrolateral position (Fig. XIV/64). This case was observed in some genera of the family *Ephemerellidae* (Landa et al., 1982), namely in *Dru-*

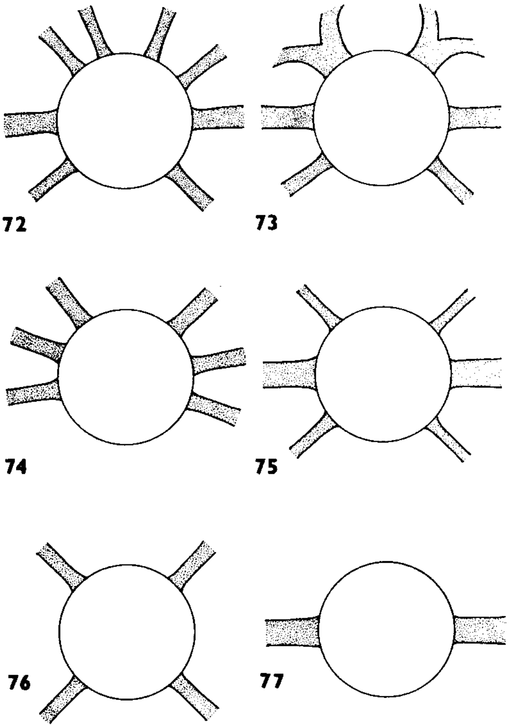

Fig. XVI. Comparative anatomy of Malpighian tubules of mayflies. 72 - *Meridialaris*. 73 - *Hermanella*. 74 - *Miroculis*. 75 - *Choroterpes* (*Euthraulus*). 76 - *Tortopus*. 77 - *Hagenulus*. For explanations see Fig. XIV.

nella submontana where nine irregularly inserted low trunks enter the alimentary canal. Other species of this genus examined possess usually eight low trunks (*D. cornuta, D. grandis, D. pelosa*). (Qb) Malpighian tubules form eight (4 pairs) of simple common trunks regularly inserted. Two trunks (one pair) are situated dorsally on the alimentary canal, two trunks usually dorsolaterally,two trunks laterally, and two trunks (last pair) ventrolaterally (Figs. XV/69, XVI/72). Typical ventral position was observed only exceptionally in some specimens of genera of the families *Ephemerellidae* and *Leptophlebiidae*. This arrangement of trunks occurs in *Isonychiinae, Chromarcyinae, Oligoneuriinae, Heptageniinae* except *Cinygmula* and in numerous genera of the family *Leptophlebiidae* (e.g. *Adenophlebia, Aprionyx, Atalophlebia, Kimminsula, Ulmerophlebia, Kirrara,Massartellopsis* and others (see Landa et al., 1980). (Qc) Common trunks are multiplied, the number of them is higher than eight. This situation was found in three genera of the family *Leptophlebiidae*. There is twelve trunks (6 pairs) in *Ulmeritus* and *Atalonella* and 10 trunks (5 pairs) in *Massartella*. In both the above cases, trunks are situated regularly round the alimentary canal, 1-2 pairs of trunks are inserted also in the ventral position (Fig. XV/70, 71). (Qd) The number of common trunks is reduced there is only six trunks (3 pairs) inserted usually in dorsolateral, lateral and ventrolateral position. This arrangement was found in the *Ametropodinae* and in 17 genera of the family *Leptophlebiidae* (e.g. *Askola, Borinquena, Megaglena, Thraulus, Choroterpes,Hermanella, Choroterpides* and others (see Landa et al., 1980).Six trunks occur also in most families of the superfamily *Ephemeroidea* (*Ephemeridae, Potamanthidae,Polymitarcyidae - Ephoroninae*,and *Palingeniidae*). Six trunks were found in *Tricorythinae* as well. (Fig. XVI/73-75).(Qe) Only four trunks (2 pairs) entering the alimentary canal, trunks inserted usually in dorsolateral and lateral position. This situation was found in the *Euthyplociidae* and *Polymitarcyidae - Campsurinae* and *Asthenopodinae*, six trunks occur also in a single genus of the family *Leptophlebiidae* (*Hagenulopsis*) (Fig. XVI/76). (Qf) Common trunks considerably reduced to a single pair (2 trunks) inserted in lateral position owing to the alimentary canal. This arrangement was discovered in a single genus of the family *Leptophlebiidae* (*Hagenulus*) and in several families of advanced *Pannota* (*Caenidae, Neoephemeridae,Prosopistomatidae* and *Baetiscidae*) (Figs. XVI/77, XVII/86).

(R) Shape and relative length of individual trunks and lower buds. Buds formed by extended bases of Malpighian tubules are always of the same shape and mostly of the some length.They can be egg-shaped (*Behningia,Dolania* - cf. Soldán,1979) or cylindrical and rounded at apex,twice as long as broad (*Ephemerellidae - Torleya, Ephemerella, Attenella* and other - see Landa et al., 1982) or even conical - some *Leptophlebiidae* - see figures by Landa et al. (1980); (Fig. XV/66-68) Rather different situation can be found in the arrangement of common trunks, the following cases were observed. (Ra) All trunks unspecialized, equal in shape and length. In this case trunks are usually only slightly distally enlarged and at least with only slight branching (e.g. *Chromarcyinae, Oligoneuriinae, Heptageniinae* (Fig. XVII/82) except *Cinygmula,* some *Leptophlebiidae,* e.g. *Adenophlebia, Atalophlebia, Hapsiphlebia, Habrophlebia, Polythelais, Farrodes, Thraulus, Indialis, Miroculis, Megaglena* and others). In *Isonychiinae* trunks are long narrow, forming thin branches (Fig. XVII/83).

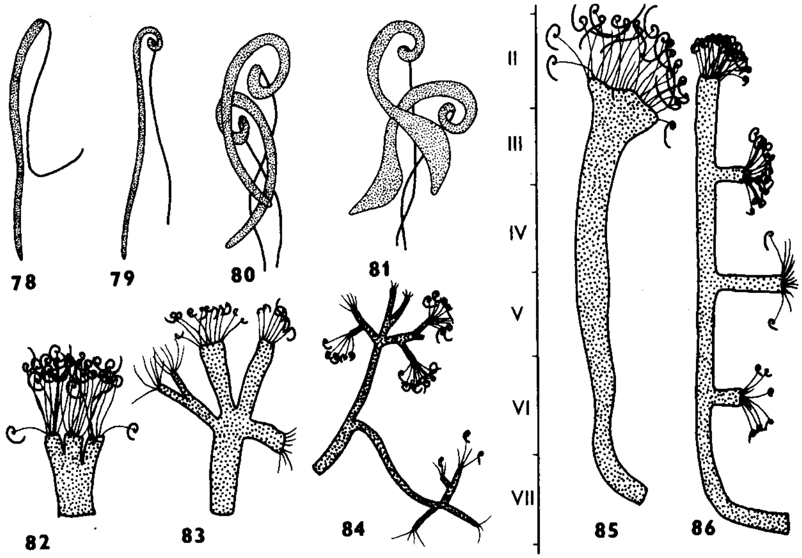

Fig. XVII. Comparative anatomy of Malpighian tubules of mayflies, individual tubules (figs. 78-81) and common trunks (figs. 82-86). 78 - *Baetis.* 79 - *Ametropus.* 80 - *Ameletoides.* 81 - *Paraleptophlebia.* 82 - *Hepagenia.* 83 - *Isonychia.* 84 - *Ichthybotus.* 85 - *Choroterpides.* 86 - *Baetisca.* II - VII - abdominal segments.

(Rb) some of trunk pairs are longer than the others and mostly also a little broader at bases. This cases occur especially in some genera of the family *Leptophlebiidae* and in *Ametropodidae*. Lateral pair of trunks is usually longer than other pairs, but approximately equal in shape (*Kirrara, Massartellopsis, Meridialaris, Petersophlebia, Choroterpes* - subgenera *Euthraulus* and *Neochoroterpes* (Fig. XVII/85).

(Rc) Some trunk pairs are specialized, considerably longer and differently shaped than the other ones. Lateral trunks longer,all trunks bush-like branched occurs in *Potamanthidae, Ephemeridae* (Fig. XVII/84). *Polymitarcyidae - Polymitarcyinae* and *Palingeniinae,* two trunks long and two short in *Euthyplociidae, Asthenopodinae* and *Campsurinae.* Specialized trunks were found also in *Leptophlebiidae* and *Ephemerellidae.* Dichotomically branched trunks occurs e.g. in *Ulmeritus* and *Hermanella* (only dorsal pair branched)(Fig. XVI/73). Lateral and dorsolateral pairs of trunks are considerably specialized in *Acerella,* being at least twice length of ventral and dorsal ones (Fig. XV/68). Lateral trunks of *Homothraulus,Traverella, Choroterpides* and *Hagenulopsis* are 2-3 times longer and considerably calix-like extended at apex, reaching as far as segment IV of abdomen. There are 6 trunks, two of them considerably shorter and differently shaped in *Tricorythinae* (*Tricorythus*).

(De) Trunks very specialized, forming either sharply bent tubules (*Prosopistomatidae*) or with 3 unbranched processes extending to the alimentary canal (*Baetiscidae, Neoephemeridae*). These processes are perpendicular the main stem-trunk paralell to mesenteron and reaching even to abdominal segment I in *Neoephemera* (Fig. XVII/86).

Based on comparative study of the arrangement of Malpighian tubules and their trunks, the anagenesis of this organs can be well understood especially because of relatively high number of various transitory types conserved in recent genera. Without any doubt, tubules entering individually alimentary canal represent (Fig. XIV/60) the most plesiomorphic situation. This situation is now considered as hypothetic-we did not find it in any recent genus. Very similar arrangement of Malpighian tubules occurs in some genera of families *Siphlonuridae* and *Baetidae.* For instance, in *Siphlonurus* lacustris, there are only slightly expanded bases of proximal portions of tubules not communicating each other so that tubules enter the alimentary canal nearly individually.

Next step in Malpighian tubules anagenesis is represented by fusion of the bases of proximal tubules. Fused bases form a band on colon. Band on the alimentary canal gives rise to two principal types of Malpighian tubules arrangement. First of all,it is further concentration of tubules bases into buds (P) and, later concentration into common trunks (Q). We believe that both the above types emerged from a band on colon independently by desintegration of original band. Buds would be considered as isolated projection of relative broad band. There is an interstage represented by Malpighian tubules of *Attenella* (*Ephemerellidae*). There are several triangular irregular projections of still not desintegrated band (Fig. XIV/63). Further anagenesis tended to disappearing of "interprojectional" portions of original band. Typical lower buds which emerged as a result of this process always show a typical radial symmetry (a pair of dorsal, dorsolateral, ventrolateral and ventral buds). Buds, although variously shaped (egg-shaped, cylindrical,conical etc.), they are always of the same length and not specialized.Owing to their symmetry,they probably represent more or less finished and blind anagenetic trend.

As indicated above we suppose that common trunks evolved from colon band independently by desintegration of original band as a whole. Desintegration was originally chaotic without symmetry. This process seems to be documented by some species of recent genera *Drunella* and *Timpanoga* (family *Ephemerellidae*).

In these species there are usually nine (or even more) irregularly shaped low triangular common trunks which are still inserted round the alimentary canal without defined dorsal or lateral position. Further development tend to eight (4 pairs) trunks with supression of trunks in ventral position. Lack of ventral trunks represents the main difference in comparison with buds. Except the cases of multiplyfication of trunks in some *Leptophlebiidae*, there are no recent forms with ventral trunks present. The most primitive situation within forms possessing common trunks is represented by genera having eight unspecialized and relatively short trunks.

Next specialization within the above groups is well characterised by two evolutionary tencencies: (1) tendency to reduction of number of common trunks and (2) tendency to specialization of one (usually lateral) pair of trunks. Multiplication of trunks to 5 or 6 pairs (*Atalonella*, *Massartella*, *Ulmeritus*) represents probably a secondary phenomenon. Multiplied trunks could be easily derived from types with 8 unspecialized trunks by their branching at basis. Moreover, at least in *Massartella* multiplication of trunks is undoubtedly affected by the need of multiplication of tubules because of comparatively very large body size. As far as reduction of common trunks is concerned,there is a large number of interstages between most primitive types with 8 pairs of trunks through 6 and 4 pairs to only a single pair of mostly very specialized trunks. Single pair of trunks which remained nearly unspecialized is very rare in present genera (e.g. *Caenis*,*Caenomedea* and others).

Tendency to the specialization of one pair of trunks is apparent even in the most primitive types having four pairs of trunks. Lateral pair is apparently longer in some genera of the family *Leptophlebiidae*. Specialization of lateral pair of trunks is more pronounced in types with six trunks; in *Choroterpides* (*Leptophlebiidae*) lateral trunks are even 2-3 times longer, robust with calix-like apex, while the other pair remains unspecialized. The types where two pairs are longer and one pair of trunk reduced are relatively rare but occur within this group as well (*Tricorythinae*). On the other hand, genera having only four trunks (two pairs) possess mostly only slightly specialized trunk pair (some *Ephemeroidea* - e.g. *Euthyplociidae, Campsurinae* and *Asthenopodinae*). Highest degree of specialization can be recognized in some genera with only a single pair of trunks. Except for *Caenidae,* this specialization is well apparent in advanced *Pannota,* especially in *Prosopistomatidae* (trunks bent at right angle) or in *Neoephemeridae* and *Baetiscidae*. The situation in two latter families represents undoubtedly the most specialized, autapomorphic Malpighian tubules arrangement. Common trunks form several processes extending to the alimentary canal. This formation represent very derived type of excretory organs emergence of common "ureter" with associated trunks of tubules).

Certain anagenetic trends can be distinguished also in the arrangement of tubule itself. Malpighian tubules of mayflies would be derived from unspecialized and homogeneous tubules of insect ancestor by enlarging of distal portion which contains excretory epithelium. Extretory cells are relatively large so that distal portion is many times broader than proximal part of tubule which changed in duct-like formations.The most primitive tubules occur in *Baetidae* - distal portion is still tube-like and uncoiled only slightly broader than proximal portion. The next step in tubules anagenesis is characterized by club-like tubules of *Ameletopsidae*. More derived tubules are possessed by most of remaining families (tubules coiled at the end or even at both ends). Most derived tubules were found in some genera of the family *Leptophlebiidae*. Although the shape of distal part of tubule was not investigated in detail there is an apparent tendency to forming a discoidal plate from originally coiled basis of distal part of tubule. Apart from the only case (some genera of the *Ephemerellidae* - two larger tubules directed foreward enter the alimentary canal individually - Landa, 1967) there are no apparent tendency to specialization of some tubules. Although some relative differences among individual tubules of the same bud or trunk or among tubules of different trunks are recognisable, differences never represent departure from individual variability in length and shape. Number of tubules is not conditioned by anagenesis but it is clearly dependent on the size of specimen, as documented above (Landa et al., 1980; 1982).

Another anagenetic trend is represented by tendency to shifting of tubules to anterior abdominal segments. Primitive arrangement of tubules (no trunks, distal portions uncoiled) is manifested by tubules in anterion abdominal segments (segments VI-VIII or V-VII in *Baetidae* and some other families). Specialization of trunks is closely connected with shifting of tubules into segments IV or III (e.g. some *Leptophlebiidae* and primitive *Pannota*) or segments II-I (advanced *Pannota*). In *Baetisca* (most derived arrangement of trunks) Malpighian tubules reach even to metathorax.Tendency to place tubules to segments VII and IX is much less pronounced, seen only in some genera of families of the *Ephemeroidea* where trunks are deeply branched.

Internal reproductive organs

Internal reproductive organs of mayflies (testes, ovaries and their envelopes and ducts) are deposited in the body cavity along the alimentary canal. Gonads are usually elongated, cylindrical or spindle-shaped attached to peritoneal structures by a suspensory ligament in thorax.The outer membraneous cover of gonads is formed by the peritoneal membrane. Contrary to the gonads of other insects, mayfly testes and ovaries are well recognisable in the early stage of development, even in very young larvae (cf. Soldán 1979b, 1979c). In comparison with other internal organs the gonads undertook considerable changes during ontogenesis. Both testes and ovaries are fully developed in older larvae (e.g. those from approximately 10th instar). Testes in imagos and subimagoes are shrunken, follicles partially or entirely disintegrated, and the seminal vesicles are hypertrophied, full of mature spermatozoa. Ovaries of subimagoes and imagos are apparent as extremely extended oviducts completely filled up with mature eggs,and the ovarioles (or at least their germaria and previtellaria) are atrophied and membraneous. Degenerative changes are visible also in the arrangement of the peritoneal tissues. For details concerning changes of gonads in last larval instars and imagos see Soldán (1979b, 1979c). The older larvae (differentiation of gonad is completely finished and the changes connected with descent of mature spermatozoa and eggs have not occurred yet) represent the best model for study of comparative anatomy of the gonads. All the descriptions below concern exclusively older larvae.

Testes are paired usually cylindrical and not flattened.Each testis is enveloped by a large number of follicles (testicular follicles) from above and from the sides. The number of follicles enveloping the testis is not constant in individual species or even in specimens of the same population.Moreover,the number of follicles is apparently not correlated with body size. There is only several tens of follicles in *Ametropus* (*Ametropodinae*) with larvae of 20-30 mm in body length and several hundreds of follicles in *Choroterpes* (5-10 mm body length).Follicles are directly attached to a seminal duct, and no vasa efferentia are developed. Follicles are usually arranged in longitudinal rows in dorsal view (Fig. XX/104,106-111). The seminal duct or vas deferens is a simple tubular duct extending from apical portion of testis in thorax or first abdominal segment to the posterior margin of abdominal segment IX. It consists of an inner layer of epithelium and an outer layer of circular muscles capable of a considerably expanding, as seen in seminal vesicle. The seminal vesicles are formed by expanded seminal ducts in the last abdominal segments. The seminal vesicle is well recognizable even in half-grown larvae, long before the descent of mature spermatozoa starts. In the last larval instar the seminal vesicles are directly connected with the ejaculatory ducts (ductus ejaculatorius) which open at apex of the penis lobes. Ejaculatory ducts are very narrow with inner layer of chitinous intima. Follicles contain germ cell undertaking gradual spermatogenesis.Transformation of spermatids and secondary spermatocytes into presperms and spermatozoa start in the last larval instars. For details concerning histology of testis and spermatogenesis see Soldán (1979b). Grimm (1977) studied in detail the arrangement of muscles attached to the posterior portion of male outflow ways which form "sperm-pump" assisting in ejaculatory process in some species. Spermatozoa of mayflies show several basic types as far as the arrangement of head and length of flagellum are concerned.In some groups (*Leptophlebiidae*) even spermatozoa without discernible flagellum in light microscope were found (for details see Soldán, 1979d). Ultrastructure of spermatozoon of *Cloeon dipterum* is described by Baccetti et al. (1969). There is no doubt that morphology and ultrastructure will provide us with very valuable data from the comparative point of view.

Ovaries are paired, usually subcylindrical or conical and at least slightly flattened or tongue-shaped. Each ovary is envelopped by a large number of ovarioles from above and from the sides. (Fig.XX/105,113-115). Similarly to testis,the number of ovarioles is not constant in specimens of the same population and does not mostly depend on the size of eggs (except *Behningiidae* and some *Oligoneuriinae* - *Oligoneurisca* and *Homoeoneuria*). On the other hand, the number of ovarioles is roughly correlated with fecundity (number of eggs produced by individual specimen). There are also certain relationships between fecundity and body size as seen even in the same species (cf. Hunt,1951).Ovarioles are attached to oviduct (oviductus lateralis) through connective cells forming a pedicel. Ovarioles,when still short (previtellogenetic stage), are arranged in several longitudinal rows seen from above. Ovarioles are deposited in usually oblique position to the oviduct.They are differentiated into germarium containing germ cells (oogonia and primary oocytes) and vitellarium in which individual follicles are contained. Follicles consisting of one oocyte encircled by follicular epithelium start to form in older larvae. Secretion of chorion takes part in the older (distal to germarium) follicle. For details concerning mayfly oogenesis see Soldán (1979c).

The oviduct is, similarly to the seminal duct,a simple tubular duct of the same structure of inner and outer layers.It extends from the apex of the ovary (usually in thorax) sometimes touching the suspensori ligament of the ovary to the intersegmental area of segments VII and VIII. Before **descent** of mature eggs into the oviducts, the oviduct is of approximately the same width in both distal and proximal portions.

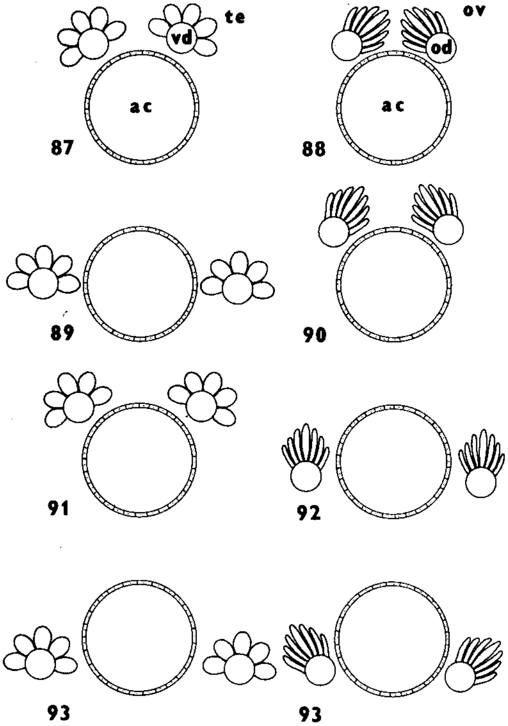

Fig. XVIII. **Comparative anatomy of internal** reproductive organs of mayflies, position of gonads to the alimentary canal: 87 - dorsal (testes).88 - dorsal (ovaries). 89 - lateral (testes). 90 - dorsolateral (ovaries). 91 - dorsolateral (testes). 92 - lateral (ovaries). 93 - ventrolateral (testes left, ovaries right). ac - alimentary canal, vd - seminal ducts, te - testicular follicles, od - oviducts, ov - ovarioles. Sketch,relative length of body segments not followed. (According to Soldán, 1981).

Openings of female gonads are arranged in several ways. There are transitions from simple membraneous openings to relatively complicated bursae and copulatory pouches of ectodermal origin (for details see Brinck,1957).Fecundity of mayflies is very high in comparison with other insect orders and data concerning egg number laid by many species have been published (cf. Degrange, 1960, Clifford & Boerger 1974 and others).

As far as comparative anatomy of gonads is concerned the following characters were investigated:

(S) Position of gonads to the alimentary canal. (Sa) Testes and ovaries are deposited dorsally to the alimentary canal (Fig. XVIII/87, 88), sometimes contiguous in thorax and connecting the dorsal body wall - *Siphlonurinae, Acanthametropodinae, Rallidentinae, Baetidae* and *Metretopodinae*. (Sb) Gonads deposited dorsolaterally to the alimentary canal sometimes contiguous in thorax not connecting dorsal body wall - *Ameletopsinae, Oniscigastrinae, Isonychiinae, Oligoneuriinae, Ametropodinae, Pseudironinae*. (Sc) Testes and ovaries deposited laterally to the alimentary canal, sometimes closely contiguous to the wall of gut (mesenteron). This position of gonads occurs in *Coloburiscinae, Heptageniinae,Arthropleinae, Anepeorinae, Leptophlebiidae, Ephemerellidae, Tricorythidae, Behningiidae, Potamanthidae, Neoephemeridae, Caenidae, Baetiscidae* and *Prosopistomatidae*.In some genera of the family *Ephemerellidae* gonads (especially testes) remain in dorsolateral position in thorax (*Timpanoga,Attenella, Dannella* and others). (Sd) Gonads in ventrolateral position occurs in the families *Ephemeridae, Polymitarcyidae, Euthyplociidae*, and *Palingeniidae*.

(T) Position of gonads to the body segmentation (Fig. XIX/94-103). (Ta) Testes deposited in only abdominal segments I-VI or in metathorax and segments I-VI- *Isonychiinae, Oligoneuriinae, Heptageniinae* (some genera), *Leptophlebiidae* (primitive groups of genera - cf. Landa et al., 1980), *Ephemerellidae* (some genera), *Behningiidae, Euthyplociidae,Asthenopodinae, Campsurinae, Siphlonurinae, Acanthametropodinae, Ametropodinae, Metretopodinae, Dicercomyzinae, Leptohyphinae, Potamanthidae* and others; ovaries usually only in abdominal segments II-VII: *Coloburiscinae,Heptageniinae* (some genera), *Leptophlebiidae* (e.g. *Atalomicria, Atalophlebia,Jappa*), *Euthyplociidae,Asthenopodinae,Campsurinae*. (Tb) Testes extend either from mesothorax or prothorax,suspensory ligament can occur even in head (*Pseudironinae, Ephemerellidae - Teloganodes; Ephemeridae* - most of genera, *Leptophlebiidae* - e.g. *Hagenulus, Traverella; Caenidae, Neoephemeridae, Baetiscidae, Prosopistomatidae*); ovaries deposited in metathorax and segments I-VI or in mesothorax and segments I-VI. Most recent genera belong to this group (for detailed list see Soldán, 1981, p. 35-36, paragraphs "Jb" and "Jc"). Ovaries are produced even into head

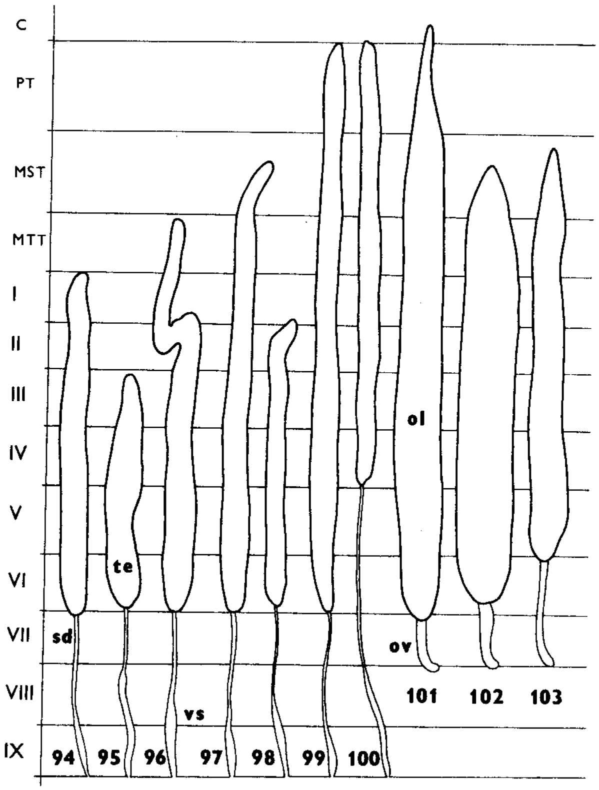

Fig. XIX. Comparative anatomy of internal reproductive organs of mayflies, position of gonads to body segmentation. 94 - testis, *Lachlania*. 95 - testis, *Coloburiscoides*. 96 - testis, *Siphlonurus*. 97 - testis, *Tasmanophlebia*. 98 - testis, *Chiloporter*. 99 - testis, *Neoephemera*. 100 - testis, *Eurylophella*. 101 - ovary, *Caenis*. 102 - ovary, *Mirawara*. 103 - ovary, *Baetis*. sd - seminal duct, te - testis, vs - seminal vesicle, ov - oviduct, ol - ovary, C - head, PT - prothorax, MST - mesothorax, MTT - metathorax, I-IX - abdominal segments.

in some genera of the family *Caenidae* (*Caenis*, *Caenomedea*, *Tasmanocoenis*). (Tc) Testes are produced into thorax but they do not reach VIth abdominal segment. This type of testis position occurs only in the family *Baetidae* (*Baetis* - some species, *Baetodes*, *Pseudocloeon* - some species: mesothorax - V or mesothorax-IV) and *Ephemerellidae* (genera *Drunella* and *Eurylophella* testis in prothorax - V or prothorax - IV respectively). In female larvae, ovaries do not reach abdominal segment VI in *Baetidae* (*Baetodes*, *Pseudocloeon*), some *Leptophlebiidae* and some *Ephemerellidae*. (Td) Testes deposited only in abdominal segments, but not in segments I-VI: *Ameletopsinae* (*Chiloporter* II-VI), *Coloburiscinae* (III-VI), *Leptophlebiidae* (*Kimminsula*, *Thraulus*). No such case has been observed in position of ovaries.

(U) Shape of testis and ovary and shape of their apical portion. (Ua) Testis cylindrical or subcylindrical, in thorax bent or s-curved, with apical portion rounded or slightly pointed, ovary cylindrical or subcylindrical, only slightly flattened, in thorax bent or s-curved, apical portion bluntly pointed or rounded: *Siphlonurinae, Acanthametropodinae, Rallidentinae, Oniscigastrinae, Coloburiscinae, Metretopodinae*. (Ub) Gonads cylindrical or subcylindrical, straight, bluntly pointed or rounded at apex, ovary slightly flattened. This group contains most of the genera investigated, for list see Soldán (1981, p. 28 and 36). (Uc) Gonads narrowly cylindrical or spindle-shaped with apical portion produced into a point - some genera of the family *Leptophlebiidae* (e.g. *Paraleptophlebia, Traverella, Hagenulus* and other). Ovaries may be bilaterally flattened. (Ud) Testis straight, slightly or apparently bilaterally flattened, ovary tongue shaped, considerably flattened: *Behningiidae, Potamanthidae, Ephemeridae, Polymitarcyidae, Palingeniidae, Euthyplociidae, Neoephemeridae, Prosopistomatidae, Baetiscidae* (testis dorsolaterally flattened).

(V) Size and arrangement of testicular follicles. While the ovarioles are arranged usually in regular longitudinal rows and all ovarioles are equal in size, testicular follicles can be arranged as follows: (Va) Follicles different in size (these differences can be very conspicuous - *Ameletus, Ametropus*) and arranged into irregular longitudinal rows (follicles usually large, shortly cylindrical or spherical) - *Siphlonurinae* except *Siphlonurus, Acanthametropodinae, Ametropodinae, Rallidentinae, Metretopodinae, Chiloporter, Pseudironinae,* some *Ephemerellidae*. (Vb) Follicles equal in size, mostly arranged in regular longitudinal rows, two subgroups: (Vb_1) Follicles large, short and cylindrical (at most four longitudinal rows consisting of 100-250 follicles) - *Siphlonurus, Oniscigastrinae, Ameletopsinae, Oligonuriidae, Baetidae, Heptageniidae,* some *Leptophlebiidae* and *Ephemerellidae, Ephemeroidea;* (Vb_2) Follicles relatively small or very small, longer and multiplied (each testis consists of approximately 200-650 follicles arranged into 4-7 longitudinal rows) some genera of the *Leptophlebiidae* and *Ephemerellidae* (e.g. *Habrophlebia, Habroleptoides, Traverella, Hagenulus, Thraulus, Ephemerella, Torleya, Chitonophora*), *Tricorythidae, Neoephemeridae, Caenidae, Baetiscidae, Prosopistomatidae* (Fig. XX/107-111).

(X) Position of individual follicles (ovarioles) to seminal duct (oviduct). (Xa) Follicles are perpendicular to seminal duct, ovarioles perpendicular or nearly perpendicular to oviduct (the angle between axis of ovariole and axis of oviduct 70-90°) - *Siphlonurinae, Oniscigastrinae, Acanthametropodinae,* most genera of *Heptageniidae, Pseudironinae,* some *Leptophlebiidae* and *Ephemerellidae, Tricorythidae* and most families of

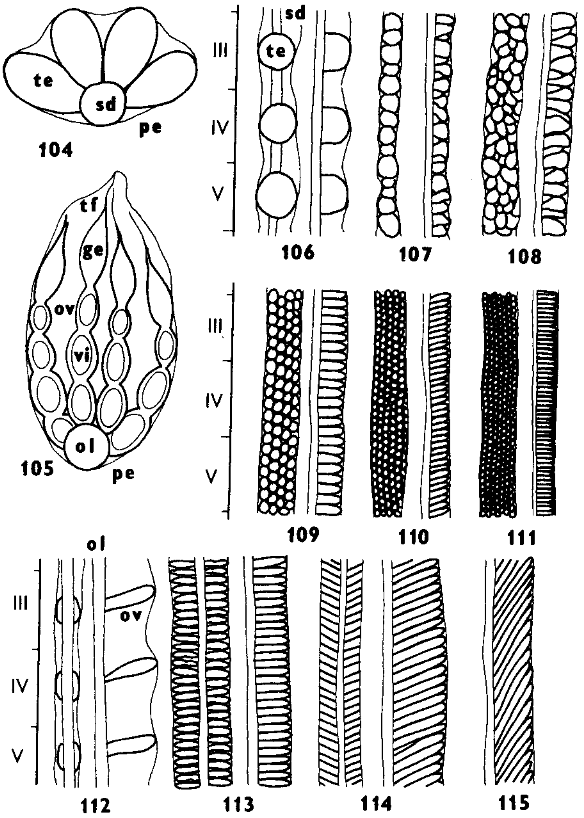

Fig. XX. Comparative anatomy of internal reproductive organs of mayflies, sketch of testis (104), sketch of ovary (105) and arrangement of testicular follicles (106-111, dorsal and lateral view) and ovarioles (112-115,ventral and lateral view).106 - hypothetical ancestral testis. 107 - *Ametropus*. 108 - *Parameletus*. 109 - *Stenonema*. 110 - *Thraulus*. 111 - *Brachycercus*. 112 - hypothetical ancestral ovary. 113 - *Siphlonurus*. 114 - *Campylocia*. 115 - *Hagenulus*. Te - testicular follicles, sd - seminal duct, ol - oviduct, pe - peritoneal epithelium, tf - terminal filament, ge - germarium, vi - vitellarium, ov - ovarioles, III-V - abdominal segments.

the *Ephemeroidea*. (Xb) Follicles slightly or apparently oblique to seminal duct (the angle between axis of seminal duct and axis of follicle is about 60-80°) *Coloburiscinae*, *Leptophlebiidae* (*Hagenulus*, *Traverella*, *Thraulus*, *Choroterpes*), *Tricorythinae*, *Leptohyphinae*,*Campsurinae*; ovarioles apparently oblique to oviduct (30-60°): *Isonychiinae*, some *Leptophlebiidae*, and *Ephemerellidae* (e.g. *Leptophlebia*, *Paraleptophlebia*, *Habrophlebia*, *Traverella*, *Hagenulus*, *Teloganodes*, *Ephemerella*, *Torleya*, *Leptohyphinae*, *Ephemeridae*, *Neoephemeridae*, *Caenidae*, *Baetiscidae*, *Prosopistomatidae*).

(Y) Shape of seminal vesicle. (Ya) seminal vesicle inconspicuous, duct only slightly expanded (*Coloburiscinae, Oligoneuriinae, Leptophlebiidae* - e.g. *Atalophlebia, Jappa*), *Ephemerellidae* - *Teloganodes, Tricorythidae, Behningiidae, Neoephemeridae, Caenidae, Prosopistomatidae.* (Yb) Seminal vesicle apparent, duct expanded gradually caudad; visicle cylindrical or elongated (*Oniscigastrinae, Ameletopsinae; Arthropleinae; Leptophlebiidae* - *Leptophlebia, Kimminsula, Kirrara; Ephemerellidae* - *Ephemerella, Drunella, Eurylophella, Torleya, Chitonophora*),*Ephemeridae, Euthyplociidae,Polymitarcyinae,Campsurinae, Palingeniidae*). (Yc) Seminal vesicle conspicuous, duct extended suddenly,vesicle cylindrical funneliform,or spindle shaped (*Siphlonurinae, Isonychiinae, Rallidentinae, Heptageniinae,Pseudironinae,Ametropodinae, Metretopodinae, Leptophlebiidae, Ephemerellidae* - *Attenella, Timpanoga*), *Potamanthidae, Asthenopodinae, Baetiscidae*). (Yd) Seminal vesicle nearly spherical, rounded, apparently expanded in segments VII-VIII and constricted caudad; this type of seminal vesicle occurs only in some genera of the family *Leptophlebiidae*.

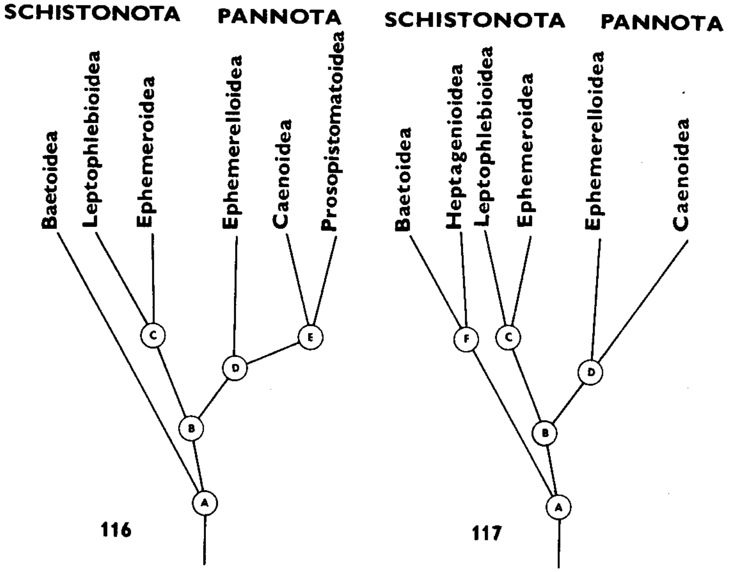

Fig. XXI. Phylogeny of the extant suborders of *Ephemeroptera* (ancestors lettered). 117 - schema by McCafferty & Edmunds (1979:7). 117 - taxonomic shifts within *Schistonota* and *Pannota* presented herein.

(Z) Position of seminal vesicle to body segmentation. (Za) Vesicle deposited in abdominal segments VIII and IX,only exceptionally exceeding to VII of VI, shape of vesicle usually cylindrical (Ya) - *Chiloporter, Coloburiscinae, Oligoneuriinae, Artheropleinae, Ephemerellidae - Teloganodes, Timpanoga), Leptohyphinae, Behningiidae - Behningia, Neoephemeridae, Caenidae, Prosopistomatidae.* (Zb) Vesicle in segment IX (may exceed into VIII - shape usually of the Yb type) - this type contains the most of genera investigated (for detailed list see Soldán, 1981, p. 30-31). (Zc) Vesicle deposited only in segment IX (shape of the Yc or Yd type) - *Siphlonurinae (Ameletoides), Rallidentinae, Isonychiinae, Baetidae, Ametropodinae, Metretopodinae,* some *Leptophlebiidae.*

Since hypothetical scheme of anagenesis of internal reproductive organs of mayflies is extensively discussed by Soldán (1981) we briefly outline only the main anagenetic tendences here. Although no paleontologic data exist the hypothesis of metameric origin of insect gonads is generally accepted. Originally, ancestral insects possessed probably 10 pairs of metamerically arranged gonads entirely independent on one another communicating with the outside environment by quite separated openings. The gonads of recent mayflies can be derived directly from the above situation by association of individual gonoducts to simple elongated common duct and by multiplication of originally metameric follicles or ovarioles. The follicles in posterior abdominal segments, which are modificated into mesadenia of males and spermatheca of females in other insects, are probably entirely reduced in recent *Ephemeroptera.* The seminal vesicle in males and openings in females undoubtedly represent secondary structures. Contrary to other recent insect orders (except *Thysanura*) both mayfly testes and ovaries remain quite separated, not connected by common outflow ways.

Primitive characters recognizable on mayfly gonads are as follows: gonads deposited in dorsolateral position (shifting of gonads to ventrolateral position is probably connected with gradual transformation of larval body from "swimming" to "crawling" or "burrowing" body type since ancestral fossil forms possessed mostly "swimming" body type probably corresponding with dorsal or dorsolateral position of gonads - cf. Soldán, 1981:88), gonads deposited only in abdominal segments (shifting of gonads to thorax or even to head is considered as derived situation for many reasons - cf. Soldán, 1981), relatively small number of follicles and ovarioles (follicles of the unequal shape show beginning of multiplication of originally metameric organs), follicles and ovarioles perpendicular to ducts (oblique position is characteristic for secondarily elongated follicles and ovarioles), and only inconspicuously indicated seminal vesicle deposited in segments VI-IX (situation near to originally unspecialized ducts).

If we compare character of testis and those of ovaries of the same

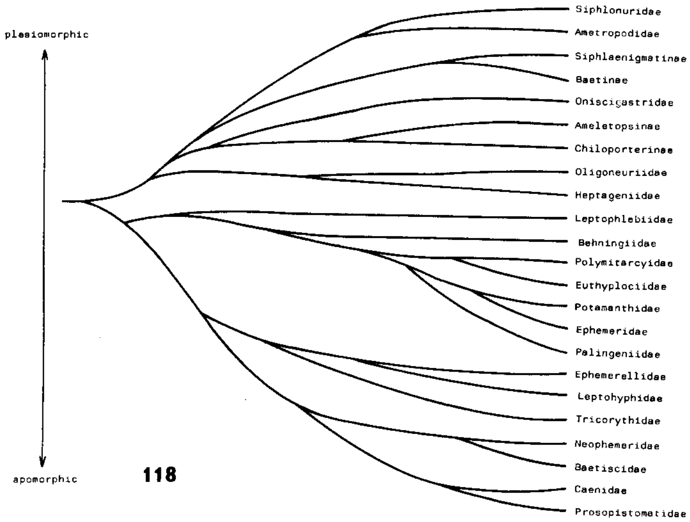

Fig. XXII. Hypothetical scheme of the evolution of the *Ephemeroptera*.

species we can recognize that the ovary seems to be more "anagenetically advanced" than testis. Ovaries always reach more cranially than testis, ovarioles are always of the same shape and mostly more oblique to oviduct than follicles to seminal ducts. Moreover, ovarioles are mostly more numerous in comparison with follicles of testis of the same species. This difference is markedly apparent especially in the genus *Ametropus* (family *Ametropodidae*).

As far as the anagenesis of mayfly gonads is concerned there are several obvious developmental tendencies: (i) tendency to shifting of gonads from dorsal to ventral position to the alimentary canal. Most derived situation within recent mayflies is in some families of the superfamily *Ephemeroidea* (ii) tendency of producing of gonads cranially to the thorax or to the head (some *Caenidae*) (iii) tendency to shape changes of both testes and ovaries. Originally cylindrical and or subcylindrical gonads gradually change to bilaterally flattened or tongue-shaped ones (as seen especially in shape of ovary). These changes are connected with elongation of ovarioles. (iv) tendency to multiplication of number of testicular follicles and ovarioles, in the case of testis also tendency to diminish the follicles of the same size and length. In females,there is tendency to increase the length of ovarioles,especially that of the vitellarium in order to produce higher number of eggs. The situation is quite different in ovoviviparous species of the family Baetidae and in larvae of the family Behningiidae. In both cases ovarioles are short,containing at most 2-3 functional follicles. The former case is connected with the ovoviviparity, the latter with unique reproductive adaptation (cf. Degrange, 1959; Soldán, 1979a; Soldán & Fink, 1982) (v) tendency to slanting of testicular follicles and ovarioles from perpendicular to oblique position to the seminal duct or oviduct. (vi) tendency to form a specialized, rounded and nearly spherical seminal vesicles from the original type of unspecialized elongated vesicle and tendency to shift the seminal vesicle from the abdominal segments VII-IX only to segment IX.

Discussion

The *Ephemeroptera* represent an insect order the evolutionary relationships of which are relatively well understood among its higher groups. Recently some authors (e.g. Edmunds & Traver, 1954; Demoulin, 1958; Tshernova, 1970, 1980; Koss, 1968, 1973; Riek, 1973; Landa, 1973; Koss & Edmunds,1974; McCafferty & Edmunds, 1979; Soldán,1981 and others) have obtained a large number of data concerning application of characters studied (exoskeleton, soft anatomy, behavioral data, egg characters and fossil evidence as well) to the phylogeny and higher classification of mayflies. That is why the *Ephemeroptera* became a model for studies integrating phylogeny, classification and biogeography.In this respect, it is probably one of the best konwn groups of extant insects.

Since we have no direct data concerning the soft anatomy of fossil taxa our following discussion concerns mainly recent families and subfamilies. The considerable or total reduction of nearly all internal organ systems (perhaps except for the ventral nerve cord) in adult *Ephemeroptera* results in the necessity to pay attention to larval stages where most anatomical characters are well manifested. In the following paragraphs we discuss a contribution of larval comparative anatomy to mayfly phylogeny and higher classification. Our discussion is based on the classification by McCafferty & Edmunds (1979) which represents a basic background for every consideration of this type. Suborders, superfamilies, major stem-groups and some problems concerning families and subfamilies are discussed. Naturally,our discussion of families and subfamilies is limited to those groups that will be affected by our classificatory modifications.

Our system reflecting all the changes suggested is presented at the end of this chapter. In order to compare it with the most important earlier systems we included some synonyms at family and subfamily level. An attempt to list all extinct and extant genera is made at the same place. It summarizes, except for some exceptions, genera described till the end of 1979 (cf. list by Hubbard, 1979).

Proposals on higher taxons of the order *Ephemeroptera:*

Suborders

The question of suborders of recent representatives of the order *Ephemeroptera* emerged several years ago. McCafferty & Edmunds (1979) discovered new thoracic characters (arrangement of larval mesonotum and wing pads) which enabled them to establish two suborders of extant mayflies. Former suborders erected by Ulmer (1920) in fact represented taxa at only superfamily level and the question of suborders of fossil *Ephemeroptera* will be discussed later.

According to McCafferty & Edmunds (1979) the larvae of the *Pannota* (more derived suborder) tend to be structurally (arrangement of thoracic nota, abdomen and gills) as well as behaviorally (generally slow moving crawlers or clingers) more homogeneous than those of *Schistonota* (more primitive suborder). As far as the arrangement of internal organs is concerned we can characterize the suborder *Pannota* as follows:

Ventral nerve system: clear tendency to further association of ganglia in thorax and in last abdominal segments to emerging of two or even a single ganglionic centre in abdomen. In *Pannota* in general the fusion of especially abdominal ganglia is correlated with the fusion of fore wing pads with mesonotum (less than a half wing pad fused - McCafferty & Edmunds, 1979). Maximum expression of this fusion is seen in the *Prosopistomatidae* and *Baetiscidae* forming a thoracic "carapace". That is reflected in the CNS by forming of a ganglionic mass in the head and thorax without discernible ganglia and connectives. In primitive *Pannota* (*Ephemerellidae*) we can find relatively unassociated CNS (see Landa et al., 1982) while in advanced *Pannota* (e.g. *Caenidae*) there is more associated ventral nerve cord, as seen in the arrangement of the last ganglionic centre. On the other hand the fusion of see metathoracic ganglion with mesothoracic one and fusion of connectives them selves show certain independence on general trend. It is manifested in both the suborders, the former being in close connection with the loss of hind wings (hind wings lost independently several times within recent mayflies), the latter occurring even independently on fusions of ganglia (some *Siphlonuridae* and *Baetidae*).

Tracheal system: Tracheal system of *Pannota* is well distinguishable from that of *Schistonota*. Commonly derived characters of improved tracheal system of *Pannota* (cf. McCafferty & Edmunds, 1979; as indicated by Landa, 1973) are the following: (a) reduction of visceral tracheae that is well apparent also in relatively primitive *Ephemerellidae* (e.g. peculiar reduction of TV 4 - *Attenella* or TV 7 - *Ephemerella*, some species, with well developed TV 3 or TV 6 respectively); occurrence of

(b) asymmetry in the visceral tracheization; (c) position of visceral tracheae - they are inserted at the same place not only with neural tracheae but also with some ventral anastomoses (if present). The above common derived characters within the *Pannota* are undoubtedly closely connected with enlargement of mesonotum and with shortening of the abdominal part of body of inactive pannotan clingers and crawlers. There is no doubt, that the shift of TV insertions is connected also with respiratory physiology - emerging of opercular gills, gill covers, and gradual gill reduction. Contrary to visceral tracheae the arrangement of ventral tracheal anastomoses do not provide us with commonly derived characters within the *Pannota*. Weakly developed communications between lateral trunks in derived *Pannota* (e.g. *Caenidae* and *Baetiscidae*) might represent larval convergency or, more probably, secondary loss of anastomoses, the function of which is replaced by connected neural tracheae.

Tracheization of the head is somewhat simplified in *Pannota* in comparison with those of *Schistonota*. Both dorsal and ventral tracheal trunks are not so branched, air sacks or their indications are always lacking. Detailed study of head tracheization would be very useful since detailed topography of head tracheization of *Pannota* remains unknown (cf. Landa, 1948).

Alimentary canal: The arrangement of the alimentary canal does not provide us with any common apomorphic character within the *Pannota*. Although there is a clear tendency to form projections on the rectum resulting in well developed, unpaired projections in *Caenidae* and *Baetiscidae*, we can find the same phenomenon also within advanced *Schistonota*. Some adaptations to predatory habits described above probably represent convergences within both *Schistonota* and *Pannota* (see situation e.g. in *Ephemerellidae* and *Behningiidae*).

Malpighian tubules: The suborder *Pannota* do not possess any synapomorphic character of Malpighian tubules. All the anagenetic types of Malpighian tubules arrangement occur within this group, from a single ring of expanded tubules bases in *Ephemerellidae* to the "ureter" of *Baetiscidae*. On the other hand, there is a clear tendency to shift tubules and trunks cranially. In general, the Malpighian tubules of *Pannota* are more specialized than those of advanced *Schistonota* (see situation in *Leptophlebiidae* and in *Ephemerellidae*, cf. Landa et al., 1980, 1982).

Internal reproductive system: Gonads of *Pannota* are characterized, first of all,by its position to body segmentation. They are (both testes and ovaries) conspicuously shifted into enlarged metathorax, in some cases even into head (*Caenidae*, some genera). Otherwise the gonads conserved some very primitive characters in *Pannota*, like testicular follicles of different shape in some genera of the family *Ephemerellidae*.

Taking into account the above facts we can characterize the suborder *Pannota* as homogeneous from the comparative anatomical point of view. First of all, it is characterized by improved tracheal system and advanced association of ventral nerve cord. These characters are closely connected, together with shifting of gonads into thorax and specialization of distal portions of Malpighian tubules,with gradual fusion of the wings pads with the mesonotum. These characters are most pronounced in larvae where large mesonotal shield covering wing pads entirely is formed (*Prosopistomatidae* and *Baetiscidae*). The most primitive group of the suborder *Pannota* is represented by the family *Ephemerellidae* where many primitive characters are retained, some of them nearly in the ancestral state (e.g. testicular follicles and arrangement of Malpighian tubules in *Timpanoga*, *Attenella* and *Dannella*). These characters show certain relationships even to siphlonurid-like groups or at least to their descendants.

The more primitive suborder *Schistonota* consists of more heterogeneous groups in comparison with the *Pannota*. Anatomical schemes are very differentiated within individual families and the differences among superfamilies are more pronounced than those in the suborder *Pannota*. The anatomical characters of individual groups of *Schistonota* and their interrelationships will be discussed in the following paragraphs.

Naturally, there is a large number of convergences among both the *Schistonota* and *Pannota*. They are presented, for example, by the arrangement of Malpighian tubules (only a single pair of common trunks) in *Hagenulus* (*Leptophlebiidae*, *Schistonota*) and the *Caenidae* (*Pannota*) or position of gonads in *Traverella* (*Leptophlebiidae*,*Schistonota*) and *Caenoidea* (*Pannota*). On the other hand, the covergences which have been found by McCafferty & Edmunds (1976) based on thoracic morphology (*Murphyella*, *Coloburiscoides* - *Schistonota* - wing pads of larvae fused for a considerable distance; *Neoephemeridae* - *Pannota* - adults possess thorax of the schistonotan type) are not manifested in the arrangement of internal organs at all. The anatomical characters of these groups fully agree with typical anatomical scheme of *Schistonota* or *Pannota* respectively. As noted by McCafferty & Edmunds (1979) other convergences will be found probably among the *Siphlonuridae* and *Leptophlebiidae*.

As far as fossil mayflies are concerned most extinct species apparently belong to the suborder *Schistonota* as documented by conserved characters of skeletal morphology of fossil material (extremely free wing pads very narrowly attached to meso- and metathorax). Reconstructions show (see Handlirsch, 1905-1906; Kukalová, 1968; Kukalová-Peck,1978 and Hubbard & Kukalova-Peck, 1980) these primitive larvae (*Protereismatoidea*, Permian) to be "an extreme schistonotan (precursor) type" (McCafferty & Edmunds,1979). These larvae possessed more than seven gill pairs (usually nine, eight in *Mesoplectopteron*) so that their tracheal system was most likely more autonomous, with probably only weakly developed lateral trunks or with bundle of tracheae branched independently from each gill.

The fossil suborder *Protephemeroptera* contains the only genus *Triplosoba* Handlirsch (Upper Carboniferous). It was established by Demoulin (1956) in order to distinguish its peculiar wing venation (simple MA, separated R_4 and R_5) from other fossil material assigned to the *Ephemeroptera*. This genus (and suborder) probably represented a blind evolutionary line (Carpenter, 1963). Since the larvae of *Triplosoba* are not known its equivalency within the McCafferty's & Edmunds' (1979) subordial scheme cannot be determined at present. There is no doubt that this suborder shoved relationships to later Permian pre-*Schistonota* (e.g. *Prosopistomatoidea*). Till the larvae and/or descendants of *Triplosoba* remain unknown we believe that it is reasonable to conserve this suborder (cf. Tshernova, 1970, 1980).

The fossil genus *Litoneura* Carpenter (Upper Carboniferous of Illinois), which has been often considered an ephemeropteran of a monotypic family, belongs to the *Palaeodictioptera* (cf. Hubbard & Kukalova-Peck, 1980). Although its venation seems to be near the ideal ancestral wing form of *Ephemeroptera* (Edmunds, 1972) it lacks the costal brace, an important apomorphic ephemeropteroid character (Hubbard & Kukalova-Peck, 1980).

Superfamilies

The classification of mayflies at the superfamily level has been very unstable in the past 20-30 years. Soldán (1981) cited the example of the family *Baetiscidae* classified in the superfamily *Prosopistomatoidea* by Edmunds et al. (1963) in the superfamily *Oligoneurioidea* by Demoulin (1958), in the *Ephemerelloidea* by Tshernova (1970), in the *Leptophlebioidea* by Landa (1967, 1969a) and in the *Baetiscoidea* by Spieth (1933) although this confusion is often caused by chaotic application of superfamily names despite the law of priority. The following discussion is based mainly on the classification by McCafferty & Edmunds (1979) who recognize 6 extant superfamilies (3 within *Schistonota* and 3 within *Pannota*).

We suggest to classify the suborder *Schistonota* as having 4 recent superfamilies and the suborder *Pannota* as consisting of 2 recent superfamilies. If accepted, the *Schistonota-Pannota* subordial classification recognizes common ancestor of all modern mayfly groups (ancestor B in McCafferty & Edmunds, 1979 - see Fig. XXI/116). Since all these advanced groups (all the superfamilies except for the *Baetoidea* and *Heptagenioidea* in our classification) share common apomorphic characters in the arrangement of internal organs (e.g. ventral anastomoses, reduction of TV, position of gonads, coiled distal portion of Malpighian tubules) we can suppose this ancestor to be a direct descendant of a hypothetical ancestor (A in McCafferty & Edmunds, 1976 - see Fig. XXI/116,117) of all recent mayflies. The former ancestor was probably leptophlebioid-like while the latter ancestor was most likely an ancestral *Baetoidea* (cf. McCafferty & Edmunds, 1979).

Edmunds (1972) and Edmunds et al. (1976) derived a caenoid-prosopistomatoid and an ephemerellid-tricorythid lineage independently similarly to Landa (1967). This opinion leads to the erection of a superfamily (*Leptophlebiodea* sensu Edmunds et al., 1963, 1976 and Landa, 1967) consisting of *Ephemerellidae* and *Tricorythidae* together with the *Leptophlebiidae*. Taking into account relatively homogeneous anatomical characters of the family *Leptophlebiidae* (see Landa et al., 1980) and unstable and widely fluctuating anatomical characters of the *Ephemerellidae* (see Landa et al., 1982) this grouping is a contradiction to anagenetic trends of individual internal organs systems as recognized first by Landa (1973). In Landa s (1973) classification the *Leptophlebiidae--Ephemeroidea* line (*Schistonota*) form different lineage from those of the *Ephemerellidae-Tricorythidae-Caenoidea* line. McCafferty & Edmunds (1979) are of the same opinion (cf. Landa, 1973: 156) classifying the latter lineage as *Ephemerelloidea, Caenoidea* and *Prosopistomatoidea.*

Also Riek (1973) although admitting that the *Leptophlebioidea* includes the *Ephemerellidae,* noted a marked difference between the Ephemerellidae and the *Leptophlebiidae* itself.Tshernova (1980) separated the leptophlebiid lineage completely from the ephemerellid-tricorythid lineage contrary to her and Demoulin´s (1958, 1961) opinion where the *Leptophlebiidae* is contained in the superfamily *Siphlonuroidea* (sensu Tshernova, 1970) or in the *Heptagenioidea* respectively. According to her (Tshernova, 1980) phylogenetic diagram the branching of these lineages took place in the Upper Triassic or lower Jurassic,much earlier than the splitting of the extinct superfamily Hexagenitoidea from today's pannotan families (*Ephemerelloidea, Caenoidea*).

We fully agree with McCafferty & Edmunds (1979) that the hypothetical common ancestor of *Pannota* (D in Fig. XXI/116,117) was most probably ephemerelloid-like and gave rise to the extant families *Ephemerellidae, Tricorythidae* and *Leptohyphidae* and a caenoid ancestor (E in McCafferty & Edmunds, 1979: 7 - see Fig. XXI/116). We agree to establish the superfamily *Ephemerelloidea* for the more ancient *Pannota Ephemerellidae* and *Leptohyphidae* still possessing numerous visceral tracheae and original arrangement of Malpighian tubules and for the more specialized family *Tricorythidae*. Tshernova (1970,1980), contrary to Edmunds et al., (1976) and McCafferty & Edmunds (1979), supposed a common ancestor of this group and the family *Baetiscidae* (now in *Caenoidea*) living in the Upper Jurassic. We found only very weak anatomical background for such a conclusion since there are nearly no apomorphic characters possessed by both these recent groups, apart from some similarities in wing venation (cf. Riek, 1973). Absence of TAV in the *Baetiscidae* ranges the only extant genus of this family to the *Caenoidea*.

We suggest to establish the only common superfamily *Caenoidea* in order to emphasize the anatomical unity of the *Caenidae, Neoephemeridae, Baetiscidae,* and *Prosopistomatidae*. Such a classification is contrary to the findings of Edmunds (1972),Edmunds et al. (1976: table 1) and McCafferty & Edmunds (1979: 7) who present,mainly on a skeletal morphological basis, the superfamily *Caenoidea* for the two former families and the superfamily *Prosopistomatoidea* for the two latter ones.

From the anatomical point of view this conclusion is supported only by the arrangement of visceral tracheae (TV 6 - TV 10 in *Caenoidea* s.str.; TV 1, TV 4 - TV 10) and CNS (ganglionic mass in the *Prosopistomatoidea*) but other characters (e.g. arrangement of the alimentary canal, Malpighian tubules or absence of TAV clearly approaching *Caenidae* to *Prosopistomatidae*) show distict relationships between *Caenidae* and *Prosopistomatidae* on one hand and between *Neoephemeridae* and *Baetiscidae* on the other hand.Also Landa (1967,1969a,1973) emphasized the anatomical similarities between *Neoephemera* and *Baetisca* ("ureter" of trunks of Malpighian tubules) and between *Caenis* and *Prosopistoma* (arrangement of alimentary canal and other characters).

Riek (1973) stated that "although the *Prosopistomatidae* and *Baetiscidae* are referred to the same superfamily at present, the differences, both in nymphs and adults are such that a more detailed study may indicate that they are not as closely related as at present assumed." Tshernova (1970) united the families *Caenidae* and *Prosopistomatidae* into the superfamily *Caenoidea* and established a separate superfamily for the *Neoephemeridae*. Later (Tshernova, 1980 the separated the family *Baetiscidae* from the remaining three families left in the *Caenoidea* assuming that the *Baetiscidae* had split from the ephemerrelloid-tricorythid lineage in the Lower Cretaceous independently from the on caenoid-prosopistomatoidneoephemeroid lineage. Demoulin (1958) left the *Caenidae* and the *Prosopistomatidae* in the *Ephemerelloidea* while the family *Baetiscidae* classifies as a member of the *Oligoneurioidea*.

The suborder *Schistonota* comprises most of the extant representatives of the order as is more diverse as the suborder *Pannota*. McCafferty & Edmunds divided this suborder into three superfamilies forming two main phylogenetic lineages. As noted above, the hypothetical ancestor of all recent mayflies was most probably a baetoid (McCafferty & Edmunds, 1979; 7 - see Fig. XXI/116, 117) which gave rise to a common ancestor of advanced *Schistonota* and all the *Pannota* (B - see Fig. XXI/116, 117). We fully agree with a classification of advanced *Schistonota* into superfamilies *Leptophlebioidea* (to include the *Leptophlebiidae* - cf. Tshernova, 1980) and *Ephemeroidea* (to include the *Behningiidae*, *Potamanthidae*, *Euthyplociidae*, *Polymitarcyidae*, *Ephemeridae*, and *Palingeniidae*) since these two superfamilies are very well defined anatomically as well (cf. Landa, 1967, 1969a, 1973; Landa et al.,1980; Soldán, 1981). The ancestor (C - see Fig. XXI/116, 117) was most likely leptophlebioid like or potamanthoid-like (cf. McCafferty & Edmund, 1979). On the other hand, the *Leptophlebiodea* show apparent morphological (cf. Demoulin,1958; Edmunds, 1962,1972; Edmunds et al.,1963, Tshernova,1970) and anatomical relationships to the *Pannota* (superfamily *Ephemerelloidea* (cf. Landa, 1967, 1969a).This is the reason several authors (see above) united or combined the superfamilies *Leptophlebioidea* and *Ephemerelloidea* (sensu McCafferty & Edmunds, 1979).

Nearly all the authors which have had some interest in the phylogeny of mayflies classify the superfamily *Ephemeroidea* (comprising families with burrowing or semi-burrowing larvae) in the original sense (cf. Edmunds & Traver (1954). Demoulin (1958) united the *Behningiidae* and *Palingeniidae* into a common superfamily *Palingenioidea* in order to emphasize the relationships of these groups to the extinct family *Hexagenitidae* (as *Mesephemeridae* in Demoulin, 1958) also included here.

The superfamily *Ephemeroidea* is anatomically very well defined, first of all by shifting the gonads to the ventrolateral position and presence of numerous ventral anastomoses in tracheal system: (TAV 4) TAV 5 - TAV 10 (visceral tracheae TV 6 - TV 10 (IX)).The family *Behningiidae* represents in many respects a transition from the *Leptophlebioidea* to the *Ephemeroidea* (e.g. arrangement of Malpighian tubules and the alimentary canal - cf. Soldán, 1979).

The most primitive group of recent mayflies can be probably derived directly from hypothetical ancestor A (baetoid-like, McCafferty & Edmunds, 1979: 7, see Fig. XXI/116, 117). McCafferty & Edmunds classified this lineage as a single superfamily *Baetoidea* (*Heptagenioidea* sensu Edmunds et al., 1963,1976 and Edmunds & Traver,1954) consisting of 5 families with 18 subfamilies. There are principally two distinct groups of families well characterized by external morphology, body shape, anatomy of internal organs and behaviour (e.g. trophic relationships etc.). The first group consists of the families *Siphlonuridae* and *Baetidae* (body elongated, "shrimp-like" swimmers derived from machiloid body type, generally collectors, gatherers, scrapers). The second group consists of the families *Oligoneuriidae* and *Heptageniidae* (body mostly dorsovetrally flattened, femora flat, generally scrapers, filterers).

The above two groups are well distiguished also according to the arrangement of internal organs.The second group (*Oligoneuriidae* and *Heptageniidae*) shows several common apomorphic characters: 1-2 simple tracheal anastomoses appearing in abdominal segments VIII and/or IX, gonads shifted from dorsal or dorsolateral position to lateral position, bases of individual Malpighian tubules are mostly associated into common trunks, alimentary canal specialized in some predaceous groups. These characters divide this group from the *Siphlonuridae* and *Baetidae* although there are some transitory forms represented e.g. by the subfamily *Isonychiinae* (*Oligoneuriidae*) the larvae of which retaine shrimp-like body shape.

Siphlonuridae (most of the subfamilies), *Baetidae* and some small siphlonurid-like families possess a very primitive tracheal system (nearly no anastomoses and a large number of visceral tracheae), gonads in dorsal or dorsolateral position, and a primitive arrangement of Malpighian tubules. On the other hand, similar specialization of the alimentary canal (formation of a crop) can be observed in some groups (*Acantametropodinae* and especially *Ameletopsidae*).

Both these groups evolved from primitive ancestral siphlonurid-like forms (F - see Fig. XXI/117) and at present they represent in many respects independent evolutionary lineages (cf. Landa, 1973). Since the differences are nearly as pronounced as those as between the *Leptophlebioidea* and the *Ephemeroidea* we prefer, contrary to McCafferty & Edmunds (1979), to classify the families *Oligoneuriidae* and *Heptageniidae* into the separate superfamily *Heptagenioidea* (nec sensu Edmunds & Traver, 1954; Edmunds, 1962 and Edmunds et al., 1963, 1976).

Riek (1973) pointed out the differences between the *Heptageniidae* (using adult characters as well) and the remaining *Baetoidea* but left the *Oligoneuriidae* in the *Baetoidea*.This is an apparent contradiction to classificatory rules as formulated by McCafferty & Edmunds,1976. Similar solutions of this problem can be found also in systems by Demoulin (1955a, 1956, 1958, 1961) and by Tshernova (1970). Tshernova (1970) emphasizing the relationships between *Isonychiinae* (*Isonychiidae* here) and *Siphlonurinae* left this family in the *Baetoidea* and established a separate superfamily for the *Oligoneuriidae* and *Chromarcyidae* (here separated families). She (Tshernova, 1980) supposed that both the *Heptageniidae* and the *Oligoneuriidae* split their lineages independently in the Lower Jurassic.

Fossil superfamilies are relatively numerous, containing only a single or two families (*Mesephemeroidea*, *Hexagenitoidea*) except for 4 families included in the Permian *Protereismatoidea* (see Demoulin, 1958; Tshernova, 1970, 1980; Demoulin, 1980; Carpenter, 1979 and others). The superfamily *Triplosoboidea* is the only superfamily of the extinct suborder *Prothephemeroptera*. The placement of the Triassic superfamily *Litophlebioidea* (1 family, 1 genus from South Africa) within the order *Ephemeroptera* seems to be doubtfull; this superfamily might be referred to the *Megasecoptera* (cf. Riek, 1976; Hubbard & Riek, 1978 and Hubbard & Kukalova-Peck, 1980).

Major stem-groups

Specialization in characters of the adults in *Ephemeroptera* have not paralelled those in the larvae. Edmunds (1972),Riek (1973 and others showed that characters of adults were affected by a large number of factors which were not manifested in larvae at all. The adults of *Pannota* and *Schistonota* are not so easily distinguishable (cf. McCafferty & Edmunds, 1979) since morphological characters (especially thoracic morphology, and wing size reduction) have evidently evolved many times in various groups of *Pannota* and *Schistonota*). Moreover,some adults of *Pannota* are reduced to such a considerable degree that they do not provide us with any comparative characters. These are the reasons that the following considerations are based mainly on larvae.

In any one recent genus of the order we are not able to find all ancestral ephemeropteran characters which appear in fossil material. As far as skeletal morphology and body shape is concerned the ancestors of the extant *Ephemeroptera* were probably most similar to some siphlonurid genera, especially to the genus *Parameletus* (body generally machiloid, legs unmodified, 7 pairs of equally shaped gills). Eight pairs of gills were observed in the only species of the genus *Baetis* recently described from Caucasus. Whether this condition is secondary or ancestral (like in the Upper Permian *Mesoplectopteridae*) and whether the ancestral gills did or did not possess bundles of fibriliform filaments is open to question (cf. Riek, 1973; Štys & Soldán, 1980).

From the comparative anatomical point of view the most primitive genus of extant mayflies is the genus *Ametropus*. Larvae possess no tracheal anastomoses,CNS with well developed first abdominal ganglion (autplesiotypic within the order), individually entering Malpighian tubules and testes with only a single row of follicles of different size and some other very primitive characters although skeletal morphological characters are somewhat specialized in comparison with the *Siphlonuridae*. The origin of the family *Ametropodidae* remains unclear (cf. Demoulin, 1955b, 1974) since the characters according to McCafferty & Edmunds (1979) most related group - *Acanthametropodinae* - are plesiomorphic. These authors consider fused adult penes and especially elongate curved, adenticulate claws of sand-dwelling larvae to be synapomorphic. Our findings of arrangement of internal organs only weakly support this conclusion. The above authors indicated the possibility of placement of the *Acanthametropodinae* (because of possible intermediancy between *Ametropodidae* and *Siphlonuridae*) in the family *Ametropodidae*, as a primitive subfamily.

Despite to nearly ancestral anatomical stage of *Ametropus* the family *Siphlonuridae* undoubtedly represents recent descendants of the earliest mayfly adaptive radiation. As it has been postulated by McCafferty & Edmunds (1979) the phylogeny of the major groups of *Ephemeroptera* cannot be fully understood without a detailed study of this group. These authors showed that each of the five main non-siphlonurid lineages contains commonly derived siphlonurids at their base.The same phenomenon can be demonstrated also by conditions in the arrangement of internal organs. Anagenesis of all the organ systems studied in recent representatives of the order starts within the *Siphlonuridae* (see respective paragraphs concerning the anagenesis of internal organs), continues through commonly derived siphlonurids at the base of *Heptagenioidea* (in our sense) - *Isonychiinae*- and of *Leptophlebioidea* to most apomorphic conditions of advanced *Pannota*.

The family *Siphlonuridae* (or even superfamily *Baetoidea*) in general is clearly paraphyletic since it has given rise to lineages which became considerably evolved into other groups. In order to prevent extreme fragmentation of higher classification it is necessary to erect paraphyletic taxa (cf. McCafferty & Edmunds,1979) and thus accept paraphyly in higher classification of the order.

Paraphyletic lineages within the *Siphlonuridae* are represented by subfamilies *Oniscigastrinae*, *Ameletopsinae* and probably also *Rallidentinae* (cf. Demoulin, 1969). *Oniscigastrinae* although has retained many ancestral siphlonurid features (e.g. arrangement of Malpighian tubules) probably shares a common ancestor with the more derived leptophlebiid--like lineage because of occurrence of strong TAV 6 - TAV 10 (IX) and very derived characters of gonads (cf. Landa, 1969b; Soldán, 1981). Similar conditions (TAV 4 - TAV 10, VIII; TAV 10, IX) were found in the Neotropical genus *Chiloporter* of *Ameletopsinae*. These facts lead Landa (1973) to place this genus, which possesses also differently arranged gills than other *Ameletopsinae*, in a separate phyletic lineage together with *Oniscigastrinae*. The *Rallidentinae* (gills with a primitive filamentous part) differs from other *Siphlonuridae* by the presence of strong TV 2 and ventral nerve cord similar to *Baetidae* but shares remaining characters with *Siphlonurinae*.

Another paraphyletic lineage is represented by the family *Baetidae* characterized first of all by fused nerve connectives. This family is very large, widespread, inhabiting all continental aquatic habitats and with intensive present process of speciation. Common origin of this family can be found with the *Metamonius-Nesameletus* group of the *Siphlonuridae* (Edmunds et al., 1963; Riek, 1973; McCafferty & Edmunds, 1979). This fact is documented by some common characters on gonads and ventral nerve cord. Also the family *Metretopodinae* can be derived directly from *Siphlonurinae* having nearly identical anatomical scheme of internal organs. This group shares most likely common ancestors with the *Siphlonurus-Parameletus* complex of the *Siphlonurinae*. It is, according to our opinion, much more related to *Siphlonurinae* than the family *Baetidae* is.

Further paraphyletic group of siphlonurids is represented by the subfamily *Pseudironinae* (formerly in *Heptageniidae*).Its anatomical scheme (extremely weak or not developed 1-2 ventral anastomoses, gonads in dorsolateral position, primitive arrangement of Malpighian tubules) closely resembles that of *Siphlonurinae*. Apomorphic common characters are partly fused connectives of ventral nerve cord and specialized fore gut (larvae predaceous).

As indicated in the foregoing paragraphs, the lineage of the *Heptagenioidea* (in our sense) had to have split from the siphlonurid ancestor. It consists of more primitive filter-feeders (*Oligoneuriidae*) and more advanced collectors and scrapers (*Heptageniidae*). Anatomical characteristics of these groups is given above. McCafferty & Edmunds (1979) count the synapomorphic adaptations of mouthparts of this lineage stating: "... other than the hypothetical, we know of no 'siphlonurids' which are left to represent this particular lineage."

The family *Leptophlebiidae* representing the other major stem-group of extant *Ephemeroptera* consists of a large number of both relatively very ancestral and highly derived genera with an extremely high species diversity especially in the southern hemisphere. Among very specialized and apomorphic genera there are (as seen in anatomical characters as well) several very primitive genera (e.g. *Leptophlebia* and *Paraleptophlebia* - see Landa et al., 1980).

The superfamily *Ephemeroidea* represents a highly derived group not only as seen in skeletal morphological characters but also from the comparative anatomical point of view.It originates within the leptophlebiid ancestors (cf. an early gill pattern in the *Leptophlebiids* - a simple fork like in recent *Paraleptophlebia* - McCafferty & Edmunds, 1979). On the other hand, Riek (1973) and Peters (pers. comm.) suppose that the primitive gill of *Leptophlebiidae* was not a narrow *Paraleptophlebia*-like gill but a plate-like gill (*Leptophlebia*-like). Since tendencies to burrowing habits throughout the larval stages occur also in "non-burrowing" families *Potamanthidae* and *Euthyplociidae* (McCafferty, 1975) and even in some leptophlebiid larvae (e.g. Australian *Jappa* - see Riek, 1973) it is possible to suppose that these habits were present also in the first ephemeroid. McCafferty (1978) showed that burrowing habits evolved independently in the *Behningiidae*, the *Polymitarcyidae* and the *Ephemeridae-Palingeniidae* lineages.

These groups can also be characterized by the arrangement of the internal organs (cf. Landa,1969b, Soldán, 1981). The family *Behningiidae* still shows some primitive characters (Malpighian tubules) although the arrangement of the tracheal system shares several apomorphic characters with remaining *Ephemeroidea*. The families *Polymitarcyidae* and *Euthyplociidae* are characterized by presence of TV 1 (visceral trachea in mesothorax),anastomoses TAV 4 - TAV 10 (IX) and by four trunks of Malpighian tubules. The families of the *Ephemeridae-Palingeniidae* lineage are characterized by presence of TV 2 (metathoracic) and anastomoses (TAV 4) TAV 5 - TAV 10 (IX) and by six common trunks of Malpighian tubules.Based on the anatomical arrangement we must include also the family *Potamanthidae* into this lineage (cf. Landa, 1973). It probably evolved from the ancestor of the *Ephemeridae* perhaps later than the family *Palingeniidae* had split (*Potamanthidae* anatomically identical with primitive group of genera of the *Ephemeridae* - Landa, 1976,1969b).Tshernova (1980) indicated that these events occurred in the Lower and Middle Jurassic.

To summarize, there are two main lines in the evolution of mayflies (see Fig. XXII/118). Landa (1967, 1969) supposed that they have existed as early as in the Permian, Tshernova (1980) showd their origin in the Triassic or even in the Lower Jurassic. The first line characterized first of all by very simple tracheal system contained in the two main lineages. The more primitive one (Fig. XXII/118) is characterized by absence of anastomoses, well separated nerve ganglia, nearly straight tubules of Malpighian organs entering gut individually, and by the primitive gonads deposited in dorsal or dorsolateral position. It leads to the families *Siphlonuridae* and *Ametropodidae* (primitive branch) and to the *Baetidae*, *Oniscigastridae* and *Ameletopsidae* (advanced branch - anastomoses, specialization of gut in two latter families). The second lineage of the first line leads to the families *Oligoneuriidae* (primitive branch) and *Heptageniidae* (more advanced branch). This lineage is characterized by a tracheal system in the original simple form with presence of 1-2 anastomoses in abdominal segments VIII and IX, by emerging of common trunks in the arrangement of Malpighian tubules and especially by shift of gonads to lateral position to the alimentary canal and diminishing of follicles and ovarioles which became equal in size.

The second main evolutionary line shows profound changes in the tracheal system.Numerous strong anastomoses occur ventrally and numerous visceral tracheae are reduced, the ventral nerve cord becomes more associated, Malpighian tubules specialized and gonads are considerably shifted cranially. This line consists of two main lineages again. The first one (schistonotan) contains the *Leptophlebiidae* (gonads in lateral position, extremely diversified but evolutionary homogeneous anatomically) and the *Ephemeroidea* (more derived, gonad in ventrolateral position, 4-6 trunks of Malpighian tubules, 6-7 strong anastomoses). However, Dr. Peters (pers. comm.) is not convinced that the *Ephemeroidea* arose from the *Leptophlebiinae*. He has yet to find one single external apomorphic character which holds together *Leptophlebiinae* and *Ephemeroidea*.The second lineage (pannotan) comprises two main branches (see Fig. XXII/118).The ephemerelloid-tricorythid branch leads to genera with many anatomical characters retained in nearly ancestral stage (Malpigian tubules, arrangement of testicular follicles) but with very improved tracheal system (contiguous insertions of anastomoses, visceral tracheae and neural tracheae,reduced TV) and considerably shifted gonads cranially. The caenoid (*Caenidae*, *Prosopistomatidae*, *Neoephemeridae* and *Baetiscidae*) branch is represented by the most derived genera of recent mayflies. Despite the absence of anastomoses (might be secondary) they possess highly associated CNS, long projections of the alimentary canal, Malpighian tubules forming "ureter" and gonads shifted sometimes even into head.

Some problems of taxa at the family level

Taking into account basic principles of recently defined classificatory philosophy within the *Ephemeroptera* (McCafferty & Edmunds, 1976, 1979; Edmunds, 1962,1973) and our results of anatomical study we present some taxonomic shifts of taxa at the family level in the foregoing paragraphs.

The former family *Siphlonuridae* (as defined by Edmunds & Traver, 1954; Edmunds et al., 1963, and Demoulin, 1958) represents the most discussed classificatory problem within the *Ephemeroptera* since small groups involved here tend to obscure the definition of either plesiotypic or apotypic groups. First of all, the former subfamilies *Ameletopsinae* and *Oniscigastrinae* have to be removed from the *Siphlonuridae* owing to tendency to form numerous anastomoses (strong anastomoses in *Oniscigastrinae* and *Chiloporter*) and to the dorsolateral position of the gonads (see Soldán, 1981). We classify, as indicated above, the *Oniscigastridae* (*Oniscigaster, Siphlonella* and *Tasmanophlebia*) as a separate family showing certain relationships to the pre-*Leptophlebioidea* ancestor (anastomoses, specialization of gills, two ganglia in abdominal segment VII).

Riek (1973), though leaving the *Oniscigastridae* within the *Siphlonuridae,* showed also its relationships to other groups within clearly separated phyletic lineage (specialization of gills). Landa (1973) established a separate family *Chiloporteridae* for the Neotropical genus *Chiloporter* based on unique occurrence of strong anastomoses and different gill arrangement from other *Ameletopsinae* (cf. Edmunds,1973b). Edmunds (1972) stated: "*Chiloporter* (Chile-Argentina) is clearly a member of the *Ameletopsinae* and shares numerous apomorphic characters with the other three genera, hence, similarity of its tracheal system to higher forms must be explain by parallel evolution." Since *Chiloporter* shows other anatomical characters (gonads of unique arrangement, CNS identical with *Mirawara* and *Chaquihua,* the same apomorphic character of the alimentary canal - occurrence of a crop) and the same autapomorphic arrangement of mouthparts (flagellate palpi) we classify this genus within the family *Ameletopsidae,* as a separate subfamily. Riek (1973), contrary to McCafferty & Edmunds (1979), Edmund et al. (1976) and Tshernova (1980), also separated the family *Ameletopsidae* from the remaining *Siphlonuridae.* This group shows clear relationships to the family *Baetidae* (e.g. arrangement of CNS in *Ameletopsis* etc. - see Landa, 1969b).

On the other hand, the siphlonurid subfamily *Rallidentinae* can be placed in the *Siphlonuridae* although it manifests distinct relationships to the *Baetidae* in the arrangement of the internal organs (Landa,1969b). Landa (1973) and Demoulin (1979, 1974) separated this group from the *Siphlonuridae*.Penniket (1966) and Riek (1973) showed clear relationships to the *Nesameletus-Metamonius* complex of the *Siphlonurinae* (*Nesameletinae* Riek, 1973).

The subfamily *Metretopodinae* (originally in *Ametropodidae* - see Bengtsson, 1917 and Edmunds et al., 1963) manifests nearly identical anatomical scheme with the subfamily *Siphlonurinae* (TV 2 - TV 10,no anastomoses, 8 short buds of Malpighian tubules,connectives of ventral nerve cord fused, identical arrangement of gonads). That is why we classify this group as a subfamily of *Siphlonuridae* although there are some common characters also with the *Baetidae* (McCafferty & Edmunds, 1979). Demoulin (1955b), Tshernova (1970), Riek 1973 and Edmunds (1973b) are of the same opinion, other authors classify this group as a separate family (McCafferty & Edmunds, 1979; Berner, 1978; Edmunds et al., 1976).

Another taxonomic shift is represented by the subfamily *Pseudironinae* (TV 2 - TV 10, weak 1-2 or none anastomoses, gonads in dorsolateral position with testicular follicles of different size, primitive arrangement of Malpighian tubules, specialization of fore gut, predatory habits) which is classified herein as a subfamily of the family *Siphlonurinae*. Edmunds et al. (1963, 1976),McCafferty & Edmunds (1979), Tshernova (1970) and Edmunds & Jensen (1973) refer this subfamily (the only genus *Pseudiron*) to the family *Heptageniidae* although the venation of *Pseudiron* (and that of *Ametropodidae* and *Metretopodinae* as well - see Riek, 1973) and some larval characters (reduced segmentation of hind tarsi and only lateral rows of fringes on cerci) place this subfamily clearly to the *Siphlonuridae*. Burks (1953) referring this genus to *Ametropodidae* (s.lat.) noted also the shape of the larval frons - it is not produced over the labrum as is usual in *Heptageniidae*.

The taxonomic position of the monotypic subfamily *Siphlaenigmatidae* (New Zealand) has been discussed many times (Penniket, 1962; Edmunds et al., 1963; Demoulin, 1968 and others). Riek (1973) first reduced the original family to a subfamily of the *Baetidae*. McCafferty & Edmunds (1979) also showed,besides some morphological characters (narrow glossae and paraglossae in larvae; detached veins IMA and MA_2 and reduced penis in adults), also several behavioral characteristics place it in the family *Baetidae*. Tshernova (1970, 1980) defended a independent position of *Siphlaenigmatidae*. The arrangement of internal organs fully supports the former conclusions being nearly identical with that of the family *Baetidae* (*Baetinae*);only some characters (lacking TV 3,arrangement of gonads) show on its intermediary position between the *Siphlonuridae* and *Baetidae*. We suppose that the subfamilial classification introduced by Kazlauskas (1969) concerning the former *Baetidae* meets the demands of evaluating of numerous genera of the family. The subfamily *Cloeoninae* (=*Callibaetinae* Riek, 1973, syn.n.), although weakly defined in original description, is very well characterized by two rows of relatively minute spines on larval claws (cf. Riek, 1973). There are also some anatomical characters common for *Cloeoninae* (e.g. the arrangement of gonads - Soldán,1981 and others). We attempt to devide all the genera described into these two subfamilies (some of them only tentatively) although we are aware that most of the genera of this family are yet to be described and this problem requires detailed morphological and anatomical study.

The heptageniid lineage (see above) is characterized by strongly depressed larval body and flattened femora.Anatomically,it is characterized by emerging of ventral anastomoses, further reduction of visceral tracheae,shifting of gonads to lateral position and emerging of somewhat more specialized Malpighian tubules.All these features appear within the subfamilies *Isonychiinae* and *Coloburiscinae* formerly classified within the family *Siphlonuridae*.In these groups we can find the same apomorphic characters as in the *Oligoneuriinae* namely the tracheization of accessoric gills (and their occurrence itself) and lacking of the ventral cephalic tracheal trunks besides the characters of external morphology (a double row of long setae on the larval prothoracic femora and tibiae). That is why these subfamilies are now classified within the family *Oligoneuriidae*. Riek (1973) first introduced such a classification. McCafferty & Edmunds (1979) followed this opinion based on principles of higher classification defined earlier.

On the other hand, many retained anatomical siphlonurid characters (e.g. all possible visceral tracheae in *Isonychia*, singly entering malpighian tubules in *Coloburiscus* and *Coloburiscoides*,no anastomoses in *Murphyella*) show an intermediancy of these two subfamilies (cf. Edmunds & Trave,1954; Edmunds et al., 1963,1976; Demoulin,1953; Tshernova, 1970, 1980; Koss & Edmunds, 1974). McCafferty & Edmunds (1979) outlined the relationships of these group using also behavioral characteristics of primitive active strong swimming larvae (*Isonychia*, *Chromarcys*), slow crawlers (*Oligoneuriella*, *Lachlania*) and soft bodied sand dwellers (*Homoeoneuria*, *Oligoneurisca*). Though they evolved from *Isonychia*-like ancestors, McCafferty & Edmunds found the precise point of phyletic origin of the *Isonychiinae* and *Coloburiscinae*, relative to each other, unclear since none of the derived characters of either lineage is shared by the other. The same can be applied also for the anatomical characters.

We fully agree with the recent subfamilial classification of the family *Leptophlebiidae* introduced by Peters (1980).The genera comprising the subfamily *Leptophlebiinae* (e.g. *Leptophlebia*, *Paraleptophlebia*, *Habrophlebia*) are well characterized by the arrangement of the tracheal system and especially the Malpighian tubules (for details see Landa et al.,1980).The more derived subfamily *Atalophlebiinae* consists of a large number of genera (over 80) extremely variable in arrangement of internal organs but, as emphasized above, anagenetically relatively homogeneous (Landa et al., 1980).

Among the *Pannota*, the basic classificatory questions concern the superfamily *Ephemerelloidea*. Since we have no data concerning anatomy of the Neotropical genus *Melanemerella* (larvae yet undescribed) we refer only to subfamilies *Ephemerellinae* and *Teloganodinae* of the family *Ephemerellidae*. *Melanemerellidae* is classified as a member of the family *Ephemerellidae* by Edmunds et al. (1963, 1965), Allen (1965), McCafferty & Edmunds (1979) or the family *Tricorythidae* (Demoulin, 1955c). Based on anatomical study we agree that the *Teloganodinae* appears to be the most ancestral group of the ephemerelloids (cf. McCafferty & Edmunds, 1979) despite some derived characters in the arrangement of gonads (Landa et al.,1982).According to McCafferty & Edmunds (1979) this group also seems to be paraphyletic with both the *Ephemerellidae* and *Tricorythidae* being derived from within it.

The family *Tricorythidae* consists of two heterogeneous groups from the comparative anatomical point of view.The subfamily *Tricorythinae* exhibits apparent relationships to the advanced *Pannota* (especially *Caenidae*) possessing 5 abdominal anastomoses (synapomorphic with several genera of the *Ephemerellidae*) but very derived arrangement of Malpighian tubules and CNS (shift of abdominal ganglia). On the other hand,the subfamilies *Leptohyphinae* and *Dicercomyzinae* have nearly identical scheme with some groups of genera of the family *Ephemerellidae* (Landa et al., 1982) possessing 6 abdominal anastomoses (autapomorphic within *Leptohyphinae*), 6 visceral tracheae and very primitive arrangement of Malpighian tubules. Another characters can be seen also on gonads (see Soldán, 1981). These are the reasons for separating the two latter subfamilies from the *Tricorythidae* and establishing the separate family *Leptohyphidae* (cf. Landa, 1973). Riek (1973) also considers *Leptohyphinae* a separate family. The remaining tricorythid subfamilies *Machadorythinae* and *Ephemerythinae* are left within *Tricorythidae* since their anatomical characters are very poorly known.

Higher classification of the *Ephemeroptera*

A. suborder –*Prothephemeroptera* Demoulin, 1956.

Prothephemeroptera Demoulin, 1956. *Prothephemeroptera*: Demoulin, 1958; Tshernova, 1962, 1970; Carpenter, 1963.
Prothephemeroidea Handlirsch, 1908.
Prothephemeroides Laméere, 1917 (partim).
Triplosobina Tshernova, 1980.

I. superfamily –*Triplosoboidea* Handlirsch, 1908.

Triplosoboidea Handlirsch, 1908. *Triplosoboidea*: Demoulin, 1956, 1958; Tshernova, 1970, 1980.

1. family +*Triplosobidae* Handlirsch, 1908.

Triplosobidae Handlirsch, 1908. *Triplosobidae*: Demoulin, 1956, 1958; Tshernova, 1962, 1970, 1980.
Genera included: +*Triplosoba* Handlirsch, 1908 (Upper Carboniferous).

B. suborder *Schistonota* McCafferty & Edmunds, 1979.

Plectoptera Packard, 1886 (partim). *Plectoptera*: Demoulin, 1956, 1958 (partim); Tshernova, 1970 (partim).
Mesoplectoptères Laméere, 1917.
Plectoptères Laméere, 1917 (partim).
Baetoidea Ulmer, 1920 (partim).
Heptagenioidea Ulmer, 1920 (partim).
Ephemeroidea Ulmer, 1920 (partim).
Permoplectoptera Tillyard, 1932, Tshernova, 1962.
Euplectoptera Tillyard, 1932 (partim); Tshernova, 1962 (partim).
Ephemerina Tshernova, 1980 (partim).
Schistonota McCafferty & Edmunds, 1979.

+) extinct taxa

II. superfamily -*Protereismatoidea* Sellards, 1907.

Protereismatoidea Sellards, 1907. *Protereismatoidea*: Demoulin, 1958; Tshernova, 1970, 1980.

Proteresmatidea: Tshernova, 1962 (partim).

2. family +*Misthodotidae* Tillyard, 1932.

Misthodotidae Tillyard, 1932. *Misthodotidae*: Demoulin, 1958; Tshernova, 1962, 1970, 1980; Carpenter, 1979.

Eudoteridae Demoulin, 1954, 1958; Tshernova, 1962, 1970, 1980.

Genera included: +*Misthodotes* Sellards, 1909 (Lower Permian).

3. family +*Protereismatidae* Sellards, 1907.

Protereismatidae Sellards,1907. *Protereismatidae*: Laméere,1917 (partim); Tillyard, 1932; Demoulin, 1958; Handlirsch, 1919; Carpenter, 1933, 1979; Tshernova, 1962, 1970, 1980; Hubbard & Kukalova-Peck, 1980.

Protereismephemeridae Sellards, 1907.

Kukalovidae Demoulin, 1970; Tshernova, 1980.

Genera included: +*Protereisma* Sellards, 1907 (Lower Permian). - +*Kukalova* Demoulin, 1970 (Lower Permian).

4. family +*Jarmilidae* Demoulin, 1970.

Jarmilidae Demoulin, 1970. *Jarmilidae*: Hubbard & Kukalova-Peck, 1980; Tshernova, 1980.

Genera included: +*Jarmila* Demoulin, 1970 (Lower Permian).

5. family +*Oboriphlebiidae* Hubbard & Kukalova-Peck, 1980.

Oboriphlebiidae Hubbard & Kukalova-Peck, 1980.

Genera included: +*Oboriphlebia* Hubbard & Kukalova-Peck, 1980 (Lower Permian).

6. family +*Mesoplectopteridae* Demoulin, 1955.

Ametropodidae-Mesoplectopterinae Demoulin, 1955.

Protereismidae Laméere, 1917 (partim).

Mesoplectopteridae: Tshernova, 1980.

Genera included: +*Mesoplectopteron* Handlirsch, 1918 (Triassic).

Incertae sedis: +*Phthartus* Handlirsch, 1908 (Permian).

III. superfamily -*Mesephemeroidea* Laméere, 1917

Mesephemeroidea: Tshernova, 1970, 1980.

Mesephemeridea Tshernova, 1962 (partim).

Palingenioidea Demoulin, 1958. (partim).

7. family +*Mesephemeridae* Laméere, 1917.

Mesephemeridae Laméere, 1917 (partim); Carpenter, 1932, 1979, Demoulin, 1958, Tshernova, 1962, 1970, 1980.

Palingenopsidae Martynov, 1938; Carpenter, 1979.

Genera included: +*Mesephemera* Handlirsch, 1903 (Upper Permian). - +*Palingenopsis* Martynov, 1932 (Upper Jurassic).

IV. superfamily -*Litophlebioidea* Hubbard & Riek, 1978*

Litophlebioidea Hubbard & Riek, 1978.

Xenophlebioidea Riek, 1976.

8. family +*Litophlebiidae* Hubbard & Riek, 1978.

Litophlebiidae Hubbard & Riek, 1978.

Xenophlebiidae Riek, 1978.

Genera included: *Litophlebia* Hubbard & Riek, 1978 (Upper Triassic).

V. superfamily *Baetoidea* Leach, 1815.

Baetoidea: Riek, 1973 (partim), McCafferty & Edmunds, 1979.

Siphlonuroidea Spieth, 1933 (partim); Demoulin, 1958; Tshernova, 1962, 1970 (partim), 1980 (partim); Landa, 1967 (partim), 1969 (partim).

Heptagenioidea: Edmunds & Traver, 1954 (partim); Edmunds, 1964 (partim); Edmunds et al., 1963 (partim), 1976 (partim); Demoulin, 1958 (partim); Landa, 1967 (partim), 1969a (partim).

Ephemerelloidea: Landa, 1967 (partim).

9. family *Siphlonuridae* Ulmer, 1920 (1888).

Siphlonuridae Ulmer, 1920 (partim). *Siphlonuridae*: Spieth, 1933 (partim); Ulmer, 1933 (partim); Edmunds & Traver, 1954 (partim); Edmunds, 1962 (partim); Edmunds et al., 1963, (partim), 1976 (partim); Landa, 1967 (partim), 1969a (partim), 1973 (partim); Tshernova, 1970 (partim), 1980

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*) referred to the order *Megasecoptera* (cf. Hubbard & Kukalova-Peck, 1980)

(partim); Demoulin, 1958 (partim); Edmunds, 1972 (partim); Riek, 1973 (partim); McCafferty & Edmunds, 1979 (partim).

Siphlurini: Lameére, 1917; Handlirsch, 1925.

Baetidae-Siphlonurinae: Lestage,1917, Needham et al.,1935, Berner, 1950, Burks, 1953.

Heptageniidae: Edmunds & Traver, 1954 (partim); Edmunds et al., 1963 (partim), 1976 (partim); McCafferty & Edmunds, 1979 (partim).

Ametropodidae: Burks, 1953 (partim), Lestage, 1938 (partim).

a) subfamily *Siphlonurinae* Ulmer, 1920 (1888)

Siphlonurinae: Edmunds & Koss, 1972; Edmunds, 1972; Landa, 1973; Edmunds et al.,1976; McCafferty & Edmunds,1979; Edmunds & Traver, 1954 (partim); Demoulin, 1958 (partim); Edmunds et al., 1963 (partim); Tshernova, 1970 (partim); Riek, 1973 (partim).

Genera included: +*Baltameletus* Demoulin, 1968 (Eocene, Baltic amber). - +*Proameletus* Sinitchenkova,1976 (Lower Cretaceous). - +*Olgisca* Demoulin, 1970 (Upper Jurassic). - *Ameletoides* Tillyard, 1933 (Aus)[*]. *Ameletus* Eaton, 1885 (As,E,N,NA). - *Dipterominus* McLachlan, 1875 (As). - *Edmundsius* Day, 1953 (NA). - *Metamonius* Eaton, 1885 (SA). *Metreletus* Demoulin, 1951 (E). - *Nesameletus* Tillyard, 1933 (NZ). *Parameletus* Bengtsson, 1908 (As,E,NA). - *Siphlonisca* Needham, 1909 (As,NA). - *Siphlonurus* Eaton,1868 (As,E,NA).

b) subfamily *Acanthametropodinae* Edmunds, 1963.

Acanthametropodinae Edmunds et al., 1963 (partim). *Acanthametropodinae*: Edmunds & Koss, 1972; Landa,1973; Riek,1973; McCafferty & Edmunds, 1979; Edmunds et al., 1976; Edmunds, 1972.

Analetridinae Demoulin, 1974.

Genera included: +*Stackelbergisca* Tshernova, 1967 (Middle Jurassic). - *Acanthametropus* Tshernova, 1948 (As,NA). - *Analetris* Edmunds, 1972 (NA). - *Siphluriscus* Ulmer, 1920 (As).

c) subfamily *Metretopodinae* Needham, Traver & Hsu, 1935.

Metretopodinae: Riek, 1973.

Ametropinae Lestage, 1917 (partim).

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[*] Af - Africa including the Canary Islands; As - Asia indluding the East Indies and New Guinea; Aus - Australia and Oceania; E - Europe including Turkey and the Azores; NA - The North America, north of Mexico, including the Hawaian Islands; NZ - New Zealand; SA - The Americas south of Mexico including West Indies; Mad - Madagascar, the Comoro Islands and the Seychelles (cf. Hubbard, 1979).

Ametropodini Handlirsch, 1925 (partim).

Siphloplectonidae Lestage, 1938.

Ametropodidae-Metretopodinae: Ulmer, 1920, 1933, Burks, 1953, Edmunds & Traver, 1954, Edmunds et al., 1963, Demoulin, 1958, Edmunds, 1962, 1972, Landa, 1967, 1969a, 1973.

Metretopinae: Needham et al., (partim), Berner, 1950 (partim), Demoulin, 1958 (partim),

Metretopodidae: Lestage, 1938, Tshernova, 1970, 1980, Edmunds et al., 1979, McCafferty & Edmunds, 1979.

Genera included: *Metretopus* Eaton, 1901 (As,E,NA). - *Siphloplecton* Clemens, 1915 (NA).

d) subfamily *Pseudironinae* Edmunds & Traver, 1954.

Pseudironinae: Riek, 1973.

Ametropidae: Needham et al., 1935; Lestage, 1938; Berner, 1950; Burks, 1953.

Heptageniidae-Psedironinae: Edmunds & Traver, 1954, Demoulin, 1958, Edmunds et al., 1963, 1976, McCafferty & Edmunds, 1979.

Genera included: Pseudiron McDunnough, 1931 (NA).

e) subfamily *Rallidentinae* Penniket, 1966.

Rallidentinae Penniket, 1966. *Rallidentinae*: Riek, 1973; Edmunds et al., 1976; McCafferty & Edmunds, 1979.

Rallidentidae: Landa, 1973.

Genera included: *Rallidens* Penniket, 1966 (NZ).

10. family *Baetidae* Leach, 1815.

Baetidae: Needham et al., 1935 (partim); Lestage, 1917 (partim); Berner, 1950 (partim); Burks,1953 (partim); Edmunds et al., 1963, 1976 (partim); Edmunds, 1962,1972 (partim); Tshernova, 1970,1980 (partim); Landa, 1967, 1969a, 1973 (partim); Ulmer, 1920, 1933, Spieth, 1933; Edmunds & Traver, 1954; Demoulin, 1958; Riek, 1973; McCafferty & Edmunds, 1979.

Baetini Laméere, 1917.

Oligoneuriidae Lestage, 1917 (partim).

Baetidinae Handlirsch, 1925.

a) subfamily *Siphlaenigmatidae* Penniket, 1962.

Siphlaenigmatidae: Edmunds et al., 1962: Tshernova, 1970, 1980; Edmunds et al., 1976.

Siphlaenigmatinae: Riek, 1973; McCafferty & Edmunds, 1979.

Genera included: *Siphlaenigma* Penniket, 1962 (NZ).

b) subfamily *Baetinae* Leach, 1815.

Baetinae (partim) auct. (see above).

Baetidae (partim).

Genera included: *Acentrella* Bengtsson, 1912 (Af,E,As). - *Afrobaetodes* Demoulin, 1970 (Af). - *Apobaetis* Day, 1955 (NA). - *Baetiella* Uéno, 1931 (As). - *Baetis* Leach, 1815 (Af,As,Aus,E,NA,SA,Mad). - *Baetodes* Needham & Murphy, 1924 (SA,NA). - *Bungona* Harker, 1957 (Aus). - *Camelobaetidius* Demoulin,1966 (SA). - *Centroptiloides* Lestage, 1918 (Af,Mad). - *Dactylobaetis* Traver & Edmunds, 1968 (NA,SA). - *Heterocloeon* McDunnough, 1925 (NA). - *Indocloeon* Müller-Liebenau, 1982 (AS) - *Indobaetis* Müller-Liebenau, 1982 (As). - *Jubabaetis* Müller-Liebenau, 1980 (As). - *Nesoptiloides* Demoulin, 1973 (Mad). - *Platybaetis* Müller-Liebenau, 1980 (As). - *Pseudocloeon* Klapálek,1905 (Af,As,E,NA,SA,Mad). - *Rhaptobaetopus* Müller-Liebenau, 1978 (E,As).

c) subfamily *Cloeoninae* Kazlauskas, 1969.

Cloeoninae Kazlauskas, 1969.

Callibaetinae Riek, 1973.

Baetidae (partim).

Baetinae (partim) auct. see above.

Genera included: *Baetopus* Keffermüller,1960 (E,As). - *Callibaetis* Eaton, 1881 (NA,SA). - *Centroptilum* Eaton,1869 (Af,As,Aus,E,NA,Mad). - *Centroptella* Braasch & Soldán, 1980 (As). - *Cloeodes* Traver,1938 (SA). - *Cloeon* Leach, 1815 (Af,As,Aus,E,NA,SA,Mad). - *Notobaetis* Morihara & Edmunds, 1980 (SA). - *Paracloeodes* Day, 1955 (NA,SA). *Procloeon* Bengtsson, 1915 (Af,As,E). - *Symbiocloeon* Müller-Liebenau, 1979 (As).

11. family *Oniscigastridae* Laméere, 1917.

Oniscigastridae: Landa, 1973.

Oniscigastrina Laméere, 1917

Siphlonuridae: Edmunds & Traver, 1954 (partim); Demoulin, 1958 (partim); Edmunds, 1962, 1972 (partim); Riek, 1973 (partim); McCafferty & Edmunds, 1979.

Genera included: *Oniscigaster* McLachlan,1873 (NZ). - *Siphlonella* Needham & Murphy, 1924 (SA). - *Tasmanophlebia* Tillyard, 1921 (Aus).

12. family *Ameletopsidae* Edmunds, 1957, stat. nov.

Ameletopsidae: Landa, 1973, Riek, 1973.

Siphlonuridae: Edmunds & Traver, 1954 (partim); Demoulin, 1958 (partim); Edmunds, 1972 (partim); Edmunds et al., 1963, 1976 (partim); Tshernova, 1970, 1980 (partim); McCafferty & Edmunds, 1979 (partim).

a) subfamily *Ameletopsinae* Edmunds, 1957, stat. nov.

Ameletopsinae: Demoulin, 1958 (partim); Edmunds, 1972 (partim); Edmunds et al., 1963, 1976 (partim); Tshernova, 1970, 1980 (partim); McCafferty & Edmunds, 1979 (partim).

Genera included: +*Balticophlebia* Demoulin, 1968 (Eocene,Baltic amber). - *Ameletopsis* Phillips, 1930 NZ . - *Chaquihua* Demoulin, 1955 (SA). - *Mirawara* Haker, 1954 (Aus).

b) subfamily *Chiloporterinae* Landa, 1973, stat. nov.

Ameletopsinae (partim) auct. (see above).

Chiloporteridae Landa, 1973.

Genera included: *Chiloporter* Lestage, 1931 (SA).

13. family *Ametropodidae* Bengtsson, 1913.

Ametropodidae: Lestage, 1938; Tshernova 1970,1980; McCafferty & Edmunds, 1979; Ulmer, 1920, 1933 (partim); Edmunds & Traver, 1954 (partim); Edmunds, 1958, 1962, 1972 (partim); Edmunds et al., 1963 (partim); Burks, 1953 (partim); Landa, 1967, 1969a, 1973 (partim).

Ametropini Laméere, 1917.

Baeridae: Lestage, 1917 (partim).

Siphlonuridae: Riek, 1973 (partim); Demoulin, 1951 (partim); Tshernova, 1948 (partim).

Metretopsinae: Needham et al., 1935; Berner, 1950.

Genera included: +*Brevitibia* Demoulin, 1968 (Eocene, Baltic amber). - *Ametropus* Albarda, 1878 (As,E,NA).

VI. superfamily ***Heptagenioidea*** Needham, 1901.

Heptagenioidea: Edmunds & Traver, 1954 (partim); Edmunds et al., 1964 (partim), 1976 (partim); Tshernova, 1962, 1970, 1980 (partim); Demoulin, 1958 (partim); Edmunds, 1962 (partim); Landa, 1967,1969a (partim); Riek, 1973.

Baetoidea: Riek, 1973 (partim); McCafferty & Edmunds, 1979 (partim),

Siphlonuroides: Tshernova, 1962 (partim), 1970 (partim), 1980 (partim); Spieth, 1934 (partim); Landa, 1967 (partim), 1969a (partim).

Oligoneurioides: Demoulin, 1958 (partim); Tshernova, 1962 (partim), 1970 (partim), 1980 (partim).

14. family +*Epeoromimidae* Tshernova, 1969.

Epeoromimidae Tshernova, 1969. Epeoromimidae: Tshernova, 1970, 1980.

Heptageniidae:Demoulin, 1969 (partim).

Genera included: +*Epeoromimus* Tshernova, 1969 (Lower Jurassic).

15. family *Oligoneuriidae* Ulmer, 1914.

Oligoneuriidae: Lestage, 1917 (partim); Ulmer, 1920 (partim), 1933 (partim); Edmunds & Traver, 1954 (partim); Demoulin, 1958 (partim); Edmunds, 1962 (partim), 1972 (partim); Tshernova, 1962 (partim), 1970 (partim), 1980 (partim); Edmunds et al., 1963 (partim), 1976 (partim); Burks, 1953 (partim); Landa, 1967 (partim), 1969a (partim), 1973 (partim); Riek, 1973; McCafferty & Edmunds, 1979.

Siphlurini: Laméere, 1917 (partim).

Oligoneuriinae: Handlirsch, 1925.

Baetidae: Needham et al., 1935 (partim); Berner, 1950 (partim).

a) subfamily *Isonychiinae* Edmunds & Traver, 1954.

Isonychiinae: Edmunds, 1972, 1962; Edmunds et al., 1963, 1976; Riek, 1973; McCafferty & Edmunds, 1979.

Oligoneurina: Laméere, 1917 (partim).

Baetidae-Isonychiinae:Burks, 1953.

Siphlonuridae: Needham et al., 1935 (partim); Berner, 1950 (partim).

Isonychiidae: Edmunds & Traver, 1954 (partim); Demoulin, 1958 (partim); Kimmins, 1960 (partim); Landa, 1967, 1969a, 1973; Tshernova, 1970, 1980.

Genera included: +*Siphlurites* Cockerell, 1923 (Miocene). - *Isonychia* Eaton, 1871 (As,E,NA,SA) (sg. Isonychia s.str.; Prionoides Kondratieff & Voshell, 1983).

b) subfamily *Coloburiscinae* Edmunds, 1963.

Coloburiscinae: Edmunds et al., 1963, 1976, Edmunds, 1972, Riek, 1973, McCafferty & Edmunds, 1979.

Isonychiidae: Edmunds & Traver, 1954 (partim), Demoulin, 1958 (partim), 1970 (partim),

Coloburiscidae: Landa, 1973.

Genera included: +*Cronicus* Eaton, 1871 (Eocene, Baltic amber). - *Coloburiscoides* Lestage, 1935 (Aus). - *Coloburiscus* Eaton, 1888 (NZ). - *Murphyella* Lestage, 1929 (SA).

c) subfamily *Chromarcyinae* Demoulin, 1958.

Chromarcyinae: Edmunds et al., 1963, 1976; Riek, 1973; McCafferty & Edmunds, 1979.

Genera included: *Chromarcys* Navás, 1932 (As).

d) subfamily *Oligoneuriinae* Ulmer, 1914.

Oligoneuriinae: Edmunds & Traver, 1954, Demoulin, 1958, Edmunds et al., 1963, 1976, Riek, 1973, McCafferty & Edmunds, 1979.

Oligoneuriina: Laméere, 1917 (partim).

Genera included: +*Protoligoneuria* Demoulin, 1955 (Eocene?). - *Elassoneuria* Eaton, 1881 (sg. *Elassoneuria* s.str., *Madeconeuria* Demoulin, 1973) (Af,Mad). - *Homoeoneuria* Eaton, 1881 (NA,SA). - *Lachlania* Hagen, 1868 (NA,SA). - *Oligoneuria* Pictet, 1844 (SA). - *Oligoneuriella* Ulmer, 1924 (Af,As,E). - *Oligoneurioides* Demoulin, 1955 (SA). - *Oligoneuriopsis* Crass,1947 (Af). - *Oligoneurisca* Lestage,1938 (E).- *Spaniophlebia* Eaton, 1881 (SA).

16. family *Heptageniidae* Needham, 1901.

Heptageniidae: Riek,1973; Lestage, 1917 (partim); Spieth, 1933 (partim); Needham et al., 1935 (partim); Berner, 1950 (partim); Burks, 1953 (partim); Demoulin, 1958 (partim); Edmunds, 1962 (partim), 1972, (partim); Edmunds & Traver,1954 (partim); Edmunds et al., 1963 (partim),1976 (partim); Landa, 1967 (partim), 1969a (partim). 1973 (partim); Tshernova, 1970 (partim), 1962 (partim), 1980 (partim); McCafferty & Edmunds, 1979 (partim).

a) subfamily *Arthropleinae* Balthasar, 1939.

Arthropleinae: Demoulin, 1956,1958, Edmunds, 1962, 1972; Edmunds et al., 1963, 1976.

Heptageniinae: Edmunds & Traver, 1954 (partim); Burks, 1953 (partim); Berner, 1950 (partim).

Arthropleidae Balthasar, 1939: Landa, 1967, 1969a, 1973.

Genera included: +*Electrogenia* Demoulin, 1956 (Eocene, Baltic amber). - *Arthroplea* Bengtsson, 1909 (E,NA).

b) subfamily *Heptageniinae* Needham, 1901.

Heptageniinae: Lestage,1917; Demoulin, 1958; Edmunds et al., 1963, 1976; Edmunds, 1972; McCafferty & Edmunds, 1979.

Rhithrogeninae Lestage, 1917.

Genera included: +*Miocoenogenia* Tshernova, 1969 (Miocene). - +*Succinogenia* Demoulin, 1965 (Eocene, Baltic amber). - *Afghanurus* Demoulin, 1964 (As). - *Afronurus* Lestage,1924 (Af,As,E). - *Atopopus* Eaton, 1881 (As). - *Belovius* Tshernova, 1981 (As) - *Bleptus* Eaton, 1885 (As). - *Cinygma* Eaton, 1885 (As,NA). - *Cinygmina* Kimmins, 1937 (As). - *Cinygmoides* Matsumura 1931 (As). - *Cinygmula* McDunnough, 1933 (As,NA). - *Compsoneuria* Eaton, 1881 (As). - *Compsoneuriella* Ulmer, 1939 (Af,As,Mad). - *Ecdyonuroides* Dang,1967 (As). - *Ecdyonurus* Eaton, 1871 (Af,As,E). - *Epeiron* Demoulin, 1964 (As,E). - *Epeorella* Ulmer, 1939 (As). - *Epeorus* Eaton, 1881 (As,E,NA,SA) (sg. *Epeorus* s.str., *Ironopsis* Traver, 1935). - *Iron* Eaton, 1883 (As,E,NA). - *Ironodes* Traver, 1935 (NA). - *Leucrocuta* Flowers, 1980

(NA). - *MacDunnoa* Lehmkuhl, 1979 (NA). - *Nixe* Flowers,1980 (NA)(sg. *Nixe* s.str., *Akkarion* Flowers, 1980). - *Notacanthurus* Tshernova, 1974 (As). - *Ororotsia* Traver,1939 (As). - *Rhithrogena* Eaton, 1881 (Af,As,E,NA,SA). - *Rhithrogeniella* Ulmer, 1939 (As). - *Sigmoneuria* Demoulin, 1964 (As). - *Stenacron* Jensen, 1974 (NA). - *Stenonema* Traver, 1933 (NA) (sg. *Stenonema* s.str., *Maccaffertium* Bednarik, 1979). - *Thalerosphyrus* Eaton, 1881 (As). - *Paegniodes* Eaton, 1881 (As).

c) subfamily *Anepeorinae* Edmunds & Traver, 1954.

Heptageniinae: Needham et al., 1935 (partim); Berner, 1950 (partim); Burks, 1953 (partim).

Pseudironinae Edmunds & Traver,1954. *Pseudironinae*: Edmunds et al.,1963, 1976; Edmunds, 1972; Landa, 1967; Demoulin, 1958; McCafferty & Edmunds, 1979.

Genera included: *Anepeorus* McDunnough, 1925 (NA,As?).

d) subfamily *Spinadinae* Edmunds & Jensen, 1974.

Spinadinae Edmunds & Jensen, 1974. *Spinadinae*: Edmunds et al., 1976, McCafferty & Edmunds, 1979.

Genera included: *Spinadis* Edmunds & Jensen, 1974 (NA).

VII. superfamily *Leptophlebioidea* Banks, 1900.

Leptophlebioidea: Edmunds & Traver, 1954 (partim); Edmunds, 1962 (partim); Edmunds et al.,1963 (partim), 1976 (partim); Landa, 1967 (partim), 1969 (partim); Riek, 1973 (partim); Tshernova 1980 (partim); McCafferty & Edmunds, 1979.

Siphlonuroidea: Tshernova, 1962 (partim), 1970 (partim).

Heptagenioidea: Demoulin, 1958 (partim).

Ephemeroidea: Spieth, 1933 (partim).

Oligoneurioidea: Tshernova, 1970 (partim).

17. family *Leptophlebiidae* Banks, 1900.

Leptophlebiidae: Spieth, 1933; Burks, 1953; Ulmer, 1920, 1933; Edmunds & Traver, 1954; Demoulin, 1958; Tshernova, 1962, 1970, 1980; Edmunds,1962, 1972; Edmunds et al., 1963, 1976; Landa, 1967, 1969a; McCafferty & Edmunds, 1979.

Leptophlebiinae: Lameére, 1917.

*Leptophlebini*Handlirsch, 1925.

a) subfamily +*Mesonetinae* Tshernova, 1969.

Mesonetinae: Tshernova, 1971; Demoulin, 1969.

Ametropodidae: Demoulin, 1968 (partim).
Ephemerellidae: Tshernova, 1962 (partim).
Mesonetidae: Tshernova, 1969, 1970.
Genera included: +*Mesoneta Brauer, Redtenbacher* & Ganglbauer, 1889 (Jurassic). - +*Cretoneta* Tshernova, 1971 (Upper Cretaceous).

b) subfamily *Leptophlebiinae* Banks, 1900.
Leptophlebiinae (partim) auct. (see above).
Leptophlebiinae: Peters, 1980.
Genera included: *Calliarcys* Eaton, 1881 (E). - *Dipterophlebiodes* Demoulin, 1954 (As). - *Gilliesia* Peters & Edmunds,1970 (As). - *Habroleptoides* Schoenemund, 1930 (Af,E). - *Habrophlebia* Eaton, 1881 (E,NA) (sg. *Habrophlebia* s.str., *Hesperaphlebia* Peters, 1979). - *Habrophlebiodes* Ulmer, 1920 (As,NA,SA?). - *Leptophlebia* Westwood, 1840 (As,E,NA). - *Paraleptophlebia* Lestage, 1917 (As,E,NA).

c) subfamily *Atalophlebiinae* Peters, 1980.
Atalophlebiinae Peters, 1980.
Genera included: +*Blasturophlebia* Demoulin, 1968 (Eocene, Baltic amber). - +*Lepismophlebia* Demoulin, 1958 (Miocene). - +*Xenophlebia* Demoulin,1968 (Eocene, Baltic amber). - *Adenophlebia* Eaton, 1881 (Af). - *Adenophlebiodes* Ulmer, 1924 (Af) (*Adenophlebiodes* s.str., *Hyalophlebia* Demoulin, 1955). - *Aprionyx* Barnard,1940 (Af) - *Archethraulodes* Pescador & Peters, 1982 (SA). - *Arachnocolus* Towns & Peters,1979 (NZ). - *Askola* Peters,1969 (SA). - *Atalomicria* Harker, 1954 (Aus). - *Atalonella* Needham & Murphy, 1924 (Aus). - *Atalophlebia* Eaton, 1881 (Aus,SA). - *Atalophlebioides* Phillips, 1930 (Aus, NZ). - *Atopophlebia* Flowers, 1980 (SA). - *Austroclima* Towns & Peters, 1979 (NZ). - *Borinquena* Traver, 1938 (SA) (*Boriquena* s.str., *Australphlebia* Peters, 1971). - *Careospina* Peters, 1971 (SA). - *Kariona* Peters & Peters,1981 (Aus). - *Chiusanophlebia* Uéno, 1969 (As). - *Choroterpes* Eaton,1871 (Af,As,E,NA,SA) *Choroterpes* s. str., *Euthraulus* Barnard, 1932, *Neochoroterpes* Allen, 1974). - *Choroterpides* Ulmer, 1939 (As). - *Celiphlebia* Peters & Peters, 1979 (Aus). - *Coula* Peters & Peters, 1979 (As). - *Cryophlebia* Towns & Peters, 1979 (NZ). - - *Cryptopenella* Gillies, 1951 (As). - *Dactylophlebia* Pescador & Peters, 1980 (SA). - *Deleatidium* Eaton, 1899 (Aus,SA). - *Demoulinellus* Pescador & Peters, 1982 (SA). - *Farrodes* Peters, 1971 (SA). - *Fittkaulus* Savage & Peters, 1978 (SA). - *Fulleta* Navás, 1930 (Af). - *Fulletomimus* Demoulin, 1956 (Af). - *Hagenulodes* Ulmer, 1920 (Mad). - *Hagenulopsis* Ulmer, 1920 (SA). - *Hagenulus* Eaton, 1882 (As,SA). - *Hapsiphlebia* Peters & Edmunds, 1972 (SA). - *Hermanella* Needham & Murphy, 1924 (SA). - *Hermenellopsis* Demoulin,1955 (SA). - *Homothraulus* Demoulin,1955 (SA). - *Indialis* Peters

& Edmunds, 1970 (As). - *Isca* Gillies, 1951 (Sa) (*Isca* s. str., *Minyphlebia* Peters & Edmunds, 1970, *Tanycola* Peters & Edmunds,1970). - *Isothraulus* Towns & Peters, 1979 (NZ). - *Jappa* Harker, 1954 (Aus). - *Kimminsula* Peters & Edmunds, 1970 (As). - *Kirrara* Harker, 1954 (Aus). - *Leentvaaria* Demoulin, 1966 (SA). - *Lepegenia* Peters, Peters & Edmunds, 1978 (Aus). - *Lepeorus* Peters, Peters & Edmunds, 1978 Aus . - *Magallanella* Pescador & Peters, 1980 (SA). - *Maheathraulus* Peters,Gillies & Edmunds, 1964 (Mad). - *Massartella* Lestage, 1930 (SA). - *Massartellopsis* Demoulin, 1955 (SA). - *Mauiulus* Towns & Peters,1979 (NZ). - *Megaglena* Peters & Edmunds, 1970 (As). - *Meridialaris* Peters & Edmunds, 1972 (SA). - *Microphlebia* Savage & Peters 1982 (SA). - *Miroculis* Edmunds, 1963 (SA) (*Miroculis* s.str., *Ommaethus* Savage & Peters 1982, *Atroari* Savage & Peters, 1982; *Yaruma* Savage & Peters, 1982). - *Miroculitus* Savage & Peters, 1982 (SA). - *Mathanella* Demoulin, 1955 (As). - *Neohagenulus* Traver, 1938 (SA). - *Nesophlebia* Peters & Edmunds, 1964 (Mad). - *Notachalcus* Peters & Peters,1981 (Aus). - *Notophlebia* Peters & Edmunds 1970 (As). - *Nousia* Navás, 1918 (SA). - *Papposa* Peters & Peters, 1981 (Aus). - *Peloracantha* Peters & Peters, 1979 (Aus). - *Penaphlebia* Peters & Edmunds, 1972 (SA). - *Penniketellus* Towns & Peters,1979 (NZ). - *Perissophlebiodes* Savage 1983 (As). - *Petersophlebia* Demoulin,1973 (Mad). - *Polythelais* Demoulin,1973 (Mad). - *Poya* Peters & Peters, 1979 (Aus) - *Rhigotopus* Pescador & Peters, 1982 (SA). - *Simothraulopsis* Demoulin, 1966 (SA). - *Simothraulus* Ulmer, 1939 (As) - *Secochela* Pescador & Peters, 1982 (SA). - *Terpides* Demoulin, 1966 (SA). - *Thraulodes* Ulmer, 1920 (NA,SA). - *Thraulophlebia* Demoulin, 1955 (Aus). - *Thraulus* Eaton, 1881 (Af,Aus,As,E). - *Tindea* Peters & Peters, 1979 (Aus). - *Traverella* Edmunds, 1948 (NA,SA). - *Traverina* Peters, 1971 (SA). - *Ulmeritus* Traver, 1956 (SA) (*Ulmeritus* s.str., *Pseudulmeritus* Traver, 1959, *Ulmeritoides* Traver, 1959). - *Ulmerophlebia* Demoulin, 1955 (Aus, Mad). - *Zephlebia* Penniket, 1961 (NZ) (*Zephlebia* s. str., *Neozephlebia* Penniket, 1961).

Incertae sedis: +*Mesobaetis* Brauer, Redtenbacher & *Ganglbauer, 1889* (Lower Jurassic).

VIII. superfamily *Ephemeroidea* Leach, 1815.

Ephemeroidea: Demoulin, 1958,(partim), 1961 (partim); Spieth, 1933 (partim); Edmunds & Traver, 1954; Tshernova, 1962, 1970, 1980; Riek, 1973; McCafferty & Edmunds, 1979.

*Ephemerinae*Handlirsch, 1925.

Ephemeridae: Needham et al., 1935; Berner, 1950; Burks, 1953.

Palingenioidea: Demoulin, 1958 (partim); 1961 (partim).

18. family *Behningiidae* Motas & Bacesco, 1937.

Behningiidae Motas & Bacesco. *Behningiidae*: Demoulin,1952,1958; Edmunds, 1962, 1972; Edmunds et al., 1963, 1976; Edmunds & Traver, 1954, 1959; Tshernova, 1962, 1970, 1980; Landa, 1967, 1969a, 1973; Riek,1973, McCafferty & Edmunds, 1979.

Oligoneuriidae: Lestage, 1938 (partim).

Genera included: +*Archaeobehningia* Tshernova, 1978 (Upper Jurassic). - - *Behningia* Lestage, 1929 (As,E). - *Dolania* Edmunds & Traver, 1959 (NA). - *Protobehningia* Tshernova, 1960 (As).

19. family *Potamanthidae* Albarda in Selys-Longchamps, 1888.

Potamanthidae: Ulmer, 1920,1933; Edmunds & Traver, 1954; Demoulin, 1958; Edmunds, 1962, 1972; Tshernova, 1962, 1970, 1980; Edmunds et al., 1963, 1976; Landa, 1967, 1969a, 1973; McCafferty & Edmunds, 1979.

Potamanthini: Laméere, 1917; Handlirsch, 1925.

Potamanthinae: Lestage, 1917; Needham et al., 1936; Berner, 1950; Burks, 1953.

Genera included: *Neopotamanthodes* Hsu, 1938 (As). - *Potamanthindus* Lestage, 1930 (As). - *Potamanthodes* Ulmer, 1920 (As). - *Potamanthus* Pictet,1843 (Af,As,E,NA,SA?). - *Rhoenanthopsis* Ulmer, 1932 (As). - *Rhoenanthus* Eaton, 1881 (As).

20. family *Euthyplociidae* Lestage, 1921.

Euthyplociidae: Edmunds & Traver, 1954; Demoulin, 1958; Tshernova, 1962, 1970, 1980; Edmunds, 1962, 1972; Edmunds et al., 1963, 1976; Landa,1967, 1969a, 1973; McCafferty & Edmunds, 1979.

Euthyplociinae: Lestage, 1921.

Ephemerini: Laméere, 1917 (partim).

Polymitarcyini: Handlirsch, 1925 (partim).

Polymitarcyinae: Lestage, 1917 (partim).

a) subfamily *Euthyplociinae* Lestage, 1921.

Euthyplociidae auct. (partim), see above.

Genera included: *Campylocia* Needham & Murphy, 1924 (SA). - *Ethyplocia* Eaton, 1871 (As,SA). - *Mesoplocia* Demoulin, 1952 (SA). - *Polyplocia* Lestage, 1921 (SA). - *Proboscíplocia* Demoulin, 1966 (Mad).

b) subfamily *Exenthyplociinae* Gillies, 1980.

Extenthyplociinae Gillies, 1980.

Euthyplociidae auct. (partim) - see above.

Genera included: *Afroplocia* Lestage, 1939 (Af). - *Exeuthyplocia* Lestage 1919 (Af).

21. family *Polymitarcyidae* Banks, 1900.

Polymitarcyidae: Edmunds & Traver, 1954; Demoulin, 1958; Ulmer, 1920, 1933; Tshernova, 1962, 1970, 1980; Edmunds, 1962, 1972; Edmunds et al., 1963, 1976; Landa, 1967, 1969a, 1973; McCafferty & Edmunds, 1979.

a) subfamily *Polymitarcyinae* Banks, 1900.

Polymitarcyinae: Edmunds & Traver, 1954; Demoulin, 1958; Edmunds et al., 1963, 1976; Edmunds, 1972; Landa, 1967; McCafferty & Edmunds, 1979.

Genera included: *Ephoron* Williamson, 1802 (Af,As,E,NA).

b) subfamily *Campsurinae* Traver in Needham et al., 1935.

Campsurinae Traver, 1935. *Campsurinae*: Demoulin, 1958 (partim); Berner, 1950; Burks, 1953; Edmunds & Traver, 1954; Edmunds,1962; Edmunds et al., 1963, 1976; Landa, 1967; McCafferty & Edmunds, 1979.

Campsuridae: Tshernova, 1970, 1980.

Genera included: *Campsurus* Eaton, 1868 (NA,SA). - *Tortopus* Needham & Murphy, 1924 (NA,SA).

c) subfamily *Asthenopodinae* Edmunds & Traver, 1954.

Asthenopodinae Edmunds & Traver, 1954.

Campsurinae: Demoulin, 1958 (partim).

Campsuridae: Tshernova, 1970, 1980 (partim).

Genera included: *Asthenopodes* Ulmer, 1920 SA . - *Asthenopus* Eaton, 1871 (SA). - *Povilla* Navás, 1912 (Af,As).

22. family *Ephemeridae* Leach, 1815.

Ephemeridae: Edmunds & Traver,1954 (partim); Ulmer, 1920, 1933 (partim); Spieth,1933 (partim); Demoulin, 1958 (partim); Tshernova, 1962 (partim), 1970 (partim), 1980 (partim); Edmunds et al., 1963 (partim); Landa, 1967 (partim), 1969a (partim), 1973 (partim); Edmunds, 1962 (partim), 1972 (partim); Riek, 1973 (partim); McCafferty & Edmunds, 1976, 1979; Edmunds et al., 1976.

Ephemerini: Laméere, 1917; Handlirsch, 1925.

Ephemerinae: Needham et al., 1935 (partim); Berner,1950 (partim); Burks, 1953 (partim); Lestage, 1917 (partim).

Ichthybotidae: Demoulin, 1957, 1958; Tshernova, 1970, 1980.

Genera included: +*Parabaetis* Haupt, 1956 (Eocene). - *Afromera* Demoulin, 1955 (Af). - *Eatonica* Navás, 1913 (Af,Mad). - *Eatonigenia* Ulmer, 1939

(As). - *Ephemera* Linné, 1758 (Af,As,E,NA) (*Ephemera* s.str., *Aethephemera* McCafferty & Edmunds, 1973, *Dicrephemera* McCafferty & Edmunds, 1973). - *Hexagenia* Walsh,1863 (As?NA,SA)(*Hexagenia* s.str., *Pseueatonica* Spieth, 1941). - *Ichthybotus* Eaton, 1899 (NZ). - *Litobrancha* McCafferty, 1971 (NA).

23. family *Palingeniidae* Albarda in Selys-Longchamps, 1888.

Palingeniidae: McCafferty & Edmunds, 1976, 1979; Edmunds et al., 1976.

Ephemerini: Laméere, 1917 (partim).

Palingeniini: Handlirsch, 1925.

Palingeniinae: Lestage, 1917; Ulmer, 1920, 1933; Needham et al., 1935; Berner,1950; Burks,1953; Edmunds & Traver,1954; Demoulin, 1958; Edmunds, 1962, 1972; Tshernova, 1962, 1970, 1980; Edmunds et al., 1963; Landa, 1967, 1969a, 1973.

a) subfamily *Palingeniinae* Albarda in Selys-Longchamps, 1888.

Palingeniinae: McCafferty & Edmunds, 1976, 1979; Edmunds et al., 1976.

Palingeniidae auct. (see above).

Genera included: +*Mesogenesia* Tshernova, 1977 (Upper Jurassic). - Anagenesia Eaton, 1883 (As). - *Chankagenesia* Buldovskij, 1935 (As). - *Cheirogenesia* Demoulin,1952 (Mad). - *Mortogenesia* Lestage, 1923 (As). - *Palingenia* Burmeister, 1839 (Af?As,E,SA?). - *Plethogenesia* Ulmer, 1920 (As).

b) subfamily *Pentageniinae* McCafferty, 1972.

Pentageniinae: McCafferty & Edmunds, 1976, 1979, Edmunds et al., 1979.

Pentageniidae McCafferty, 1972.

Ephemeridae (partim) auct. (see above).

Genera included: *Pentagenia* Walsh, 1863 (NA).

IX. superfamily -*Hexagenitoidea* Laméere, 1917.

Hexagenitoidea: Tshernova, 1970, 1980.

Paedephemeridea: Tshernova, 1962.

Oligoneurioidea: Demoulin, 1958 (partim).

24. family +*Hexagenitidae* Laméere, 1917.

Hexagenitidae: Tshernova, 1970, 1980.

Prosopistomatidae: Laméere, 1917 (partim).

Paedephemeridae Laméere, 1917, Demoulin, 1958 (partim).

Ephemeropsidae Cockerell, 1924.

Stenodicranidae Demoulin, 1954.

Genera included: +*Ephemeropsis* Eichwald, 1864 (Upper Jurassic). - +*Hexagenites* Scudder, 1880 (Upper Jurassic).

25. family +*Aenigmephemeridae* Tshernova, 1968.

Aenigmephemeridae Tshernova, 1968. *Aenigmephemeridae*: Tshernova, 1970, 1980.

Genera included: +*Aenigmephemera* Tshernova, 1968 (Middle Jurassic).

Incertae sedis:

26. family +*Aphelophlebodidae*, Pierce, 1945.

Aphelophlebodidae Pierce, 1945.

Genera included: + *Aphelophlebia* Pierce, 1945 (Upper Miocene).

C. subordo *Pannota* McCafferty & Edmunds, 1979.

Pannota McCafferty & Edmunds, 1979.

Plectoptera Packard, 1886 (partim); Demoulin, 1956, 1958, Tshernova,1970 (partim).

Plectopteres Laméere, 1917 (partim).

Baetoidea: Ulmer, 1920 (partim).

Heptagenioidea: Ulmer, 1920 (partim).

Euplectoptera Tillyard, 1932 (partim), Tshernova, 1962 (partim).

Ephemerina: Tshernova, 1980 (partim).

X. superfamily *Ephemerelloidea* Klapálek, 1909.

Ephemerelloidea: Demoulin, 1958 (partim); Landa, 1967 (partim); Tshernova, 1970 (partim), 1980; McCafferty & Edmunds, 1979.

Ephemeroidea: Spieth, 1933 (partim).

Siphlonuroidea: Tshernova, 1962 (partim).

Leptophlebioidea: Edmunds & Traver, 1954 (partim); Edmunds, 1962 (partim); Edmunds et al.,1963 (partim), 1976 (partim); Landa, 1967 (partim); 1969a (partim); Riek, 1973 (partim).

27. family *Ephemerellidae* Klapálek, 1909.

Ephemerellidae: Edmunds & Traver, 1954; Ulmer, 1920, 1933; Spieth, 1933; Burks, 1953; Edmunds, 1962, 1972; Edmunds et al., 1963, 1976; Tshernova, 1970,1980; Allen, 1965; Landa, 1967, 1969a, 1973; Riek, 1973; McCafferty & Edmunds, 1979.

Ephemerellini Laméere, 1917; Handlirsch, 1925.

Baetidae-Ephemerellinae: Lestage, 1917; Needham et al., 1935; Berner, 1950.

Tricorythidae: Demoulin, 1955 (partim), 1958 (partim).

a) subfamily *Teloganodinae* Allen, 1965.

Teloganodinae: Allen, 1965. *Teloganodinae*: Edmunds,1972;Edmunds et al., 1976; McCafferty & Edmunds, 1976.

Ephemerellinae: Edmunds & Traver, 1954 (partim); Demoulin,1958 (partim); Edmunds et al., 1963 (partim); Landa, 1967 (partim); Tshernova, 1970 (partim).

Genera included: *Austremerella* Riek,1966 Aus . - *Ephemerellina* Lestage, 1924 (Af,As)(*Ephemerellina* s.str. *Lithogloea* Barnard, 1932).
- *Lestagella* Demoulin, 1970 (Af). - *Manohyphella* Allen, 1973 (Mad).
- *Teloganella* Ulmer, 1939 (As). - *Teloganodes* Eaton, 1882 (As).

b) subfamily *Ephemerellinae* Klapálek, 1909.

Ephemerellinae: Allen, 1965.

Ephemerellinae (partim) auct. (see above).

Genera included: a) tribe *Ephemerellini* Laméere, 1917: *Acerella* Allen, 1971 (As). - *Attenella* Edmunds, 1971 (NA). - *Caudatella* Edmunds, 1959 (NA). - *Cincticostella* Allen,1971 (As) (*Cincticostella* s. str.,*Rhionella* Allen, 1980, *Vietnamella* Tshernova, 1972 . - *Crinitella* Allen & Edmunds, 1963 (As). - *Dannella* Edmunds, 1959 (NA) (*Dannella* s.str., *Dentanella* Allen, 1980). - *Drunella* Needham, 1909 (As, NA) (*Drunella* s.str., *Tribrachella* Allen, 1980, *Unirhachella* Allen, 1980, *Myllonella* Allen, 1980, *Eatonella* Needham, 1927). - *Ephemerella* Walsh,1862 (As,Af,E,NA). - *Eurylophella* Tiensuu, 1935 (As,E,NA). - *Serratella* Edmunds, 1959 (NA,As). - *Timpanoga* Needham, 1927 (NA). - *Teloganopsis* Ulmer, 1939 (As). - *Torleya* Lestage, 1917 (E,As). - *Uracanthella* Belov, 1979 (As). b) tribe *Hyrtanellini* Allen, 1980: *Hyrtanella* Allen & Edmunds, 1976 (As).

c) subfamily *Melanemerellinae* Demoulin, 1955.

Melanemerellinae Demoulin, 1955. *Melanemerellinae*: Demoulin, 1958; Edmunds et al., 1963, 1976; Edmunds, 1972; McCafferty & Edmunds, 1979.

Ephemerellinae: Edmunds & Traver, 1954 (partim).

Genera included: *Melanemerella* Ulmer, 1920 (SA).

Incertae sedis: +*Turfanella* Demoulin, 1954 (Upper Jurassic).

28. family *Leptohyphidae* Edmunds & Traver, 1954.

Leptohyphidae: Riek, 1973; Landa, 1973.

Tricorythidae: Edmunds & Traver, 1954 (partim); Demoulin, 1958 (partim);

Edmunds, 1962 (partim), 1972 (partim); Edmunds et al., 1963 (partim), 1976 (partim); Landa, 1967 (partim), 1969a (partim); Tshernova, 1962 (partim), 1970 (partim), 1980 (partim); McCafferty & Edmunds, 1979.

a) subfamily *Leptohyphinae* Edmunds & Traver, 1954.

Leptohyphinae Edmunds & Traver, 1954. *Leptohyphinae*: Demoulin, 1958; Edmunds et al., 1963, 1976; Landa, 1967, 1969a; McCafferty & Edmunds, 1979.
Genera included: *Cotopaxi* Mayo, 1968 (SA), - *Haplohyphes* Allen, 1966 (SA). - *Leptohyphes* Eaton, 1882 (NA,SA). - *Leptohyphodes* Ulmer, 1920 (SA). - *Tricorythafer* Lestage, 1942 (Af). - *Tricorythodes* Ulmer, 1920 (NA,SA). - - *Tricorythopsis* Traver, 1958 (SA).

b) subfamily *Dicercomyzinae* Edmunds & Traver, 1954.

Dicercomyzinae Edmunds & Traver, 1954. *Dicercomyzinae*: auct. (see above).
Genera included: *Dicercomyzon* Demoulin, 1954 (Af).

29. family *Tricorythidae* Lestage, 1942.

Tricorythidae: Edmunds & Traver, 1954 (partim); Lestage, 1941 (partim); Demoulin, 1955 (partim), 1958 (partim); Edmunds, 1962 (partim), 1972 (partim); Edmunds et al., 1963 (partim), 1976 (partim); Landa, 1967 (partim), 1969a (partim) 1973; Tshernova, 1970 (partim), 1980 (partim); Riek, 1973 (partim); McCafferty & Edmunds, 1979 (partim),

a) subfamily *Tricorythinae* Lestage, 1941.

Tricorythinae: Edmunds & Traver, 1954; Demoulin, 1958; Edmunds, 1962, 1972; Edmunds et al., 1963, 1976; Landa, 1967; McCafferty & Edmunds, 1979.
Genera included: *Neurocaenis* Navás, 1936 (Af,As,Mad). - *Tricorythus* Eaton, 1968 (Af,As) (*Tricorythus* s.str., *Tricorythurus* Lestage, 1942).

b) subfamily *Machadorythinae* Demoulin, 1959.

Machadorythinae Demoulin, 1959. *Machadorythinae*: Edmunds et al., 1963, 1976; Edmunds, 1972; McCafferty & Edmunds, 1979.
Genera included: *Machadorythus* Demoulin, 1959 (Af). - *Coryphorus* Peters, 1981 (SA).

c) subfamily *Ephemeryrhinae* Gillies, 1960.

Ephemerythinae Gillies, 1960. *Ephemerythinae*: auct. (see above).
Genera included: *Ephemerythus* Gillies, 1960 (Af)(*Ephemerythus* s.str. *Tricomerella* Demoulin, 1964).

XI. superfamily *Caenoidea* Newman, 1853.

Caenoidea: Edmunds & Traver,1954; Edmunds, 1962; Ulmer, 1933; Edmunds et al., 1963,1976; Tshernova, 1970, 1980; Riek, 1973; McCafferty & Edmunds, 1979.

Baetiscidea: Spieth, 1933.

*Ephemeroidea*Demoulin, 1958 (partim), 1961 (partim).

Ephemerelloidea: Demoulin, 1958 (partim); Tshernova, 1970 (partim).

Leptophlebioidea: Landa, 1967, 1969 (partim).

Neoephemeroidea: Tshernova, 1970

Oligoneurioidea: Demoulin, 1958 (partim).

Prosopistomatoidea: Edmunds & Traver,1954; Edmunds,1962; Edmunds et al., 1963, 1976; Riek, 1973; McCafferty & Edmunds, 1979.

30. family *Neoephemeridae* Traver in Needham et al., 1935.

Neoephemeridae Traver, 1935.

Neoephemerinae: Needham et al., 1935; Berner, 1950.

Baetiscidae: Edmunds & Traver, 1954; Demoulin,1958; Edmunds, 1962, 1972; Edmunds et al., 1963,1976; Landa, 1967, 1969a, 1973; Burks, 1953; Tshernova, 1970, 1980; Riek, 1973; McCafferty & Edmunds, 1979.

Genera included: *Neoephemera* McDunnough, 1925 (As,E,NA) (*Neoephemera* s. str., *Leucorhoenanthus* Lestage, 1930, *Oreianthus* Traver, 1931). - *Neoephemeropsis* Ulmer, 1939 (As). - *Potamanthellus* Lestage, 1930 (As).

31. family *Baetiscidae* Laméere, 1917.

Baetiscidae: Ulmer, 1920, 1933; Spieth, 1933; Burks, 1953; Edmunds & Traver, 1954; Demoulin, 1958; Edmunds, 1962, 1972; Edmunds et al., 1963, 1976; Landa, 1967, 1969a, 1973; Tshernova, 1970, 1980; Riek, 1973; McCafferty & Edmunds, 1979.

Genera included: Baetisca Walsh, 1862 (NA).

32. family Caenidae Newman, 1853.

Caenidae: Ulmer, 1920, 1933; Spieth, 1933; Burks, 1953; Edmunds & Traver, 1954; Demoulin, 1958; Edmunds, 1962, 1972; Edmunds et al., 1963, 1976; Landa, 1967, 1969a, 1973; Tshernova, 1970, 1980; Riek, 1973; McCafferty & Edmunds, 1979.

Brachycercidae Lestage 1924.

Genera included: Afrocaenis Gillies, 1982 (Af). - Brachycercus Curtis, 1834 (As,E,NA,Af). - Brasilocaenis Puthz, 1975 (SA). - Austrocaenis Barnard, 1932 (Af,Mad). - Caenis Stephens, 1835 (Af,As,E,NA,SA,Aus). - Caenodes Ulmer, 1924 (Af,As). - Caenomedea Thew, 1960 (Af,As). - Clypeocaenis Soldán, 1978 (As,Af). - Tasmanocaenis Lestage, 1930 (=Pseudocaenis Soldán, 1978 syn.n.) (Aus). - Caenopsella Gillies, 1977 (Af).

33. family Prosopistomatidae Laméere, 1917

Prosopistomatidae: Lestage, 1917; Ulmer, 1920, 1933; Edmunds & Traver, 1954; Demoulin, 1958; Edmunds, 1962, 1972; Edmunds et al., 1963, 1976; Landa, 1967, 1969a, 1973; Tshernova, 1970, 1980; Riek, 1973; McCafferty & Edmunds, 1979.

Binoculidae Demoulin, 1954.

Genera included: *Prosopistoma* Letreille, 1833 (Af,As,E,Mad).

Summary

Based on both published and unpublished results obtained during the past 30 years by dissection of larvae of more than 400 recent species (about 170 genera all extant known families) from all the biogeographic regions we summarise anagenetic trends and tendencies forming the arrangement of ventral nerve cord, tracheal system, alimentary canal, malpighian tubules,and internal reproductive organs.The results obtained are applied in reconstruction of phylogeny and in higher classification of the order *Ephemeroptera*.

Within the arrangement of ventral nerve cord the folloving characters are considered as those of comparative value: position of methathoracic ganglion and a relative length of thoracic connectives (A);position of anterior abdominal ganglia (ganglia 1-5) (B);arrangement of posterior ganglionic centers (ganglia 7 and 8) (C); arrangement of connectives (D). Main anagenetic trends are as follows: to shift metathoracic ganglion to mesothorax (1); to fuse first abdominal ganglion with metathoracic one (2); to shift anterior ganglia toward thorax (3); to more associate and to shift last ganglionic center forewards (cranially) (H); to fuss both connectives (5). These trends result in thoracic ganglionic mass in *Prosopistomatidae* and *Baetiscidae*.

Within the arrangement of tracheal system there are these characters of comparative value: absence, presence and number of ventral tracheal anostomoses (TAV)(E,F,G);gradual reduction of visceral tracheae (TV) (H,I,J,K). Anagenesis of thoracic and abdominal tracheal system tends to increase number of TAV and to reduce number of TV resulting in anastomoses in all the abdominal segments (*Hexagenia*, *Pentagenia*- *Ephemeridae*) and visceral tracheae only in segments IV-VIII (*Neoephemeridae*, *Caenidae*). The reduction of TAV in some derived *Pannota* is most likely secondary.

Alimentary canal provides us with the following comparative characters: degree of apparent macroscopic differentiation of stomodaeum (L);position of pyloric valve and colon to body segmentation (M); arrangement of anterior part of rectum (N);Anagenesis of the alimentary canal tends to differentiation (extension) of stomodaeum, to elongation of oesophagus and to forming of oesophagial crop (1);to emergency of rectal projections, to their branching and elongation into anterior abdominal

segments (2), and shortening of colon and rectum (proctodaeum) with simultaneous cranially directed shifting (3).Most specialised alimentary canal is possessed by the *Caenidae* and *Baetiscidae* (long unpaired projections).

Malpighian tubules manifest the following character with comparative value: arrangement of distal portions of individual tubules (O); arrangement of bases of proximal portions of individual tubules (P); number of common trunks (if present) (Q); relative lenght and specialization of individual trunks (R).Anagenetic trends within the arrangement of Malpighian tubules are well manifested.They are:tendency to specialization of distal portion of tubule (spiral coiling, enlarging) (1); tendency to form common trunks, to reduce their number to a single pair (2) and tendency to specialize one and elongate pair (usually lateral). These tendencies lead to forming "ureter" of recent *Neoephemeridae* and *Baetiscidae*.

Internal reproductive organs provide us with the following characters with comparative value:position of gonads to alimentary canal (S); position of gonads to body segmentation (T); shape of testes and ovaries (U); shape and relative length of testicular follicles (V); position of follicles and ovarioles to seminal ducts and oviducts (X) and shape and position of seminal vesicle (Y). Within the arrangement of internal reproductive organs the following anagenetic trends can be recognized:to shift gonads to ventrolateral position to alimentary canal (1); and cranially to prothorax and head (2) to diminish the size of follicles which have became equal in length (3), to slant follicles to ducts (4) and to form rounded seminal vesicle deposited in posterior abdominal segments. Anagenesis of gonads results in gonads with minute follicles reaching head capsula (some *Pannota*).

Recently erected subordes *Schistonota* and *Pannota* (McCafferty & Edmunds, 1979) can be characterized by the arrangement of internal organs as well. Derived suborder *Pannota* shows the following common characters: lack of first abdominal ganglion, remaining abdominal ganglia shifted forewards; relatively well associated last ganglionic centre; visceral tracheae (TV) inserted at the same place not only with neural tracheae but also with ventral anastomoses (if present); gonads shifted largerly at least to meso- or metathorax, sometimes even to the head. The arrangement of alimentary canal and malpighian tubules exihibit both primitive and derived characters within the *Pannota*, although there are clear tendencies to specialization ("ureter" in *Caenoidea*, projections of hind gut).

We suggest to classify the suborder *Schistonota* as having 4 superfamilies and the suborder *Pannota* consisting of two superfamilies. The main taxonomic shifts are manifested by separating the superfamily *Heptagenioidea* from the *Baetoidea* since it is well characterized by the arrangement of internal organs (occurence of TAV and reduction of TV, gonads in lateral position, common trunks of malpighian tubules) and by fusion of former *Prosopistomatoidea* and *Caenoidea* since there are very pronounced anatomical relationships between *Caenidae* and *Prosopistomatidae* and between *Neoephemeridae* and *Baetiscidae*.

Major stem-groups are illustrated and characterized by the arrangement of internal organs. Most primitive characters were found in *Ametropodidae* and *Siphlonuridae* in families representing descendants of earlier mayfly ancestors. There are two main phyletic lines. Primitive (schistonotan) line is represented by paraphyletic lineages of recent *Siphlonuridae* (from which split the lineage of *Heptageniidae*) and *Baetidae* with *Ameletopsidae* (highly derined characters in *Oniscigastridae* and *Chiloporter*) and by leptophlebioid-ephemerid lineage. Derived (pannotan) line is represented by two lineages recently manifested by *Ephemerelloidea* and *Caenoidea* respectively.

We present a higher classificatory system of mayflies consisting of 3 (1 fossil) suborders, 11 (5 fossil) superfamilies and 32 (11 fossil) families with 54 subfamilies comprising 302 (38 fossil) genera. Based on comparative anatomy characters we classify the former subfamilies *Oniscigastrinae* and *Ameletopsinae* (now two subfamilies *Ameletopsinae* and *Chiloporterinae*) as separated families and former families *Metretopodidae* and *Siphlaenigmatidae* as subfamilies of the *Siphlonuridae* and *Baetidae* respectively. *Isonychiinae* and *Coloburiscinae* are transferred from *Siphlonuridae* to the *Oligoneuriidae* and *Pseudironinae* from the *Heptageniidae* to the *Siphlonuridae*. Within the *Pannota*, we separate the family *Leptohyphidae* (formerly in the *Tricorythidae*) to consist of the *Leptohyphinae* and *Dicercomyzinae*.

Souhrn

Na základě publikovaných i nepublikovaných výsledků,které byly získány během posledních 30 let pomocí pitev larev více než 400 recentních druhů (přes 170 rodů, všechny recentní čeledi řádu), jsou shrnuty anagenetické trendy a tendence formující utváření ventrální nervové pásky, tracheálního systému, trávicí trubice, malpighických orgánů (trubic) a vnitřních reproduktivních orgánů. Získané výsledky jsou aplikovány při rekonstrukci fylogenetického vývoje a v systému vyšší klasifikace řádu *Ephemeroptera*.

Z hlediska srovnávací anatomie ventrální nervové pásky mají srovnávací hodnotu následující znaky: pozice metathorakálního ganglia a relativní délka hrudních konektivů (A);pozice předních abdominálních ganglií (ganglia 1-5) (B); uspořádání zadního ganglionického centra (ganglia 7 a 8) (C); uspořádání a stupeň splynutí konektivů (D). Hlavní anagenetické trendy formující ventrální nervovou pásku jsou tyto: posunout metathorakální ganglion do mezothoraxu (1); spojit první abdominální ganglion s metathorakálním (2);posunout přední abdominální ganglia směrem ke (do) hrudi (3); asociovat poslední ganglionické centrum a posunout je dopředu (kraniálně) (4); spojit oba konektivy (5). Tyto trendy ústí ve vytváření thorakálních ganglionických mas u čeledí *Prosopistomatidae* and *Baetiscidae*.

U tracheálního systému nacházíme následující znaky s vysokou srovnávací hodnotou: absenci,prezenci a počet ventrálních tracheálních anastomóz (TAV)(E,F,G); postupnou redukci viscerální tracheizace (TV)(H,I,J,K). Anageneze thorakálního a abdominálního tracheálního systému směřuje ke zvýšení počtu TAV a k redukci viscerálních trachejí (TV). Konečným stavem je výskyt anastomóz ve všech abdominálních segmentech (*Hexagenia*, *Pentagenia-Ephemeridae*) a výskyt viscerálních trachejí pouze v abdominálních segmentech IV-VIII (*Neoephemeridae*, *Caenidae*). Redukce TAV u některých odvozených skupin podřádu *Pannota* je pravděpodobně sekundární.

Trávicí trubice nám poskytuje následující srovnávací znaky: stupeň zřejmé makroskopické diferenciace stomodea (L); pozici pylorické valvy a kolonu vzhledem k tělní segmentaci (M); tvar a uspořádání přední části rekta (N). Anageneze trávicí trubice směřuje k diferenciaci (rozšíření) stomodea, prodloužení oesophagu a vzniku jícnového volete (1); ke vzniku rektálních výběžků,k jejich větvení a protažení do zadních abdominálních segmentů (2) a ke zkrácení kolonu a rekta (proctodea) a k jejich současnému posunutí kraniálním směrem. Nejodvozenější stavbu trávicí trubice vykazují *Caenidae* a *Baetiscidae* (dlouhé, nepárové výběžky).

Malpigické trubice vykazují tyto srovnávací znaky: uspořádání distálních částí jednotlivých tubulů (O); uspořádání bází proximálních částí tubulů (P); počet společných kmenů jestliže jsou vyvinuty (Q); relativní délku a specializaci jednotlivých kmenů (R). Anagenetické trendy vývoje malpigických trubic jsou dobře manifestovány. Jsou to: tendence ke specializaci distální části tubulů (prodloužení,spirální stáčení)(1), tendence ke tvorbě společných kmenů,k redukci jejich počtu na jediný pár (2) a tendence ke specializaci a prodloužení jediného (většinou laterálního) páru. Tyto tendence vedou k formování "ureteru" současných čeledí *Neoephemeridae* a *Baetiscidae*.

Vnitřní reproduktivní orgány poskytují následující srovnávací znaky: pozici gonád vzhledem k trávicí trubici (S); pozici gonád vzhledem k tělní segmentaci (T); tvar varlat a vaječníků (U); tvar a relativní délku testikulárních folikulů (V); pozici folikulů a ovariol vzhledem k chámovodům a vejcovodům (X); tvar a pozici semenného váčku. V uspořádání vnitřních reproduktivních orgánů je možno rozlišit následující anagenetické trendy: posun gonád do ventrolaterální pozice k trávicí soustavě (1) a kraniálně do prothoraxu a hlavy (2); zmenšení velikosti folikulů, které se již staly rovnocenné (3); zešikmení folikulů i ovariol (4) a formování zaobleného semenného váčku, který je uložen v zadních abdominálních segmentech (5). Anageneze gonád vrcholí gonádami s malými folikuly, dosahujícími až k hlavové kapsuli (někteří zástupci *Pannota*).

Nedávno ustanovené podřády *Schistonota* a *Pannota* (McCafferty & Edmunds, 1979) mohou být charakterizovány také uspořádáním vnitřních orgánů. Odvozený podřád *Pannota* vykazuje následující společné znaky: chybějící prvé abdominální ganglion, zbývající ganglia posunuta směrem dopředu;poměrně značný stupeň asociace posledního ganglionického centra; viscerální tracheje (TV) jsou připojeny na stejném místě nejen s neutrálními trachejemi, ale i s ventrálními anastomózami (jestliže ty jsou vyvinuty); gonády silně posunuty kraniálně,přinejmenším do mezo- či metathoraxu,někdy až do hlavy. Uspořádání trávicí trubice a malpigických trubic vykazuje obojí,primitivní i odvozené znaky u podřádu *Pannota*, ačkoliv se zde objevují jasné tendence ke specializaci ("ureter" a výběžky trávicí trubice u *Caenoidea*).

Navrhujeme klasifikovat podřád *Schistonota* do čtyř a podřád *Pannota* do dvou nadčeledí. Hlavní taxonomické přesuny v tomto směru reprezentují separace nadčeledi *Heptagenioidea* od nadčeledi *Baetoidea*, neboť je velmi dobře charakterizována uspořádáním vnitřních orgánů (výskyt TAV a redukce TV, gonády v laterální pozici, výskyt společných kmenů malpigických trubic, a dále spojením původních nadčeledí *Caenoidea* a *Prosopistomatoidea*, neboť existují výrazné anatomické vazby mezi čeleděmi *Caenidae* a *Prosopistomatidae* a mezi čeleděmi *Meoephemeridae* a *Baetiscidae*.

Hlavní vývojové linie jsou ilustrovány a charakterizovány pomocí anatomického uspořádání vnitřních orgánů. Nejprimitivnější znaky byly nalezeny u čeledí *Ametropodidae* a *Siphlonuridae*, které reprezentují potomky původních předků jepic. Existují dvě hlavní fyletické linie. Primitivní (schistonotní) linie je reprezentována současnými rody čeledí *Siphlonuridae* (od které se odštěpila větev vedoucí k čeledi *Heptageniidae*) a *Baetidae* s *Ameletopsidae* (vysoce odvozené znaky u čeledi *Oniscigastridae* a rodu *Chiloporter*) a větví leptophlebio-ephemeridní.Odvozená (pannotní) linie je reprezentována 2 větvemi nadčeledí *Ephemerelloidea* a *Caenoidea*.

Námi navrhovaný systém se skládá ze 3 podřádů (1 fosilní), 11 nadčeledí (5 fosilních), 32 čeledí (11 fosilních) s 54 podčeleděmi (12 fosilních), které celkem obsahují 302 rodů (38 fosilních). Na základě výsledků srovnávací anatomie klasifikujeme původní podčeledi *Oniscigastrinae* a *Ameletopsinae* (nyní dvě podčeledi *Ameletopsinae* a *Chiloporterinae*) jako samostatné čeledi a původní čeledi *Metretopodidae* a *Siphlaenigmatidae* jako podčeledi čeledí *Siphlonuridae* a *Baetidae*. *Isonychiinae* a *Coloburiscidae* jsou převedeny ze *Siphlonuridae* do *Oligoneuriidae* a podčeleď *Pseudironinae* z čeledi *Heptageniidae* do čeledi *Siphlonuridae*. V rámci podřádu *Pannota* vyčleňujeme čeleď *Leptohyphidae* (dříve podčeleď čeledi *Tricorythidae*) se dvěma podčeleděmi *Leptohyphinae* a *Dicercomyzinae*.

Zusammenfassung

Auf Grund der publizierten und unpublizierten Ergebnisse, die während der letzten 30 Jahren durch die Sezierung der Larven von mehr als 400 rezenten Arten erworben wurden (über 170 Gattungen, alle rezente Familien der Ordnung) werden die anagenetischen Richtungen und Tendenzen, die Bildung des Ventralnervenbandes, des Tracheensystems, der Verdauungsrohr, der Malpighischen Gefässe und der inneren Geschlechtsorgane formieren zusammengefasst. Die Resultate werden bei der Rekonstruktion der phyllogenetischen Entwicklung und im System der höheren Klassifizierung der Ordnung *Ephemeroptera* verwendet.

Vom Gesichtspunkt der vergleichenden Anatomie des Ventralnervenbandes sind folgende Merkmale vom Vergleichswert: die Position des Metathorakalganglions und relative länge der Thoraxconnektiven (A); die Position der vorderen Abdominalganglien (Ganglien 1 bis 5) (B);die Anordnung des hinteren Ganglienzentrums (Ganglien 7 bis 8) (C); die Bildung und Verschmelzungsstufe der Connektiven (D). Die anagenetischen Hauptrichtungen die das Ventralnervenband formieren sind folgende: das Metathorakalganglion nach Mesothorax zu verschieben (1); das erste Abdominalganglion mit dem Metathorakalganglion zu vereinigen (2); die vorderen Abdominalganglien in der Richtung zum Thorax zu verschieben (3); das letzte Ganglienzentrum zu vereinigen und nach vorne (kranial) zu verschieben (4); beide Connektiven zu vereinigen (5). Diese Richtungen münden in die Bildung der thorakalen Ganglienmassen bei den Familien *Prosopistomatidae* und *Baetiscidae*.

Beim Tracheensystem findet man folgende Merkmale die ein hohes Vergleichswert aufweisen: die Abwesenheit, die Anwesenheit und die Anzahl der ventralen Tracheenanastomosen (TAV) (E,F,G,); fortschreitende Reduktion der visceralen Tracheisation (TV) (H,I,J,K). Anagenie des thorakalen und abdominalen Tracheensystems zielt zur Erhöhung der Anzahl der TAV und zur Reduktion der Visceraltracheen (TV). Der Endstand ist das Vorkommen von Anastomoses in allen Abdominalsegmenten (*Hexagenia, Pentagenia - Ephemeridae*) und das Vorkommen der Visceraltracheen nur in den Abdominalsegmenten IV. - VIII. (*Neoephemeridae, Caenidae*). Reduktion der TAV bei einigen abgeleiteten Gruppen der Unterordnung *Pannota* ist wahrscheinlich sekundär.

Die Verdauungsrohr bietet folgende Vergleichsmerkmale an: die Stufe der offensichtlichen makroskopischen Differenzierung von Stomodaeum (L.); die Position der Valvula pylorica und des Colon in bezug zur Körpergliederung (M); die Form und Anordnung des Vorderteils des Rectums (N). Anagenie der Verdauungsrohr zielt zur Differenzierung (Verbreitung) von Stomodaeum, der Verlängerung des Oesophagus und zum Entstehen des Ingluviaes (Kropf) (1); zur Entstehung der Rectalausläufern, zu ihrer Verzweigung und Verlängerung in die hintere Abdominalsegmente (2); und zur Verkürzung des Colons und des Rectums (Proctodaeum), und zu ihren gleichzeitigen Verschiebung in der Kranialrichtung. Den meist abgeleiteten Bau der Verdauungsrohr weisen *Caenidae* und *Baetiscidae* (lange unpaarige Ausläufer) auf.

Die Malpighischen Gefässe weisen folgende Vergleichsmerkmale auf; die Anordnung der Distalteilen der einzelnen Tubuli (O); die Anordnung der Basis der Proximalteilen der Tubuli (P); die Anzahl der gemeinsamen Stämme falls sie gebildet sind (Q); die Relativlänge und Spezialisierung der einzelnen Stämme (R). Die anagenetischen Richtungen der Entwicklung der Malpighischen Gefässen, die sich gut sichtbar machen, sind folgende: die Spezialisierung der Distalteile der Tubuli (Verlängerung, das Drehen in die Spirale) (1), die Tendenz zur Bildung der gemeinsamen Stämme, zur Reduktion auf ein einziges Paar (2) und die Tendenz zur Spezialisierung des einzelnen meistens des Lateralpaares). Diese Tendenzen münden in die Bildung eines "Urethers" bei den gegenwärtigen Familien *Neoephemeridae* und *Baetiscidae*.

Die inneren Geschlechtsorgane bieten folgende Vergleichsmerkmale an: die Position der Gonaden in bezug zur Verdauungsrohr (S), die Position der Gonaden in bezug zur Körpergliederung (T), die Form der Hoden und Ovarien (U); die Form und Relativlänge der Testikularfollikeln (V); die Position der Follikeln und Ovariolen in bezug zu dem Samen- und Eileitern (X); die Form und Position der Samenblase. In der Anordnung der inneren Geschlechtsorgane kann man folgende anagenetische Richtungen unterscheiden: die Verschiebung der Gonaden in die ventrolaterale Position zur Verdauungsrohr (1) und kranial in den Prothorax und den Kopf (2); die Verkleinerung der Follikelgrösse die schon gleichgülting geworden sind (3); und zur Verschiefung der Follikeln und Ovariolen (4) und zur Formierung einer abgerundeten Samenblase, die in den hinteren Abdominalsegmenten plaziert wird (5). Die Anagenie der Geschlechtsorgane mündet in die Gonaden mit kleinen Follikeln die Kopfkapsel erreichen (einige Vertreter der *Pannota*).

Die unlängst festgesetzten Unterordnungen *Schistonota* und *Pannota* (McCafferty & Edmunds, 1979) können auch durch die Anordnung der inneren Organe bestimmt werden. Die abgeleitete Unterordnung *Pannota* weist folgende gemeinsame Merkmale auf: das erste Abdominalganglion fehlt, die übrigen Ganglien sind nach vorne verschoben, relativ hohe Stufe der Vereinigung der letzten Ganglienzentrums; Visceraltracheen (TV) setzen auf gleicher Stelle nicht nur mit den Neuraltracheen, sondern auch mit den Ventralkomissuren (falls diese gebildet sind an; die Gonaden stark kranial verschoben,mindestens ins Meso- oder Metathorax,manchmal bis in den Kopf. Die Anordnung der Verdauungsrohr und der Malpighischen Gefässe weist beide, die primitiven und abgeleiteten Merkmale bei der Unterordnung *Pannota* auf, obwohl hier klare Tendenzen zur Spezialisierung ("Urether" und die Ausläufer der Verdauungsrohr bei den *Caenoidea*) erscheinen.

Wir schlagen vor die Unterordnung *Schistonota* in vier und die Unterordnung Pannota in zwei Überfamilien zu klassifizieren. Die meisten taxonomischen Veränderungen in dieser Richtung stellen die Trennung der Überfamilie *Baetoidea*, weil sie sehr gut durch die Anordnung der inneren Organe (das Vorkommen von TAV und Reduktion von TV, Gonaden in der Lateralposition, das Vorkommen der gemeinsamen Stämme der Malpighischen Gefässe und weiter die Vereinigung der Überfamilien *Caenoidea* und *Prosopistomatidea* vor, da es eine ausdruckvolle anatomische Bildung zwischen den Familien *Neoephemeridae* und *Baetiscidae* gibt.

Die Hauptentwicklungslinien werden mit Hilfe der anatomischen Anordnung der inneren Organe illustriert und charakterisiert. Die primitivsten Merkmale wurden bei den Familien *Ametropodidae* und *Siphlonuridae*, die Nachkommen der ursprünglichen Vorfahren der Eintagsfliegen vertreten. Es gibt zwei phyllogenetischen Hauptlinien. Die primitive Linie (*Schistonota*), wird durch die rezenten Gattungen der Familien *Siphonuridae* (von deren sich der Zweig, der zur Familie *Heptageniidae* führt trennte) und *Baetidae* mit *Ameletopsidae* (stark abgeleitete Merkmale bei der Familie *Oniscigastridae* und bei der Gattung *Chiloporter*) und den leptophlebio - ephemeriden Zweig vertreten.Die abgeleitete Linie (*Pannota*) bilden zwei Zweige der Überfamilien *Ephemerelloidea* und *Caenoidea*.

Das von uns vorgeschlagene System setzt sich aus 3 Unterordnungen (1 fossile), 11 Überfamilien (5 fossile), 32 Familien (11 fossile) die insgesamt 302 Gattungen (38 fossile), enthalten. Auf Grund der Resultate der vergleichenden Anatomie klassifizieren wir die ursprünglichen Unterfamilien *Oniscigastrinae* und *Ameletopsinae* (jetzt zwei Unterfamilien *Ameletopsinae* und *Chiloporterinae*) als selbstständige Familien und die urspünglichen Familien *Metretopodidae* und *Siphlaenigmatidae* als Unterfamilien der Familien *Siphlonuridae* und *Baetidae*. *Isonychiinae* und *Coloburiscidae* sind von *Siphlonuridae* ins *Oligoneuriidae* und die Unterfamilie *Pseudironinae* von der Familie *Heptageniidae* in die Familie *Leptophlebii-*

dae (früher Unterfamilie der Familie *Tricorythidae*) mit zwei Unterfamilien *Leptohyphinae* und *Dicercomyzinae* überfürt.

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STUDIE ČSAV
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Akademik Vladimír Landa,
RNDr. Tomáš Soldán, CSc.

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The present volume is the outcome of prolonged studies on the internal reproduction organs of the mayfly (*Ephemeroptera*). It is introduced by a description of working procedures, and a list of species,genera and families of ephemeropterans examined, with notes on their sites of incidence. The following chapters give valuable informations on the structure of sexual organs examined, and a description of basic types. These original resultes are complemented with 261 drawings illustrating the structure and the shape of the male and female reproductive organs and their location in individual segments of the body. Results of comparative studies with other insect orders are of primary importance in the field of evolutionary biology. Appended to the text is an extensive list of references.

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