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DEVELOPMENTAL CYCLES OF CENTRAL EUROPEAN EPHEMEROPTERA AND THEIR INTERRELATIONS

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Little data on the development of individual mayfly species have been available until recent years. As late as the 1940's information was limited mainly to the occurrence periods of adults mentioned in taxonomic papers, and in only a few instances from actual studies of larvae. Comprehensive investigations into the developmental cycles are now being stimulated by the study of hydrobiology.

MOON (1939) described the developmental cycles in the species *Caenis horaria* (L.), *Leptophlebia vespertina* (L.) and *Leptophlebia marginata* (L.) and HARKER (1952) in the species *Rhithrogena semicolorata* (CURT.) and *Ecdyonurus torrentis* KIMM. Similar modern investigations have been carried out by MACAN (1957, 1957) who for several years studied the development of the river fauna in the North of England and obtained data on the species *Ameletus inopinatus* EAT., *Ecdyonurus torrentis* KIMM., *Ecdyonurus venosus* (FABR.), *Ecdyonurus dispar* (CURT.), *Rhithrogena semicolorata* (CURT.), *Heptagenia lateralis* (CURT.), *Baetis rhodani* (PICT.), *Baetis pumilus* (BURM.), *Ephemerella ignita* (PODA), *Paraleptophlebia submarginata* (STEPH.), *Baetis scambus* EAT., *Heptagenia sulphurea* (MÜLL.), *Siphlonurus lacustris* (EAT.), *Centroptilum luteolum* (MÜLL.), *Centroptilum pennulatum* EAT., *Procloen rufulum* (MÜLL.) (*Procloeon pseudorufulum* KIMM.), *Rhithrogena haarupi* ESB. — PET., *Ephemerella notata* EAT. and *Paraleptophlebia cincta* (RETZ.). Similarly, in Austria PLESKOT (1953, 1958) obtained data on the species *Paraleptophlebia submarginata* (STEPH.), *Ephemerella* (*Torleya*) *major* (KLAP.), *Habroleptoides modesta* (HAGEN), *Ephemera danica* MÜLL., *Ephemerella ignita* (PODA), *Baetis subalpinus* BENGTS., *Baetis rhodani* (PICT.), *Habrophlebia lauta* MCLACHL. and *Baetis vernus* CURT. LANDA (1957) compared the developmental cycles of the two closely related species *Habrophlebia fusca* (CURT.) and *Habrophlebia lauta* MCLACHL. GLEDHILL (1959) studied the development of the species *Ameletus inopinatus* EAT. MACAN (1961) summed up the available information, and on analysis distinguished several developmental types of different character. He also gave diagrams showing the seasonal dynamics of the species *Leptophlebia* sp., *Paraleptophlebia submarginata* (STEPH.), *Heptagenia lateralis* (CURT.), *Cloeon dipterum* (L.), *Ameletus inopinatus* EAT., *Rhithrogena semicolorata* (CURT.), *Ecdyonurus torrentis* KIMM., *Ecdyonurus venosus* (FABR.), *Cloeon simile* EAT. and *Ephemerella ignita* (PODA). Recently BRETSCHKO (1965) has published a paper dealing with the development of the species *Cloeon dipterum* (L.), *Cloeon simile* EAT., *Centroptilum luteolum* (MÜLL.) and *Baetis rhodani* (PICT.). Data from which the development of individual species may be reconstructed is found in a great number of hydrobiological papers concerning investigations of the seasonal changes in the fauna of certain biotopes. Among the more important papers reporting investigations carried out in Czechoslovakia are those by LELLÁK (1953, 1958), VONDREJS (1958), PETR (1961), etc.

The extensive research carried out on the distribution and seasonal dynamics of mayflies in Czechoslovakia during the last 15 years, has brought rich material and much new data. As a result we can now classify the developmental cycles of the Central European mayfly species. The developmental cycles may be divided into the groups and types as defined in the first part of this paper. The knowledge of the developmental cycles of practically all the mayfly species occurring in a given area discloses certain general dependences of relations with the different developmental cycles on the biotope.

Also that the developmental cycles are important for the distribution of the species, origin of second generations and possibly new races and species. These general dependences are dealt with in the second part of the paper

DEVELOPMENTAL CYCLES OF MAYFLIES

The developmental cycles of mayflies can be divided into the following groups and types:

Group A. The species has one generation in the year. The annual developmental cycle is closely connected with the seasonal cycle of the year. Three types constitute this group:

A 1. The eggs hatch about one month after oviposition and reach the stage of "older larva" in autumn. (The term "older larva" is meant in the morphological sense, i.e. a larva from about the 10th instar.) Larvae continue growing during the winter and then more vigorously in spring months, the adults emerge in spring, or in summer at higher altitudes. Species having this type of development can be called "winter" species, and include the following:

Ameletus inopinatus EAT.
Baetis alpinus (PICT.) (in higher altitudes)
Rhithrogena semicolorata (CURT.)
Rhithrogena georgii LANDA
Rhithrogena hybrida EAT.
Rhithrogena hercynia LANDA
Epeorus assimilis EAT.
Heptagenia flava ROST.
Heptagenia coerulans ROST.
Heptagenia sulphurea (MÜLL.)
Heptagenia fuscogrisea (RETZ.)
Heptagenia lateralis (CURT.)
Heptagenia quadrilineata LANDA
Ecdyonurus torrentis KIMM.
Ecdyonurus venosus (FABR.)
Ecydonurus forcipula (PICT.)
Ecydonurus austriacus KIMM.
Ephemerella notata EAT.
Ephemerella krieghoffi (ULM.)
Ephemerella major (KLAP.)
Paraleptophlebia submarginata (STEPH.)
Leptophlebia marginata (L.)
Leptophlebia vespertina (L.)
Habroleptoides modesta (HAG.)

The above mentioned type naturally varies in individual cases in the total length of time taken for the development in older larvae, and as to the season of the year in which the main growth is concentrated (autumn in ***Rhithrogena georgii***, ***R. hercynia***, but in most species during the spring months, as in ***R. semicolorata***), or as to the degree to which the development slows down during winter (e.g. in ***Rhithrogena semicolorata*** and ***Ecdyonurus torrentis*** it slows down negligibly, in ***Ameletus inopinatus***, ***Heptagenia lateralis*** considerably).

A 2. After oviposition in the autumn, eggs remain in diapause until spring or even summer the following year (it is probable that in some cases early instar larvae may also remain in diapause). Older larvae develop very quickly during 2—3 months in summer. Species having this type of development can be called "summer" species, and include the following:

Siphlonurus lacustris (EAT.)
Siphlonurus aestivalis (EAT.)
Siphlonurus armatus (EAT.)
Siphlonurus linnaeanus (EAT.)
Baetis scambus EAT.
Centroptilum pennulatum EAT.
Oligoneuriella rhenana (IMH.)
Arthroplea congener BENGTS.
Rhithrogena aurantiaca (BURM.)
Rhithrogena alpestris EAT.
Rhithrogena tatrica ZELINKA
Heptagenia affinis (EAT.)
Ecdyonurus insignis (EAT.)
Ecdyonurus fluminum (PICT.)
Ecdyonurus dispar (CURT.)
Ecdyonurus submontanus LANDA
Ephemerella ignita (PODA)
Caenis pseudorivulorum KEFFERMÜLLER
Caenis undosa TIENSUU
Brachycercus harrisella CURT.
Paraleptophlebia cincta (RETZ.)
Paraleptophlebia werneri ULM.
Choroterpes picteti (EAT.)

The northern species *Arthroplea congener* is a characteristic representative of the above mentioned type of development. As a typical summer species it inhabits the small water pools and lakes in Norway, Finland and the northern-most parts of the USSR. The eggs of this species hatch and the larvae develop rapidly in July and August in the course of the short northern summer. In the other seasons of the year the eggs remain in diapause. In the more southerly latitudes of Czechoslovakia it retains the same developmental pattern, but the two-month period of main growth occurs earlier, March, April or May, varying a little according to the altitude.

A 3. The older larvae develop in autumn and then cease growing during the winter (apparently entering a state of diapause) until late spring or summer when, like the summer species, they quickly complete their development and reach maturity in the course of 2—3 months. This type of development occurs in the following species:

Habrophlebia fusca (CURT.)
Habrophlebia lauta MCLACHL.
Ephoron virgo (OLIV.)
Potamanthus luteus (L.)

It may be anticipated that when the embryonic development and the development of early instar larvae of the individual species has been further studied, some of the species now listed under the A 1 type may then be classified under this type of development.

Group B. The species has two generations in the year. The developmental cycle of the two generations is closely connected with the seasonal cycle of the year. Four types constitute this group:

B 1. The developmental cycle of the first generation corresponds on the whole to that of the type A 1. Eggs hatch as late as the autumn, but the larvae develop quickly and reach the stage of older larva by late autumn; the adults emerge the following spring and commence ovipositing. The eggs hatch within 2—3 weeks, and the larvae of this new generation develop rapidly in the 2—3 summer months like those of the summer species in A 2. From the eggs laid by the adults of the second generation, older larvae mature in autumn and the cycle is repeated. This type can be observed in the following species:

Baetis rhodani (PICT.)
Baetis vernus CURT.
Baetis alpinus (PICT.) (in lower altitudes)
Baetis buceratus EAT.
Baetis niger (L.)
Baetis pumilus (BURM.)
Baetis atrebatinus EAT.
Centroptilum luteolum (MÜLL.)
Cloeon dipterum (L.)
Cloeon simile EAT.
Procloeon pseudorufulum KIMM.
Ecdyonurus subalpinus KLAP.
Caenis macrura STEPH.
Caenis moesta BENGTS.
Caenis robusta EAT.
Caenis horaria (L.)

B 2. Two generations follow in a rapid succession in the summer months. The first generation compares generally with type A 2. This type of double summer brood occurs in some species of type A 2 under extremely favourable conditions. It has so far been ascertained in the following species:

Baetis bioculatus (L.)
Siphlonurus aestivalis (EAT.)
Caenis pseudorivulorum KEFFERMÜLLER

In *Baetis bioculatus* this type is observed quite frequently, so that it may be considered as the basic one.

B 3. In species of this group the development is similar to that of type B 1, but instead of one summer generation, there are two summer generations, thus the species in this group have in all three generations. Basically this type is a combination of the developmental types B 1 and B 2. This type of development takes place only under exceptionally favourable conditions and has only been found in the following two species:

Cloeon dipterum (L.) *Caenis horaria* (L.)

B 4. A proportion of the eggs oviposited in autumn hatch and gives rise to older larvae in autumn, the remaining eggs overwinter before hatching, the young larvae quickly developing and reaching the older larva stage in the spring. During the following summer the fully developed adults emerge in two separate periods, the specimens of each emergence differing in size. However, this is not a case of two generations in the accepted sense of the word. This type of development occurs only exceptionally, and has been ascertained in the species *Ameletus inopinatus* (GLEDHILL, 1959); available data indicates that it may occur in *Baetis vernus* CURT.

Group C. The species in this group have only one generation in two or more years. The developmental cycle is thus equivalent to a two-season cycle of a univoltine species. Two types constitute this group:

C 1. The development lasts two years. The older larvae develop from the autumn of one year through the whole of the following year, the adults emerging in the spring or summer of the third year. This type was found in the following species:

Ephemera vulgata (L.) *Ephemera danica* MÜLL.
Ephemera lineata EAT.

C 2. The development lasts three years. A three year life cycle is usually attributed to species of the family *Palingeniidae*. My own observations carried out on limited material have so far provided no evidence of such a long-term development. This category therefore remains to be confirmed, and is tentatively included in the classification.

Group D. The relations of the developmental cycles and the seasons year cycles change:

D 1. Species with three generations in two years. In species with the developmental type B 2 the development of the first generation is prolonged, so that the summer, i.e. the second generation, does not develop in that year. The adults of this generation emerge in the early spring of the following year. In this second year there is a sufficiently long period for the development of two generations. This type of development was described as the basic type in *Baetis vagans* MCDUNNOUGH by MURPHY (1922). However, in Czechoslovakia this type has been observed in *Baetis rhodani* (PICT.), but not as the basic type but as an exceptional one.

D 2. Species with two generations in three years. This also is a case of an exceptional type of development, which has not yet been confirmed. The evidence hitherto collected indicates that it may occur in the species *Ephemera danica* (MÜLL.).

An analysis of the developmental types in the individual species occuring in the Central Europe is given in table 1.

TABLE 1

Developmental cycles of mayflies

Species	Number of generation	Groups and types	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII
Siphlonuridae	1													
A. inopinatus EAT.	1	A 1 (B 4)												
S. lacustris (EAT.)	1	A 2												
S. aestivalis (EAT.)	1	A 2 (B 2)												
S. armatus (EAT.)	1	A 2												
S. linnaeanus (EAT.)	1	A 2												
Baetidae														
B. rhodani (PICT.)	2	B 1 (D 1)												
B. vernus CURT.	2	B 1 (B 4)												
+*B. buceratus* EAT.	2	B 1 (B 2)												
B. alpinus (PICT.)	2 (1)	B 1 (A 1)												
B. bioculatus (L.)	2	B 2												
B. scambus EAT.	1	A 2												
B. niger (L.)	2	B 1												
B. pumilus (BURM.)	2	B 1												
B. atrebatinus EAT.	2	B 1												
C. luteolum (MÜLL.)	2	B 1												
C. pennulatum EAT.	2	B 1												
C. dipterum (L.)	2	B 1 (B 3)												
C. simile EAT.	2	B 1												
P. pseudorufulum KIMM.	2	B 1												
Oligoneuriidae														
O. rhenana (IMH.)	1	A 2												
Arthropleidae														
A. congener BENGTSS.	1	A 2												
Heptageniidae														
R. semicolorata (CURT.)	1	A 1												
R. aurantiaca (BURM.)	1	A 2												
R. alpestris EAT.	1	A 2												
R. georgii LANDA	1	A 1												
R. tatrica ZELINKA	1	A 2												
R. hybrida EAT.	1	A 1												
R. hercynia LANDA	1	A 1												
E. assimilis EAT.	1	A 1												
H. flava ROST.	1	A 1												
H. coerulans ROST.	1	A 1												
H. sulphurea (MÜLL.)	2	B 1 (A 1)												
H. fuscogrisea (RETZ.)	1	A 1												
H. lateralis (CURT.)	1	A 1												
H. quadrilineata LANDA	1	A 1												
H. affinis (EAT.)	1	A 2												
E. insignis (EAT.)	1	A 2												
E. fluminum (PICT.)	1	A 2												
E. dispar (CURT.)	1	A 2												

(+ only limited data available)

TABLE 1 (continuation)

Species	Number of generation	Groups	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII
E. submontanus LANDA	1	A 2												
E. torrentis KIMM.	1	A 1												
E. venosus (FABR.)	1	A 1												
E. forcipula (PICT.)	1	A 1												
E. subalpinus KLAP.	2	B 1												
+*E. austriacus* KIMM.	1	A 1												
Ephemerellidae														
E. ignita (PODA)	1	A 2												
+*E. mesoleuca* (BRAUER)	1	A 2												
E. notata EAT.	1	A 1												
E. krieghoffi (ULM.)	1	A 1												
E. major (KLAP.)	1	A 1												
Caenidae														
C. macrura STEPH.	2	B 1												
C. moesta BENGTSS.	2	B 1												
C. pseudorivulorum KEFFERMÜLLER	1	A 2 (B 2)												
C. undosa TIENSUU	1	A 2												
C. robusta EAT.	2	B 1												
C. horaria (L.)	2	B 1 (B 3)												
B. harrisella CURT.	1	A 2												
Leptophlebiidae														
P. submarginata (STEPH.)	1	A 1												
P. cincta (RETZ.)	1	A 2												
P. werneri ULM.	1	A 2												
L. marginata (L.)	1	A 1												
L. vespertina (L.)	1	A 1												
Ch. picteti (EAT.)	1	A 2												
H. modesta (HAGEN)	1	A 1												
H. fusca (CURT.)	1	A 3												
H. lauta MCLACHL.	1	A 3												
Polymitarcidae	1													
E. virgo (OLIV.)		A 3												
Ephemeridae														
E. vulgata L.	1 in 2 years	C 1												
E. danica MÜLL.	1 in 2 years	C 1 (D 2)												
E. lineata EAT.	1 in 2 years	C 1												
Potamanthidae														
P. luteus (L.)	1	A 3												

(+ only limited data available)

The following general conclusions may be deduced from our present knowledge of the developmental cycles of mayflies:

1. Four distinct seasonal aspects are evident in the mayfly fauna of Central Europe, and in the development of their larvae. These may be classed as pre-spring, spring, summer, and autumn aspects. The spring aspect is characterised by a smaller number of individuals of each species. In the summer aspect the number of individuals of each species is higher and frequently there is a mass occurrence of them. The pre-spring and autumn aspects occur mainly in the piedmont rivers and streams. The spring aspect is richest in small rivers of upland areas, the summer one in ponds and larger rivers of lowland areas. The summer aspect is rich in the mountain streams as well.

2. The development of the species is not equable. Each species, irrespective of the total time taken for development, has a more or less defined period of main growth, when rapid and progressive development takes place. In the majority of species the main growth period takes place about two months prior to the date of emergence of the imago.

3. In certain biotopes, the developmental cycles of mayflies and especially their main growth periods are distributed throughout the whole year, or in some water types, throughout the vegetation period. This fact greatly enhances the importance of mayflies in the biocenosis, influencing the productivity aspect and self-purification capability of the waters. A good example of sequence of the main developmental periods in species of the genus *Caenis* is to be found in the biocenosis of the benthos in the ponds in Southern Bohemia. There the developmental periods of the larvae of *Caenis horaria* (L.) follow that of the larvae of *Caenis robusta* EAT. The first generation occurs from late April to mid-June, the second from mid-June to early September. In the interim period between the two generations the summer northern species with one generation, *Caenis undosa* TIENSUU, appears.

4. From table 1 it can be seen that the genera which are represented in Central Europe by several species are to be found at various stages of development throughout the year. These genera contain winter and summer species. It is of interest to note that these two group are balanced, the total number of winter species occuring in this area corresponding approximately to that of summer species. In other genera a balance is achieved by having two generations. The winter species of type A 1 are distinctly morphologically, phylogenetically and zoogeographically defined and they are more autochtonous in this area. The summer species of the type A 2 on the other hand are generally rather markedly variable, and cannot at present be critically defined. This fact seems to indicate that the summer species evolved gradually in the course of the warming of the climate between each glacial period or after the last glacial period under the pressure of a certain vacuum or vacant ecological niche in aquatic biotopes during the successive prolongation of the vegetation period. This theory is supported also by the fact, that in a number of summer species a relationship to the basic winter species can be seen. [*Rhithrogena semicolorata* (CURT.), *R. aurantiaca* (BURM.), *R. semicolorata* (CURT.), *R. alpestris* EAT., *Ecdyonurus torrentis* KIMM., *E. dispar* (CURT.), *E. torrentis* KIMM., *E. submontanus* LANDA; *Paraleptophlebia submarginata* (STEPH.), *P. cincta* (RETZ.) and other.] When taking into consideration the greater variability of the second generation of type B 1, it

seems probable that it was the original summer generations of the basic winter species that gave rise to species of the summer type.

5. The distribution of the main developmental periods of species is of primary importance when considering the distribution and formation of the fauna in a certain area, and the formation of biocenoses in certain biotopes. New elements penetrate with great difficulty into the closed biocenosis by a number of original species. With the prolonging of the vegetation period there appeared new possibilities for the penetration of new elements into the summer aspect. At the present time the situation appears most favourable for the northern species where summer species well adapted to a short summer predominate. This would also account for the penetration of northern species into Central Europe.

SUMMARY

Analysis of available information on the developmental cycles of the mayflies of Central Europe reveals that they may be classified under four main groups, each comprising one or more types. These are arranged as follows: Group A: Species with one generation in the year. A 1. Larvae hatched in autumn, continue to grow throughout winter, adults emerge in spring or summer. A 2. Eggs are in diapause till spring or summer, the growth of larvae is short and rapid. A 3. Larvae hibernate over winter to spring without any growth, recommence the development in spring and summer. Group B: Species with two generations in the year. B 1. First generation eggs hatch in autumn, the larvae develop during winter and adults emerge in spring, the second generation develops rapidly in the course of summer. B 2. Eggs are in diapause up till spring or summer, two generations develop in rapid succession in summer. B 3. In species of type B 1 instead of one summer generation, two generations occur. The species has then three generations. Group C: Species with a two-year developmental period (C 1) or a three-year period (C 2). Group D : Species with three generations in two years (D 1) or two generations in three years (type D 2).

On the basis of present knowledge of the mayfly developmental cycles, the following conclutions on their interrelationship may be deduced. 1. In the mayfly fauna of Central Europe there appear four distinct aspects during the year: pre-spring, spring, summer and autumn aspect. 2. The development of the species is not equable. Each species has more or less defined period of main growth. 3. In certain biotopes the developmental cycles of mayflies and especially their main growth periods are distributed throughout the whole year, or, in some water types, to the vegetation period. 4. In genera which are represented in Central Europe by a greater number of species the developmental cycles of individual species are also distributed throughout year. 5. The distribution of the periods of main growth is of great importance for the distribution of mayflies, for the formation of the fauna in a given area and for the formation of biocenoses in certain biotopes.

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