

## A comparative study of spermatozoa of some Central European Ephemeroptera

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### Morphology, smears, staining, measurements, light microscopy, 25 genera

**Abstract.** The spermatozoa of species from 25 genera (11 families, 51 species) representative of Central European mayflies were investigated. Squashes and smears of seminal vesicles of adult testes fixed in osmium tetroxide vapours were stained by Pappenheim's method. There are four principal groups of spermatozoa: (i) rod-shaped spermatozoa with relatively short head (3–8  $\mu\text{m}$  in length) and with flagellum, these subdivide into two distinct types: smaller, well stainable, rod-shaped spermatozoa (about 75–90%) and large, less well stainable, usually spindle-shaped spermatozoa (about 25–10%) (Siphonuridae, *Ephoron*, *Ephemer*, *Potamanthus*); (ii) rod-shaped, elongated spermatozoa with relatively long (8–20  $\mu\text{m}$  in length) head and with flagellum similar in shape, these also differentiated into two staining types (Baetidae); (iii) rod-shaped spermatozoa with shorter or longer head and well developed flagellum equal in both length and shape, these all of well staining type (Heptageniidae, *Arthroplea*, *Ephemerella*, *Caenidae*); (iv) rounded spermatozoa differentiated into two staining types as in groups (i) and (ii) but flagellum not discernible under light microscope (Leptophlebiidae). The arrangement of the morphological characters of mayfly spermatozoa is supposed to be related to the main phylogenetic trends within the order.

Our knowledge of mayfly eggs and especially of chorion structure, micropyle and sperm guide is relatively very extensive. The eggs of most of the European genera were dealt with by DEGRANGE (1960) who also studied the fecundity of females. KOSS (1968) and KOSS & EDMUNDS (1974) described the eggs of more than 100 representative genera of all known recent families of the order. Despite these extensive comparative studies very little attention has been devoted to the structure of the mayfly spermatozoa. The success achieved in comparative study of other insect and Arthropod spermatozoon ultrastructure has prompted interest in those of the Ephemeroptera. BACCETTI, DALLAI & GIUSTI (1969) examined the ultrastructure of the spermatozoon of *Cloeon dipterum* (L.), but so far no other data concerning mayfly spermatozoa have been published.

While studying the spermatogenesis and structure of the mayfly testes (SOLDÁN, 1979) I observed conspicuous differences in the spermatozoa shape and size in six selected European genera which represent different morphological, ecological and life cycle types. A comprehensive analysis of more than 50 Central European species available at Czechoslovak localities, has shown that similar differences occur in other genera and families and are significant. The shape and measurements of the spermatozoa of species from 25 European genera are described in the present paper.

### MATERIAL AND METHODS

Fifty-one Central European species (156 specimens examined) of mayflies were investigated. The species investigated are listed in paragraphs describing the spermatozoa of the respective families. These species are arranged according to the classification by LANDA (1969); see this

monograph also for the authors of species, genera and families. With the exception of *Pseudocloeon inexpectatum* and *Rhithrogena ferruginea* collected at localities in the Danube basin in Slovakia, all the material investigated was collected at localities in the Elbe basin, mostly in Central and South Bohemia.

Fresh material of the adults or subimagos before moulting was used for the study of spermatozoa. The specimens were opened dorsally, the seminal vesicles as well as shrunken remnants of testes and vas deferens were loosened with a thin trickle of Pringle's solution. Squashes of the dissected organs and smears of sperm content of seminal vesicle were made on cover glasses and then fixed in 1% osmium tetroxide solution vapours for 2–5 min. Pappenheim's method (May-Grünwald, Giemsa) was used for staining squashes and smears. Some squashes were stained with Giemsa (10% solution) for 10–20 minutes. Dehydrated squashes and smears were embedded in Canada balsam with Cellosolve.

As is usually in the literature dealing with mayfly eggs (e.g. DEGRANGE, 1960) only the maximal range of spermatozoon head length and width, and range of flagellum length are given for species investigated. The measurements are based always on several (5–15) spermatozoa; the measurements of less stainable spermatozoa are given in parentheses. The ocular micrometer and magnification with objective 100× (oil immersion) and projection 12.5 were used for measuring spermatozoa. Preparations were examined and microphotographs taken with a Zetopan microscope.

## RESULTS

### Siphonuridae

(Plate II, 7)\*

Measurements: *Ameletus inopinatus*: 3.3–6.2 × 0.5–1.3 μm – well stainable type, (4.8–7.6 × 2.0–3.1 μm – less stainable type); *Metreletus balcanicus*: 3.6–5.4 × 0.8–1.3 (5.2–9.0 × 1.9–2.9); *Siphonurus aestivalis*: 3.8–5.6 × 0.8–1.2 (5.6–8.5 × 2.2–2.8); *S. lucustris*: 4.0–6.2 × 0.7–1.4 (6.0–9.5 × 2.3–3.5); *S. linnaeanus*: 3.5–6.5 × 0.9–1.5 (5.5–8.3 × 2.0–4.0). Flagellum hardly distinguishable in all species examined. (All measurements in μm.)

Head of spermatozoon roughly rod-shaped, slightly bent or straight. Spermatozoa mostly irregular in shape; they can be club-shaped or spindle-shaped with more or less extended anterior or posterior portion. Differences in the length of head are relatively high even in the well stainable type; the less stainable spermatozoa are present but very rare (about 5–15% of total). Spermatozoa of this type are conspicuously irregular in shape, usually spindle-shaped or even rounded with pointed anterior and posterior portion. Both types of spermatozoa with hardly distinguishable flagellum. Flagellum most probably present but virtually indiscernible except for its basis under the light microscope.

### Baetidae

(Pl. II, 2, 3, 4, 5)

Measurements: *Baetis alpinus*: 10.3–12.8 × 0.3–0.6 μm, flagellum 25–30 μm (17.5 to 19.3 × 0.5–0.7, fl. 30–45); *B. buceratus*: 7.4–8.7 × 0.6–0.8, fl. 30–40 (11.5–12.9 × 1.4–1.7, fl. 50); *B. fuscatus*: 14.8–16.3 × 0.5–0.8, fl. 40–55 (16.9–18.4 × 2.0–2.5, fl. 50); *B. lutheri*: 7.0–8.2 × 0.6–0.9, fl. 30–45 (10.8–11.6 × 0.8–1.2, fl. 60); *B. muticus*: 7.5–9.7 × 0.5–0.7, fl. 30–40 (10.5–11.3 × 0.7–0.8, fl. 50); *B. niger*: 8.0–9.8 × 0.4–0.6, fl. 20–30 (10.3–11.0 × 0.6 to 0.8, fl. 30–45); *B. rhodani*: 11.2–14.5 × 0.3–0.5, fl. 30–45 (14.3–16.1 × 0.5–0.7, fl. 45 to 50); *B. vernus*: 7.0–9.0 × 0.7–0.9, fl. 20–35 (10.1–11.0 × 1.0–1.2, fl. 30–40); *Centroptilum luteolum*: 5.6–7.9 × 0.6–0.8, fl. indistinguishable (9.8–10.6 × 0.9–1.7); *Cloeon dipterum*: 9.6–11.6 × 0.5–0.7, fl. 30–45, all spermatozoa approximately equal in size; *C. simile*: 8.7 to 10.8 × 0.5–0.7, fl. 30–45 (12.2–14.0 × 0.8–1.0, fl. 40–55); *Procloeon bifidum*: 9.4–11.2 × 0.4 to 0.6, fl. 35–45 (12.3–14.1 × 0.8–1.4, fl. 50–60); *Pseudocloeon inexpectatum*: 7.4–9.3 × 0.5 to 0.7, fl. 30–50 (11.8–12.9 × 1.0–1.6, fl. 30–55).

\* Plates I–III will be found at the end of this issue.

Head of spermatozoon regularly rod-shaped, elongated and straight. The anterior portion rounded or bluntly pointed. With the exception of *Cloeon dipterum* spermatozoa of the less stainable type were present in all specimens investigated. They are similarly shaped as spermatozoa of the normal type and the differences in size are only slight (*B. rhodani*, *B. fuscatus*). These spermatozoa are very rare (less than 10%). Flagellum present in both types, about 3—4 times longer than the length of the head. In *Centroptilum luteolum* flagellum present but barely distinguishable. There are considerable differences in the length of spermatozoa within the genus *Baetis*. In *Baetis buceratus*, *B. lutheri*, *B. niger* and *B. vernus* spermatozoa with relatively shorter head (up to 8—10  $\mu\text{m}$ ) occur; longer spermatozoa (approximately 12—15  $\mu\text{m}$  head length) present in *B. fuscatus*, *B. alpinus* and *B. rhodani*. Similar differences were found between the genus *Centroptilum* and the genera *Cloeon* and *Procloeon*.

### Oligoneuriidae

(Pl. II, 12)

Measurements: *Oligoneuriella rhenana*: 7.8—9.8  $\times$  0.5—0.8, flagellum 30—50), all spermatozoa equal in length.

Head of spermatozoon regularly rod-shaped, straight or slightly bent, the anterior portion rounded or slightly pointed. Flagellum present, long, approximately 3—4 times longer than the head. All spermatozoa belong to the well stainable type. Spermatozoa of *Oligoneuriella rhenana* show affinities to those of the Heptageniidae (length and shape of the head). They differ in the length of flagellum.

### Arthropleidae

Measurements: *Arthroplea congener*: 8.8—10.3  $\times$  0.5—0.8, flagellum 15—25, all spermatozoa equal in length.

Head of spermatozoon rod-shaped or club-shaped with slightly extended and rounded anterior portion. Flagellum present, approximately twice or three times as long as the head. Only the well stainable type of spermatozoa was observed. Spermatozoa of the only European species show close affinities with those of the Heptageniidae, especially the genus *Ecdyonurus*.

### Heptageniidae

(Pl. I, 1—5)

Measurements: *Ecdyonurus aurantiacus*: 12.0—14.2  $\times$  0.4—0.6, flagellum 8—15; *E. lateralis*: 9.6—11.1  $\times$  0.4—0.6, fl. 5—15; *E. dispar*: 12.8—15.4  $\times$  0.5—0.7, fl. 8—20; *E. subalpinus*: 12.8—15.2  $\times$  0.4—0.7, fl. 5—15; *E. torrentis*: 10.4—11.2  $\times$  0.7—1.0, fl. 8—15; *E. venosus*: 12.1 to 13.8  $\times$  0.6—0.8, fl. 10—15; *Epeorus sylvicola*: 11.8—12.9  $\times$  0.6—0.9, fl. 10—25; *Heptagenia flava*: 10.6—13.9  $\times$  0.7—0.9, fl. 5—10; *H. fuscogrisea*: 12.1—13.2  $\times$  0.4—0.8, fl. 8—12; *H. sulphurea*: 11.5—14.2  $\times$  0.5—0.8, fl. 6—15; *Rhithrogena ferruginea*: 12.2—14.6  $\times$  0.4—0.6, fl. 20—40; *R. hercynia*: 13.9—16.5  $\times$  0.8—1.1, fl. 30—55; *R. semicolorata*: 12.6—14.9  $\times$  0.5—0.7, fl. 10—35.

Head of spermatozoon rod-shaped, elongated, usually straight or slightly bent. Both anterior and posterior portions rounded or slightly pointed. In some species of the genus *Ecdyonurus* the head is club-shaped with extended anterior part (*E. subalpinus*, *E. torrentis*). Flagellum present in all genera and species investigated; approximately as long as the head or shorter.

Flagellum twice or three times longer than the head in the genus *Rhithrogena*. All spermatozoa approximately equal in length and shape. Less stainable ones apparently absent; all spermatozoa belong to the well stainable type.

Unlike the genus *Baetis*, there are no considerable differences in size and shape of spermatozoa within the genus *Ecdyonurus* (six species examined). The family Heptageniidae is well characterized by the size and shape of the spermatozoa; the genus *Rhithrogena* differs from *Ecdyonurus*, *Epeorus* and *Heptagenia* in the length of flagellum. This family shows affinities to the Oligoneuriidae and Ephemerellidae.

### Ephemerellidae

(Pl. I, 6)

Measurements: *Ephemerella* (*Ephemerella*) *ignita*: 24.5–26.3 × 0.4–0.6, fl. 8–20; *E.* (*Chitonophora*) *Krieghoffi*: 11.9–13.5 × 0.8–1.0, fl. 15–20; *E.* (*Torleya*) *major*: 12.0–13.2 × 0.6 to 0.8, fl. 10–25, all spermatozoa equal in length.

There are two groups of subgenera in the only European genus *Ephemerella*. Spermatozoa of the subgenus *Ephemerella* s. str. (*E. ignita*) are conspicuously long and bent, with anterior part of the head produced into a point and flagellum much shorter than the head. The second group comprises the subgenera *Chitonophora* and *Torleya*. The head of spermatozoon is rod-shaped and elongated with rounded or bluntly pointed anterior portion and flagellum at least as long as the head. Spermatozoa of these subgenera are practically identical with those of the family Heptageniidae. All spermatozoa equal in shape and size in the Ephemerellidae, and belong to the well stainable type.

### Caenidae

(Pl. III, 15)

Measurements: *Brachycercus harrisella*: 4.8–6.3 × 0.4–0.6, flagellum 15–25; *Caenis macrura*: 4.8–5.5 × 0.5–0.8, fl. 10–20; *C. robusta*: 4.2–6.5 × 0.5–0.9, fl. 10–25, all spermatozoa equal in length.

Head of spermatozoon rod-shaped with bluntly pointed or rounded anterior part and much shorter than in the Heptageniidae and Ephemerellidae. Flagellum present, about 3–4 times longer than the head. All spermatozoa equal in size and shape; less stainable ones absent in all species investigated.

The family Caenidae shows affinities to the Heptageniidae and Ephemerellidae from which it differs by the shortened head. This character places the Caenidae nearer to the Ephemeridae and Potamanthidae.

### Leptophlebiidae

(Pl. III, 13, 14)

Measurements: *Leptophlebia marginata*: 2.7–3.5 (3.7–4.5 in less stainable type); *L. vespertina*: 1.8–2.6 (2.9–3.3); *Paraleptophlebia submarginata*: 1.8–2.4 (1.9–2.7); *P. cincta*: 1.6–2.0 (1.8–2.3); *Habroleptoides modesta*: 1.3–2.1 (1.8–2.4); *Habrophlebia fusca*: 1.3 to 2.0 (1.5–2.2); *H. lauta*: 1.5–2.2 (1.8–2.4); *Choroterpes picteti*: 0.8–1.2 (2.2–2.6), flagellum indiscernible in all species investigated.

Spermatozoa regularly rounded, resembling blood corpuscles on smears or squashes. They are probably spherical in ducts or seminal vesicles. Head

with a translucent area in the middle which is easily distinguishable, especially in the genera *Leptophebia* and *Choroterpes*. In these genera spermatozoa are apparently differentiated into two types: less and well stainable, and also distinguished by the size of the head. Both types are similar in shape. Less stainable spermatozoa are relatively abundant (about 20%). In the genera *Paraleptophebia*, *Habroleptoides* and *Habrophlebia* only slight differences in size were observed, less stainable spermatozoa being relatively rare (less than 10–15%).

Spermatozoa of the Leptophebiidae represent the most remarkable ones within Central European mayflies. The shape of the head is completely atypical, flagellum not discernible by means of light microscopy or reduced. The family is well characterized by arrangement of spermatozoa; no close affinities with any other European family of mayflies is apparent.

### Polymitarcidae

Measurements: *Ephoron virgo*:  $4.2-5.4 \times 0.5-0.7$ , flagellum 20–40 ( $8.9-14.8 \times 1.2$  to 2.5, fl. 30–55 in less stainable type).

Head of spermatozoon rod-shaped, straight with rounded posterior and anterior portions. Two types of spermatozoa distinguished by size and staining ability. Spermatozoa of less stainable type irregular in shape, roughly rod-shaped. Flagellum normally developed. Spermatozoa of the only genus *Ephoron* occurring in Europe are very similar to those of the Ephemeridae.

### Ephemeridae

(Pl. III, 17, 18)

Measurements: *Ephemera vulgata*:  $4.2-5.1 \times 0.6-0.9$ , flagellum 15–30 ( $8.9-14.7 \times 1.1$  to 2.9, fl. 20–45 in less stainable type); *E. danica*:  $4.4-5.0 \times 0.7-0.9$ , fl. 15–35 ( $11.1-15.2 \times 1.5$  to 3.4, fl. 30–50); *E. lineata*:  $4.5-5.0 \times 0.7-0.9$ , fl. 15–35 ( $10.4-15.8 \times 1.1-3.6$ , fl. 35–50).

Head of spermatozoon regularly rod-shaped, slightly bent with bluntly pointed anterior part (well stainable type). Spermatozoa of the less stainable type irregular in shape. They are irregularly rod-shaped, spindle-shaped, bent or straight, or even nearly rounded. Difference in size between the two types is considerable. Flagellum present and easily distinguishable in both types, approximately 3–6 times longer than the head. Spermatozoa of the less stainable type relatively numerous (more than 20%).

The family Ephemeridae is well characterized by morphological characters of the spermatozoa, especially by the difference in the size of the head. The family is in close affinity with the Polymitarcidae and shows relationship also to the Potamanthidae and Siphonuridae.

### Potamanthidae

(Pl. III, 16)

Measurements: *Potamanthus luteus*:  $4.3-5.1 \times 0.5-0.7$ , flagellum 15–25 ( $5.6-5.9 \times 0.8$  to 1.2, fl. 20–40 in less stainable type).

Head of spermatozoon regularly rod-shaped, straight. Spermatozoa differentiated into two types. Less stainable ones equal in shape, rod-shaped;

these spermatozoa very rare (less than 10%). Flagellum present, well distinguishable in both types.

The family Potamanthidae shows close relationship to the Siphonuridae and also to the Ephemeridae and Polymitarciidae. Shortened spermatozoa of this family are similar to those of the Caenidae.

#### DISCUSSION AND CONCLUSIONS

Using Pappenheim's method of staining smears and squashes, we can readily compare the shape and size of spermatozoa. This method shows the general characters satisfactorily but does not provide cytological data (size and position of nucleus, mitochondria, crystalline bodies etc.). A comparative study of spermatozoa of more than 50 Central European genera shows relatively great differences in both shape and size of the spermatozoon head and in the length of flagellum. The differences are very remarkable. Spermatozoa of species investigated measure from 1.0  $\mu\text{m}$  (*Choroterpes picteti*) to 25  $\mu\text{m}$  (*Ephemerella ignita*) in length of the head. The spermatozoa of species examined consist of four principal groups, as follows:

(i) rod-shaped, elongated spermatozoa with relatively short head (about 3–8  $\mu\text{m}$  head length) and apparent (except Siphonuridae) tail, which is usually twice or 3–5 times longer than the head. Always two types of spermatozoa occur: smaller and well stainable type and large, less stainable type. Most spermatozoa belong to the well stainable type (approximately 75–80% in *Ephemerella* and *Ephoron*; more than 90% in Siphonuridae and *Potamanthus*). Less stainable spermatozoa can be different in shape (rod- or spindle-shaped, rounded, irregularly elongated), and are found in the families Siphonuridae, Polymitarciidae, Ephemeridae and Potamanthidae.

(ii) rod-shaped, elongated spermatozoa with relatively long head (5–15  $\mu\text{m}$  head length) and flagellum twice or 3–5 times longer than the head. Spermatozoa of the less stainable type present, but usually very rare. This group comprises only the family Baetidae.

(iii) rod-shaped spermatozoa with shorter or longer head and flagellum as long as the head or shorter. All spermatozoa equal in both shape and size; less stainable type absent. This group comprises the families Oligoneuriidae, Heptageniidae, Arthropleinac, Ephemerellidae and Caenidae.

(iv) rounded and probably spherical spermatozoa without any distinguishable flagellum. Spermatozoa of the less stainable type present, relatively abundant. Both types of spermatozoa equal in shape, with a translucent area in the middle of the head. This group comprises only the family Leptophlebiidae.

The mayfly spermatozoon is atypical within the Arthropods. While the typical feature of the insect spermatozoon is a generally very slim shape with an extremely elongated head (PHILLIPS, 1970; BACCETTI, 1972), the mayfly spermatozoon possesses a shortened rod-shaped head or even a rounded head in the Leptophlebiidae. Mayfly spermatozoa are relatively very small, especially in the genera *Choroterpes*, *Caenis* and *Potamanthus*.

The ultrastructural characters of the mayfly spermatozoon are in a comparatively independent and isolated position (BACCETTI, DALLAI & GIUSTI, 1969). The following characters single it out from spermatozoa of other insects: the flagellar filament of the 9 + 9 + 0 type, very brief acrosome,

crystalline proteinaceous complex within a single membrane, mitochondrial complex separated from crystalline mass. Some of these characters are supposed to be very primitive. I believe, contrary to BACCETTI et al. (1969), that the spermatozoon of *Cloeon dipterum* (L.) (family Baetidae) does not represent a typical mayfly spermatozoon but only one of the four different types found in Central European mayflies. The many striking differences between the spermatozoa of each group must be involved in the ultrastructure of head and flagellum as well.

There are two more remarkable aspects of the morphology of the mayfly spermatozoa: their polymorphism (dimorphism) in some families and the unique, non-flagellate spermatozoa of the Leptophlebiidae. Spermatozoa polymorphism as a result of typical two-fold spermatogenesis has been found in many Arthropods. The most relevant aspects of this phenomenon were summarized by FAIN-MAUREL (1966) and ZYLBERBERG (1969) who studied these problems in the Lepidoptera. As has been already pointed out (SOLDÁN, 1979), the less well stainable spermatozoa may belong, analogously to some other insects, to the apyrene or diploid (polyploid) hyperpyrene lines, and the well stainable ones to the eupyrene line. Obviously, little can be said about spermatozoa polymorphism and genetics in the Ephemeroptera without detailed cytological analysis.

Non-flagellate spermatozoa of the Leptophlebiidae, which are dimorphic as well, represent seemingly paradoxical conditions. This type of spermatozoa was previously described only in four insect groups (BACCETTI, 1972). Non-flagellate spermatozoa can be associated with non-motility. Rounded non-flagellate spermatozoa of the Leptophlebiidae resemble immature presperms or even spermatids in other families. However, the spermatozoa of the Leptophlebiidae were taken for examination from the seminal vesicles of mature males 1 day old which are ready for mating flight. On the other hand, in some other insects groups the maturation of spermatozoa is achieved in the female organism (HUGHES & DAVEY, 1969). This problem requires further examination of the ultrastructure.

It is difficult to reconstruct phylogenetic trends from the relatively few characters which the spermatozoa provide. The four groups mentioned in the previous section correspond with the main phylogenetic trends within the order Ephemeroptera derived from other data (LANDA, 1969b — comparative anatomy of tracheal system; RIEK, 1973 — external morphology; KOSS & EDMUNDS, 1974 — morphology of the eggs). As far as the morphology of mayfly spermatozoa is concerned, it seems to be premature to make any phylogenetical conclusions because of the fragmentary knowledge of the ultrastructure.

According to KOSS & EDMUNDS (1974) chorionic sculpturing evolved independently in nearly every family or subfamily, and therefore these characters are useful for phylogenetic studies of the order. I believe that spermatozoa, whose shape and size must be closely related to microphyle sculpturing, can provide us with further data useful for phylogenetic study.

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### Сравнительное изучение сперматозоидов некоторых средневропейских поденок (Ephemeroptera)

Морфология, мазки, световая микроскопия, 25 родов

**Резюме.** Были исследованы сперматозоиды представителей 25 родов (11 семейств, 51 вида) средневропейских поденок. Мазки из семенных пузырьков или семенников взрослых особей фиксировались парами четырехоксида осмия и окрашивались по Пашпгенгейму. Были установлены 4 основных группы сперматозоидов: (I) палочковидные с относительно короткой головкой (длина 3—8 мкм) и жгутиком; среди них встречаются два разных типа: более мелкие, хорошо окрашивающиеся, палочковидные (около 75—90%) и крупные, менее хорошо окрашивающиеся, обычно веретеновидные (10—25%) (*Siphonuridae*, *Ephoron*, *Ephemera*, *Polamanthus*); (II) палочковидные, удлиненные, с относительно длинной головкой (8—20 мкм) и жгутиком одинаковой формы, дифференцированные как и в первой группе (*Baetidae*); (III) палочковидные с более короткой или длинной головкой и жгутиком одинаковой длины и формы (*Heptageniidae*, *Ephemerella*, *Arthroplea*, *Caenidae*); (IV) округлые сперматозоиды без различного в оптический микроскоп жгутика и дифференцированные в два типа как и в группах (I) и (II) (*Leptophlebiidae*). Предполагается, что расположение морфологических признаков сперматозоидов поденок соответствует основным направлениям филогенеза в рамках этого порядка.

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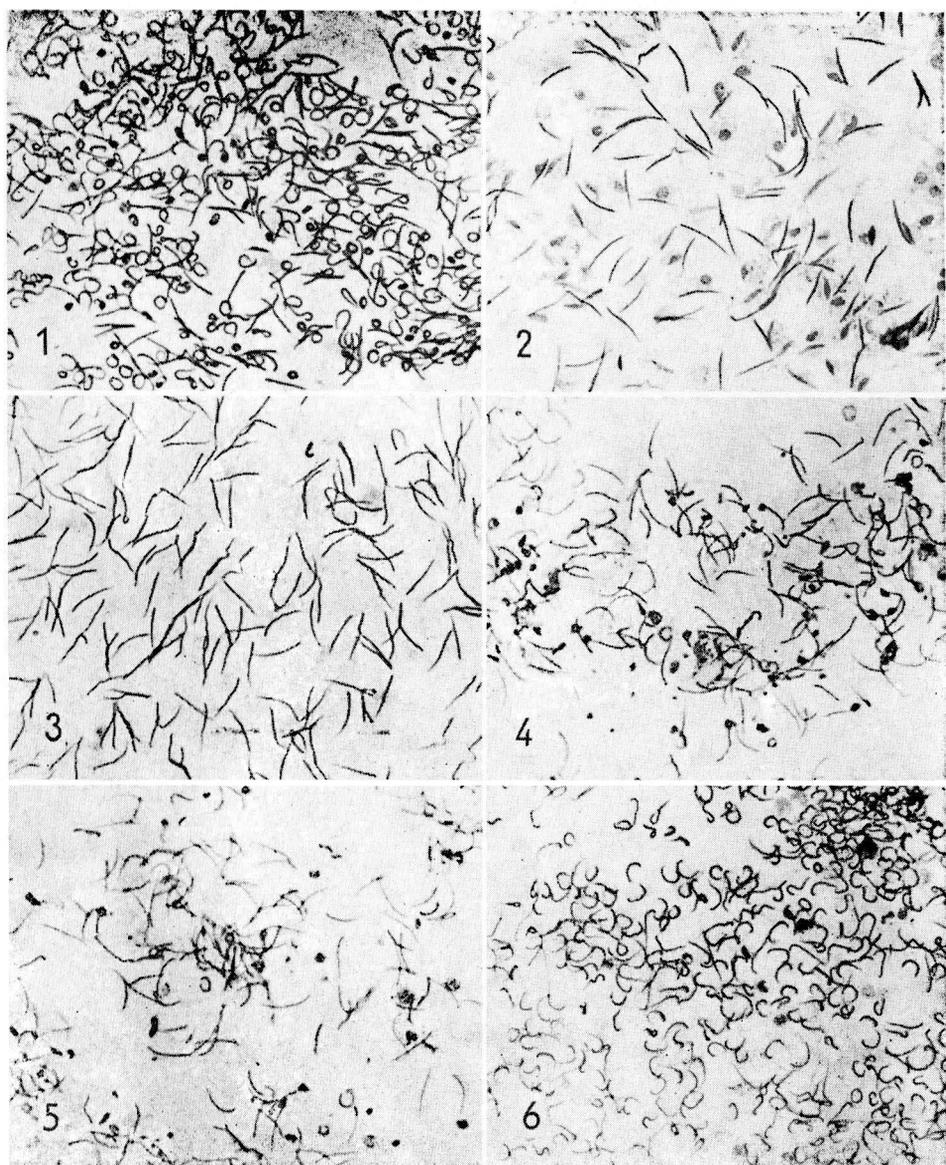


PLATE I, 1-6: Spermatozoa of Central European mayflies. 1 - *Ecdyonurus venosus*. 2 - *E. subalpinus*. 3 - *Rhithrogena semicolorata*. 4 - *Heptagenia fuscogrisea*. 5 - *Epeorus sylvicola* (Heptageniidae). 6 - *Ephemerella (Chitonophora) krieghoffi* (Ephemerellidae). Objective 63 $\times$ , projection 8 $\times$ .

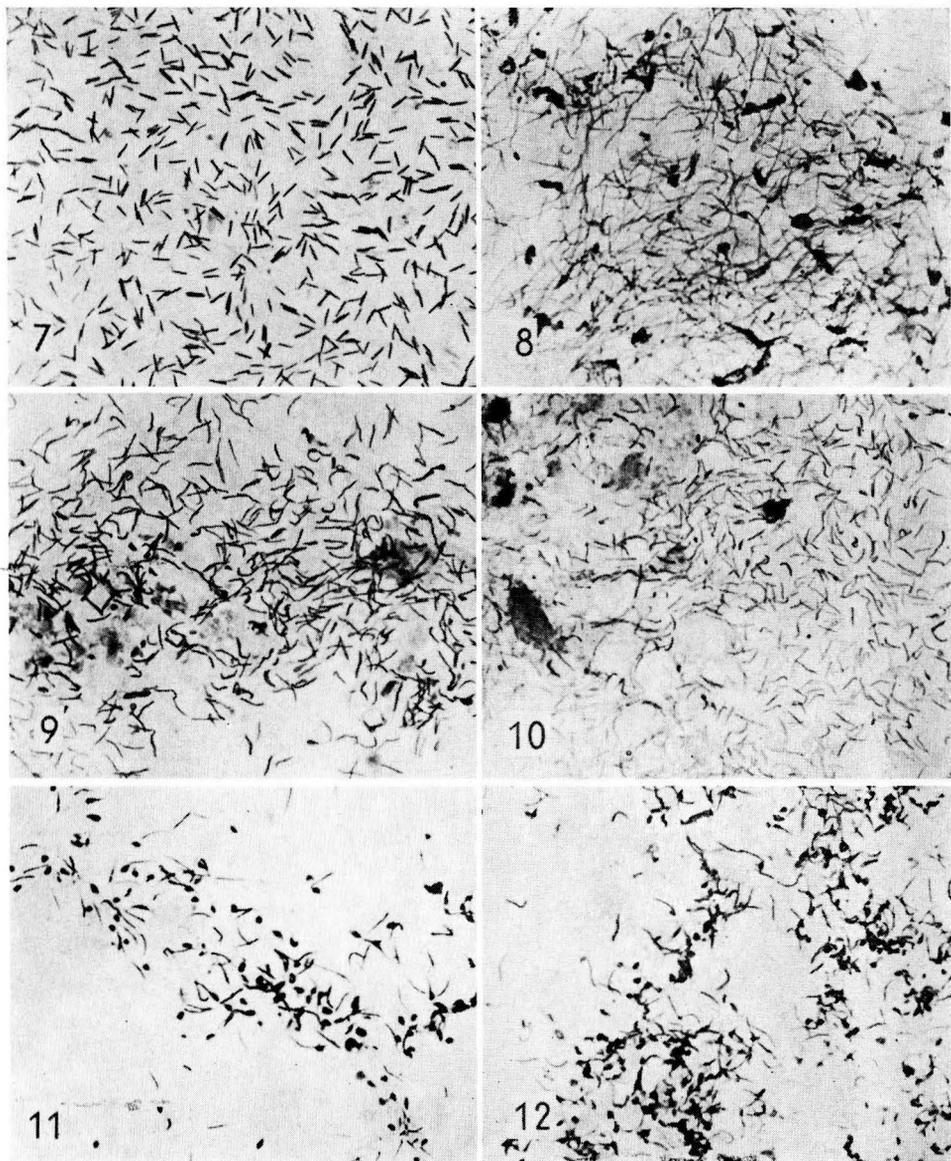


PLATE II, 7-12: Spermatozoa of Central European mayflies. 7 - *Siphonurus aestivalis* (Siphonuridae). 8 - *Baetis rhodani*. 9 - *Baetis niger*. 10 - *Centroptilum luteolum*. 11 - *Pseudocloeon inexpectatum* (Baetidae). 12 - *Oligoneuriella rhenana* (Oligoneuriidae). Objective 63 $\times$ , projection 8 $\times$ .

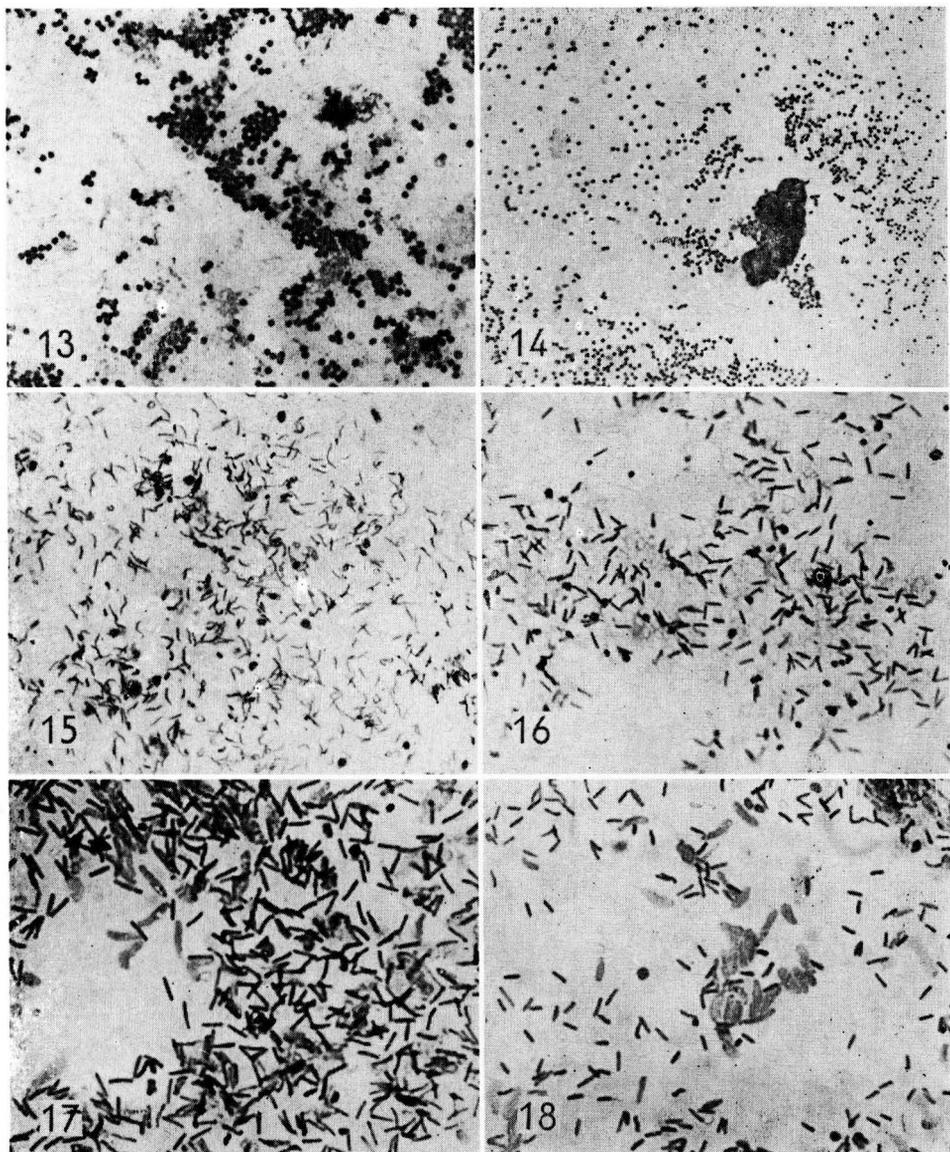


PLATE III, 13-18: Spermatozoa of Central European mayflies. 13 - *Paraleptophlebia cincta*. 14 - *Choropterus picteti* (Leptophlebiidae). 15 - *Caenic macrura* (Caenidae). 16 - *Potamanthus luteus* (Potamanthidae). 17 - *Ephemera vulgata*. 18 - *Ephemera lineata* (Ephemeridae), detail of less stainable spermatozoa. Objective 63 $\times$ , projection 8 $\times$ .