

Tomáš Soldán	Comparative anatomy of the internal reproductive organs of mayflies ( <i>Ephemeroptera</i> )	Studie ČSAV	č. 6 1981
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Comparative anatomy of the internal  
reproductive organs of mayflies (*Ephemeroptera*)

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Corresp. member of ČSAV Jaroslav Weiser, DrSc.

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Tomáš Soldán

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# INTRODUCTION

Lately it has been showed that more detailed study of comparative anatomy can bring about valuable information not only for the developmental morphology, physiology and comparative physiology, but also for the taxonomy, higher classification and phylogenesis of insects (Landa, 1959). The classical comparative anatomy as separated branch of science was developed especially in the first third of this century, when a great deal of data concerning a large number of insect orders was obtained. A weak point of the classical comparative anatomy is the insufficiency of more detailed data about organ systems in the frame of whole insect orders or larger taxonomic groups, outlasting till now. With the lack of palaeontological material, which is considerable in many groups, these data can contribute essentially to the reconstruction of phylogenetic development and to the classification of recent representatives of given taxon.

In this respect, the order *Ephemeroptera* is an exception. In the scope of the whole order, detailed data about the structure of tracheal system, malpighian tubules and ventral nerve cord are published (Landa, 1948, 1949, 1967, 1969b). This information have been used earlier for the reconstruction of main phylogenetic lineages of the order (Landa, 1973). In some Palaearctic species the muscles of abdomen and thorax (Grandi, 1947, 1962), the muscles of gills (Eastham, 1958) and the alimentary system (Grandi, 1950) have been studied from the comparative anatomy point of view. In many Palaearctic families even the endocrine system (corpora allata, corpora cardiaca) is described (Arvy & Gabe, 1951, 1952a,b, 1953a,b; Cazal, 1948). In several European species also the structure of circulatory system has been studied (Popovici-Bazosanu, 1905; Meyer, 1931). On the basis of comparative study of the external morphology of larvae and adults of almost all the recent genera, the key to families and subfamilies based on larvae has been constructed (Edmunds, Allen & Peters, 1963) and the basic principles of the higher classification of mayflies has been summarized (Edmunds, 1962, 1973a).

The lack is that the reproductive system of *Ephemeroptera* has not been yet elaborated in a similar way. With the exception of some European and North American species and with the exception of male external genitalia we have no detailed data concerning the gonads of may-

flies. The objective of this study is to acquire information about male and female reproductive system from the comparative anatomy point of view concerning as many genera as possible from all the zoogeographic regions. These data should partly complete the anatomical data concerning other organ systems partly contribute to solving of some points of higher classification and phylogenetic development of the order *Ephemeroptera*. The comparative data concerning reproductive organs may be important also for the study of the physiology of reproduction and the acquired information can be used to precise the relation of internal reproductive organs of *Ephemeroptera* to gonads of other insect groups with panoistic type of ovarioles (*Apterygota*, *Odonata*, *Polyneoptera*). The data concerning the reproduction of water insects can also have practical significance in connection with using the biological indication of water quality. Perfect anatomical knowledge enables besides to use *Ephemeroptera* as a model for solving some general biological questions.

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## SURVEY OF LITERATURE

We find the first reference concerning the reproductive system of *Ephemeroptera* in Schwammerdam's work *Ephemerivita* (1975), where besides other organ systems also gonads of *Palingenia longicauda* (Oliv.) are described and illustrated. As he was studying testes especially in adults, he came to many uncorrect conclusions because in adults these organs are very modified in connection with the descent of mature spermatozoa into the seminal vesicle. Besides the author figures a pair of elongated bodies, which he indicates as accessoric organs, but they probably represent a part of malpighian tubules or parts of fat body (Brinck, 1957). But for that time the illustrations are really true.

Earlier authors who studied reproductive organs of *Ephemeroptera* (Joly, 1977a; Joly and Joly, 1876a, 1876b) dealt with gonads of *Palingenia longicauda* (Oliv.), *Ephoron virgo* (Oliv.), *Ephemera vulgata* L. and other large species. Gonads of *Caenis macrura* (Steph.) (adult) are mentioned by Eaton (1867). At that time the attention was devoted especially to ovaries. Brandt (1878) studied their histological structure and described ovarioles of mayfly ovary as panoistic for the first time. The most important work from that period is the first monograph on insect gonads by Palmén (1884) where gonads of the genera *Ecdyonurus* and *Rhithrogena* (as *Heptagenia*), *Oligoneuriella* (as *Oligoneuria*), *Caenis*, *Palingenia*, *Potamanthus* and *Ephoron* (as *Polymitaecys*) are described more detailed. In all the genera investigated a great number of testicular follicles and ovarioles was found out and with the exception of males of the genus *Ephoron*, where anastomosis between seminal vesicles is stated to be present, the gonads are entirely separated. Besides the basic anatomic data also the first more detailed histological data are presented and gonads of mayflies are confronted to gonads of related insect orders. The changes occurring during the ontogenetic development are mentioned in more details, too. The Palmén's monography assumes also some former uncorrect data. Palmén believes that the openings of testes and ovaries as well are of the mesodermal origin. These data were corrected by Wheeler (1893) and Quadri (1940) above all on the basis of study of embryogenesis and larvae of the first instars.

By the end of the last century and in the first half of this century the intensive development of the comparative anatomy occurs. In the

framework of the study of general anatomical conditions a great attention is paid to reproductive organs of mayflies though the gonads are studied rather from the descriptive anatomy point of view. Drenkelfort (1910) describes gonads of *Siphonurus lacustris* Etn., Heiner (1914) deals with anatomy of *Cloeon dipterum* (L.), *Baetis fuscatus* (L.) and *Habrophlebia fusca* (Curt.), Vayssière (1882, 1890) deals in details with the anatomy of *Prosopistoma* and later (Vayssière, 1934, 1937) describes the gonads of *Baetisca carolina* Traver, *B. obesa* Say and *Probosciodoplocia sikorai* (Vayss.). Levy (1948) deals with gonads, their openings and copulatory organs of the genus *Hexagenia*. More data concerning the reproductive system in some European species are introduced by Verrier (1942), Bayard and Verrier (1950), and Grenier and Verrier (1950), who were dealing with the anatomy of *Ecdyonurus lateralis* (Curt.), *Ephemerella*, *Chitonophora* sp. and *Ephemera vulgata* L. All the data obtained this way are summarized in respective chapters of some compendia, e.g. Schroeder (1912-1929), Weber (1933), Imms (1951) and in the general compilations of the order *Ephemeroptera*, e.g. Ulmer (1924, 1929) or Despax (1949) and others.

The first more detailed anatomical and histological data concerning the reproductive system of mayflies were published by Needham, Traver and Hsu (1935) in their monography on biology and taxonomy of Nearctic mayflies. As to the male reproductive system, the main attention was given to changes of gonads after moulting of larva into subimago and histology of seminal and ejaculatory ducts, seminal vesicles, penis and forceps in a subimago and an adult. As to the female reproductive system, the study was concentrated on the development of growing oocytes, forming of chorionic structures, and the descent of mature eggs to oviducts and the changes of the eggs and attachment structures after an oviposition. This work is important above all because histological changes of gonads during ontogenesis are studied for the first time. All the observations were made on larvae and adults of Nearctic genus *Stenonema* (family *Heptageniidae*).

One of the most important works concerning the reproductive system of mayflies is that by Brinck (1957) which deals not only with a testis, an ovary and copulatory organs of males and females but also with body segmentation during embryogenesis on the basis of embryological data known till now and on the basis of detailed study of the first larvae instar (larvulle), placement of gonopores and innervation of last abdominal segments and copulatory organs. Besides the relation between ventral muscles and gonoducts at place of their openings has been studied. In the genera *Siphonurus*, *Parametetus*, *Baetis*, *Cloeon*, *Ephemerella*, *Leptophlebia*, *Heptagenia* and *Ephemera* gonads, ducts and copu-

latory organs of larvae, males and females are being studied. A great attention has been paid to both copulation and mating flight in some groups of mayflies and many former confusing data have been changed or corrected. Also the summary of terminology of mayfly external genitalia in five languages which unifies often uncorrect terms is very valuable and introduces the definition of concepts. This work is, of course, of a general character, dealing with problems of arrangement and ontogenetic development of mayfly reproductive system and that is why only a little attention was turned to more detailed study of histological structures of gonads.

The reproductive organs of *Coloburiscus humeralis* (Walker) from New Zealand were described by Wisely (1965). He studied mostly gonads of subimagos and adults. He describes the degeneration of testicular follicles, the descent of mature eggs into oviducts, and openings of both ovaries and testes, male and female copulatory organs, copulation and ovoposition. He also deals with histological structure of ovarioles and histological changes of ovarioles during the termination of oogenesis and the descent of eggs.

The detail description of reproductive organs in larvae, subimagos and adults of *Ecdyonurus lateralis* (Curt.) and *Rhithrogena semicolorata* (Curt.) is introduced by Codreanu (1939) who studies the effects of ectoparasite *Symbiocladius rhithrogenae* Zav. (Chironomidae, Orthocladiinae) on the mayfly larvae. He describes in detail the development of ovary and testis and the development of copulatory organs in infected and control larvae. In males of *E. lateralis* he describes in a similar way as Palmén (1884) the transversal anastomosis between seminal vesicles. Besides, he deals with the histological structure of gonads and describes the changes caused by a parasite. For the first time spermatogenesis is mentioned. While infected female larvae stay even sterile after moulting to subimago, there are no essential changes of spermatogenesis in male larvae and subimagos. The development of copulatory organs is mentioned as well.

While only a little attention was paid to internal reproductive organs of mayflies and their histological structure or ultrastructure was not studied at all, great attention was paid to male copulatory organs. The male external genitalia and mainly penis and forceps were studied, especially because they provide very important and often even the only reliable critical characters for determination at the species level. The descriptions and illustrations of male copulatory organs with almost all mayfly species described until now can be found in some more important monographs: Eaton (1883-1888), Grandi (1960a), Landa (1969a)-Palearctic fauna, Needham, Traver and Hsu (1935), Edmunds, Jensen &

Berner (1976) - Nearctic fauna, Ulmer (1949) - Oriental fauna, Crass (1947) - Ethiopian fauna, Phillips (1930) - Australian fauna, Needham and Murphy (1924) - Neotropical fauna etc. Postembryonal development of penis and other external genitalia structures were studied by Grandi (1964) in larvae of several European species and she found out that the foundations of penis appear during the last larval instars and also forceps are already visible in older larvae. Ide (1935) describes the development of male copulatory organs in Nearctic species of the genera *Stenonema* and *Ephemera*. The fundaments of the styli are distinguishable 8-9 instars before the moulting of larva into subimago already. Development of male copulatory organs are described also by Needham, Traver and Hsu (1935) and Brinck (1957). From the point of view of the comparative morphology copulatory organs were dealt with by Levy (1948) and Grandi (1960b). Postembryonal development of male and female gonoducts was studied in European species of the genus *Rhithrogena* and *Heptagenia* by Quadri (1940) and it was found that the posterior portion of gonoducts were of the ectodermal origin.

Copulatory organs of mayflies are dealt with by a number of authors also from the general entomology point of view. There are above all the studied aimed at the study of phylogenesis of apterygote insects on the basis of abdominal appendages (Crampton, 1917, 1918, 1929 and others) or general works concerning the morphology of insect genitalia and their interpretation (Snodgrass, 1931, 1936, 1957). Birket-Smith (1971) studied in detail the copulative organs, their muscles and innervation in female larvae and adults of both sexes *Povilla adusta* Návas (family *Polymitarcidae*). He has found out that gonostylus is appended by a pair of condyli to gonocoxa and is controlled by a couple of muscles which are identical to pleural muscles. Gonoporus is placed on gonocoxae not on gonostylus as usual in many mayfly genera. Grimm (1977) discovered sperm-pump mechanism assisting the transfer of spermatozoa in *Habrophlebia lauta* Etn. This mechanism consists of the posterior portion of ducts and a thick layer of circular muscles. Sperm-transfer in *Rhithrogena semicolorata* (Curtis) and *Cloeon* sp. is briefly mentioned by Schlee (1959).

Less attention was paid to female copulatory organs though they have been studied in details in a number of genera. Female copulatory organs, however, are by far not so variable in arrangement as male copulatory organs and they probably do not yield taxonomic characters. The developmental tendency to fusion of the posterior parts of oviducts into the unpaired common oviduct (oviductus communis) is distinctly recognisable in several families. Brinck (1957) distinguishes 6 fundamental types of arrangement of female copulatory organs. The most simple

situation is manifested by a pair of simple openings of oviducts between sterna VII-VIII. A more complicated arrangement of female external genitalia is represented by situation when posterior margin of sternum VII is produced to cover a simple vestibulum or a genital chambre with a sac-shaped seminal receptacle which may serve as copulatory pouches. Grandi (1947, 1955) describes female copulatory organs of European species of genera *Siphonurus*, *Cloeon*, *Centroptilum*, *Baetis*, *Rhithrogena*, *Epeorus*, *Heptagenia*, *Ecdyonurus*, *Ephemerella*, *Caenis*, *Paraleptophlebia*, *Choroterpes*, *Habroleptoides*, *Habrophlebia*, and *Ephemera*. Important data concerning female external genitalia were published by Morrison (1919) and Pleskot (1953) who described copulatory organs and ducts openings of a number of genera, especially from the family *Leptophlebiidae*, where in the genus *Hagenulus* and some related genera we find the most derived type of female copulatory organs in *Ephemeroptera*. The posterior margin of sternum VII is analogous to the ovopositor of orthopteroid insects. Copulatory organs of adults in the genus *Campsurus* are described by Morgan (1913), and Needham & Murphy (1924). The development of ovopositor and copulatory organs in male larvae was dealt with by Quadri (1940). There are only slight differences between subimagos and imagoes. Male and female copulatory organs in subimagos of 10 European genera were studied by Grandi (1964).

All literary data concerning testes, ovaries, duct openings and copulatory organs published until now, together with data about the segmentation of the abdomen in larvae and adults are summarized in monograph dealing with the insect abdomen by Matsuda (1976), where also relations of abdominal structures of mayflies to similar structures in other insect orders are discussed.

Our knowledge concerning spermatogenesis and oogenesis of mayflies is very insufficient. With the exception of several data published by Codreanu (1939) spermatogenesis remains entirely unknown until now. According to some preliminary results the study of structure of spermatozoa spermatogenesis is supposed to bring relevant data for solving of some phylogenetical problems. The knowing of ultrastructure of spermatozoa of *Cloeon dipterum* (L.) (*Baetidae*), which differs from spermatozoa of related insect groups evidently by the unique structure of flagellum, indicates it. The flagellum of *C. dipterum* spermatozoa is without the central pair of microfibrils and spermatozoon head bears further remarkable characters as well (Baccetti, Dallai & Giusti, 1969).

Oogenesis was studied especially in larvae of the last instar, subimagos and adults, essentially in the connection with the descent of mature eggs to oviducts (Needham, Traver & Hsu, 1935; Wisely, 1965 and others).

More detailed histological data, especially concerning the ovaries of younger larvae, have not yet been published. Otherwise oogenesis was studied only in the connection with the cytological study, especially in the determination of the number of chromosomes. Number of chromosomes and chromosome determination of sex were deduced in greater part from the study of growing oocytes chromosomes or from the spermatocytes (Bernhard, 1907; Bohle, 1969; Kiauta & Mol, 1977) or from the chromosomes of the dividing oogonia and spermatogonia (Wolf, 1946). Oogenesis in *C. dipterum* (L.) was dealt more detailly by Wolf (1960) during the study of cytology of oocytes.

The European species *C. dipterum* is probably the best elaborated species from the point of view of oogenesis and the development of ovaries in general especially because it became the model for the study of viviparity (more precisely ovoviviparity) within the Ephemeroptera. A great attention has been devoted to this phenomenon (Joly, 1877b; Causard, 1896; Coggi, 1897; Heymons, 1897), however, these studies concern mostly a mere description of ovoviviparity. From the embryological point of view the ovoviviparity in this species was dealt with by Bernhard (1907) and especially by Degrange (1959). The eggs lack the exochorion and the embryogenesis lasts about 10 - 14 days in the oviducts of the female. Mostly, already newly hatched or hatching larvae of the first instar are to be laid. The fecundity of the female is about 400-600 larvae. The ovoviviparity was observed also in some Nearctic species of the genus *Callibaetis* (Berner, 1941; Edmunds, 1945).

Eggs of mayflies are relatively well elaborated and at present they are already described in the most of genera known till now. In some cases the chorionic structures represent also an important character for determination of species; in addition to this, according to the eggs of adult female and mature female larva the association of larvae and adults can be made. The first data concerning mayfly eggs were published by Ratzel (1867) and Brandt (1878). Eggs of the European species of genera *Ameletus*, *Siphonurus*, *Baetis*, *Centroptilum*, *Gloeon* (oviparous species), *Metretopus*, *Arthroplea*, *Heptagenia*, *Ecdyonurus*, *Ephemerella*, *Caenis*, *Leptophlebia*, and *Ephemer* were described by Bengtsson (1913). Eggs of a large number of remaining European species were described and illustrated by Degrange (1960). He studies chorionic and attachment structures, position and number of micropyle in detail for the first time (Degrange, 1956, 1967). Ovoposition and eggs of numerous Nearctic genera are described by Smith (1935). Eggs of 101 species from all zoogeographic regions were studied by Koss (1968). He paid a considerable attention to the morphology of micropyle and to adhesive structures. This author also calls attention to the signifi-



cance of chorionic structures and adhesive organs for phylogenesis and higher classification of the order (Koss, 1973). Besides, he dealt more detailly also with the formation and origin of adhesive layers (Koss, 1970) and he found out, that the adhesive layer of mature egg must be formed by follicular cells of oocyte after the forming of chorion, it means before the descent of eggs (ovulation) to oviducts and probably before fertilizing, because mayfly gonads lack any accessoric organs entirely. The position of micropyle as well as polar caps is constant. A detailed study of a great number of genera was published by Koss & Edmunds (1974). Except the description and classification of all types of chorionic and adhesive structures, they deal with the evolution of chorion within the order *Ephemeroptera*, on basis of data acquired this way. Plesiomorphic type is represented by oval, smooth chorion with nonfibrillar adhesive layer, funneliform micropyle and suprachorionic sperm guide. It is possible to derive several more advanced types in arrangement of chorionic structures from this basic type. Based on the study of chorion the intrafamilial and interfamilial phylogenetic relationships are discussed in this paper. Suggested classification is based on 6 superfamilies and 21 families of extant *Ephemeroptera*.

Our knowledge about the fecundity of mayflies is relatively extensive, especially, because the questions of fecundity connected with the productivity of water animals have been previously studied in a number of hydrobiological papers. The number of ovoposited eggs in most *Ephemeroptera* is, except the social insects (*Isoptera*, *Hymenoptera*), the highest within the insects in general. The average fecundity ranges from 1000 - 6000 (cf. Clifford & Boerger, 1974); the extreme values are 174 eggs in *Prosopistoma foliaceum* (Fourcr.) (*Prosopistomatidae*) and 12 000 eggs in *Palingenia sublongicauda* Tshern. (*Palingeniidae*). Even less than 100 eggs per female is produced by *Dolania americana* Edmunds & Traver (Peters & Peters, 1977). Until now the fecundity of more than 60 species from 14 families is known (cf. Smith, 1936; Degrange, 1960; Clifford & Boerger, 1974 and others). Palaearctic and Nearctic species are mostly concerned.

## MATERIAL AND METHODS

The following species, genera and families were used for study of reproductive system comparative anatomy. The genera and families are arranged according to the classification by Edmunds, Allen & Peters (1963) see this publication also for the authors of genera, subfamilies and families investigated.

Abbreviations used: A - Australian region; E - Ethiopian region; NA - Nearctic region; NT - Neotropical region; O - Oriental region; P - Palaearctic region; leg. (coll.) - collected by (collection of). The number and sex of specimens investigated is presented in brackets.

### *Siphonuridae*

#### *Siphonurinae*

A - *Ameletoides locusalbiniae* Tillyard, Hedley Creek, New South Wales, Australia, 9.ii.1966 leg. E.F.Riek (4♂, 2♀); P - *Ameletus alexandrae* Brodsky, tributary of Kisilsu Riv., Ačik-Taš, Kirkizian SSR, USSR, 20.vii.1977 leg. M.Hlináková (6♂, 8♀); P - *Ameletus inopinatus* Eaton, Studená Vltava, Stožec, South Bohemia, Czechoslovakia, 12.vii.1971 leg. T. Soldán (11♂, 9♀); NA - *Ameletus velox* Dodds, Mill Creek, Salt Lake Co., Utah, USA, 3.vi.1965 leg. V.Landa (2♂, 1♀); NT - *Siphonella* sp., Rio Illapel, Coquimbo Prov., Caren., Chile 15.xi.1963 leg. G.F. Edmunds (3♂, 1♀); P - *Metreletus goetghebueri* Lest., brook, Dobříš, Central Bohemia, Czechoslovakia, 25.vi.1976 leg. T. Soldán (8♂, 7♀); NA - *Parameletus columbiae* McDunnough, Big Cottonwood Creek, Brighton, Utah, USA, 3.vi.1965 leg. V.Landa (1♂, 1♀); P - *Siphonurus aestivalis* Eaton, Smutná, Bechyně, South Bohemia, Czechoslovakia, 16.v.1974 leg. T. Soldán (4♂, 7♀); P - *Siphonurus lacustris* Eaton, Mumlava, Kořenov, North Bohemia, Czechoslovakia, 4.ix.1973 leg. T. Soldán (11♂, 9♀); P - *Siphonurus armatus* Eaton, pools near Lužnice Riv., Sezimovo Ústí, South Bohemia, Czechoslovakia, 10.v.1973 leg. T. Soldán (4♂, 5♀); NT - *Siphonurus (Siphonurella) occidentalis* Eaton, Mill Creek, Salt Lake Co., Utah, USA, 3.vi.1965 leg. V. Landa (2♂, 1♀).

### *Acanthametropodinae*

P - *Acanthametropus nikolskyi* Tshernova, Amur riv., USSR, v.1956 leg.O. A.Tshernova (1♂); NA - *Acanthametropus* sp., Savannah riv., Georgia, USA, leg. G. F. Edmunds (coll. Landa) (1♀).

### *Oniscigastriinae*

A - *Oniscigaster* sp., Taranski Co., Taranski Prov., New Zealand, 5.ii.1958 leg.McFarlane (coll.V.Landa) (1♂, 1♀) A - *Tasmanophlebia nigrescens* Tillyard, Alpine Creek, Kiandra, New South Wales, Australia, 29.i.1970 leg.E.F.Riek 1♂, 2♀).

### *Ameletopsinae*

A - *Ameletopsis* sp., Taranski Co., Taranski Prov., New Zealand, 5.ii.1958 leg.McFarlane (coll.V.Landa) (1♀); NT - *Chiloporter* sp., Rio Llancahue, Villarica, Cautin, Chile, 11.ii.1958 leg.J.Illies (coll. V. Landa) (1♂, 1♀); A - *Mirawara* sp., stream, Mt. Buffalo, New South Wales, Australia, 3.iii.1967 leg.E.F.Riek (1♂, 1♀).

### *Isonychiinae*

P - *Isonychia ignota* (Walker), Ondava, Čičava, East Slovakia, Czechoslovakia, 17.vii.1975 leg.T.Soldán (1♂, 1♀); NT - *Isonychia* sp., Cullasaja Riv., Macon Co., North Carolina, USA, 30.vii.1966 leg.V.Landa (2♂, 3♀).

### *Coloburiscinae*

A - *Coloburiscoides* sp., Gang Gang Creek, Kiandra, New South Wales, Australia, 13.xii.1974 leg.E. F. Riek (2♂, 4♀). A - *Coloburiscus* sp., Huatoki Stream, Taranski Co., Taranski Prov. New Zealand, 21.iii.1957 leg.A.Hirsch (coll.V.Landa) (1 ♀).

### *Rallidentinae*

A - *Rallidens macfarlanei* Penniket, Pelorus Riv., Pelorus Bridge, Malboro Prov., New Zealand, 7.iii.1966 leg.G.F.Edmunds (coll.V.Landa) (2♂, 1♀).

### *Baetidae*

P - *Baetis alpinus* (Pictet), Hron, Hronská Dúbrava, Central Slovakia, 6.vii.1972 leg.T.Soldán (8♂, 5♀); P - *Baetis muticus* (Linné), Rokytná, Moravské Budějovice, Moravia, Czechoslovakia, 3.viii.1972 leg.T.Soldán (6♂, 3♀); NA - *Baetis tricaudatus* Dodds, East Canyon Creek, Summit Co., Utah, USA, 7.vi.1965 leg.V.Landa (2♂, 3♀); A - *Baetis* sp., Bellinger Riv., Bellingen, New South Wales, Australia, 23.ii.1966 leg.E.F.Riek (1♂, 1♀); O - *Baetis* sp., Poona, Mula-mula Riv., India, 6.ii.1960 leg. V.Landa (1♂, 1♀); NT - *Baetodes* sp., Rio Huallaga, Tingo Maria, Huanuco Prov., Peru,

16.viii.1963 leg.W.L.Peters (coll.V.Landa) (1♂); P - *Baetopus* sp., Somon Žinst, Tujn Gol, Mongolia, 26.vi.1966 leg.Z.Kaszab (coll.V.Landa) (1♂, 1♀); NA - *Callibaetis coloradensis* Banks, Mill Creek, Salt Lake Co., Utah, USA, 3.vi.1965 leg.V.Landa (2♂, 2♀); NT - *Callibaetis* sp., pools, Soledad, Cuba, 9.xi.1964 leg. V. Landa (2♂, 1♀); P - *Centroptilum luteolum* (Müller), Rokytka, Říčany, Central Bohemia, Czechoslovakia, 20.v.1972 leg.T.Soldán (8♂, 10♀); P - *Centroptilum pennulatum* Eaton, Štampoch Brook, Bohunice South Slovakia, Czechoslovakia, 3.vi.1974 leg.T.Soldán (11♂, 4♀); NA - *Centroptilum rubropictum* McDunnough, Nantahala Riv., Nantahala, North Carolina, USA, 1.vii.1965 leg.V.Landa (1♂, 1♀); A - *Centroptilum* sp., McLaughton Riv., Mafra, New South Wales, Australia, 19.8.1972 leg.V.Landa (1♂, 1♀); E - *Centroptilum* sp., Blue Nile, Bahar Dar, Ethiopia, 15.iv.1967 leg.P.Štys (2♂, 1♀); P - *Cloeon dipterum* (Linné), Sekerník pond, Křelov, Moravia, Czechoslovakia, 28.iv.1972 leg. T. Soldán (14♂, 17♀); E - *Cloeon* sp., Blue Nile, Wad Medani, Blue Nile Prov., 23.ii.1966 leg. P.Štys (4♂, 2♀); A - *Cloeon* sp., Armindale, New South Wales, Australia, 19.ii.1966 leg.E.F.Riek (1♂, 1♀); P - *Procloeon bifidum* Bengtsson, Nežárka, Stráž, South Bohemia, Czechoslovakia, 10.v.1973 leg. T.Soldán (12♂, 10♀); P - *Pseudocloeon inexpectatum* Tshernova, Hron, Kamenica, South Slovakia, Czechoslovakia, 20.v.1975 leg. T. Soldán (6♂, 7♀); O - *Pseudocloeon* sp., Mula-mula-Riv., Poona, India, 6.ii.1960 leg.V.Landa (2♂, 1♀).

## Oligoneuriidae

### Oligoneuriinae

E - *Elassoneuria* sp., Bahar Dar, Ethiopia, 3.iv.1967 leg.P.Štys (2♂). NA - *Homoeoneuria dolani* Edmunds, Blackwater Riv., Bryant Bridge, Okaloosa Co., Florida, USA, 11.vii.1967 leg. W.L.Peters (coll.V.Landa) (2♂, 3♀). NT - *Lachlania* sp., Rio Huallaga, Tingo Maria, Huanuco Prov., 29.-31.vii.1963 leg.W.L.Peters (coll.V.Landa) (3♂, 3♀). P - *Oligoneuriella rhenana* (Imhoff), Orava, Podbiel, West Slovakia, Czechoslovakia, 22.vii.1973 leg.T.Soldán (12♂, 19♀). P - *Oligoneuriella mikulskii* Sowa, Tisza Riv., Malé Trakany, East Slovakia, Czechoslovakia, 9.vii.1975 leg. T. Soldán (1♂, 1♀). P - *Oligoneurisca borysthénica* (Tshernova), Dnjepr, Vilnogo, 17.viii.1928 leg.O.A.Tshernova (coll.V.Landa) (1♀).

## Heptageniidae

### Heptageniinae

NA - *Cynigmula* par Eaton, Mill Creek, Salt Lake Co., Utah, USA, 3.vi.1965 leg. V. Landa (4♂, 1♀); P - *Cynigmula* sp., Listvjanka Riv., Khabarovsk Co., USSR, 30.vi.1977 leg. P. Štys (7♂, 6♀); P - *Ecdyonurus*

*austriacus* Kimmins, Hamerský stream, Horská Kvilda, South Bohemia, Czechoslovakia, 24.iv.1976 leg. T. Soldán (6♂, 11♀); P - *Ecdyonurus lateralis* (Curtis), brook, Davle-Libřice, Central Bohemia, Czechoslovakia, 15.vi.1973 leg. T. Soldán (14♂, 10♀). P - *Ecdyonurus venosus* (F.), Otava Riv., Sušice, South Bohemia, Czechoslovakia, 14.iv.1974 leg. T. Soldán (5♂, 7♀); E - *Afronurus* sp., Blue Nile, Wad Medani, Blue Nile Prov., Sudan, 23.ii.1966 leg. P. Štys (1♂, 1♀); P - *Epeorus* (*Epeorus*) *sylvicola* (Pitet), Otava Riv., Sušice, South Bohemia, Czechoslovakia, 14.iv.1974 leg. T. Soldán (6♂, 9♀); P - *Epeorus* (*Iron*) *yugoslavicus* Šámal, Rilska Reka, Rila, Bulgaria, 25.vii.1963 leg. V. Landa (5♂, 5♀); NA - *Epeorus* (*Iron*) *longimanus* Eaton, Mill Creek, Salt Lake Co., Utah, USA, 3.vi.1965 leg. V. Landa (1♂, 1♀); P - *Epeorus* (*Iron*) sp. brook, Gegard, Armenia, USSR, 15.vii.1974 leg. Z. Pádrová (2♂, 2♀); NT - *Epeorus* (*Ironopsis*) *grandis* McDunn., Wolf Creek, Lake Co., Montana, USA, 15.vii.1965 leg. R. K. Allen (coll. V. Landa) (1♂); O - *Epeorus* (*Ironodes*) sp., stream near Doi Sutep, W of Chiangmai, Chiangmai Prov., 18.xi.1964 leg. W. L. Peters (coll. V. Landa) (2♂, 1♀); P - *Heptagenia flava* Rostock, Litavka, Dvůr Králové, Central Bohemia, Czechoslovakia, 22.viii.1974 leg. T. Soldán (8♂, 12♀); P - *Heptagenia fuscogrisea* (Retz.), Lužnice Riv., Roudná, South Bohemia, Czechoslovakia, 29.iv.1976 leg. T. Soldán (5♂, 9♀); NT - *Heptagenia simplicioides* McDunn., Green Riv., Dinos. Nat. Park., Utah, USA, 6.vi.1965 leg. V. Landa (1♂, 2♀); P - *Rhithrogena semicolorata* (Curt.), Zahořanský brook, Davle-Libřice, Central Bohemia, Czechoslovakia, 15.v.1976 leg. T. Soldán (10♂, 7♀); P - *Rhithrogena hercynia* Landa, Otava Riv., Sušice, South Bohemia, Czechoslovakia, 14.iv.1974 leg. T. Soldán (5♂, 6♀); NA - *Rhithrogena robusta* Dodds, Grove Creek, Salt Lake Co., Utah, USA, 6.vi.1965 leg. V. Landa (2♂, 1♀); NA - *Stenacron smithae* (Traver), Hogtown Creek, Gainesville, Florida, USA, 15.vi.1965 leg. V. Landa (2♂, 2♀); NA - *Stenonema pudicum* Hagen, Cullasaja Riv., Macon Co., North Carolina, USA, 10.vii.1966 leg. V. Landa (1♂, 2♀); P - *Thalerosphyrus* sp., Mouche Riv., Nahr. Besri vic., Deir mash, Lebanon, 9.viii.1952 leg. K. Christiansen (1♂, 1♀); E - *Thalerosphyrus* sp., Khor Harasab, Erkwit, Kassala Prov., Sudan, 19.ix.1966 leg. P. Štys (1♂, 1♀).

#### *Anepeorinae*

NA - *Anepeorus* sp., Cherokee Riv., Cherokee Co., South Carolina, USA, vii.1952 leg. L. Berner (coll. V. Landa) (1♂, 1♀).

#### *Arthropleinae*

P - *Arthroplea congener* Bengtsson, pools near Vltava Riv., Pěkná, South Bohemia, Czechoslovakia, 18.v.1976 leg. T. Soldán (15♂, 9♀).

### *Pseudironinae*

NA - *Pseudiron meridionalis* Traver, Blackwater Riv., Deaton Bridge, Santa Rosa Co., Florida, USA, 5.-6.iv.1968 leg. W. L. Peters (coll. V. Landa) (2♂, 2♀).

## *Ametropodidae*

### *Ametropodinae*

NA - *Ametropus albrighti* Traver, Green Riv., Uintah Co., Utah, USA, 3.-5.v.1963 leg. W. L. Peters (coll. V. Landa) (2♂, 3♀); P - *Ametropus eatoni* Brodsky, Latorica Riv., Leles, East Slovakia, Czechoslovakia, 3.vi.1974 leg. T. Soldán (1♀).

### *Metretopodinae*

P - *Metretopus norvegicus* Eaton, Ly Imp, Vindelälven, Sverige, v.1952 leg. A.F. Ulfstrand (coll. V. Landa) (1♂); NA - *Siphloplecton basale* Traver, Bear Creek, St. Hwy, Gadsden Co., Florida, USA, 17.iii.1968 leg. W. L. Peters (coll. V. Landa) (1♂, 2♀).

## *Leptophlebiidae*

A - *Atalomicria* sp., New Eng. Nat. Park, New South Wales, Australia, 20.ii.1966 leg. E.F. Riek (3♂, 4♀); A - *Atalophlebia* sp., McLaughlin Riv., Mafra, New South Wales, Australia, 20.8.1972 leg. V. Landa (2♂, 4♀); A - *Atalophlebioides* sp., Monga Riv., New South Wales, Australia, 17.viii.1972 leg. V. Landa (3♂, 7♀); P - *Choroterpes* (*Choroterpes*) *picteti* Eaton, Lužnice Riv., Bechyně, South Bohemia, Czechoslovakia, 8.ix.1974 leg. T. Soldán (11♂, 8♀); P - *Choroterpes* (*Euthraulius*) *balcanicus* Ikonov, brook, Novo Paničarevo, Bulgaria, 7.vi.1977 leg. T. Soldán (2♂, 4♀); O - *Choroterpes* (*Euthraulius*) sp., Mula-mula Riv., Poona, India, 6.ii.1960 leg. V. Landa (2♂, 1♀); P - *Habroleptoides modesta* (Hagen), Zahofanský brook, Davle-Libřice, Central Bohemia, Czechoslovakia, 24.v.1975 leg. T. Soldán (5♂, 11♀); P - *Habrophlebia fusca* (Curt.), Smutná, Bechyně, South Bohemia, Czechoslovakia, 17.v.1973 leg. T. Soldán (8♂, 7♀); P - *Habrophlebia lauta* Eaton, Smutná, Bechyně, South Bohemia, Czechoslovakia, 17.v.1973 leg. T. Soldán (5♂, 8♀); NA - *Habrophlebia vibrans* Needham, creek, Lake Caravel, Highlands, North Carolina, USA, vii.1965 leg. V. Landa (1♂, 2♀); NT - *Hagenulus* sp., creek, Pinares de Vinares, Pinal del Rio, Cuba, 11.x.1964 leg. V. Landa (4♂, 7♀); A - *Jappa* sp., McLaughlin Riv., Mafra, New South Wales, Australia, 19.viii.1972 leg. V. Landa (5♂, 2♀); O - *Kimminsula* sp., creek, Sabaragamuwa, Maratenna Prov., Ceylon, 22.ii.1962 leg. P. Brinck (coll. Landa) (6♂, 4♀); A - *Kirrara* sp., creek,

Balairo, New South Wales, Australia, 30.i.1966 leg. E. F. Riek (coll.V. Landa) (3♂, 2♀); NA - *Leptophlebia gravastella* Eaton, Green Creek, Jensen, Utah, USA, 7.vii.1965 leg. V. Landa (1♂, 1♀); P - *Leptophlebia marginata* (L.), Nádražní pond, Havlíčkův Brod, East Bohemia, Czechoslovakia, 23. iv.1973 leg. T. Soldán (4♂, 6♀); P - *Leptophlebia vespertina* (L.); pools near Vltava Riv., Pěkná, South Bohemia, Czechoslovakia, 28.iv.1977 leg. T. Soldán (4♂, 6♀); P - *Paraleptophlebia cineta* (Retz.), Židova strouha, Bechyně, South Bohemia, Czechoslovakia, 3.vi.1973 leg. T. Soldán (7♂, 11♀); NA - *Paraleptophlebia guttata* McDunn., creek, Lake Caravel, Highlands, North Carolina, USA, vii.1965 leg. V. Landa (1♂, 2♀); NA - *Paraleptophlebia pallipes* Hagen, Mill Creek, Salt Lake Co., Utah, USA, 3.vi.1965 leg. V. Landa (2♂, 1♀); P - *Thraulius bellus* Eaton, brook, Novo Paníčarevo, Bulgaria, 7.vi.1977 leg. T. Soldán (2♂, 1♀); NT - *Traverella* sp., Rio Tulumayo, Tingo Maria, San Martin Prov., Peru, vii.1963 leg. W. L. Peters (coll. V. Landa) (1♂, 1♀).

## *Ephemerellidae*

NA - *Ephemerella* (*Attenella*) *simplex* McDunn., French Broad Riv., Transylvania Co., North Carolina, USA, 10.vii.1965 leg. V. Landa (5♂, 1♀); P - *Ephemerella* (*Chitonophora*) *kriehoffi* Ulmer, Lučanský brook, Smržovka, North Bohemia, Czechoslovakia, 22.iv.1973 leg. T. Soldán (6♂, 10♀); NA - *Ephemerella* (*Drunella*) *conestee* Traver, French Broad Riv., Transylvania Co., North Carolina, USA, 10.vii.1965 leg. V. Landa (1♂, 1♀); NA - *Ephemerella* (*Drunella*) *grandis* Eaton, Mill Creek, Salt Lake Co., Utah, USA, 3.vi.1965 (4♂, 6♀); P - *Ephemerella* (*Ephemerella*) *ignita* (Poda), Dyje Riv., Lednice, South Moravia, Czechoslovakia, 5.vi.1972 leg. T. Soldán (7♂, 8♀); NA - *Ephemerella* (*Ephemerella*) *inermis* Eaton, Provo Riv., Midway, Wasatch Co., Utah, USA, 11.vi.1965 leg. V. Landa (4♂, 2♀); P - *Ephemerella* (*Ephemerella*) *notata* Eaton, Malše Riv., Sv. Jan, South Bohemia, Czechoslovakia, 22.v.1973 leg. T. Soldán (9♂, 7♀); NA - *Ephemerella* (*Eurylophella*) *trilineata* Berner, Hatchet Creek, Alachua Co., USA, 22. vi.1965 leg. V. Landa (1♂, 1♀); P - *Ephemerella* (*Cincticostella*) sp., Listvjanka Riv., Khabarovsk Co., USSR, 30.vi.1977 leg. P. Štys (2♂); NA - *Ephemerella* (*Timpanoga*) *hecuba* Eaton, Trout Creek, Summerland, British Columbia, Canada, 16.viii.1964 leg. G. F. Edmunds (coll. V. Landa) (2♂, 2♀); P - *Ephemerella* (*Torleya*) *major* Klapálek, Zahořanský brook, Davle-Libřice, Central Bohemia, Czechoslovakia, 15.vi.1975 leg. T. Soldán (8♂, 7♀); A - *Ephemerellina picta* (Riek), Flagggy Creek, via Laidley, Mistake Mts., S.E. Queensland, Australia, 11.ii.1973 leg. S. R. Monteith (coll. E. F. Riek) (1♂, 1♀); E - *Ephemerellina* sp., Great Berg Riv., French Hoek Forest Reserve, South Africa, 21.xi.1950 leg. A. D. Harrison (coll. V. Landa) (1♂);

O - *Teloganodes* sp., Kandapola, Nuwara, Elyia, Central Prov., Ceylon, iii.1962 leg. P. Brinck (coll. V. Landa) (1♂, 1♀).

## *Tricorythidae*

### *Tricorythinae*

E - *Neurocaenis* sp., Blue Nile, Wad Medani, Blue Nile Prov., Sudan, 23.ii.1966 leg. P. Štys (1♂); O - *Tricorythus* sp., Kattur Riv., Varadapalyam, Andhra Pradesh, India, 11.xii.1964 leg. W. L. Peters (coll. V. Landa) (1♂, 2♀).

### *Leptohyphinae*

NT - *Leptohyphes* sp., Ariranha Riv., Nova Teutonia, Brasil, xi.1961 leg. F. Plaumann (coll. V. Landa) (1♂, 1♀); NT - *Leptohyphodes* sp., Bulano Riv., Campamento Galera, Dept. Olanchó, Honduras, 7.xi.1964 leg. J. Packer (coll. V. Landa) (1♂); NA - *Tricorythodes albalineatus* Berner, Santa Fe Riv., Alachua Co., Florida, USA, 22.vi.1965 leg. V. Landa (6♂, 3♀); NT - *Tricorythodes* sp., creek, Pinares de Vinales, Pinal del Rio, Cuba, 11.x.1964 leg. V. Landa (3♂, 6♀); NA - *Tricorythodes* sp., stream, Salt Lake City, Salt Lake Co., USA, 5.vi.1965 leg. V. Landa (4♂, 1♀).

### *Dicercomyzinae*

E - *Dicercomyzon costale* Kimmins, Days Riv., Gold Coast, viii.1950 leg. L. Berner (coll. V. Landa) (1♂).

## *Behningiidae*

P - *Behningia ulmeri* Lestage, Warta Riv., Kuczki, Poland, vi.1958 leg. M. Keffemüller (coll. V. Landa) (1♀); NA - *Dolania americana* Edmunds, Blackwater Riv., Deaton Bridge, Santa Rosa Co., Florida, USA, 5.-6.iv.1968 leg. W. L. Peters (coll. V. Landa) (4♂, 3♀).

## *Potamanthidae*

O - *Potamanthodes* sp., Mae Ping, Chiangmai, Chiangmai Prov., Thailand, 21.xi.1964 leg. W. L. Peters (coll. V. Landa) (1♂); P - *Potamanthus luteus* (L.), Berounka Riv., Lahovice, Central Bohemia, Czechoslovakia, 17.vii.1977 leg. T. Soldán (11♂, 16♀); NT - *Potamanthus* sp., Rock Riv., Cleveland, Illinois, USA, 9.v.1954 leg. T. Thew (coll. V. Landa) (2♀); NT - *Potamanthus rufus* Argo, Priest Riv., Priest, Bonner Co., Idaho, USA, viii.1964 leg. G. F. Edmunds (coll. V. Landa) (1♂); O - *Rhoenanthopsis* sp., Mae Ping, Chiangmai, Chiangmai Prov., Thailand, 21.xi.1964 leg. W. L. Peters (coll. V. Landa) (2♂, 2♀).



## *Euthyplociidae*

NT - *Campylocia* sp., mountain stream, Rio Marauia, NW Taparuquara, Brasil, i.1963 leg. E.J. Fittkau (coll. V. Landa) (1♂); NT - *Euthyplocia* sp., Rio Pendescia, Tulumayo Valley, San Martin Prov., Peru, 10.vi.1963 leg. W.L. Peters (coll. V. Landa) (1♂, 1♀); NT - *Euthyplocia* sp., Nova Teutonia, Brasil, ii.1962 leg. F. Plaumann (coll. V. Landa) (1♀).

## *Ephemeridae*

P - *Ephemera vulgata* L., Plzinský brook, Bechyně, South Bohemia, Czechoslovakia, 22.v.1972 leg. T. Soldán (8♂, 6♀); P - *Ephemera lineata* Eaton, Lužnice Riv., Mláka, South Bohemia, Czechoslovakia, 14.vi.1972 leg. T. Soldán (3♂, 1♀); NA - *Ephemera simulans* Walker, Cullasaja Riv., Macon Co., North Carolina, USA, 10.vi.1965 leg. V. Landa (1♂, 3♀); NA - *Hexagenia munda* Eaton, Hogtown Creek, Gainesville, Florida, USA, viii.1965 leg. V. Landa (2♂, 1♀); NA - *Hexagenia limbata* Needham, Arboretum pond, Cornwallis, Benton Co., Oregon, USA, ii.1959 leg. G.F. Kraft (coll. V. Landa) (1♂); NA - *Litobranchea recurvata* (Morgan), Michigan Hollow near Attica, New York, USA, v.1966 leg. G.F. Edmunds (coll. V. Landa) (1♂, 1♀); NA - *Pentagenia vittigera* Walsh, Guadalupe Riv., S Victoria, Texas, USA, iv.1950 leg. T. Dolan (coll. V. Landa) (1♂, 1♀).

## *Polymitarcidae*

### *Polymitarcinae*

NA - *Ephoron album* (Say), Jordan Riv. Salt Lake Co., Utah, USA, 15.vii.1954 leg. G. Smith (coll. V. Landa) (1♂, 1♀); E - *Ephoron savignyi* (Pictet), Blue Nile, Khartoum, Khartoum Prov., Sudan, 12.xi.1966 leg. P. Štys (2♂, 1♀); P - *Ephoron virgo* (Oliv.), Berounka Riv., Lahovice, Central Bohemia, Czechoslovakia, 15.viii.1975 leg. T. Soldán (3♂, 4♀); O - *Ephoron* sp., Mae Ping, Chiangmai, Chiangmai Prov., Thailand, 20.xi.1964 leg. W.L. Peters (coll. V. Landa) (1♂, 2♀).

### *Campsurinae*

NT - *Campsurus* sp., Ariranha Riv., Nova Teutonia, Brasil, xi.1961 leg. F. Plaumann (coll. V. Landa) (1♂); NA - *Tortopus* sp., Cozad, Nebraska, USA, ix.1950 leg. R. B. Selander (coll. V. Landa) (1♀); NA - Guadalupe Riv., S Victoria, Texas, USA, 6.ix.1950 leg. T. Dolan (coll. V. Landa) (1♀).

### *Asthenopodinae*

NT - *Asthenopus* sp., Rio Luna Acu at junct. with Rio Pedro Acu, Brasil,

ix.1960 leg.E.J.Fittkau (coll.V.Landa)(1♂,1♀); E - *Povilla adusta* Navás, Lake Kiwu, Wahu Island, Zaire, iv.1953(coll. G. Demoulin)(1♀).

### *Palingeniidae*

P - *Anagenesia* (*Chankagenesia*) *paradora* Buldovskij, Amur Riv., Khabarovsk Co., USSR, v.1956 leg.O.A.Tshernova (coll.V.Landa) (1♂); P - *Palingenia fuliginosa* (Georgi), Latorica Riv., Leles, East Slovakia, Czechoslovakia, 29.v.1974 leg. T. Soldán (8♂, 7♀); P - *Palingenia longicauda* (Oliv.), Latorica Riv., Leles, East Slovakia, Czechoslovakia, 19.viii.1977 leg. T. Soldán (1♂, 2♀).

### *Neophemeridae*

NA - *Neophemera* (*Neophemera*) *youngi* Berner, Savannah Riv., Georgia, USA, vii.1952 leg.T.Dolan (coll.V.Landa)(1♀); NA - *Neophemera* (*Oreianthus*) *purpurea* Traver, Nantahala Riv., Nantahala, North Carolina, USA, vii.1965 leg.V.Landa (1♂, 1♀); O - *Potamanthellus* sp., Mae Ping, Chiangmai, Chiangmai Prov., Thailand, 12.xi.1964 leg.W.L.Peters (1♂, 1♀).

### *Caenidae*

P - *Brachycercus harrisella* (Curt.), Lužnice Riv., Stříbřec, South Bohemia, Czechoslovakia, 26.vi.1974 leg. T.Soldán (8♂,10♀); NA- *Brachycercus nitidus* Traver, Cullasaja Riv., Macon Co., North Carolina, USA, 10.vii.1965 leg. V.Landa (5♂, 1♀); NA - *Caenis diminuta* Walker, Hatchet Creek, Alachua Co., Florida, USA, vi.1965 leg. V. Landa (2♂, 3♀); P - *Caenis pseudorivulorum* Keffermüller, Malše Riv., Kaplice, South Bohemia, Czechoslovakia, 22.vi.1976 leg. T. Soldán (5♂, 9♀); P - *Caenis robusta* Eaton, Holoubkovský pond, Holoubkov, South Bohemia, Czechoslovakia, 8.vi.1973 leg. T. Soldán (7♂, 6♀); E - *Caenis* sp., Blue Nile, Wad Medani, Blue Nile Prov., Sudan, 23.ii.1966 leg. P.Štys (2♂, 1♀); E - *Caenomedea* sp., Blue Nile, Khartoum, Khartoum Prov., Sudan, 12.xi.1966 leg. P.Štys (3♂, 1♀); A - *Tasmanocoenis* sp., Mongalove Riv., Monga, New South Wales, Australia, ii.1967 leg.E.F.Riek (1♂, 1♀).

### *Baetiscidae*

NA - *Baetisca bajkovi* Neave, Miami Riv., Hwy 117, Indian Lake, Iowa, USA, 20.v.1953 leg. A.R.Gauvin (coll.V.Landa)(1♂, 1♀); NA - *Baetisca rogersi* Berner, Little Escambia Creek, Escambia Co., Alabama, USA, 14.iv.1956 leg. L. Berner (coll.V.Landa)(1♂, 2♀).

## *Prosopistomatidae*

P - *Prosopistoma foliaceum* (Fourcr.), Maros Riv., Szeged, reg. Hundefvara, Hungary, v. 1957 leg. K. Straškraba (coll. V. Landa) (1♂, 1♀).

Older larvae, i.e. those from about 10th instar to the 15th instar with all larval characters fully developed, were used for the study of comparative anatomy of gonads. Only these larvae possess the characters important for comparative study. In younger larvae the development of gonads is not finished; moreover, the gonads need not be differentiated into follicles in some cases. In mature male larvae (larvae of the last instar) disintegration of follicles and shrinking of testis connected with the descend of mature spermatozoa into seminal vesicles occur. The testes nearly disappear and only seminal vesicles are apparent in male subimagos and adults. Similarly, the ovaries of mature larvae, subimagos and adults do not provide us with any characters useful for the comparative study. The developmental changes of ovaries are connected with descend of mature eggs into oviducts (ovulation). Ovarioles disappear (germarium is resorbed and vitellarium is completely pulled into considerably extended oviduct).

The material dissected was fixed with Carnoy, AGA fixation (alcohol, glycerol, acetic acid) and alcohol-formalin fixation. Preferably fresh material was examined whenever available (some Palaearctic species). Fresh material was sometimes stained with methylen blue. The larvae were dissected in a Petri dish of paraffin stained red with Sudan III for a greater contrast. The subjects were opened dorsally (species with gonads in dorsal position ventrally), edges were pinned with minutiae. Gonads and other organs were loosened with a thin trickle of water, Pringle's solution or alcohol. Important parts of the gonads and their ducts were mounted in Canada balsam with Cellosolve.

## STRUCTURE AND BASIC TYPES OF ARRANGEMENT OF TESTIS AND SEMINAL VESICLE

The paired testes are situated in the body cavity (mixocoel) along the alimentary canal in older mayfly larvae. Testes extend either from thorax or from the first abdominal segment to the posterior margin of the sixth abdominal segment in older larvae (growth of testis is finished). Testis is elongated, cylindrical, subcylindrical or spindle-shaped organ which is attached to peritoneal structures by a suspensory ligament in thorax. Each testis is enveloped by a large number of follicles (testicular follicles) from above and from the sides. The number of testicular follicles, which the testis consists of, is not constant in specimens of the same species or even in specimens of the same population. The outer membrane cover of the whole testis is formed by peritoneal membrane (Figs.1,2). The follicles are filled up by germinal cells and do not undergo any changes in the initial stages of the spermatogenesis (until spermatids and presperms appear). Follicles are directly attached to seminal ducts, no vasa efferentia are developed. They are arranged in longitudinal rows in dorsal view.

The seminal duct (vas deferens) is represented by a simple tubular duct extending from the apical part of testis to the posterior margin of the abdominal segment IX. It consists of an inner layer of epithelium and an outer layer of circular muscles (Fig. 4). Contrary to the follicles and seminal vesicles the seminal ducts do not provide us with any characters useful in comparative anatomy study although its width varies from genus to genus. Seminal ducts are expanded several times, forming a large seminal vesicle (vesicula seminalis) in the area of segments VII-IX. The histological structure of seminal vesicles is the same as that of seminal ducts. In the last larval instar the seminal vesicles are directly connected with ejaculatory ducts (ductus ejaculatorius) which open at the apexes of penis lobes. The seminal vesicle is formed in half-grown or older larvae, before descending of mature spermatozoa into seminal ducts. Taking into consideration the remarkable differences in shape and position of seminal vesicles, these structures provide important characters for comparative anatomy purposes.

From the comparative anatomy point of view the most important characters of the arrangement of testes and seminal vesicles are as follows: position of testes to the alimentary canal (A); position of

testis to the body segmentation (B); shape of testis and especially shape of its apical portion (C); relative size and arrangement of follicles (D); shape of testicular follicles and their position to seminal ducts (E); shape of seminal vesicle (F); position of seminal vesicles to the body segmentation (G). The following cases in the arrangement of these characters were observed:

(A) position of testes to the alimentary canal:

(Aa) testes are deposited dorsally to alimentary canal (Fig. 6), contiguous in thorax and first abdominal segments and connecting the dorsal body wall (thoracic nota and terga of abdomen). Dorsal position of testes occurs in *Siphonurinae*, *Acanthametropodinae*, *Rallidentinae*, *Baetidae*, and *Metretopodinae*.

(Ab) testes are deposited dorsolaterally to alimentary canal (Fig. 8), not contiguous or contiguous only in thorax, not connecting the dorsal body wall. Dorsolateral position of testes occurs in *Ameletopsinae*, *Oniscigastriinae*, *Isonychiinae*, *Oligoneuriinae*, *Ametropodinae*, *Pseudironinae*.

(Ac) testes are deposited laterally to alimentary canal (Fig. 7) sometimes closely contiguous to the wall of gut. Lateral position of testes occurs in *Coloburiscinae*, *Heptageniinae*, *Arthropleinae*, *Anepeorinae*, *Leptophlebiidae*, *Ephemerellidae*, *Tricorythidae*, *Behningiidae*, *Potamanthidae*, *Neoephemeridae*, *Caenidae*, *Baetiscidae*, and *Prosopistomatidae*. The family *Ephemerellidae* represents an intermediary type between the groups Ab and Ac having the testes deposited in dorsal or dorsolateral position in thorax and in lateral position in abdominal segments.

(Ad) testes are deposited ventrolaterally to alimentary canal (Fig. 9), usually connecting the gut and lateral tracheal trunks. Ventrolateral position of testes occurs in *Ephemeridae*, *Polymitarcidae*, *Euthyplociidae*, and *Palingeniidae*.

(B) position of testis to the body segmentation:

(Ba) testes are deposited only in the abdominal segments I-VI or in metathorax and segments I-VI. Testes extend from the first to the sixth abdominal segment in *Isonychiinae*, *Oligoneuriinae*, *Heptageniidae* (*Cinygmula*, *Rhithrogena*, *Epeorus* - subgenera *Epeorus*, *Iron*, *Ironodes*), *Leptophlebiidae* (plesiomorphic group of genera), *Ephemerellidae*, *Behningiidae*, *Euthyplociidae*, *Asthenopodinae*, *Campsurinae*, and *Palingeniidae*; testes extend from metathorax to the sixth abdominal segment in *Siphonurinae*, *Acanthametropodinae*, *Ameletopsinae* (*Ameletopsis*, *Mirawara*), *Rallidentinae*, *Baetidae* (*Callibaetis*, *Centroptilum*, *Cloeon*, *Procloeon*, *Baetis* - some species, *Baetopus*), *Heptageniinae* (*Afronurus*, *Ecdyonurus*, *Heptagenia*,

*Stenacron*, *Stenonema*, *Thalerosphyrus*), *Anepeorinae*, *Arthropleinae*, *Ametropodinae*, *Metretopodinae*, *Leptophlebiidae* (some genera), *Ephemerellidae* (some genera), *Leptohyphinae*, *Dicercomyzinae*, *Potamanthidae*, *Ephemeridae* (*Ephemera*), *Polymitarcinae*.

(Bb) testes extend either from mesothorax or from prothorax; suspensory ligament can occur even in head to the sixth abdominal segment. Testes are produced into mesothorax in *Pseudironinae*, *Ephemerellidae* (*Teloganodes*), *Ephemeridae* (*Hexagenia*, *Litobrancha*, *Pentagenia*), *Caenidae* (*Brachycercus*), *Prosopistomatidae*; testes are produced to prothorax in *Leptophlebiidae* (*Paraleptophlebia* - some species, *Hagenulus*, *Traverella*), *Caenidae* (*Caenis*, *Caenomedea*, *Tasmanocoenis*), *Baetiscidae*, *Neoephemeridae*.

(Bc) testes are produced into thorax (usually pro- and mesothorax) but they are deposited only in abdominal segments I-IV or I-V. This type of the testes arrangement was found in *Baetidae* (*Baetis* - some species, *Baetodes*, *Pseudocloeon* - some species: MST-V or MST-IV) and *Ephemerellidae* (*Ephemerella* - subgenera *Drunella* and *Eurylophella*: PT-V or PT-IV).

(Bd) testes are deposited only in abdominal segments but not in I-VI: *Ameletopsinae* (*Chiloporter* II-VI), *Coloburiscinae* (III-VI), *Leptophlebiidae* (*Kimminsula*, *Thraululus*).

(C) shape of testis and shape of its apical portion:

(Ca) testis is cylindrical or subcylindrical, in thorax or in first abdominal segments bent or even s-curved: *Siphonurinae*, *Acanthametropodinae*, *Oniscigastrinae*, *Ameletopsinae* (*Chiloporter*), *Rallidentinae*, *Metretopodinae*.

(Cb) testis is cylindrical or subcylindrical, straight, with apical part rounded or slightly pointed: *Ameletopsinae* (*Ameletopsis*, *Mirawara*), *Isonychiinae*, *Coloburiscinae*, *Baetidae*, *Oligoneuriidae*, *Heptageniinae*, *Anepeorinae*, *Pseudironinae*, *Arthropleinae*, *Ametropodinae*, *Leptophlebiidae* (*Atalomicria*, *Atalophlebia*, *Atalophlebioides*, *Leptophlebia*, *Habrophlebia*, *Habrophlebiodes*, *Habroleptoides*, *Jappa*, *Kirrara*), *Ephemerellinae*, *Tricorythidae*, *Neoephemeridae*, *Caenidae*, *Baetiscidae*, *Prosopistomatidae*.

(Cc) testis is narrowly cylindrical or spindle-shaped with apical portion produced into a point: *Leptophlebiidae*, (*Paraleptophlebia*, *Hagenulus*, *Traverella*, *Choroterpes* - all subgenera).

(Cd) testis is slightly or apparently bilaterally flattened, straight: *Behningiidae*, *Potamanthidae*, *Ephemeridae*, *Polymitarcidae*, *Palingeniidae*, *Euthyplociidae*; slightly dorsolaterally flattened in *Baetiscidae*.

(D) size and arrangement of testicular follicles:

(Da) testicular follicles are different in size, the size differences can be very conspicuous (*Ameletus*, *Ametropus*); follicles arranged into irregular longitudinal rows in dorsal view: *Siphonurinae* (*Ameletoides*, *Ameletus*, *Metreletus*, *Parameletus*), *Acanthametropodinae*, *Ameletopsinae* (*Chiloporter*), *Rallidentinae*, *Pseudironinae*, *Ametropodinae*, *Metretopodinae*, *Ephemerellidae* (some subgenera of the genus *Ephemerella*). Follicles are usually relatively large, shortly cylindrical or even spherical.

(Db) follicles equal in size, mostly arranged into regular longitudinal rows in dorsal view. This group consists of two subgroups:

(Db<sub>1</sub>) follicles relatively large, short and cylindrical (rarely spherical), each testis consists of approx. 100-250 follicles (follicles arranged at most into four longitudinal rows): *Siphonurinae* (*Siphonurus*), *Oniscigastriinae*, *Ameletopsinae* (*Ameletopsis*, *Mirawara*), *Isonychiinae*, *Coloburiscinae*, *Baetidae*, *Oligoneuriinae*, *Heptageniinae*, *Anepeorinae*, *Arthropleiinae*, *Leptophlebiidae* (*Atalophlebia*, *Atalomicria*, *Atalophlebioides*, *Jappa*, *Kirrara*), *Ephemerellidae* (*Ephemerella* - subgenera *Attenella*, *Drunella* - some species), *Behningiidae*, *Potamanthidae*, *Ephemeridae*, *Euthyplociidae*, *Polymitarcidae*, and *Palingeniidae*.

(Db<sub>2</sub>) follicles relatively small or very small, longer, multiplied (each testis consists of approx. 200-650 follicles), arranged into regular longitudinal rows in dorsal view (usually 4-7 rows): *Leptophlebiidae* (*Paraleptophlebia*, *Leptophlebia*, *Habrophlebia*, *Habroleptoides*, *Hagenulus*, *Traverella*, *Thraulius*), *Ephemerellidae* (*Ephemerella* - subgenera *Ephemerella*, *Torleya*, *Chitonophora*), *Tricorythidae*, *Neophemeridae*, *Caenidae*, *Baetiscidae*, *Prosopistomatidae*.

(E) position of testicular follicles to seminal duct:

(Ea) follicles are perpendicular to seminal duct (right angle between axis of seminal duct and axis of follicle): *Siphonurinae*, *Acanthametropodinae*, *Oniscigastriinae*, *Ameletopsinae* (*Ameletopsis*, *Mirawara*, *Chiloporter*), *Isonychiinae*, *Rallidentinae*, *Oligoneuriinae*, *Heptageniidae*, *Ametropodinae*, *Metretopodinae*, *Leptophlebiidae* (*Atalomicria*, *Atalophlebia*, *Jappa*), *Ephemerellidae* (*Ephemerella* - subgenera *Timpanoga*, *Attenella*, *Ephemerella*; *Teloganodes*, *Ephemerellina*), *Leptohyphinae*, *Dicercomyzinae*, *Behningiidae*, *Potamanthidae*, *Ephemeridae*, *Polymitarcinae*, *Asthenopodinae*, *Palingeniidae*, *Euthyplociidae*, *Neophemeridae*, *Caenidae*, *Baetiscidae*, *Prosopistomatidae*.

(Eb) follicles are 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*, *Trave-*

rella, *Thraulius*, *Choroterpes*), *Tricorythinae*, *Leptohyphinae* (*Tricorythodes*), *Campsurinae*.

(F) shape of seminal vesicle:

(Fa) seminal vesicle is inconspicuous, seminal duct only slightly extended: *Coloburiscinae*, *Oligoneuriinae*, *Leptophlebiidae* (*Atalomicria*, *Atalophlebia*, *Jappa*), *Ephemerellidae* (*Teloganodes*), *Tricorythidae* (*Leptohyphinae*, *Dicercomyzinae*), *Behningiidae*, *Neoephe-meridae*, *Caenidae*, *Prosopistomatidae*.

(Fb) seminal vesicle is apparent, seminal duct extended gradually caudad; vesicle usually cylindrical or elongated: *Oniscigastrinae*, *Ameletopsinae* (*Ameletopsis*, *Mirawara*, *Chiloporter*), *Baetidae*, *Heptageniinae* (*Stenonema*, *Stenacron*), *Arthropleinae*, *Leptophlebiidae* (*Leptophlebia*, *Pataleptophlebia*, *Kimminsula*, *Kirrara*), *Ephemerellidae* (*Ephemerellina*, *Ephemerella* - subgenera *Ephemerella*, *Drunella*, *Eurylophella*, *Torleya*, *Chitonophora*), *Ephemeridae*, *Euthyplociidae*, *Polymitarcinae*, *Compsurinae*, *Palingeniidae*.

(Fc) seminal vesicle conspicuous, seminal ducts extended suddenly; seminal vesicle cylindrical, funneliform or spindle-shaped, only slightly diminished caudad: *Siphonurinae*, *Isonychiinae*, *Rallidentinae*, *Heptageniidae* (*Cinygmula*, *Rhithrogena*, *Epeorus* - subgenera *Epeorus* and *Iron*; *Afronurus*, *Ecdyonurus*, *Heptagenia*), *Anepeorinae*, *Pseudironinae*, *Ametropodinae*, *Metretopodinae*, *Leptophlebiidae*, *Ephemerellidae* (*Ephemerella* - subgenera *Attenella* and *Timpanoga*), *Potamanthidae*, *Asthenopodinae*, *Baetiscidae*.

(Fd) seminal vesicle nearly spherical, rounded; seminal ducts extended suddenly in abdominal segments VII-VIII and apparently constricted in IX. This type of arrangement of seminal vesicles occurs only in some genera of the family *Leptophlebiidae*.

(G) position of seminal vesicle to the body segmentation:

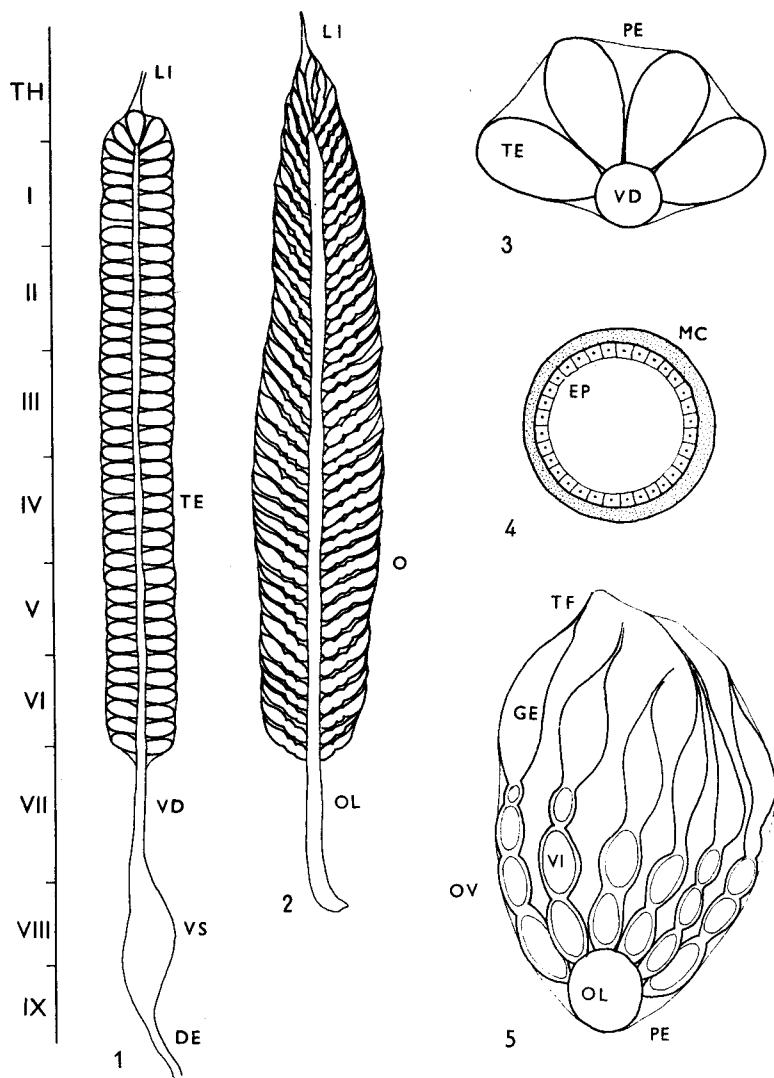
(Ga) seminal vesicle is deposited in the abdominal segments VIII and IX but may exceed to segment VII or even to segment VI; vesicle is usually cylindrical (Fa). This type of position of seminal vesicle was observed in *Ameletopsinae* (*Chiloporter*), *Coloburiscinae*, *Oligoneuriinae*, *Arthropleinae*, *Ephemerellidae* (*Teloganodes*, *Ephemerella* - subgenus *Timpanoga*), *Leptohyphinae*, *Behningiidae* (*Behningia*), *Neoephe-meridae* (*Potamanthellus*), *Caenidae* (*Caenis*, *Caenomedea*, *Tasmanocoenis*), *Prosopistomatidae*.

(Gb) seminal vesicle is deposited mainly in abdominal segment IX but may exceed to segment VIII; seminal vesicle is usually of Fb type, rarely of Fa or Fc types: *Siphonurinae* (*Ameletus*, *Siphonella*, *Metreletus*, *Parameletus*, *Siphonurus*), *Acanthametropodinae*, *Oniscigastrinae*, *Ameletopsinae* (*Ameletopsis*, *Mirawara*), *Isonychiinae*

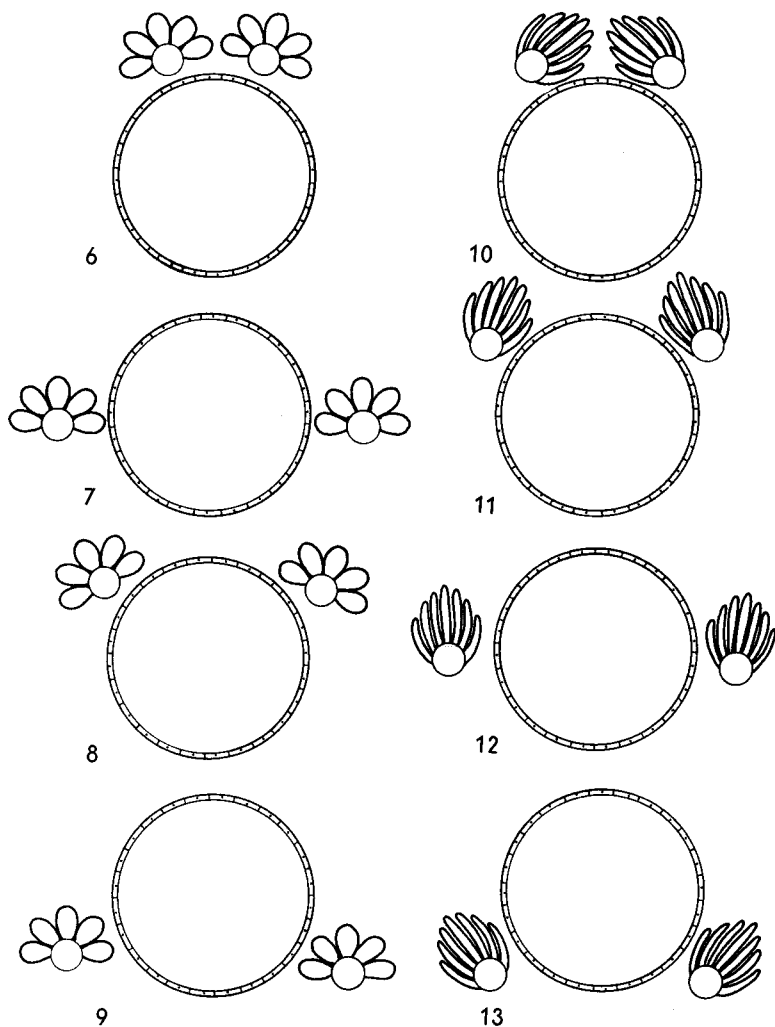


(*Isonychia* - some species), *Baetidae* (*Callibaetis*, *Baetis* - some species, *Baetopus*, *Centroptilum*, *Cloeon*, *Procloeon*), *Heptageniinae*, *Anepeorinae*, *Pseudironinae*, *Leptophlebiidae* (*Atalophlebia*, *Atalomicria*, *Jappa*), *Ephemerellidae* (*Ephemerellina*, *Ephemerella* - subgenera *Attenella*, *Drunella*, *Eurylophella*, *Chitonophora*, *Torleya*, *Ephemerella*), *Tricorythinae*, *Dicercomyzinae*, *Behningiidae* (*Dolania*), *Potamanthidae*, *Ephemeridae*, *Euthyplociidae*, *Palingeniidae*, *Neopemeridae* (*Neopphemera*), *Caenidae* (*Brachycercus*), *Baetiscidae*.

(Gc) seminal vesicle is deposited only in segment IX, slightly exceeding to segment VIII; vesicle is usually of Fc or Fd types: *Siphonurinae* (*Ameletoides*), *Isonychiinae* (*Isonychia* - some species), *Rallidentinae*, *Baetidae* (*Baetodes*, *Pseudocloeon*, *Baetis* - some species), *Ametropodinae*, *Metretopodinae*, *Leptophlebiidae* (*Leptophlebia*, *Habrophlebia*, *Habroleptoides*, *Thraululus*).



Figs. 1-5:  
 Inner reproductive organs of older mayfly larvae (sketch). 1 - testis, ventral view. 2 - ovary, ventral view. 3 - cutaway view of testis. 4 - cutaway view of duct. 5 - cutaway view of ovary. TH - thorax; I-IX - abdominal segments; LI - ligament; TE - testicular follicles; VD - vas deferens; VS - seminal vesicle; DE - ductus ejaculatorius OV - ovarioles; OL - oviductus lateralis; PE - peritoneal epithelium; MC - muscular coat; EP - inner epithelial layer; TF - terminal filament; VI - vitellarium; GE - germarium.



Figs. 6-13:  
Position of testes (Figs. 6-9) and ovaries (Figs. 10-13) in mayflies along the alimentary canal (cutaway view, sketch). 6,10 - dorsal position. 8,11 - dorsolateral position. 7, 12 - lateral position. 9, 13 - ventrolateral position.

## STRUCTURE AND BASIC TYPES OF ARRANGEMENT OF OVARY

The paired ovaries are deposited in the body cavity (mixocoel) along the alimentary canal in older mayfly larvae (growth of ovary is completely finished). Similarly to testes, the ovaries of species investigated extend either from thorax or from the first abdominal segment to the sixth abdominal segment. Ovaries may be produced even into head (*Caenidae*). Ovary is elongated, cylindrical, subcylindrical or tongue-shaped organ (Fig. 2) which is attached to peritoneal structures by a suspensory ligament in thorax. Suspensory ligament of the ovary consists of terminal filament of ovarioles from the anterior portion of ovary. Each ovary consists of a large number of ovarioles which envelope the ducts from above and from the sides. The number of ovarioles is not constant in specimens of the same species. Peritoneal membrane forms the outer membranous cover of the ovary in mayflies (Fig. 5). The ovarioles are filled up with germinal cells. They are differentiated in germarium and vitellarium in older larvae. The germarium contains oögonia and young oocytes, the vitellarium consists of several egg chambers containing growing oocytes enveloped by follicular epithelium. There are about 3-6 egg chambers apparent in older larvae. No shape changes of ovarioles occur before descending of mature eggs into oviducts. The ovarioles are directly attached to the oviduct and are arranged into several longitudinal rows in dorsal view (ovarioles are always equal in length and size).

The oviduct (oviductus lateralis) is formed by a simple tubular duct extending from the apical portion of ovary in thorax to the posterior margin of the seventh abdominal segment (Fig. 2). Lateral oviducts are always separated, their mesodermal parts never form a common oviduct (oviductus communis) as in related insect orders. Histological structure of oviduct does not substantially differ from that of seminal duct. An inner layer of epithelium is encircled by an outer muscular coat (Fig. 4). Although there are considerable differences in width of oviduct, the oviduct does not provide valuable data for comparative anatomy. This is the reason explaining that our attention must be paid to ovary preferably.

From the comparative anatomy point of view the most important characters of the arrangement of ovaries are as follows: position of

ovaries to the alimentary canal (H); position of ovaries to the body segmentation (J); shape of ovary and especially shape of its apical portion in thorax (K); position of ovarioles to oviduct (L). The following cases in the arrangement of the characters mentioned above were observed:

(H) position of ovaries to the alimentary canal:

(Ha) ovaries are deposited dorsally to alimentary canal (Fig. 11), contiguous in thorax and first abdominal segments and connecting the dorsal body wall. Dorsal position of ovaries occur in *Siphonurinae*, *Acanthametropodinae*, *Rallidentinae*, *Baetidae*, and *Metretopodinae*.

(Hb) ovaries are deposited dorsolaterally to the alimentary canal, usually contiguous only in thorax. This position of ovaries was observed in *Ameletopsinae*, *Oniscigastrinae*, *Oligoneuriinae*, *Ametropodinae*, *Isonychiinae*, *Pseudironinae*.

(Hc) ovaries are deposited laterally to alimentary canal (Fig. 12), sometimes closely contiguous to the wall of gut or to lateral tracheal trunks. This position of ovaries occur in *Coloburiscinae*, *Heptageniinae*, *Anepeorinae*, *Arthropleinae*, *Leptophlebiidae*, *Ephemerellidae* (the anterior part of ovary can be dorsolateral), *Tricorythidae*, *Behningiidae*, *Potamanthidae*, *Neophemeridae*, *Caenidae*, *Baetiscidae*, *Protopistomatidae*.

(Hd) ovaries are deposited ventrolaterally to the alimentary canal (Fig. 13). Ventrolateral position of ovaries was observed in *Ephemeridae*, *Polymitarcidae*, *Euthyplociidae*, and *Palingeniidae*. The family *Euthyplociidae* represents intermediary type between the groups Hc and Hd.

(J) position of ovaries to the body segmentation:

(Ja) ovaries are deposited only in abdominal segments extending from segment I to segment VI: *Coloburiscinae*, *Heptageniinae* (*Cinygmula*, *Epeorus* - subgenera *Epeorus*, *Iron*, *Ironopsis*), *Leptophlebiidae* (*Atalomicria*, *Atalophlebia*, *Atalophlebiodes*, *Jappa*), *Ephemerellidae* (*Ephemerella*), *Euthyplociidae* (*Euthyplocia*), *Asthenopodinae*, *Campsurinae*.

(Jb) ovaries are deposited in abdominal segments I-VI, in metathorax and I-VI or in meso-, metathorax and I-VI. Ovaries are produced into metathorax in *Ameletopsinae* (*Chilopcrter*), *Isonychiinae*, *Oligoneuriinae* (*Oligoneuriella*, *Lachlania*), *Heptageniinae* (*Epeorus* - subgenus *Ironodes*), *Anepeorinae*, *Leptophlebiidae* (some genera), *Behningiidae* (*Behningia*), *Potamanthidae* (*Rhoenanthopsis*), *Ephemeridae* (*Ephemerella*), *Euthyplociidae* (*Campylocia*), *Palingeniidae*; ovaries are produced into mesothorax in *Siphonurinae* (*Ameletoides*, *Amele-*

tus, *Siphonella*, *Metreletus*, *Parameletus*, *Acanthametropodinae*, *Ameletopsinae* (*Ameletopsis*, *Mirawara*), *Rallidentinae*, *Baetidae* (*Callibaetis*, *Baetodes*, *Cloeon*, *Procloeon*, *Centroptilum*, *Baetis* - some species), *Oligoneuriinae* (*Homoeoneuria*, *Oligoneurisca*), *Heptaneriinae* (*Stenonema*, *Stenacron*), *Ametropodinae*, *Metretopodinae*, *Leptophlebiidae* (*Paraleptophlebia* - some species, *Leptophlebia*, *Habrophlebia*, *Habroleptoides*), *Ephemerellidae* (*Ephemerella* - subgenera *Ephemerella*, *Torleya*, *Chitonophora*), *Tricorythinae*, *Leptohyphinae*, *Potamanthidae* (*Potamanthus*, *Potamanthodes*), *Ephemeridae* (*Hexagenia*, *Litobrancha*, *Pentagenia*), *Prosopistomatidae*.

(Jc) ovaries are deposited in pro-, meso- and metathorax and in abdominal segments I-VI. Ovaries or their ligaments can be produced to head. Ovaries are produced to prothorax in *Siphonurinae* (*Siphonurus*), *Oniscigastrinae*, *Heptageniinae* (*Afronurus*, *Ecdyonurus*, *Heptagenia* - some species), *Pseudironinae*, *Leptophlebiidae* (*Paraleptophlebia* - some species, *Traverella*, *Hagenulus*), *Ephemerellidae* (*Ephemerellina*, *Teloganodes*), *Neoephemeridae*, *Caenidae* (*Brachycercus*), *Baetiscidae*; ovaries are produced into head in some genera of the family *Caenidae* (*Caenis*, *Caenomedea*, *Tasmanocoenis*).

(Jd) ovaries are deposited in thorax and abdominal segments but not reaching segment VI: *Baetidae* (*Baetodes*, *Pseudocloeon*, *Baetis* - some species: PT or MST - IV-V), *Leptophlebiidae* (some genera), *Ephemerellidae* (*Ephemerella* - subgenera *Drunella*, *Eurylophella*: PT-V).

(K) shape of ovary and shape of its apical portion:

(Ka) ovary cylindrical or subcylindrical, only slightly flattened; in thorax or in first abdominal segments medially bent or even s-curved, apical part bluntly pointed or rounded: *Siphonurinae*, *Acanthametropodinae*, *Rallidentinae*, *Oniscigastrinae*, *Coloburiscinae*, *Metretopodinae*.

(Kb) ovary is cylindrical or subcylindrical, only slightly bilaterally flattened, straight, apical part bluntly pointed or rounded: *Ameletopsinae* (*Chiloporter*) *Ameletopsis*, *Mirawara*, *Isonychiinae*, *Baetidae*, *Oligoneuriinae*, *Anepeorinae*, *Arthropleinae*, *Pseudironinae*, *Ametropodinae*, *Leptophlebiidae* (*Atalomicria*, *Atalophlebia*, *Jappa*, *Atalophlebioides*), *Ephemerellidae* (*Ephemerella* - subgenera *Attenella*, *Timpanoga*, *Drunella*, *Ephemerella*, *Torleya*), *Tricorythidae*, *Leptohyphinae*, *Caenidae*.

(Kc) ovary is tongue-shaped, mostly bilaterally flattened, bluntly pointed or produced into a narrow point: *Leptophlebiidae* (*Leptophlebia*, *Paraleptophlebia*, *Habrophlebia*, *Habroleptoides*, *Traverella*, *Hagenulus*, *Thraulius*), *Potamanthidae*, *Ephemeridae*, *Euthyplociidae*,

*Polymitarcidae, Palingeniidae, Neoephemeridae, Baetiscidae, Prosopistomatidae.*

(L) position of ovarioles to oviducts:

(La) ovarioles are perpendicular or slightly oblique to oviducts (the angle between axis of ovariole and axis of oviduct is about  $70-90^{\circ}$ ): *Siphonurinae, Acanthametropodinae, Oniscigastriinae, Ameletopsinae* (*Ameletopsis, Mirawara, Chiloporter*), *Coloburiscinae, Rallidentinae, Baetidae, Oligoneuriinae, Heptageniidae* (nearly all genera investigated), *Anepeorinae, Arthropleinae, Ametropodinae, Metretopodinae, Leptophlebiidae* (*Atalomicria, Atalophlebia, Jappa*), *Ephemerellidae* (*Ephemerella* - subgenera *Attenella, Timpanoga*), *Tricorythinae, Behningiidae, Potamanthidae, Ephemeridae* (*Ephemerella*), *Euthyplociidae, Palingeniidae, Caenidae* (*Brachycercus*). Ovarioles are usually cylindrical, straight and not produced.

(Lb) ovarioles are apparently oblique to oviducts (the angle between axis of ovariole and axis of oviduct is about  $30-60^{\circ}$ ): *Isonychiinae, Leptophlebiidae* (*Leptophlebia, Paraleptophlebia, Habrophlebia, Habroleptoides, Traverella, Hagenulus*), *Ephemerellidae* (*Teloganodes, Ephemerella* - subgenera *Ephemerella, Chitonophora, Torleya*), *Leptohyphinae, Ephemeridae* (*Hexagenia, Litobrancha, Pentagenia*), *Neoephemeridae, Caenidae* (*Caenis, Caenomedeia, Tasmanocoenis*), *Baetiscidae, Prosopistomatidae*. Ovarioles are usually more numerous and smaller, produced and bent.

# ANATOMICAL SCHEMES OF INTERNAL REPRODUCTIVE SYSTEM OF THE FAMILIES, SUBFAMILIES AND GENERA OF THE ORDER *EPHEMEROPTERA*

Abbreviations used: C - head (caput); MST - mesothorax; MTT - meta-thorax; I, II, III, IV, V, VI, VII, VIII, IX, X - 1st- 10th abdominal segment; VD - seminal duct (vas deferens); DE - ejaculatory duct (ductus ejaculatorius); VS - seminal vesicle (vesicula seminalis); OL - oviduct (oviductus lateralis).

## *Siphonuridae*

### *Siphonurinae*

(Figs. 14-27)

Testis: deposited dorsally (Aa); MTT, I, II, III, IV, V, VI (Ba); cylindrical and bent medially (*Ameletus*, *Ameletoides*, *Parameletus*) or arcuately (*Siphonella*) in abdominal segments, s-curved in *Siphonurus* (Ca); testicular follicles large, different in size (the differences very conspicuous in *Ameletus*), arranged into irregular longitudinal rows (Da), less numerous, short and nearly spherical, at the right angle to VD (Ea); VS elongated, VD extended suddenly (Fc), deposited in IX (*Ameletoides*) (Gc) or in VIII and IX (*Metreletus*, *Siphonella*, *Siphonurus*) (Gb).

Ovary: deposited dorsally (Ha); MST, MTT, I, II, III, IV, V, VI (Jb); cylindrical or slightly bilaterally flattened, always bent medially (Ka), bluntly pointed or rounded in mesothorax; ovarioles large and short, cylindrical; deposited at the right angle to OL (*Siphonella*, *Parameletus*) or slightly oblique (*Ameletoides*, *Ameletus*, *Metreletus*) (La).

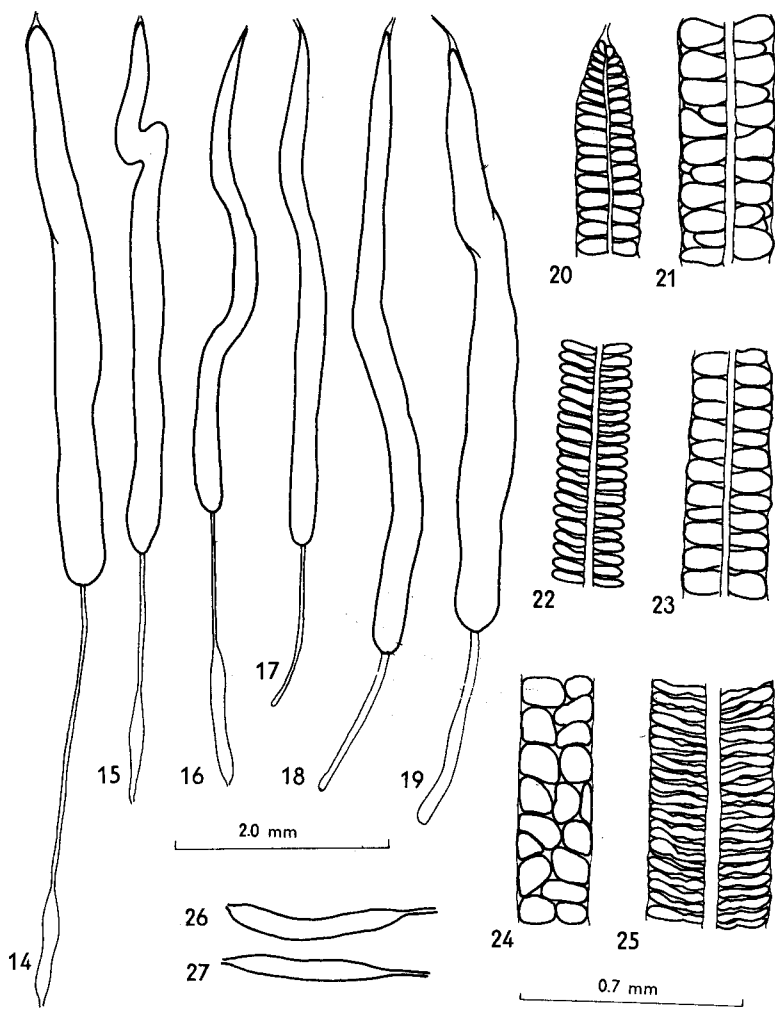
The subfamily *Siphonurinae* is quite homogeneous. Basic anatomical characters are the same in all genera investigated with the exception of Holarctic genus *Siphonurus* where testicular follicles are more numerous and nearly equal in length (Db) and ovaries extend from PT to VI (Jc).

### *Acanthametropodinae*

(Figs. 28, 33, 35, 37)

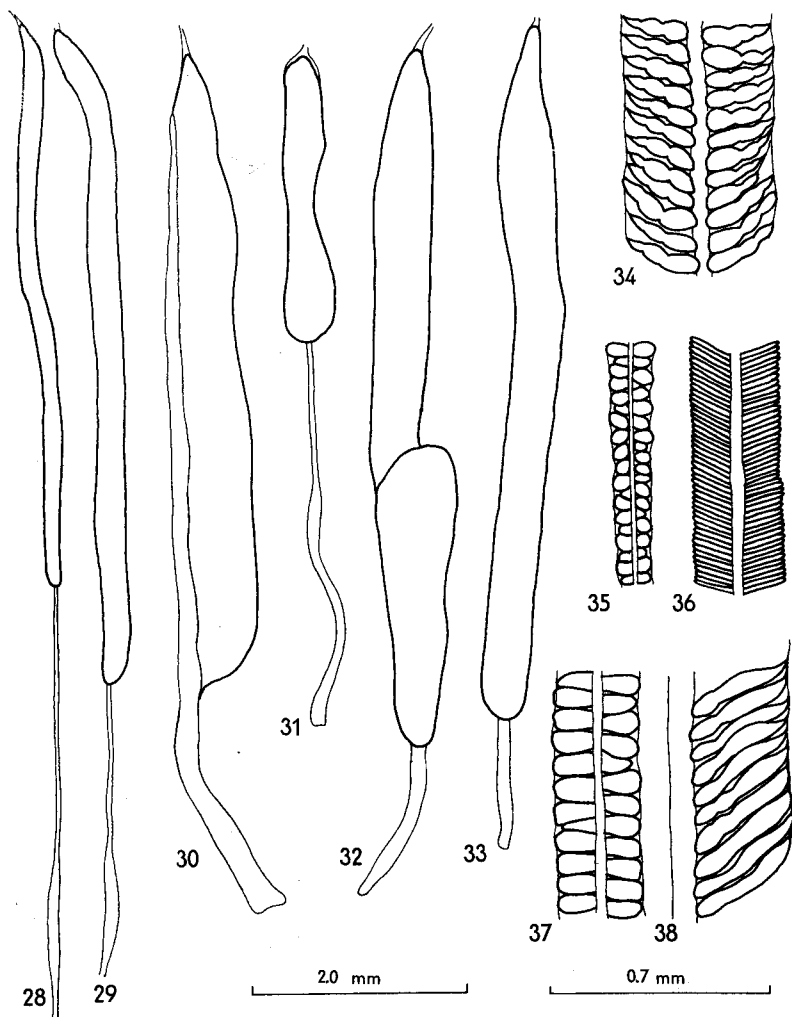
Testis: deposited dorsally (Aa); MTT, I, II, III, IV, V, VI (Ba); cylindrical, moderately bent medially, bluntly pointed in thorax (Ca); tes-





Figs. 14-27:

Gonads of the family *Siphonuridae* (subfamily *Siphonurinae*). 14,19,21, 25 - *Ameletoides locusalbiniae*. 15,18,23,27 - *Siphonurus linnaeanus*. 16,17,20,22 - *Siphonella* sp. 24 - *Ameletus alexandrae*. 14-16 - testis, dorsal view; 17-19 - ovary, dorsal view; 20,21,24 - testis, detail of follicles (20,21 - ventral, 24 - dorsal view); 22,23,25 - ovary, detail of ovarioles (ventral view); 26,27 - seminal vesicle, detail.



Figs. 28-38:

Gonads of the family Siphonuridae (subfamilies Acanthametropodinae, Oniscigastrinae and Coloburiscinae). 28,35 - *Acanthametropus nikolskyi*. 29,32,34 - *Tasmanophlebia nigrescens*. 30,31,36,38 - *Coloburiscoides* sp. 33,37 - *Acanthametropus* sp. 28,29,31 - testis, dorsal view; 30 - ovary, lateral view; 32,33 - ovary, dorsal view; 34,37 - ovary, detail of ovarioles, ventral view; 38 - the same, lateral view; 35,36 - testis, detail of follicles, ventral view.

ticular follicles different in size (difference inconspicuous), arranged into irregular longitudinal rows in dorsal view (Da), nearly spherical and deposited at the right angle to VD (Ea); VS spindle-shaped, VD extended only gradually (Fb); VS deposited in VIII and IX (Gb).

Ovary: deposited dorsally (Ha); MST, MTT, I,II,III,IV,V,VI (Jb); cylindrical, moderately bent medially in I-III (Ka), bluntly pointed in thorax; ovarioles short and large, nearly perpendicular to OL (La).

With the exception of the arrangement of seminal vesicle (Fb), anatomical scheme of the subfamily *Acanthametropodinae* does not differ from that of the *Siphonurinae*.

#### *Oniscigastreae*

(Figs. 29, 32, 34)

Testis: deposited dorsolaterally (Ab); MST, MTT, I,II,III,IV,V,VI (Bb); cylindrical, moderately bent (*Tasmanophlebia*) or straight (*Oniscigaster*) in thorax (Ca,Cb); testicular follicles equal in size, arranged into regular longitudinal rows (Db<sub>1</sub>), cylindrical, perpendicular to VD (Ea); VS elongated, narrow, VD extended gradually (Fb), vesicle deposited in VIII and IX (Gb).

Ovary: deposited dorsolaterally (Hb); PT, MST, MTT, I,II,III,IV,V,VI (Jc); cylindrical, bluntly pointed and slightly flattened in thorax, s-curved in II-IV (Ka), in *Oniscigaster* only bent medially; ovarioles large, slightly bent cranially, moderately oblique to oviduct (La).

This subfamily is quite homogeneous showing certain relationships to the subfamily *Siphonurinae*. It differs from this subfamily especially in position of gonads (Ab, Hb, Bb, Jc).

#### *Ameletopsinae*

(Figs. 39, 40, 42, 43, 46, 47, 49, 50)

##### *Ameletopsis*, *Mirawara*:

Testis: deposited dorsolaterally (Ab); MTT, I,II,III,IV,V,VI (Ba); cylindrical, pointed and straight in thorax (Cb); testicular follicles short and large, equal in size, arranged into regular rows (Db<sub>1</sub>), perpendicular to VD (Ea); seminal vesicle formed by gradually extended VD, elongated (Fb), deposited in VIII and IX (Gb).

Ovary: deposited dorsolaterally (Hb); MST, MTT, I,II,III,IV,V,VI (Jb); cylindrical, straight, not bent, bluntly pointed in thorax (*Mirawara*) or rounded at apex (*Ameletopsis*) (Kb); ovarioles minute, straight, at the right angle or slightly oblique to oviduct (La).

*Chiloporter*:

Testis: deposited dorsally (Aa), II,III,IV,V,VI (Bd); cylindrical, slightly bent medially, bluntly pointed in II (Ca); testicular follicles different in size, very short and nearly spherical, arranged into irregular longitudinal rows (Da), perpendicular to VD (Ea); VS formed by gradually extended VD (Fb), deposited in VII, VIII and IX (Ga).

Ovary: deposited dorsally (Ha), MTT, I,II,III,IV,V,VI (Jb); cylindrical, slightly medially bent and bluntly pointed in thorax (Kb); ovarioles straight, deposited slightly obliquely to oviduct, relatively numerous (La).

This subfamily apparently comprises two groups of genera. Both the New Zealand genus *Ameletopsis* and Australian genus *Mirawara* are similar in their arrangement of gonads but quite different from the subfamily *Siphonurinae* (the Neotropical genus *Chaquihua* is probably also contained in this group). The second group consists of the Neotropical genus *Chiloporter* with anatomical scheme similar to the subfamily *Siphonurinae*.

*Isonychiinae*

(Figs. 41, 44, 45, 48)

Testis: deposited dorsolaterally (Ab); I,II,III,IV,V,VI (Ba); cylindrical, bluntly pointed in I and II (Cb); testicular follicles equal in length and size, arranged into regular longitudinal rows (Db<sub>1</sub>), large and cylindrical, at the right angle to VD (Ea); VS cylindrical, VD expanded suddenly (Fc), deposited in IX (*Isonychia ignota*) (Gc) or in VIII-IX (*Isonychia* sp.) (Gb).

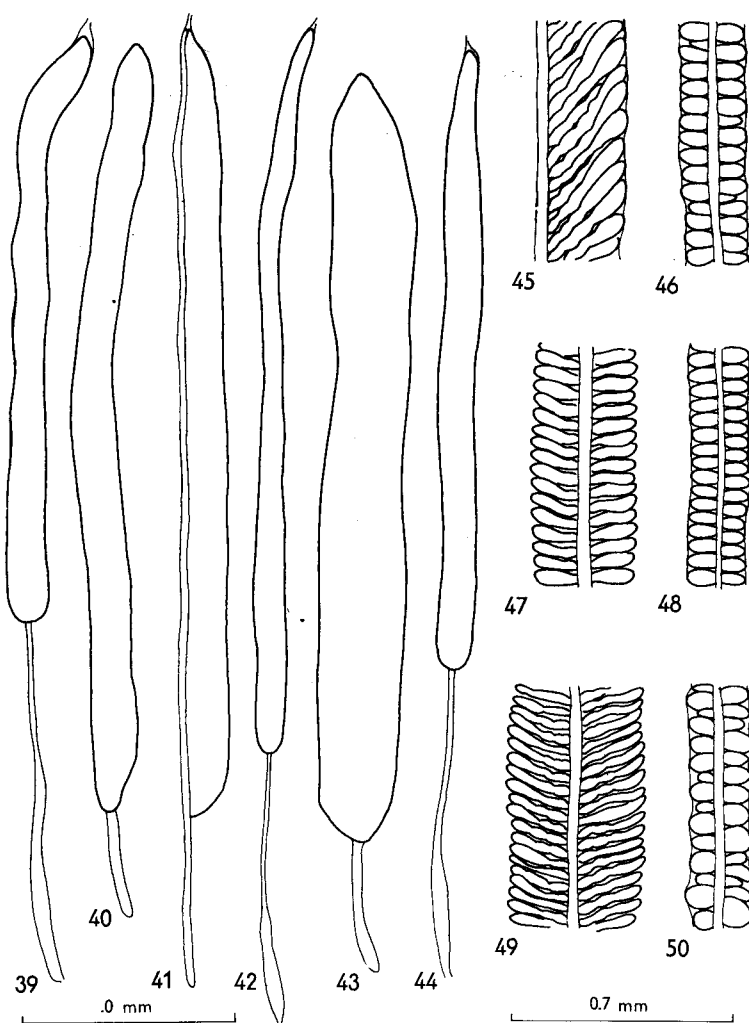
Ovary: deposited dorsolaterally (Hb); MTT, I,II,III,IV,V,VI (Jb); subcylindrical, bilaterally flattened, bluntly pointed in thorax (Kb), ovarioles large, strongly oblique to OL (Lb).

The subfamily *Isonychiinae* (a single Holarctic genus *Isonychia*) is well characterized by its anatomical characters and distinctly distinguished from all remaining subfamilies of the *Siphonuridae*. The arrangement of gonads is similar to that of the family *Oligoneuriidae*.

*Coloburiscinae*

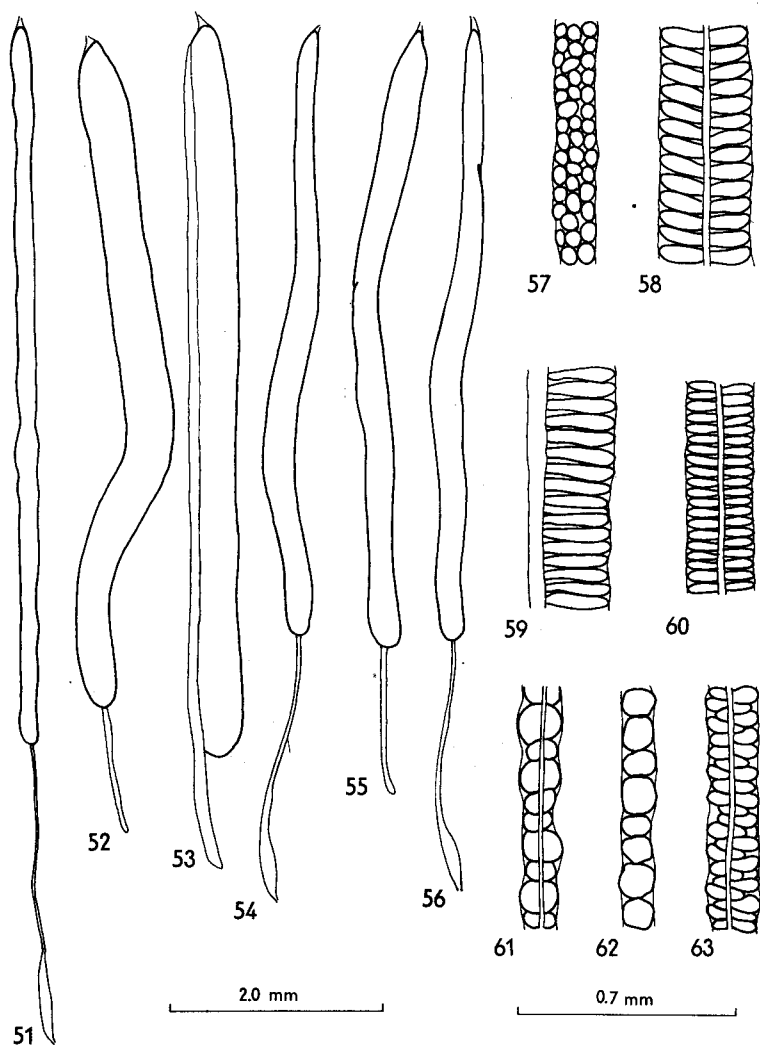
(Figs. 30, 31, 36, 38)

Testis: deposited laterally (Ac); III (II),IV,V,VI (Bd), cylindrical, in IV and V slightly constricted, in III bluntly pointed (Cb); testicular follicles equal in size, arranged into regular longitudinal rows (Db<sub>1</sub>), considerably long and slender, relatively numerous, slightly oblique to VD (Eb); VS inconspicuous, VD expanded gradually (Fa), deposited in VI-IX (Ga).



Figs. 39-50:

Gonads of the family Siphonuridae (subfamilies Ameletopsinae, Isonychiinae). 39,40,47,50 - *Chiloporter* sp. 42,43,46,49 - *Mirawara* sp. 41, 44,45 - *Isonychia* sp. 39,42,44 - testis, dorsal view; 40,43 - ovary, dorsal view; 41 - ovary, lateral view; 45,47,49 - ovary, detail of ovarioles (45 - lateral, 47,49 - ventral view); 46,48,50 - testis, detail of follicles, ventral view.



Figs. 51-63:

Gonads of the families *Siphonuridae* (subfamily *Rallidentinae*) and *Ametropodidae*. 51, 53, 59, 61, 62 - *Ametropus albrighti*. 54, 55, 57 - *Siphloplecton basale*. 60 - *Metretopus norvegicus*. 52, 56, 58, 63 - *Rallidens macfarlanei*. 51, 54, 56 - testis, dorsal view; 52, 55 - ovary, dorsal view; 53 - ovary, lateral view; 57, 61-63 - testis, detail of follicles (57, 62 - dorsal, 61, 63 - ventral view); 58, 59, 60 - ovary, detail of ovarioles (59 - lateral, 58, 60 - ventral view).

Ovary: deposited laterally (Hc); I,II,III,IV,V,VI (Ja); cylindrical, slightly bilaterally flattened and bent medially in the first and second abdominal segments (Ka); ovarioles large, oblique to OL (La).

Subfamily homogeneous, well characterized by the arrangement of gonads. It differs markedly from remaining subfamilies of the *Siphonuridae* by lateral position of both testes and ovaries and by position of testicular follicles to seminal duct (Ac, Hc, Eb).

#### *Rallidentinae*

(Figs. 52, 56, 58, 63)

Testis: deposited dorsally (Aa); MTT, I,II,III,IV,V,VI (Ba); cylindrical, moderately bent medially, bluntly pointed in thorax (Ca); testicular follicles different in size, arranged into irregular longitudinal rows (Da), relatively large, cylindrical or nearly spherical, perpendicular to VD (Ea); VS formed by cylindrically expanded VD (Fc), deposited in IX (Gc).

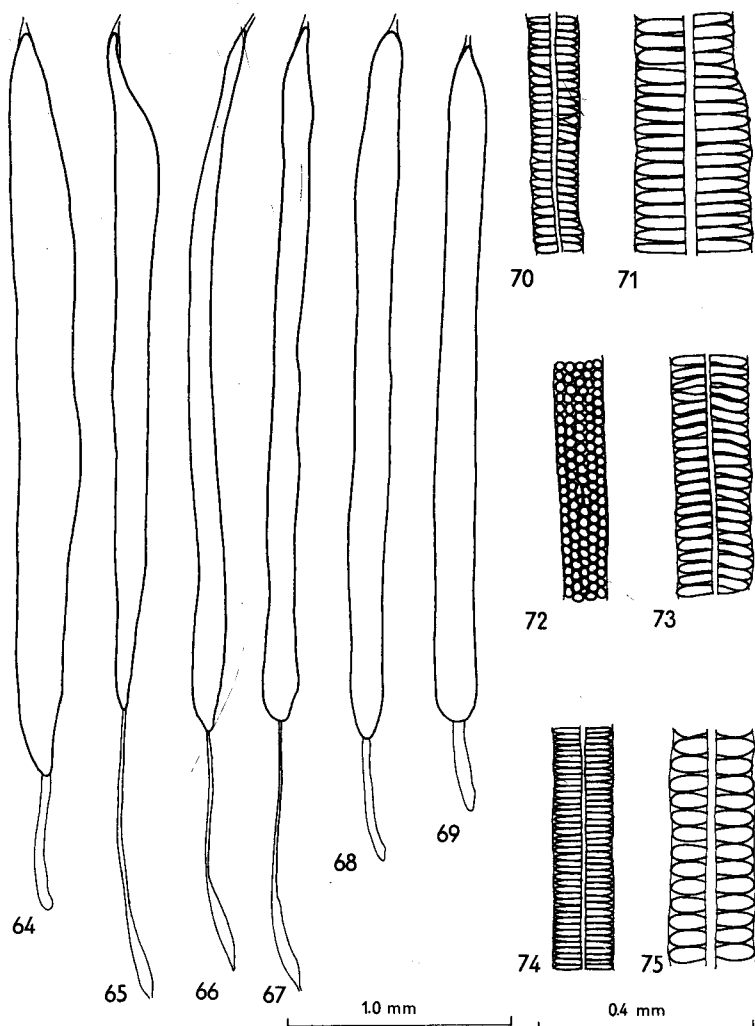
Ovary: deposited dorsally (Ha); MST,MTT, I,II,III,IV,V,VI (Jb); nearly cylindrical, strongly bent medially in III and IV, bluntly pointed in thorax (Ka); ovarioles relatively short, perpendicular or slightly oblique to OL, straight (La).

The subfamily *Rallidentinae* consisting of the only New Zealand genus *Rallidens* does not substantially differ from the *Siphonurinae* in arrangement of gonads; the genus *Rallidens* corresponds to the Australian genus *Ameletoides*.

The family *Siphonuridae* consists of group of genera with very heterogenous anatomical arrangement of gonads. The division into the following groups of subfamilies and genera results from their anatomical schemes:

- (a) *Siphonurinae*, *Acanthametropodinae*, *Rallidentinae*
- (b) *Ameletopsis*, *Mirawara* (+ *Chaquihua*) (i.e. *Ameletopsinae* excluding the genus *Chiloporter*)
- (c) *Chiloporter*
- (d) *Oniscigastriinae*
- (e) *Isonychiinae*
- (f) *Coloburiscinae*

If the scheme of gonads arrangement of subfamilies *Siphonurinae*, *Acanthametropodinae* and *Rallidentinae* is considered to be the basic scheme for the *Siphonuridae*, then it might be possible to deduce the genus *Chiloporter* with dorsal position of gonads and follicles different in size and some relatively more specialized forms of the subfamilies *Ameletopsinae* and *Isonychiinae* with gonads deposited dorsolaterally and follicles equal in size. Moreover, there are some more advanced



Figs. 64-75:

Gonads of the family Baetidae. 64,65,71,74 - *Callibaetis coloradensis*. 66,69,70,73 - *Centroptilum pennulatum*. 67,68,75 - *Baetis alpinus*. 72 - *Baetis* sp. (Australia). 65,66,67 - testis, dorsal view; 64,68,69 - ovary, dorsal view; 70,72,74 - testis, detail of follicles (72 - dorsal, 70,74 - ventral view); 71,73,75 - ovary, detail of ovarioles, ventral view.



characters in *Isonychiinae*: tongue-shaped ovary (bilaterally flattened) and ovarioles apparently oblique to oviduct. These characters approach this subfamily to the family *Siphonuridae* or to advanced group of genera of *Heptageniidae*.

The subfamily *Oniscigastriinae* is characterized by the shift of gonads into prothorax (Jc) but both testes and ovaries remain deposited dorsolaterally. While in the subfamily *Oniscigastriinae* certain elements of affinity with the family *Baetidae* may be seen, the subfamily *Coloburiscinae* differs from the *Siphonurinae* and related subfamilies (and even from the *Baetidae*) in lateral position of gonads and follicles deposited obliquely to seminal duct. These characters approach its gonads to gonads of families with lateral position of testes and ovaries.

## ***Baetidae***

### *Baetidae*

(Figs. 64-88)

*Callibaetis*, *Baetopus*, *Centroptilum*, *Cloeon*, *Procloeon*:

Testis: deposited dorsally (Aa); MST, MTT, I, II, III, IV, V, VI (Ba); cylindrical, straight, pointed or bluntly pointed in thorax (Cb); testicular follicles equal in length, arranged into regular 3-5 longitudinal rows ( $Db_1$ ), elongated, relatively numerous, at the right angle to VD (Ea); VS elongated, VD expanded gradually (Fb), deposited in VIII and IX (Gb).

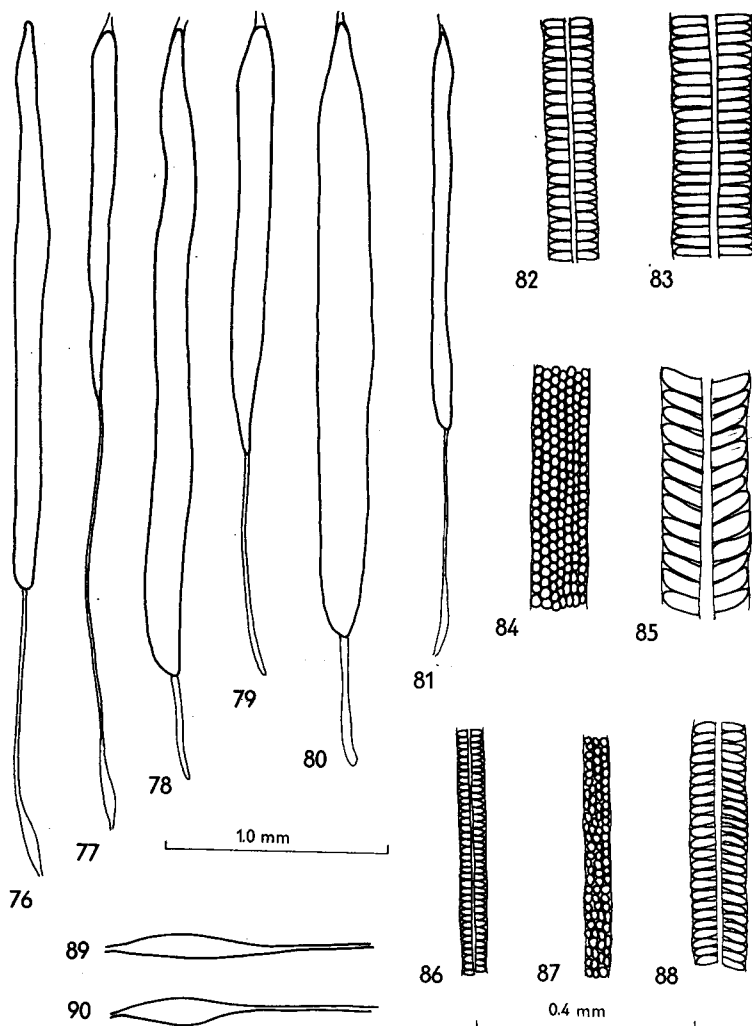
Ovary: deposited dorsally (Ha); MST, MTT, I, II, III, IV, V, VI (Jb); cylindrical or subcylindrical, straight, bluntly pointed or rounded in thorax (Ka); ovarioles short, relatively numerous, perpendicular or slightly oblique to OL (La); in ovoviviparous species of the genera *Cloeon* and *Callibaetis* only 1-2 oocytes in ovarioles.

*Baetodes*, *Pseudocloeon*:

Testis: deposited dorsally (Aa); MST, MTT, I, II, III, IV (V)(Bc); cylindrical, narrow, produced into a point in thorax (Cb); testicular follicles numerous, equal in size, arranged into regular longitudinal rows ( $Db_1$ ), at the right angle to VD (Ea); VS spindle-shaped (Fb), deposited in IX (Gc).

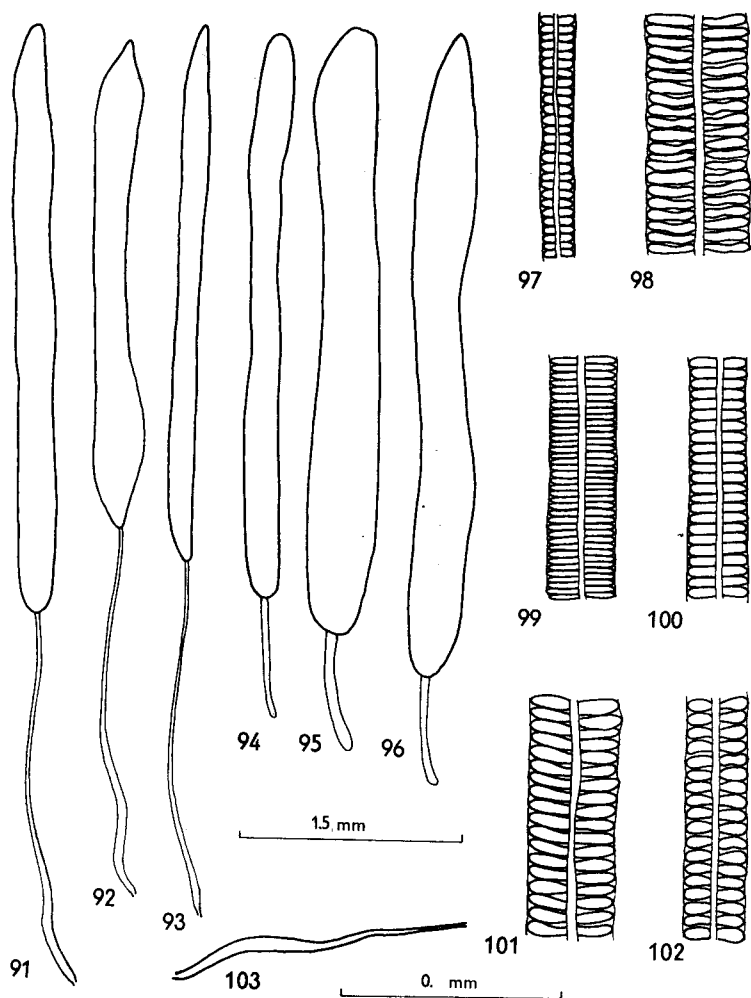
Ovary: deposited dorsally (Ha); PT, MST, MTT, I, II, III, IV, V, VI (Jd), cylindrical or slightly flattened, bluntly pointed in thorax (Ka); ovarioles perpendicular or slightly oblique to OL (La).

The family *Baetidae* comprises two basic groups of genera as to arrangement of gonads. The first group consists of genera *Callibaetis*, *Baetopus*, *Centroptilum*, *Cloeon*, and *Procloeon* with gonads showing cer-



Figs. 76-90:

Gonads of the family Baetidae. 76,80,83,85,89 - *Procloeon bifidum*. 77, 82,87,90 - *Pseudocloeon inexpectatum*. 78, 84 - *Baetopus* sp. 79, 88 - *Baetodes* sp. 81,86 - *Pseudocloeon* sp. 76,77,81 - testis, dorsal view; 78-80 - ovary, dorsal view; 82,86,87 - testis, detail of follicles (87 - dorsal, 82,86 - ventral view); 83-85,88 - ovary, detail of ovarioles (84 - dorsal, 83,85,88 - ventral view); 89,90 - seminal vesicle, detail.



Figs. 91-103:

Gonads of the family *Oligoneuriidae*. 91, 96, 99, 101, 103 - *Lachlania* sp. 92, 94, 100, 102 - *Homoeoneuria dolani*. 93, 95, 97, 98 - *Oligoneuriella rhenana*. 91, 92, 93 - testis, dorsal view; 94, 95, 96 - ovary, dorsal view; 97, 99, 100 - testis, detail of follicles, ventral view; 98, 101, 102 - ovary, detail of ovarioles, ventral view; 103 - seminal vesicle, detail.

tain relationships to gonads of the subfamilies *Oniscigastrinae* and *Ameletopsinae* (*Siphonuridae*). The second group consists of genera *Baetodes* and *Pseudocloeon* (similar arrangement of gonads was observed also in several undescribed genera from Oriental region). This group is characterized by the shift of gonad to head (apparently more derived character) which is undoubtedly due to the considerable shortening of body in some rheophile forms. In spite of these exceptions which correspond to the evolutionary tendencies of this group, the family is quite homogeneous. Moreover, numerous intermediary forms in the arrangement of gonads and especially in their position to the body segmentation can be found within the genus *Baetis*.

## *Oligoneuriidae*

### *Oligoneuriinae*

(Figs. 91-102)

Testis: deposited dorsolaterally (Ab); I,II,III,IV,V,VI (Ba); regularly cylindrical, rounded (*Lachlania*) or bluntly pointed (Cb) (*Oligoneuriella*, *Homoeoneuria*) in thorax; testicular follicles equal in size, arranged into regular longitudinal rows, elongated, (Db<sub>1</sub>), perpendicular to VD (Ea); VS inconspicuous, VD expanded gradually (Fa), deposited in VII-IX (Ga).

Ovary: deposited dorsolaterally (Hb); MTT, I,II,III,IV,V,VI (Jb), cylindrical, bluntly pointed or rounded in thorax (Ka); ovarioles at the right angle to OL (La).

Subfamily homogeneous; the Palaearctic genus *Oligoneurisca* and Nearctic genus *Homoeoneuria* deviate from the general scheme of anatomical arrangement of gonads (ovary deposited in MST-VI - Jc). The subfamily *Oligoneuriinae* shows relationships to the subfamilies *Heptageniinae* (*Heptageniidae*) and *Isonychiinae* (*Siphonurinae*); no data are known about the Oriental subfamily *Chromarcyinae*.

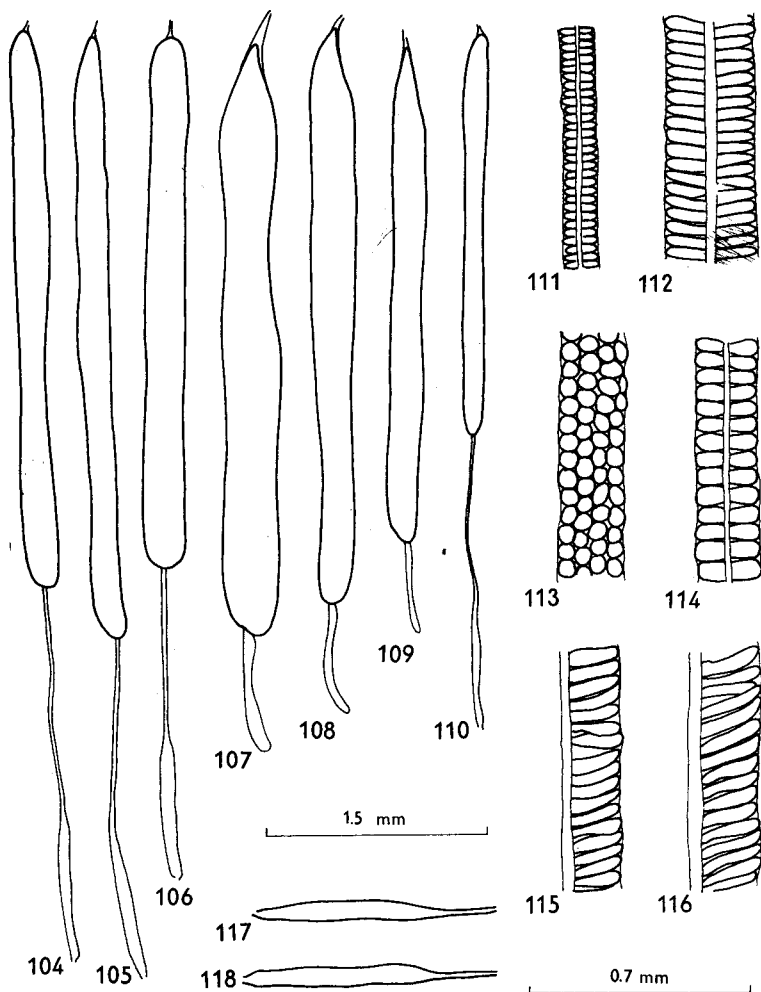
## *Heptageniidae*

### *Heptageniinae*

(Figs. 104-130)

*Cinygmula*, *Epeorus* (subgenera *Epeorus*, *Iron*, *Ironodes*), *Rhithrogena*:

Testis: deposited laterally (Ac); I,II,III,IV,V,VI (Ba); cylindrical, rounded (*Epeorus*) or bluntly pointed in thorax (Cb), straight follicles considerably large (*Epeorus*, *Rhithrogena*) or smaller, equal in size, arranged into regular longitudinal rows (Db<sub>1</sub>), perpendicular



Figs. 104-118:

Gonads of the family *Heptageniidae* (subfamily *Heptageniinae*). 104, 108, 115, 117 - *Rhithrogena hercynia*. 105, 107, 112 - *Epeorus* (*Epeorus*) *sylvicola*. 106, 109, 118 - *Epeorus* (*Iron*) *yugoslavicus*. 110, 111 - *Cinygmula* sp. 113, 114, 116 - *Epeorus* (*Ironopsis*) *grandis*. 104, 105, 106, 110 - testis, dorsal view; 107, 108, 109 - ovary, dorsal view; 111, 113, 114 - testis (111, 114 - ventral, 113 - dorsal view), detail of follicles; 112, 115, 116 - ovary, detail of ovarioles (112 - ventral, 115, 116 - lateral view); 117, 118 - seminal vesicle, detail.

to VD (Ea); VS cylindrical, VD expanded suddenly (Fb), deposited in VIII and IX (Gb).

Ovary: deposited laterally (Hc); (MTT), I,II,III,IV,V,VI (Ja, Jb); cylindrical or subcylindrical, slightly flattened, bluntly pointed in thorax (Kb); ovarioles relatively large, perpendicular or slightly oblique to OL (La).

*Afronurus*, *Ecdyonurus*, *Heptagenia*, *Stenacron*, *Stenonema*, *Heptagenia*, *Thalerosphyrus*:

Testis: deposited laterally (Ac); MTT, I,II,III,IV,V,VI (Ba); cylindrical, rounded or bluntly pointed in thorax (Cb); testicular follicles shortly cylindrical, equal in length, relatively more numerous ( $Db_1$ ), at the right angle to VD (Ea). VS formed by suddenly (*Stenonema*) or gradually expanded VD (Fb, Fc), deposited in VIII-IX (Gb).

Ovary: deposited laterally (Hc); (PT), MST, MTT, I,II,III,IV,V,VI (Jb, Jc); subcylindrical, moderately bilaterally flattened, bluntly pointed in thorax (Kb); ovarioles cylindrical, straight or slightly bent, oblique (La), in *Heptagenia* strongly oblique to OL (Lb).

The genera of the subfamily *Heptageniinae* may be divided into two groups. The group (a) is more primitive and includes genera *Cinygmula*, *Epeorus* and *Rhithrogena* - gonads only in abdomen, testicular follicles large, ovarioles nearly perpendicular to OL. The specialized group (b) includes genera *Afronurus*, *Ecdyonurus*, *Stenacron*, *Stenonema*, *Thalerosphyrus* and *Heptagenia* - gonads also in thorax, follicles numerous, ovarioles oblique to OL. Despite markedly different characters of the two groups, the subfamily *Heptageniinae* may be considered evolutionarily homogenous. The Nearctic genus *Ironopsis* and some species of the genus *Epeorus* occupy an intermediary position between the above two groups having the gonads only in abdomen but ovarioles oblique to oviduct.

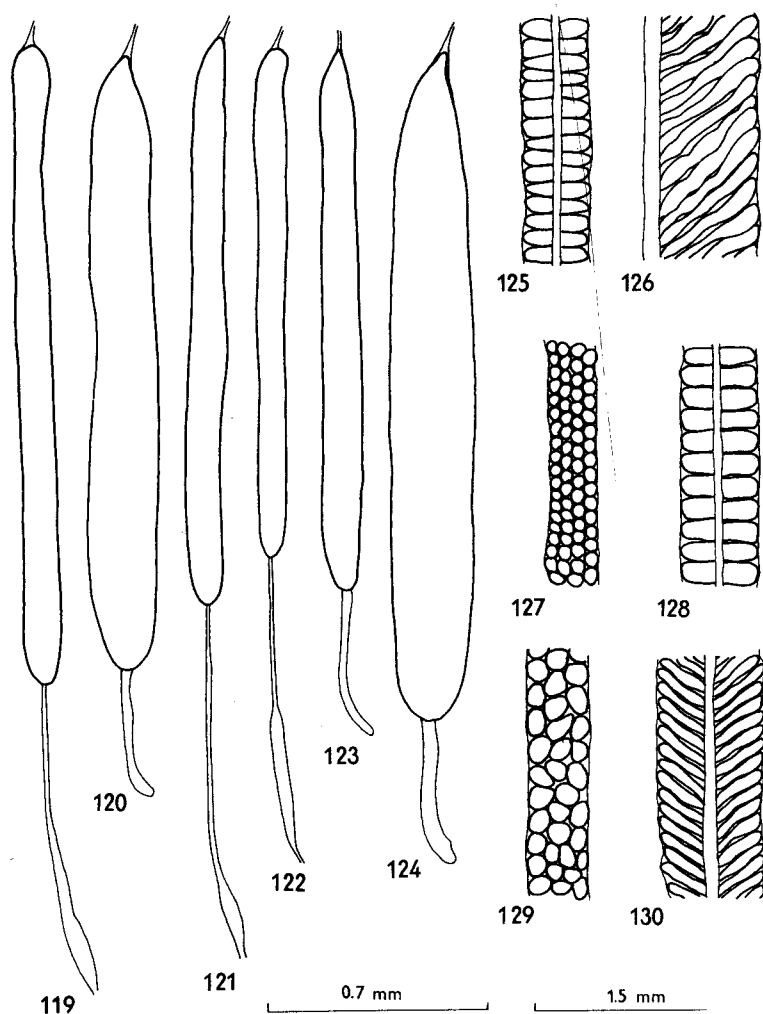
#### *Anepeorinae*

(Figs. 133, 134, 138, 142)

Testis: deposited laterally (Ac); I,II,III,IV,V,VI (Ba), cylindrical, bluntly pointed in thorax (Cb); testicular follicles equal in size, shortly cylindrical, arranged into regular longitudinal rows ( $Db_1$ ), perpendicular to VD (Ea); VS cylindrical, VD expanded suddenly (Fc), deposited in VIII and IX (Gb).

Ovary: deposited laterally (Hc); MTT, I,II,III,IV,V,VI (Jb), subcylindrical, slightly flattened, bluntly pointed in thorax (Kb); ovarioles slightly oblique to OL (La).

The subfamily *Anepeorinae* (only one Nearctic genus *Anepeorus*) does



Figs. 119-130:

Gonads of the family *Heptageniidae* (subfamily *Heptageniinae*). 119, 124, 126, 128, 129 - *Ecdyonurus venosus*. 121, 120, 125, 130 - *Heptagenia flava*. 122, 123, 127 - *Stenonema pudicum*. 119, 121, 122 - testis, dorsal view; 120, 123, 124 - ovary, dorsal view; 125, 127, 128, 129 - testis, detail of follicles (125, 128 - ventral, 127, 128 - dorsal view); 126, 130 - ovary, detail of ovarioles (126 - lateral, 130 - ventral view).

not substantially differ from the subfamily *Heptageniinae* in the arrangement of gonads, its scheme corresponds to that of primitive groups of genera.

#### *Arthropleinae*

(Figs. 132, 135, 140, 144)

Testis: deposited laterally (Ac); MTT, I,II,III,IV,V,VI (Ba); subcylindrical, slightly expanded and bluntly pointed in thorax (Cb); testicular follicles equal in size, arranged into regular longitudinal rows (Db<sub>1</sub>), perpendicular to VD (Ea); VS spindle-shaped (Fb), deposited in VII-IX (Ga).

Ovary: deposited laterally (Hc); MST, MTT, I,II,III,IV,V,VI (Jb); subcylindrical, moderately flattened, produced into a point in thorax; ovarioles relatively numerous, strongly oblique to OL (Lb).

The subfamily *Arthropleinae* (only one Holarctic genus *Arthroplea*) is well characterized by the arrangement of gonads. Its scheme apparently corresponds to that of the subfamily *Heptageniinae* (derived group of genera).

#### *Pseudironinae*

(Figs. 131, 136, 137, 139, 141, 143)

Testis: deposited dorsolaterally (Ab); MST, MTT, I,II,III,IV,V,VI (Bb), narrowly cylindrical, bluntly pointed in thorax (Cb), straight, not bent medially; testicular follicles different in size, arranged into irregular longitudinal rows (Da), large, nearly spherical, perpendicular to VD (Ea); VS formed by suddenly expanded VD (Fc), deposited in VIII-IX (Ga).

Ovary: deposited dorsolaterally (Hb), PT, MST, MTT, I,II,III,IV,V,VI (Jc), subcylindrical, produced into a point and narrow in thorax (Jc); ovarioles relatively numerous, short and cylindrical, perpendicular or slightly oblique to OL (La).

The subfamily *Pseudironinae* (only one Nearctic genus *Pseudiron*) is well characterized by the arrangement of gonads. However, its anatomical scheme is quite unique within the *Heptageniidae* and singles it out from remaining subfamilies. As far as the gonads are concerned this subfamily is closely related to the subfamilies *Siphonurinae* and *Acanthametropodinae* (*Siphonuridae*).

The family *Heptageniidae* comprises subfamilies with heterogeneous anatomical arrangement of gonads. The division into the following groups results from their schemes (monotypic Nearctic subfamily *Spinadinae* not investigated):

(a) *Heptageniinae* (two subgroups), *Anepeorinae*



(b) *Arthropleinae*

(c) *Pseudironinae*

As mentioned above the subfamilies *Anepeorinae* and *Arthropleinae* show apparent relationships to the *Heptageniinae*. The subfamily *Arthropleinae* apparently represents the most derived type within the *Heptageniidae* (Kb,Lb). On the other hand, the subfamily *Pseudironinae* occupies an isolated position within the family possessing very primitive characters (Ab,Da). These characters approach those to some subfamilies of the family *Siphonuridae*.

## *Ametropodidae*

### *Ametropodinae*

(Figs, 51, 53, 59, 61, 62)

Testis: deposited dorsolaterally (Ab), MTT, I,II,III,IV,V,VI (Ba), regularly cylindrical and very narrow, bluntly pointed or rounded in thorax (Cb); testicular follicles different in size, some of them spherical, arranged into a single longitudinal row (Da); VS cylindrical, VD expanded suddenly (Fc), deposited only in IX (Gc).

Ovary: deposited dorsolaterally (Hb); MST, MTT, I,II,III,IV,V,VI (Jb), subcylindrical, slightly bilaterally flattened, bluntly pointed in thorax (Kb); ovarioles large, straight or slightly bent, perpendicular to OL (La).

The subfamily *Ametropodinae* (a single genus *Ametropus*) is well characterized by the arrangement of gonads. It differs from following subfamily especially in position of both testes and ovaries (Ab, Hb).

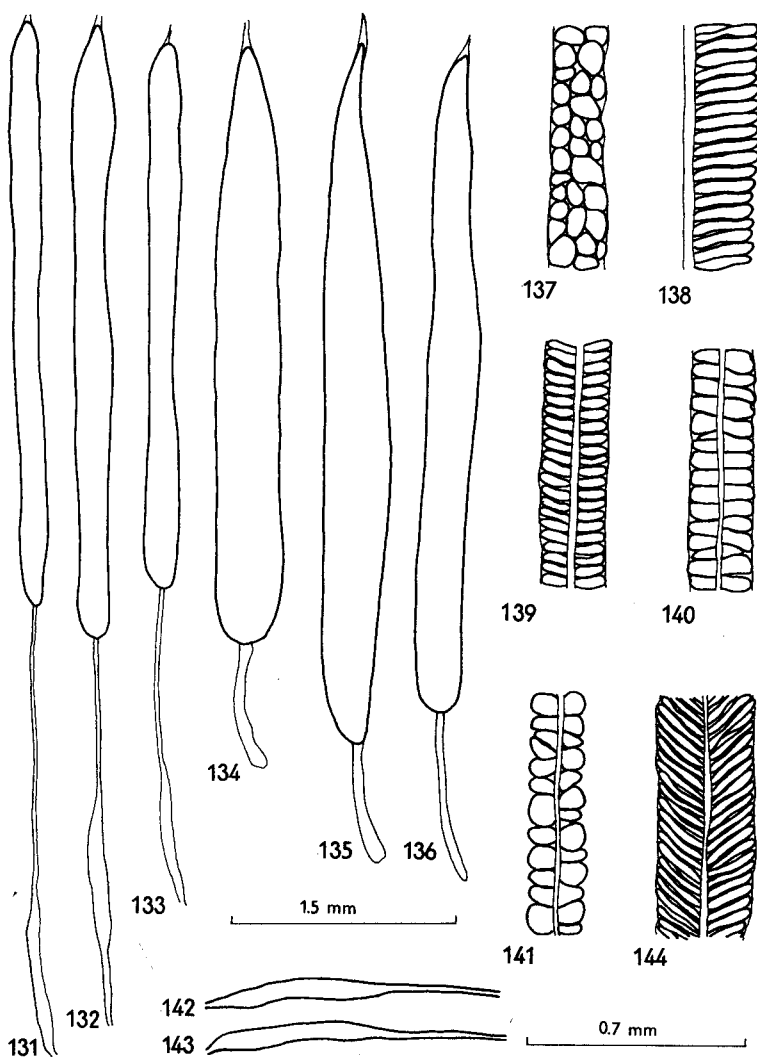
### *Metretopodinae*

(Figs. 54, 55, 57, 60, 63)

Testis: deposited dorsally (Aa); MTT, I,II,III,IV,V,VI (Ba); regularly cylindrical, slightly bent medially, bluntly pointed in thorax (Ca); testicular follicles different in size (the differences very inconspicuous), arranged into nearly regular longitudinal rows (Da), relatively short and cylindrical, perpendicular to VD (Ea); VS formed by suddenly expanded VD, cylindrical (Fc), deposited in IX (Gc).

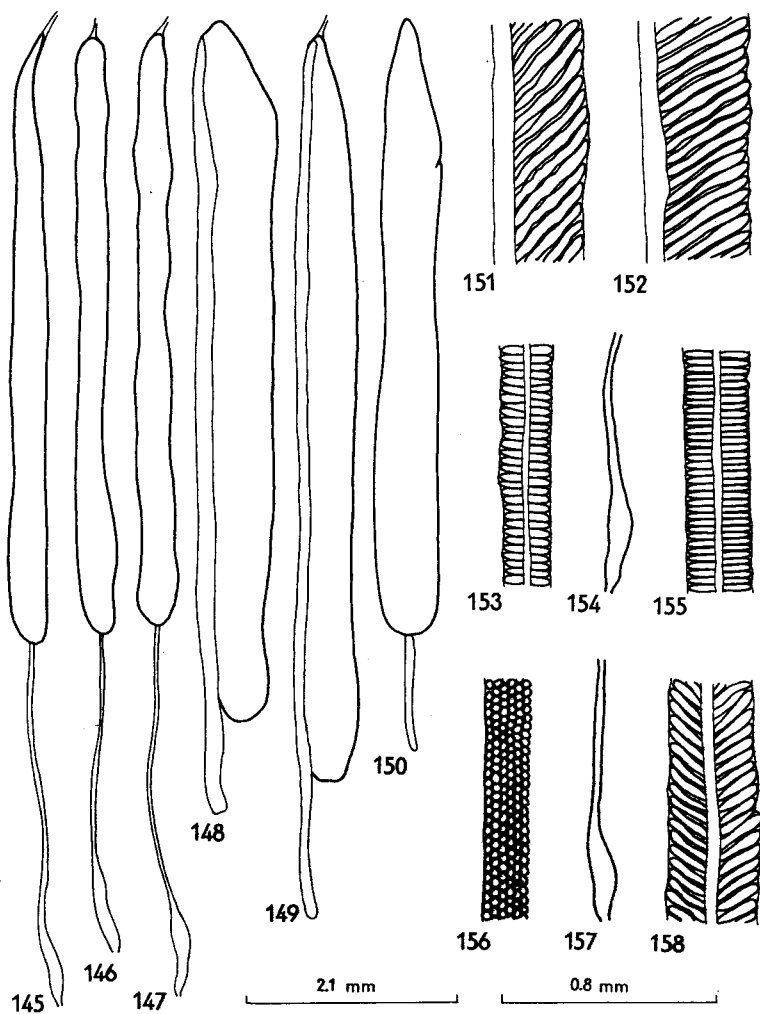
Ovary: deposited dorsally (Ha); MST, MTT, I,II,III,IV,V, VI (Jb); cylindrical, not flattened, moderately bent medially in III and IV, bluntly pointed in thorax (Ka); ovarioles relatively numerous, perpendicular to OL (La).

The subfamily *Metretopodinae* markedly differs from the *Ametropodinae* in several respects, namely in position of gonads and in their shape (Aa, Ha, Ca, Ka).



Figs. 131-144:

Gonads of the family Heptageniidae (subfamilies Arthropleinae, Anepeorinae, Pseudironinae). 131, 136, 137, 139, 141, 143 - *Pseudiron meridionalis*. 132, 135, 140, 144 - *Arthroplea congener*. 133, 134, 138, 142 - *Anepeorus* sp. 131-133 - testis, dorsal view; 134-136 - ovary, dorsal view; 137, 140, 141 - testis, detail of follicles (137, 141 - dorsal, 140 - ventral view); 138, 144 - ovary, detail of ovarioles (138 - lateral, 144 - ventral view); 142, 143 - seminal vesicle, detail.



Figs. 145-158:

Gonads of the family *Leptophlebiidae*. 145, 148, 152, 155 - *Atalomicria* sp. 146, 150, 158 - *Leptophlebia marginata*. 147, 149, 151, 153, 154, 157 - *Kirrara* sp. 145-147 - testis, dorsal view; 148, 149 - ovary, lateral view; 150 - ovary, dorsal view; 151, 152, 158 - ovary, detail of ovarioles (151, 152 - lateral, 158 - ventral view); 153, 155, 156 - testis, detail of follicles (153, 155 - ventral, 156 - dorsal view); 154, 157 - seminal vesicle, detail.

The family *Ametropodinae* includes very heterogeneous groups. While the subfamily *Metretopodinae* is nearly identical with the subfamily *Siphonurinae* in the arrangement of gonads, the subfamily *Ametropodinae* differs in position of gonads (Ab, Hb). However, there are certain elements of affinity with the subfamily *Siphonurinae* (*Siphonuridae*) as well (size of testicular follicles, Da). The genus *Ametropus* seems to possess the most plesiomorphic arrangement of testis within the *Ephemeroptera* (only a single row of follicles).

## *Leptophlebiidae*

### *Leptophlebiinae*

(Figs. 145-173)

The genera of the family may be divided into several groups resulting from their arrangement of gonads:

*Atalomicria*, *Atalophlebia*, *Atalophlebioides*, *Jappa*:

Testis: deposited laterally (Ac); I,II,III,IV,V,VI (Ba); regularly cylindrical, rounded or bluntly pointed in I-II (Cb); testicular follicles equal in size (in some specimens there are apparent differences in size of follicles - *Jappa*, *Atalophlebia*), cylindrical, arranged into regular longitudinal rows ( $Db_1$ ), perpendicular to VD (Ea); VS spindle shaped (Fb) or inconspicuous (*Atalomicria*)(Fa), deposited in VIII-IX (Gb).

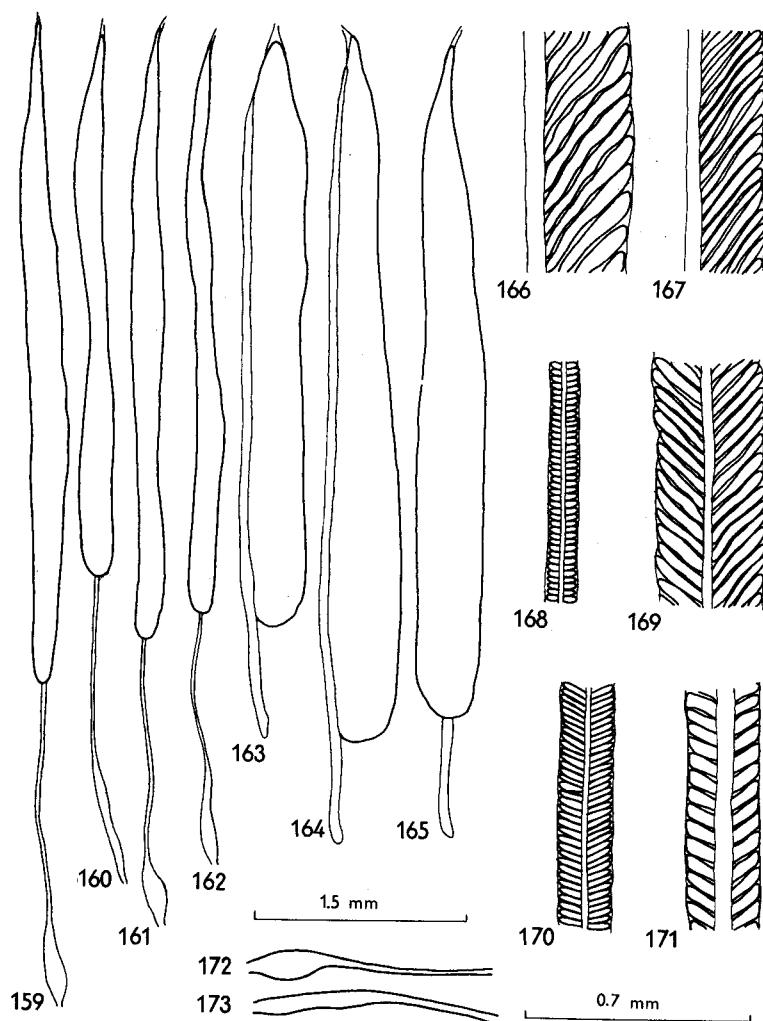
Ovary: deposited laterally (Hc); MTT, I,II,III,IV,V,VI (Ja), cylindrical, slightly bilaterally flattened, bluntly pointed or rounded in thorax (Kb); ovarioles perpendicular (*Atalophlebia*) or slightly oblique to OL (La).

*Leptophlebia*, *Paraleptophlebia*, *Habrophlebia*, *Habroleptooides*:

Testis: deposited laterally (Ac); MTT, I,II,III,IV,V,VI (Ba); cylindrical or subcylindrical, produced into a point in thorax and in I (Cb); testicular follicles cylindrical, equal in size and length, arranged in regular longitudinal rows ( $Db_1$ ), usually slightly oblique to VD (Eb); VS cylindrical (Fc) or short and rounded (Fd), deposited in VIII-IX or only in IX (Gb, Gc).

Ovary: deposited laterally (Hc); MST, MTT, I,II,III,IV,V,VI (Jb); subcylindrical, bilaterally flattened, produced into a point in thorax (Kc); ovarioles relatively more numerous and smaller, apparently oblique to OL (Lb).

The genus *Paraleptophlebia* deviates from this scheme. In some species testes are produced to MST and ovaries to PT (Bc, Jc).



**Figs. 159-173:**

Gonads of the family *Leptophlebiidae*. 159, 164, 166, 170 - *Traverella* sp. 160 - *Paraleptophlebia cincta*. 163, 167, 171, 173 - *Paraleptophlebia guttata*. 161, 165, 169, 172 - *Choroterpes* (*Choroterpes*) *picteti*. 162, 168 - *Habrophlebia lauta*. 159-162 - testis, dorsal view; 163, 164 - ovary, lateral view; 165 - ovary, dorsal view; 166, 167, 169, 171 - ovary, detail of ovarioles (166, 167 - lateral, 169, 171 - ventral view); 172, 173 - seminal vesicle, detail.

*Choroterpes* (subgenera *Choroterpes* and *Euthraulus*), *Thraulus*, *Traverella*, *Hagenulus*:

Testis: deposited laterally (Ac); PT, MST, MTT, I,II,III,IV,V,VI (Jc); cylindrical and usually bilaterally flattened, pointed or bluntly pointed in thorax (Cc); testicular follicles numerous, small, equal in length, arranged into regular longitudinal rows, perpendicular or slightly oblique to VD (Ea, Eb); VS usually short and rounded (Fd), deposited in VIII and IX (Gc).

Ovary: deposited laterally (Hc); PT, MST, MTT, I,II,III,IV,V,VI (Jc); subcylindrical, produced into a point in thorax and strongly bilaterally flattened (Kc); ovarioles small, numerous and strongly oblique to OL (Lb).

In Oriental genera *Choroterpes* and *Thraulus* the gonads need not be produced to thorax; they usually extend from I (II) to VI or VII.

The family *Leptophlebiidae* is extremely numerous (more than 70 genera described so far) with a lot of genera extraordinarily adapted to various types of habitats. The above three groups as recognized according to the arrangement of gonads evidently correspond to the evolutionary tendencies of the family. Some genera (*Kirrara*, *Kimminsula*) occupy a place in the middle between the above groups. In spite of difference between the first and the third group which are very remarkable, the generic affinity of the *Leptophlebiidae* is evident, and hence this family may be considered a natural one. The first group of genera (Australian genera *Atalophlebia*, *Atalophlebioides*, *Atalomieria*, and *Jappa*) is more plesiomorphic, the third group (*Choroterpes*, *Thraulus*, *Hagenulus*, *Traverella*) is evidently derived in arrangement of the internal reproductive system.

## *Ephemerellidae*

### *Ephemerellinae*

(Figs. 174-202)

The genera of the family *Ephemerellidae* may be divided into three groups, as follows:

(a) *Ephemerella* (subgenera *Attenella* and *Timpanoga*):

Testis: deposited laterally, in thorax dorsolaterally (Ac); (MST), MTT, I,II,III,IV,V, (VI) (Bd); cylindrical, bluntly pointed in thorax; testicular follicles considerably large, slightly different in size, arranged into irregular longitudinal rows (only a single row of follicles in thorax)(Da); perpendicular to VD (Ea); VS formed by suddenly expanded VD, cylindrical (Fc), deposited in VII-IX (*Timpanoga*) (Ga) or VIII-IX (*Attenella*)(Gb).

Ovary: deposited laterally, in thorax dorsally or dorsolaterally (Ac); MST,MTT, I,II,III,IV,V (VI) (Jb); subcylindrical, slightly flattened, bluntly pointed in thorax (Kb); ovarioles perpendicular or slightly oblique to VD (La).

(b) *Ephemerella* (subgenera *Drunella*, *Eurylophella*):

Testis: deposited laterally (Ac); PT,MST,MTT, I,II,III,IV,V (Bc); widely cylindrical, nearly rounded in thorax (Cb); testicular follicles equal in size and length, large, nearly spherical, arranged into regular longitudinal rows ( $Db_1$ ), perpendicular to VD (Ea); VS formed by VD expanded gradually, deposited in VIII-IX (Fb, Gb).

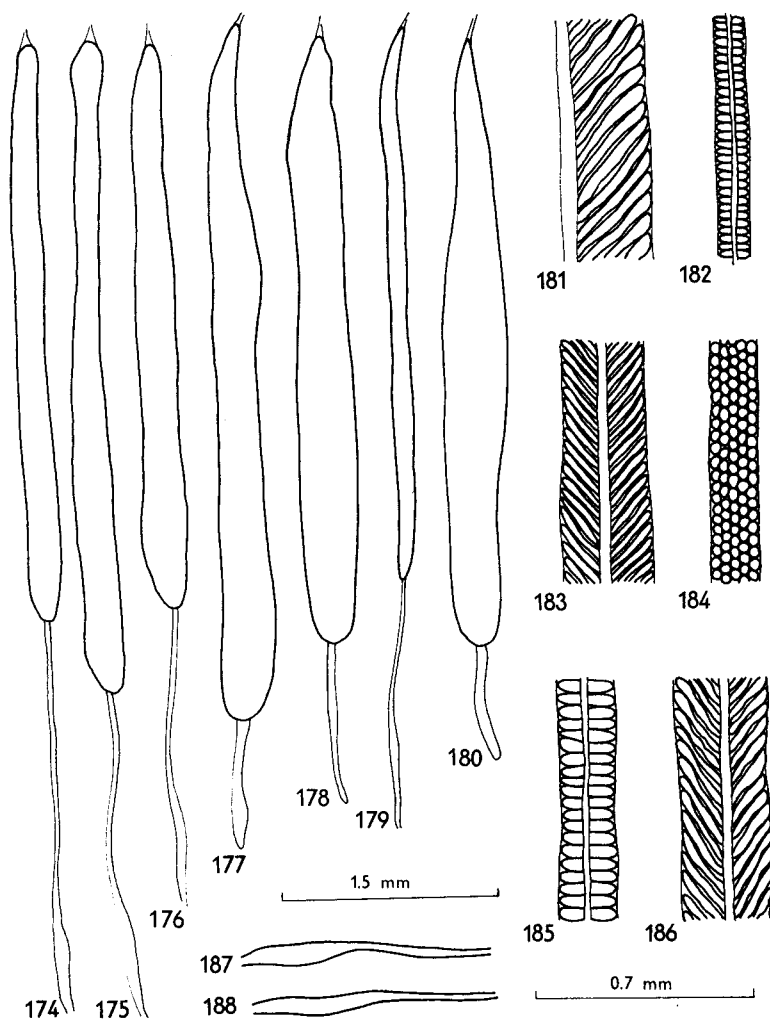
Ovary: deposited laterally (Hc); PT,MST,MTT, I,II,III,IV,V (Jd); cylindrical, slightly bilaterally flattened, bluntly pointed in thorax (Kb); ovarioles large, slightly oblique to OL (La).

(c) *Ephemerella* (subgenera *Ephemerella*, *Torleya*, *Chitonophora*), *Ephemerellina*, *Teloganodes*:

Testis: deposited laterally (Ac); MST (*Teloganodes*), MTT, I,II,III,IV,V,VI (Ba), cylindrical, straight, pointed or bluntly pointed in thorax (Cb); testicular follicles equal in length, smaller and relatively numerous, arranged into regular longitudinal rows ( $Db_2$ ); perpendicular to VD (Ea); VS formed by gradually expanded VD (Fb) or very inconspicuous (*Teloganodes*)(Fa), deposited in VII-IX (*Teloganodes*) or in VIII-IX (Gb).

Ovary: deposited laterally (Hc); (PT), MST, MTT, I,II,III,IV,V,VI (Jb) subcylindrical, bilaterally flattened (Kb); ovarioles numerous, slightly oblique (*Ephemerellina*)(La) or oblique to OL (Lb).

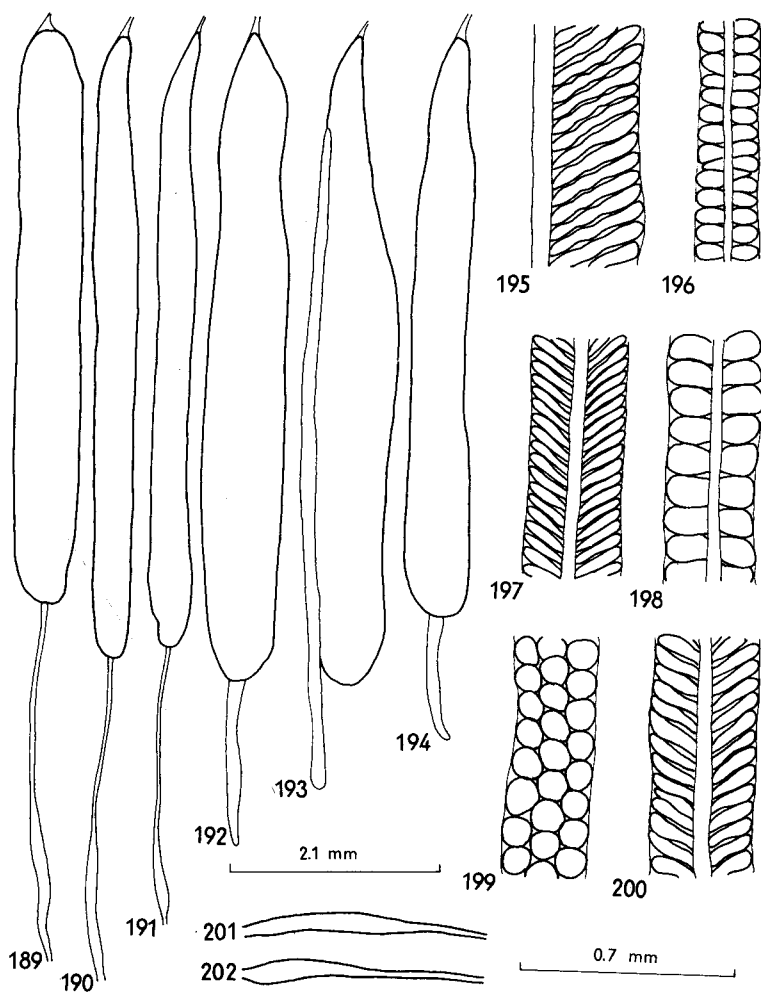
The group (a) represents the most plesiomorphic types within the family. The gonads of subgenera *Timpanoga* and *Attenella* may be derived directly from the anatomical scheme of primitive families (follicles different in size, Da; gonads deposited dorsolaterally or even dorsally in thorax). On the other hand, there are several derived characters (Bd, Jb) which unite this group with the following groups. The group (b) is characterized by the shift of gonads forward (Bc, Jd) and by relatively large follicles ( $Db_1$ ) showing distinct relationships to the group (a). The group (c) represents the most derived types within the family possessing some highly derived characters in the arrangement of their gonads (Cb,  $Db_2$ ). Despite of the differences among the above three groups, the family *Ephemerellidae* undoubtedly represents evolutionarily homogeneous group. Between the groups (a) and (b) there are intermediate forms in arrangement of gonads and between the groups (b) and (c) there



Figs. 174-188:

Gonads of the family Ephemerellidae. 174, 178, 186, 187 - *Ephemerellina picta*. 175, 185, 188, 177, 183 - *Ephemerella (Eurylophella) trilineata*. 176, 180, 181, 184 - *Ephemerella (Torleya) major*. 179, 182 - *Teloganodes* sp. 174-176, 179 - testis, dorsal view; 177, 178, 180 - ovary, dorsal view; 181, 183, 186 - ovary, detail of ovarioles, (181 - lateral, 183, 186 - ventral view); 182, 184, 185 - testis, detail of follicles (182, 185 - ventral, 184 - dorsal view); 187, 188 - seminal vesicle, detail.





Figs. 189-202:

Gonads of the family Ephemerellidae. 189,193,195,198,199 - *Ephemerella (Drunella) conestee*. 190,192,196,200,201 - *Ephemerella (Timpanoga) hecuba*. 191,194,197,202 - *Ephemerella (Ephemerella) inermis*. 189-191 - testis, dorsal view; 192,194 - ovary, dorsal view; 193 - ovary, lateral view; 195,197,200 - ovary, detail of ovarioles (195 - lateral, 197,200 - ventral view); 196,198,199 - testis, detail of follicles (196, 198 - ventral, 199 - lateral view); 201,202 - seminal vesicle, detail.

are such types as well (*Ephemerella* - subgenus *Cincticostella*: Db<sub>1</sub>, Ba, Jb). The family *Ephemerellidae* shows certain relationships to both families with dorsolateral and lateral position of gonads (*Heptageniidae*, *Leptophlebiidae*, *Tricorythidae*) having unstable and widely fluctuating characters. No data are known about the Neotropical subfamily *Melanemerellinae*.

## *Tricorythidae*

### *Tricorythinae*

(Figs. 205, 208, 213, 217)

Testis: deposited laterally (Ac), MST, MTT, I, II, III, IV, V, VI (Bb); narrowly cylindrical, bluntly pointed or pointed in thorax (Cb); testicular follicles minute, equal in length, arranged into regular longitudinal rows (Db<sub>2</sub>); slightly oblique to VD (Eb); VS inconspicuous, VD expanded gradually (Fa), deposited in VIII-IX (Gb).

Ovary: deposited laterally (Hc), (PT), MST, MTT, I, II, III, IV, V, VI (Jc), cylindrical, slightly bilaterally flattened, produced into a point in thorax (Kb); ovarioles numerous, straight, slightly oblique to OL (La).

The subfamily *Tricorythinae* is well characterized by the anatomical arrangement of gonads. Contrary to the remaining subfamilies, the gonads are considerably shifted forward, in *Tricorythus* the ovaries may be produced even to head.

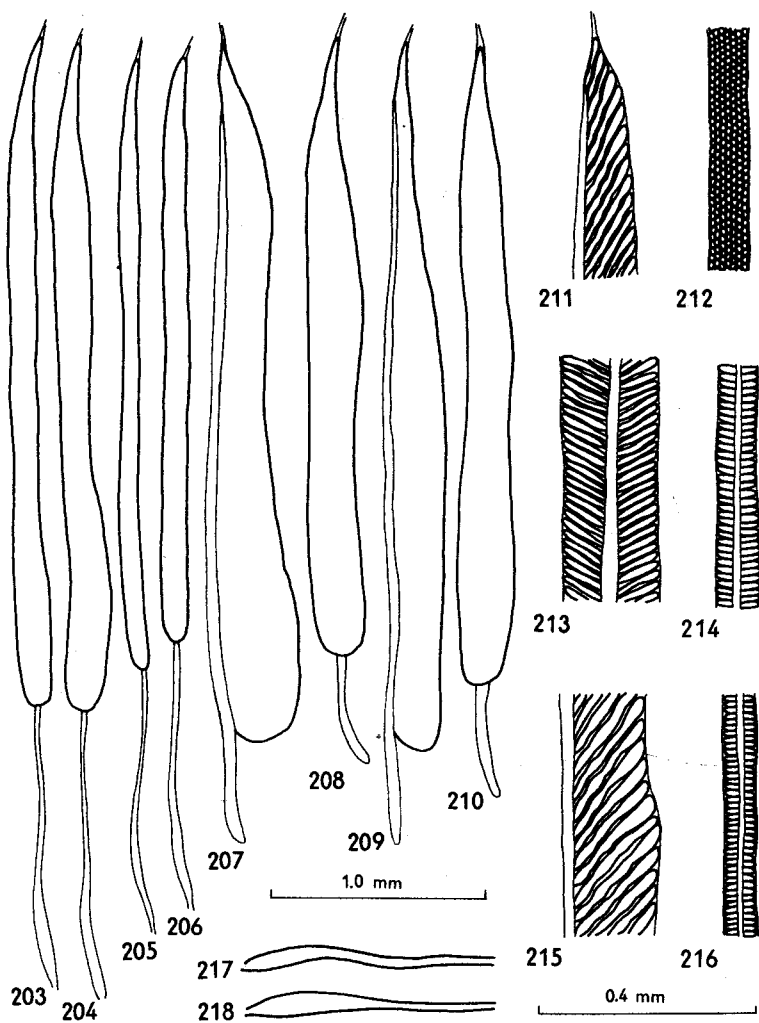
### *Leptohyphinae*

(Figs. 206, 210, 216)

Testis: deposited laterally (Ac); MTT, I, II, III, IV, V, VI (Ba); narrowly cylindrical, produced into a point in thorax (Cb); testicular follicles small, equal in size, arranged into regular longitudinal rows (Db<sub>2</sub>); perpendicular or slightly oblique to VD *Tricorythodes* (Ea, Eb); VS formed by gradually expanded (Fa), deposited in VII-IX (Ca).

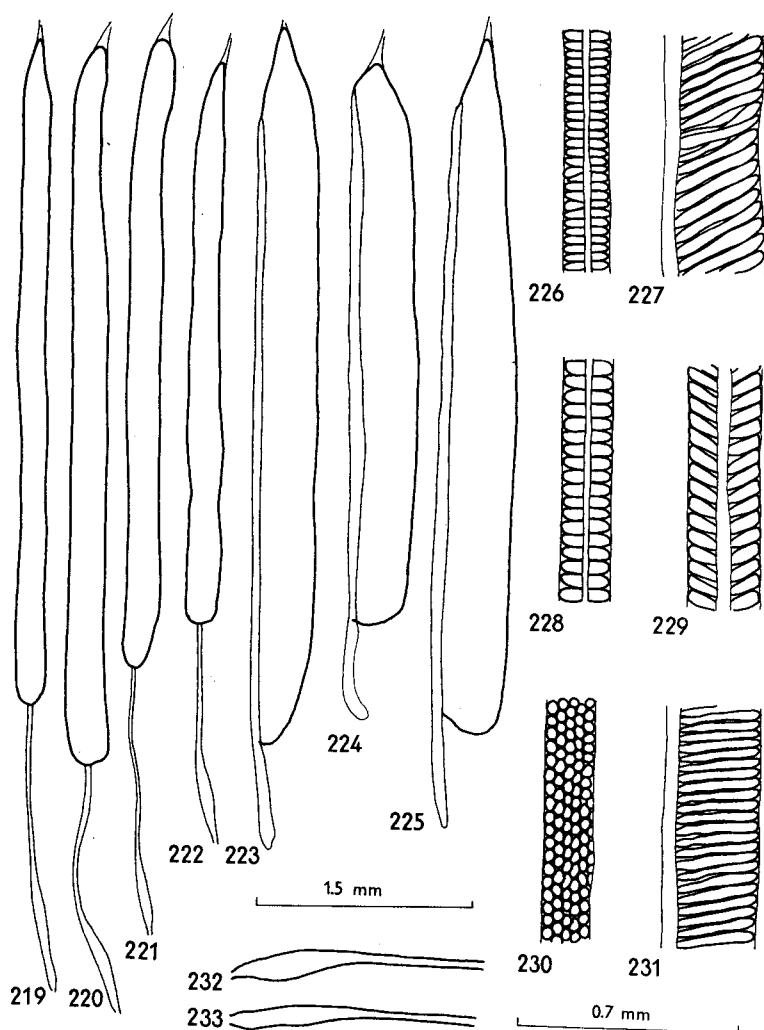
Ovary: deposited laterally (Hc); MST, MTT, I, II, III, IV, V, VI (Jb); subcylindrical, bilaterally flattened, produced into a point in thorax (Kb); ovarioles larger, straight, oblique to OL (Lb).

Subfamily homogeneous; the Neotropical genera *Leptohyphes* and *Leptohyphodes* slightly deviate from the anatomical scheme of subfamily having VS deposited in VIII-IX (Gb). This subfamily manifests relationships to remaining subfamilies of the *Tricorythidae* especially to subfamily *Dicercomyzinae*.



Figs. 203-218:

Gonads of the families *Caenidae* and *Tricorythidae* (subfamilies *Tricorythinae*, *Leptohyphinae*, *Dicercomyzinae*). 203,209,214,215,218 - *Caenis* sp. 204,207,211,212 - *Brachycercus harrisella*. 205,208,213,217 - *Tricorythus* sp. 206,210 - *Tricorythodes albalineatus*. 216 - *Dicercomyzon* sp. 203-207 - testis, dorsal view; 207,209 - ovary, lateral view; 208, 210 - ovary, dorsal view; 211,213,215 - ovary,detail of ovarioles (211, 215 - lateral, 213 -ventral view); 212,214,216 - testis, detail of follicles (212 - dorsal,214,216 - lateral view);217,218 - seminal vesicle, detail.



Figs. 219-233:

Gonads of the families Potamanthidae and Polymitarciidae. 219, 223, 227, 229, 233 - *Potamanthus luteus*. 220, 228 - *Rhoenathopsis* sp. 221, 225, 230 - *Ephoron virgo*. 222, 224, 231, 232 - *Asthenopus* sp. 226 - *Campsurus* sp. (Brasil). 219-222 - testis, dorsal view; 223-225 - ovary, lateral view; 226, 228, 230 - testis, detail of follicles (226, 228 - ventral, 230 - dorsal view); 227, 229, 231 - ovary, detail of ovarioles (227, 231 - lateral, 229 - ventral view); 232, 233 - seminal vesicle, detail.

### *Dicercomyzinae*

(Fig. 216)

Testis: deposited laterally (Ac); MTT, I,II,III,IV,V,VI (Ba); cylindrical, bluntly pointed in thorax, straight (Cb); testicular follicles very minute, equal in size, arranged in regular longitudinal rows (Db<sub>2</sub>), perpendicular to VD (Ea); VS inconspicuous, formed by gradually expanded VD (Fa), deposited in VIII-IX (Gb).

Ovary: not investigated.

Although the lacking material of female larvae made the study of gonads of the subfamily *Dicercomyzinae* incomplete, it is evident that this subfamily seems to be more related to the subfamily *Leptohyphinae* especially as far as the position of testes is concerned.

The family *Tricorythidae* (the remaining Ethiopian subfamilies *Madadorhythinae* and *Ethemerythinae* not investigated) comprises two rather heterogeneous groups. While the subfamilies *Leptohyphinae* and *Dicercomyzinae* seem to be related to the family *Ephemerellidae* (apomorphic group of genera), the subfamily *Tricorythinae* shows closer affinities to the families *Caenidae* and *Neophemeridae* (gonads in prothorax, follicles and ovarioles multiplied).

## *Behningiidae*

### *Behningiinae*

(Figs. 246, 247, 250, 258, 260)

Testis: deposited laterally (Ac); I,II,III,IV,V,VI (Ba), cylindrical, straight, rounded or bluntly pointed in thorax (Cd), slightly bilaterally flattened; testicular follicles equal in size, arranged into regular longitudinal rows (Db<sub>1</sub>), perpendicular to VD (Ea); VS inconspicuous, VD gradually expanded (Fa), deposited in VII-IX or VIII-IX (Ga, Gb).

Ovary: deposited laterally (Hc); (MTT), I,II,III,IV,V,VI (Jb) subcylindrical or tongue-shaped, bilaterally flattened, bluntly pointed or rounded (Kc); ovarioles relatively large and short, straight, slightly oblique or perpendicular to VD (La); probably only a single oocyte matures in vitellarium of ovariole.

The family *Behningiidae* is well characterized by the arrangement of gonads. Its anatomical scheme shows certain elements of affinity with families of the superfamily *Ephemeroidea* but *Behningiidae* differs markedly in position of both testes and ovaries (Ac,Hc). There are also some elements of affinity with the families *Leptophlebiidae* and *Potamanthidae*.

## *Potamanthidae*

### *Potamanthinae*

(Figs. 219, 220, 223, 227, 229, 233)

Testis: deposited laterally (Ac); MTT, I, II, III, IV, V, VI (Ba); cylindrical, moderately flattened, bluntly pointed in thorax (Cd) or rounded (*Rhoenanthopsis*); testicular follicles equal in length and size, arranged into regular longitudinal rows ( $Db_1$ ), perpendicular to VD (Ea); VS formed by suddenly expanded VD (Fc), deposited in VIII-IX (Gb).

Ovary: deposited laterally (Hc); MST, MTT, I, II, III, IV, V, VI (Jb); tongue-shaped, bilaterally flattened, pointed or bluntly pointed in thorax (Kc); ovarioles strong, slightly or moderately oblique to OL (La).

The Oriental genus *Rhoenanthopsis* and some species of the Holarctic genus *Potamanthus* deviate from the anatomical scheme of family (ovaries are produced to MST or slightly to PT). The gonads of the *Potamanthidae* show certain relationships to those of the *Leptophlebiidae* and *Ephemeridae* differing from the latter in lateral position of both testes and ovaries (Ac, Hc).

## *Ephemeridae*

### *Ephemerinae*

(Figs. 235, 239, 241, 242, 240)

The genera of the family *Ephemeridae* may be divided into two groups:

The group (a) consists of the genus *Ephemera*:

Testis: deposited ventrolaterally (Ad) MTT, I, II, III, IV, V, VI (Ba); cylindrical, moderately bilaterally flattened, rounded or bluntly pointed in thorax (Cd); testicular follicles equal in size, cylindrical, arranged into regular longitudinal rows ( $Db_1$ ), perpendicular to VD (Ea); VS subcylindrical or spindle-shaped, VD expanded gradually (Fb), deposited in VIII-IX (Gb).

Ovary: deposited ventrolaterally (Hd); (MST), MTT, I, II, III, IV, V, VI (Jb), tongue-shaped, bilaterally flattened, bluntly pointed in thorax (Kc); ovarioles moderately oblique to OL (La).

The group (b) includes the genera *Hexagenia*, *Litobrantha* and *Pentagenia*:

Testis: deposited ventrolaterally (Ad) MST, MTT, I, II, III, IV, V, VI (Bb), subcylindrical, slightly flattened, produced into a point in thorax (Cd); testicular follicles relatively numerous, equal in size, arranged into regular longitudinal rows ( $Db_1$ ), at the right angle to VD (Ea); VS as in *Ephemera* (Fb, Gb).

Ovary: deposited ventrolaterally (Hd); (PT), MST,MTT, I,II,III,IV, V,VI (Jb), tongue-shaped, considerably bilaterally flattened, produced into a point in thorax (Kc); ovarioles numerous, oblique or strongly oblique to OL (Lb).

In spite of different characters of the above two groups of genera, the family *Ephemeridae* may be considered evolutionarily homogeneous. The group (a) is more plesiomorphic (probably including the New Zealand genus *Ichthybotus* as well) manifesting a relationship to the families *Potamanthidae*, *Euthyplociidae* and *Palingeniidae*. The group (b) is more derived having some apomorphic characters (Bb, Jb, Lb) and showing certain relationships to the other families of the superfamily *Ephemeroides* (especially to the *Palingeniidae*).

## *Euthyplociidae*

*Euthyplociinae*

(Figs. 234, 238, 243)

Testis:deposited ventrolaterally (Ad), I,II,III,IV,V,VI (Ba); sub-cylindrical,slightly flattened,rounded or bluntly pointed (*Euthyplocia*) in I (Cd); testicular follicles shortly cylindrical, equal in size, in regular longitudinal rows ( $Db_1$ ); VS formed by gradually expanded VD (Fb), deposited in VIII-IX (Gb).

Ovary: deposited ventrolaterally (Hd); I,II,III,IV,V,VI (Ja); tongue-shaped, flattened, bluntly pointed in I and II (Kc); ovarioles slightly oblique to OL (La).

Subfamily quite homogeneous, well characterized by its anatomical scheme, manifesting certain relationships to the family *Polymitarcidae* or *Ephemeridae* and *Palingeniidae* respectively. The Neotropical genus *Campylocia* deviates from the scheme (ovaries in MTT: Jb).

## *Polymitarcidae*

*Polymitarcinae*

(Figs. 221, 225, 230)

Testis: deposited ventrolaterally (Ad);MTT, I,II,III,IV,V,VI (Ba); subcylindrical, moderately flattened, bluntly pointed or pointed in thorax (Cd); testicular follicles cylindrical, equal in length,arranged into regular longitudinal rows ( $Db_1$ ),perpendicular to VD (Ea);VS formed by gradually expanded VD (Fb), deposited in VIII-IX (Gb).

Ovary: deposited ventrolaterally (Hd); (MST),MTT, I,II,III,IV,V,VI (Jb); tongue-shaped, bilaterally flattened, produced and pointed in thorax (Kc); ovarioles straight, nearly perpendicular to OL (La).

The subfamily *Polymitarceinae* is well characterized by the arrangement of gonads. Some species of a single genus *Ephoron* deviate from the anatomical scheme having testes deposited only in abdomen (*E. virgo*: Ba) or ovaries in MST (Jc).

#### *Asthenopodinae*

(Figs. 222, 224, 231, 232)

Testis: deposited ventrolaterally (Ad); I,II,III,IV,V,VI (Ba) subcylindrical, slightly flattened, bluntly pointed in I and II (Cd); testicular follicles numerous, equal in size and length, arranged into regular longitudinal rows ( $Db_1$ ), perpendicular to VD (Ea); VS cylindrical, formed by suddenly expanded VD (Fc), deposited in VIII-IX (Gb).

Ovary: deposited ventrolaterally (Hd), I,II,III,IV,V,VI (Ja); tongue-shaped, bilaterally flattened, bluntly pointed in I and II (Kc); ovarioles nearly perpendicular to OL (La).

The subfamily *Asthenopodinae* is characterized mainly by the position of both testes and ovaries deposited only in abdominal segments (Ba, Ja). This character approach that to the family *Euthyplociidae* but there are also close relationships to the remaining subfamilies of the *Polymitarceidae* especially to the *Campsurinae*.

#### *Campsurinae*

(Fig. 226)

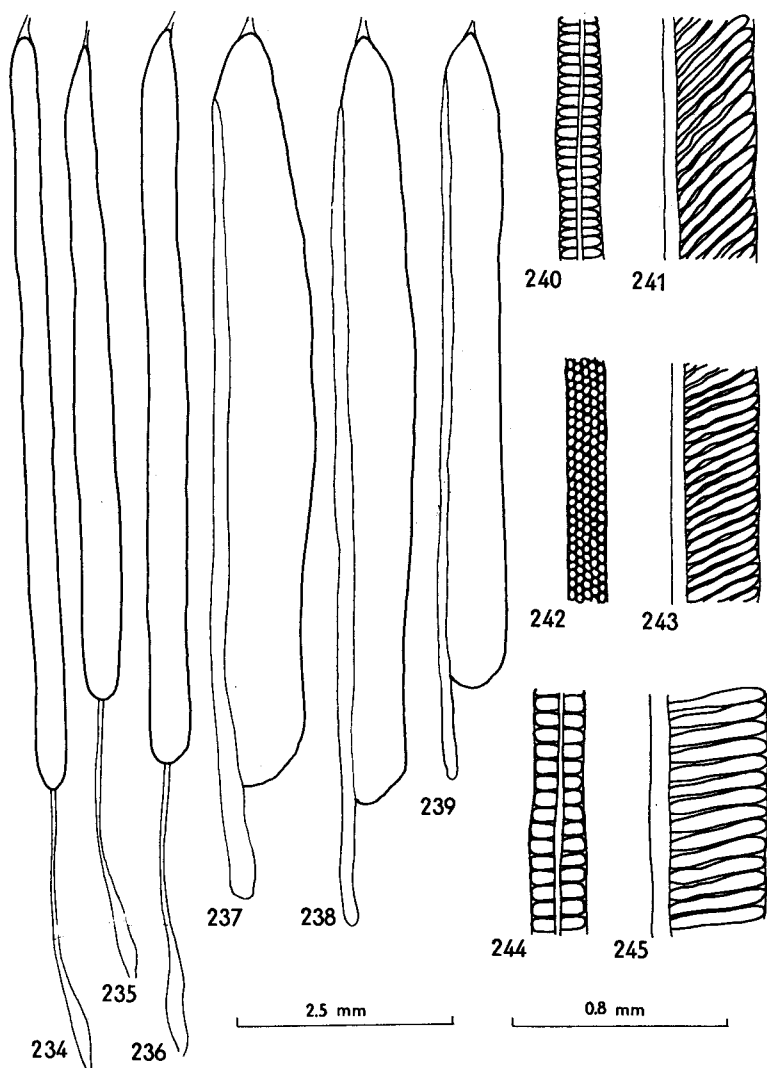
Testis: deposited ventrolaterally (Ad); I,II,III,IV,V,VI (Ba); cylindrical, bilaterally flattened, bluntly pointed in I and II (Cd); testicular follicles small and relatively numerous, arranged into regular longitudinal rows ( $Db_1$ ), deposited at the right angle, at apex slightly obliquely (Ea, Eb); VS same as in the subfamily *Asthenopodinae*.

Ovary: deposited ventrolaterally (Hd); I,II,III,IV,V,VI (Ja); tongue-shaped, strongly flattened, rounded in I and II (Kc); ovarioles smaller, slightly bent, moderately oblique to OL (La).

The subfamily *Campsurinae* is well characterized by the arrangement of gonads showing close affinity to the subfamily *Asthenopodinae*.

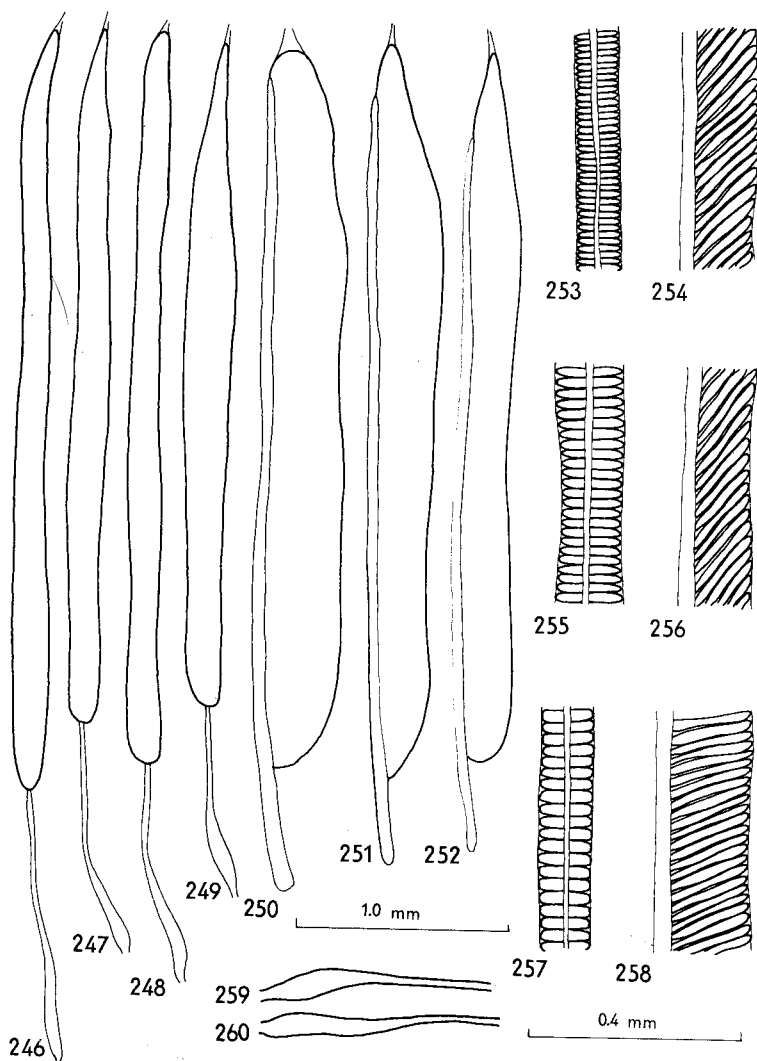
The family *Polymitarceidae* includes two closely related groups of subfamilies. The first group consists of the subfamily *Polymitarceinae* (gonads in thorax), the second one of the subfamilies *Asthenopodinae* and *Campsurinae*. These differences undoubtedly correspond to the evolutionary tendencies of this group of families (*Ephemeroidea*) and the family is quite homogeneous. It shows affinities to both *Euthyplociidae* and *Palingeniidae*.





Figs. 234-245:

Gonads of the families Euthyplociidae, Palingeniidae and Ephemeridae. 234, 238, 243 - *Campylocia* sp. 235, 239, 240, 241 - *Ephemera vulgata*. 242 - *Hexagenia limbata*. 236, 237, 244, 245 - *Palingenia fuliginosa*. 234-236 - testis, dorsal view; 237-239 - ovary, lateral view; 240, 242, 244 - testis, detail of follicles (240, 244 - ventral, 242 - dorsal view).



Figs. 246-260:

Gonads of the families *Neophemeridae*, *Behningiidae*, *Baetiscidae* and *Prosopistomatidae*. 260, 246, 257 - *Behningia ulmeri*. 247, 250, 258 - *Dolania americana*. 248, 251 - *Potamanthellus* sp. 249, 252, 255, 256, 259 - *Baetisca rogersi*. 253, 254 - *Prosopistoma foliaceum*. 246-249 - testis, dorsal view; 250-252 - ovary, lateral view; 253, 255, 257 - testis, detail of follicles, ventral view. 254, 256, 258 - ovary, lateral view, detail of ovarioles. 259, 260 - seminal vesicle, detail.

## *Palingeniidae*

### *Palingeniinae*

(Figs. 236, 237, 244, 246)

Testis: deposited ventrolaterally (Ad); I,II,III,IV,V,VI (Ba); cylindrical, moderately flattened (Cd); testicular follicles cylindrical, equal in size, arranged into regular longitudinal rows ( $Db_1$ ), perpendicular to VD (Ea); VS cylindrical (Fb), deposited in VIII-IX (Gb).

Ovary: deposited ventrolaterally (Hd), MTT, I,II,III,IV,V,VI (Jb); tongue-shaped, strongly flattened (Kc), bluntly pointed or rounded in thorax; ovarioles strong, cylindrical, slightly bent and slightly oblique to OL (La).

Family quite homogeneous; well characterized by the arrangement of gonads. The family *Palingeniidae* (only two genera investigated) seems to show certain affinity to the *Polymitarceidae* and *Euthyplocidae* and also to the family *Ephemeridae*.

## *Neophemeridae*

### *Neophemerinae*

(Figs. 248, 251)

Testis: deposited laterally (Ac); PT, MST, MTT, I,II,III,IV,V,VI (Bb); cylindrical, only slightly bilaterally flattened, rounded (*Potamanthellus*) or pointed (*Neophemera*) in thorax (Cb); testicular follicles minute, elongated and cylindrical, equal in size and length, arranged into regular longitudinal rows ( $Db_2$ ); perpendicular to VD (Ea); VS inconspicuous, formed by gradually expanded VD (Fa), deposited in VII-IX (*Potamanthellus*) (Ga) or in VIII-IX (*Neophemera*) (Gb).

Ovary: deposited laterally (Hc); PT, MST, MTT, I,II,III,IV,V,VI (Jc), moderately bilaterally flattened, produced and bluntly pointed in thorax (Kc); ovarioles minute, moderately bent, strongly oblique to OL (Lb).

The family *Neophemeridae* is well characterized by the arrangement of gonads manifesting a relationship especially to the family *Caenidae* and also to the families *Baetiscidae* and *Prosopistomatidae*.

## *Caenidae*

### *Caenidae*

(Figs. 203, 204, 207, 209, 211, 212, 214, 215, 218)

Testis: deposited laterally (Ac); PT, MST, MTT, I,II,III,IV,V,VI (Bb); narrowly cylindrical, produced into a point in thorax (Cb); tes-

ticular follicles minute, cylindrical, equal in size and length, arranged in regular longitudinal rows ( $Db_2$ ), perpendicular to VD (Ea); VS inconspicuous, formed by only slightly expanded VD (Fa); deposited in VII-IX (Ga).

Ovary: deposited laterally (Hc); (C), PT, MST, MTT, I, II, III, IV, V, VI (Jc); subcylindrical, bilaterally flattened, produced into a point in thorax (Kb); ovarioles minute, straight or moderately bent, oblique to OL, in thorax strongly oblique and produced (Lb).

The Holarctic genus *Brachycercus* deviates from the anatomical scheme of the family (testis in MST-VI:Bb; VS in VIII-IX:Gb). The family *Canidae* is characterized especially by the remarkable shift of gonads forward, the ovaries are produced to head in several genera (*Caenis*, *Caenomedea*, *Tasmanocoenis*). The family is evolutionarily quite homogeneous, despite these exceptions. The family *Caenidae* shows close affinity to the *Neophemeridae* and also to the families *Baetiscidae* and *Prosopistomatidae* in the arrangement of the internal reproductive system.

## ***Baetiscidae***

### *Baetiscinae*

(Figs. 249, 252, 255, 256, 259)

Testis: deposited laterally (Ac), PT, MST, MTT, I, II, III, IV, V, VI (Bb), cylindrical, slightly dorsolaterally flattened, produced into a point in thorax (Cb); testicular follicles, minute, elongated and cylindrical, equal in size, arranged into regular longitudinal rows ( $Db_2$ ), perpendicular to VD (Ea); VS cylindrical (Fc), deposited in VIII-IX (Gb).

Ovary: deposited laterally (Hc); PT, MST, MTT, I, II, III, IV, V, VI (Jc); cylindrical but strongly flattened, produced into a point in thorax (Kc); ovarioles relatively large, straight, strongly oblique to OL (Lb).

The family *Baetiscidae* (only one Nearctic genus *Baetisca*) is well characterized by the arrangement of gonads. The dorsoventral flattening of testes is unique character within the *Ephemeroptera*. The family manifests affinity not only to the *Prosopistomatidae* but also to the *Neophemeridae* and *Caenidae*.

## ***Prosopistomatidae***

### *Prosopistomatinae*

(Figs. 253, 254)

Testis: deposited laterally (Ac); MST, MTT, I, II, III, IV, V, VI (Bb);

cylindrical, slightly dorsoventrally flattened, pointed in thorax (Cb); testicular follicles minute, equal in size, arranged into regular longitudinal rows (Db<sub>2</sub>); perpendicular to VD (Ea); VD inconspicuous (Fa), deposited in VII-IX (Ga).

Ovary: deposited laterally (Hc); MST, MTT, I,II,III,IV,V,VI (Jb); cylindrical and strongly bilaterally flattened, pointed in thorax (Kc); ovarioles minute, strongly oblique to OL (Lb).

Family well characterized by its anatomical scheme; the gonads of the only genus *Prosopistoma* are closely related to those of the genus *Baetisca*. There are certain affinities to the families *Neophemeridae* and *Caenidae* as well.

Tab. 1

A tabular summary of the anatomical arrangement of gonads in *Epheme-*

Family (subfamily, genus)	Position of gonads (A, H)	Position of testes to segments (B)	Position of ovaries to segments (J)
<i>Siphonurinae</i>	Aa, Ha	Ba	Jb (Jc)
<i>Acanthametropodinae</i>	Aa, Ha	Ba	Jb
<i>Oniscigastrinae</i>	Ab, Hb	Bb	Jc
<i>Ameletopsis, Mirawara</i>	Ab, Hb	Ba	Jb
<i>Chiloporter</i>	Aa, Ha	Bd	Jb
<i>Isonychiinae</i>	Ab, Hb	Ba	Jb
<i>Coloburiscinae</i>	Ac, Hc	Bd	Ja
<i>Rallidentinae</i>	Aa, Ha	Ba	Jb
<i>Callibaetis, Baetopus, Centroptilum,</i>			
<i>Cloeon, Procloeon</i>	Aa, Ha	Ba	Jb
<i>Baetodes, Pseudocloeon</i>	Aa, Ha	Bc	Jd
<i>Oligoneuriinae</i>	Ab, Hb	Ba	Jb (Jc)
<i>Cinygnula, Epeorus,</i>			
<i>Rhithrogena</i>	Ac, Hc	Ba	Ja, Jb
<i>Afronurus, Ecdyonurus,</i>			
<i>Heptagenia, Stenacron,</i>			
<i>Stenonema</i>	Ac, Hc	Ba	Jb, Jc
<i>Anepeorinae</i>	Ac, Hc	Ba	Jb
<i>Arthropleinae</i>	Ac, Hc	Ba	Jb
<i>Pseudironinae</i>	Ab, Hb	Bb	Jc
<i>Ametropodinae</i>	Ab, Hb	Ba	Jb
<i>Metretopodinae</i>	Aa, Ha	Ba	Jb
<i>Atalomicria, Atalophlebia,</i>			
<i>Atalophlebiodes, Jappa</i>	Ac, Hc	Ba	Ja
<i>Leptophlebia, Habroleptoides, Habrophlebia, Kirrara</i>	Ac, Hc	Ba	Jb
<i>Kimminsula, Paraleptophlebia</i>	Ac, Hc	Bb	Jc
<i>Hagenulus, Traverella,</i>			
<i>Thraululus, Choroterpes</i>	Ac, Hc	Bd	Jd
<i>Attenella, Timpanoga</i>	Ac, Hc	Ba	Ja
<i>Drunella, Eurylophella</i>	Ac, Hc	Bc	Jd
<i>Ephemerella, Ephemerellina, Teloganodes</i>	Ac, Hc	Ba	Jb

Shape of testis (C)	Shape of ovary (K)	Arrangement of follicles (D)	Position of follicles (E)	Position of ovarioles (L)	Shape of VS (F)	Position of VS (G)
Ca	Ka	Da (Db)	Ea	La	Fc	Gc (Gb)
Ca	Ka	Da	Ea	La	Fb	Gb
Ca	Ka	Db <sub>1</sub>	Ea	La	Fb	Gb
Cb	Kb	Db <sub>1</sub>	Ea	La	Fb	Gb
Ca	Kb	Da	Ea	La	Fb	Ga
Cb	Kb	Db <sub>1</sub>	Ea	Lb	Fc	Gc (Gb)
Cb	Ka	Db <sub>1</sub>	Eb	La	Fa	Ga
Ca	Ka	Da	Ea	La	Fc	Gc
Cb	Ka	Db <sub>1</sub>	Eb	La	Fb	Gb
Cb	Ka	Db <sub>1</sub>	Ea	La	Fb	Gc
Cb	Ka	Db <sub>1</sub>	Ea	La	Fa	Ga
Cb	Kb	Db <sub>1</sub>	Ea	La	Fc, Fb	Gb
Cb	Kb	Db <sub>1</sub>	Ea	La, Lb	Fb, Fc	Gb
Cb	Kb	Db <sub>1</sub>	Ea	La	Fc	Gb
Cb	Kb	Db <sub>1</sub>	Ea	Lb	Fb	Ga
Cb	Kb	Da	Ea	La	Fc	Gb
Cb	Kb	Da	Ea	La	Fc	Gc
Ca	Ka	Da	Ea	La	Fc	Gc
Cb	Kb	Db	Ea	La	Fa, Fb	Gb
Cb	Kc	Db <sub>2</sub>	Eb	Lb	Fc	Gb, Gc
Cc	Kc	Db <sub>2</sub>	Ea	Lb	Fb	Gc
Cc	Kc	Db <sub>2</sub>	Eb	Lb	Fd	Gb, Gc
Cb	Kb	Db <sub>1</sub>	Ea	La	Fc	Ga, Gb
Cb	Kb	Db <sub>1</sub>	Ea	La	Fb	Gb
Cb	Kb	Db <sub>2</sub>	Ea	La	Fa	Gb

Tab. 1 (continued)

Family (subfamily, genus)	Position of gonads (A, H)	Position of testes to segments (B)	Position of ovaries to segments (J)
<i>Tricorythinae</i>	Ac, Hc	Bb	Jc
<i>Leptohyphinae</i>	Ac, Hc	Ba	Jb
<i>Diceromyzinae</i>	Ac	Ba	-
<i>Behningiidae</i>	Ac, Hc	Ba	Jb
<i>Potamanthidae</i>	Ac, Hc	Ba	Jb
<i>Ephemera</i>	Ad, Hd	Ba	Jb
<i>Hexagenia, Litobranchna,</i> <i>Pentagenia</i>	Ad, Hd	Bb	Jb
<i>Euthyplociidae</i>	Ad, Hd	Ba	Ja, Jb
<i>Polymitarcinae</i>	Ad, Hd	Ba	Jb
<i>Asthenopodinae</i>	Ad, Hd	Ba	Ja
<i>Campsurinae</i>	Ad, Hd	Ba	Ja
<i>Palingeniidae</i>	Ad, Hd	Ba	Jb
<i>Neophemeridae</i>	Ac, Hc	Bb	Jc
<i>Caenidae</i>	Ac, Hc	Bb	Jc
<i>Baetiscidae</i>	Ac, Hc	Bb	Jc
<i>Prosopistomatidae</i>	Ac, Hc	Bb	Jb



Shape of testis (C)	Shape of ovary (K)	Arrangement of follicles (D)	Position of follicles (E)	Position of ovarioles (L)	Shape of VS (F)	Position of VS (G)
Cb	Kb	Db <sub>2</sub>	Eb	La	Fa	Gb
Cb	Kb	Db <sub>2</sub>	Ea, Eb	Lb	Fa	Ga, Gb
Cb	-	Db <sub>2</sub>	Ea	-	Fa	Gb
Cd	Kc	Db <sub>1</sub>	Ea	La	Fa	Ga, Gb
Cd	Kc	Db <sub>1</sub>	Ea	La	Fc	Gb
Cd	Kc	Db <sub>1</sub>	Ea	La	Fb	Gb
Cd	Kc	Db <sub>1</sub>	Ea	Lb	Fb	Gb
Cd	Kc	Db <sub>1</sub>	Ea	La	Fb	Gb
Cd	Kc	Db <sub>1</sub>	Ea	La	Fb	Gb
Cd	Kc	Db <sub>1</sub>	Ea	La	Fc	Gb
Cd	Kc	Db <sub>1</sub>	Ea, Eb	La	Fc	Gb
Cd	Kc	Db <sub>1</sub>	Ea	La	Fb	Gb
Cb	Kc	Db <sub>2</sub>	Ea	Lb	Fa	Gb
Cb	Kb	Db <sub>2</sub>	Ea	Lb	Fa	Ga
Cb	Kc	Db <sub>2</sub>	Ea	Lb	Fc	Gb
Cb	Kc	Db <sub>2</sub>	Ea	Lb	Fa	Ga

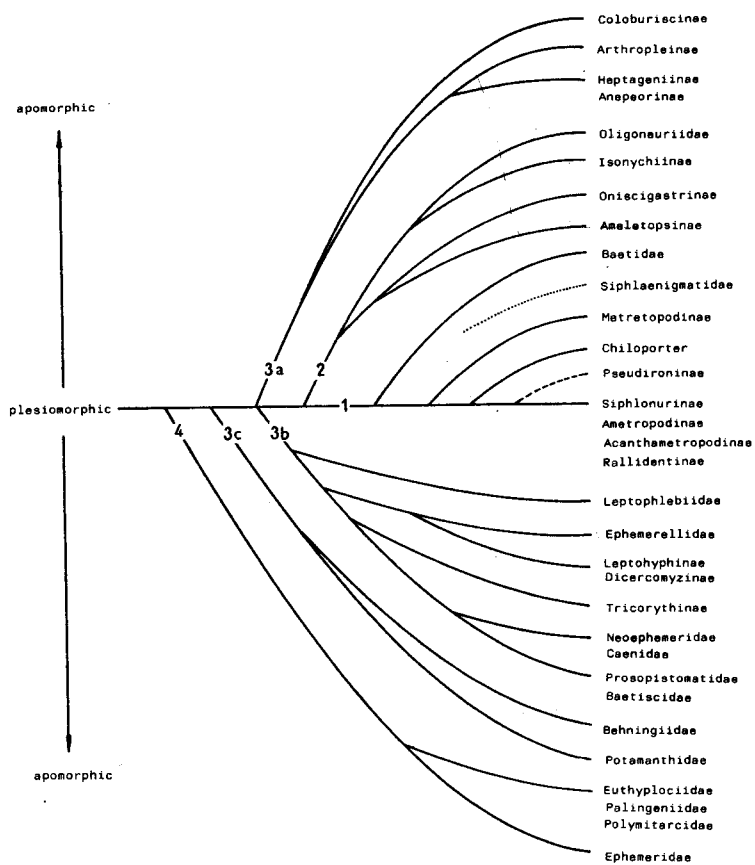


Fig. 261:  
 Tentative diagram of mayfly gonads anagenesis.

## DISCUSSION

### Comparison of results with literary data

The results obtained from the study of the testes and ovaries of species from 94 genera of mayflies can be compared with literary data published till now, even though the papers published so far refer only to several genera mostly from Holarctic region. The results obtained agree with the data published by Brinck (1957) based on examination of gonads of 8 European genera. He mentions also the shape of testes in the genus *Siphonurus* which is s-curved in the thorax or in the first abdominal segments and which is characteristic for the whole subfamily *Siphonurinae* (family *Siphonuridae*). However, on the basis of examination of several species of the genus *Siphonurus*, it was found that the ovary reaches much more further to the thorax (till the prothorax) and the testes reach to the metathorax at least in older larvae. So that the reproductive system is placed nearer to the head both in males and females than it is illustrated by Brinck (1957).

The data resulting from the investigation of gonads of different species and genera of the family *Heptageniidae* differ in some details from those published by Needham, Traver & Hsu (1935) dealing with the anatomy of testes and ovaries of the Nearctic genus *Stenonema*. They state that both testes and ovaries are deposited dorsally to the alimentary canal. Although the position of gonads can be slightly fluctuating from genus to genus, this is the contrary to the anatomical arrangement of gonads of all genera of the subfamily *Heptageniinae* (including *Stenonema* and *Stenacron*) where the gonads were found in the lateral position only, connecting the lateral tracheal trunks. The data indicating the position of testes and ovaries to the body segmentation differ as well from those obtained from the examination of older larvae of different species and genera of the subfamily *Heptageniinae*. Needham et al. (1935) state that testes are placed in the abdominal segments III-VII and ovaries in the abdominal segments I-VI in larvae. In older larvae of species of the genus *Stenonema* (recently divided into *Stenonema* and *Stenacron*) the gonads were found to reach at least to the metathorax or even to the mesothorax. These differences can be simply explained by the fact that larvae of different age were probably studied. In younger larvae the growth of the ovary can be still not finished and the ovary need not be produced to the thorax even in this

genus, in male mature larvae before the subimaginal moulting the testes can reach only to the abdominal segment three with regard to the degeneration of follicles connected with the finishing of spermatogenesis and the descent of mature spermatozoa into seminal ducts. However, in any genus of the subfamily *Heptageniinae* the testes were not found to reach further than to the abdominal segment VI, not even in mature larvae.

In all the genera and species investigated the gonads (testes and ovaries) were found entirely separated with the exception of ectodermal portions of the oviducts in some families. The paired gonads in some families (especially in those with dorsal or dorsolateral position of testes and ovaries) can touch or be contiguous in thorax or in the first abdominal segments. Rarely gonads are contiguous even in the groups having the lateral or ventrolateral position of gonads. In very case in question only passive touch of left and right gonad occurs, the peritoneal structures as well as any mesodermal structures are never fused. Palmén (1884) mentions the transverse anastomosis in the place of the seminal vesicles of European species *Ephoron virgo* (Oliv.). This anastomosis was found neither in any studied species of the genus *Ephoron* (*E. album*, *E. savignyi*, *Ephoron* sp. - Thailand) nor in any other genus of the family *Polymitaecidae*. Similar anastomosis is mentioned and figured by Codreanu (1939) in the genera *Ecdyonurus* (*E. lateralis*, as *Heptagenia*) and *Rhithrogena* (*R. semicolorata*) but repeatedly it was found neither in any species of these genera nor in any other genus of the family *Heptageniidae*. The same results (no transversal anastomoses) were obtained also by Brinck (1957) in eight Holarctic genera and Wisely (1965) in the New Zealand genus *Coloburiscus* (*Coloburiscinae*, *Siphonuridae*) and by some other authors.

As there were published only several papers dealing with the internal reproductive system of mayflies in detail, the results obtained during the study of comparative anatomy of gonads can be compared only with the works paying the attention to study of some special questions. A great attention was paid to the problems of ovoviviparity in the European species *Cloeon dipterum* (L.) (Joly, 1877b; Heymons, 1897; Degrange, 1957; Bernhard, 1907). The study of comparative anatomy of gonads of both ovoviviparous and oviparous species reveals that contrary to oviparous species (*C. simile*, *Cloeon* spp. from Africa) only a single or at most two oocytes mature in ovarioles of ovoviviparous species (*C. dipterum*) and that is why the ovarioles are usually strong and considerably short. These data correspond to those by Degrange (1957, 1960) that females lay 400-600 newly hatched or just hatching larvae of the first instar (larvullae). In the connection with the ovoviviparity not

only the number of growing oocytes but probably also the number of ovarioles are due to reduction secondarily. Similar arrangement of ovaries was observed in two genera of the family *Behningiidae* (*Behningia*, *Dolania*). This phenomenon is undoubtedly connected with remarkably large size of mature eggs (cf. Koss & Edmunds, 1974; Peters & Peters, 1977) but owing to apparent oviparity of both genera contained in the *Behningiidae* it remains quite unclear so far.

A considerable attention was paid also to the fertility of mayflies (see review by Clifford & Boerger, 1974; Smith, 1935; Degrange, 1960). The comparative anatomy of the ovaries of mature larvae of mayflies can also bring data concerning the fertility of females if we know the number of ovarioles and of oocytes maturing in one ovariole. Though no special attention was paid to this question it was possible to determine the fertility of females of some species and genera. The fertility of the most species calculated on the basis of anatomic study of the ovaries agrees with the values of producted eggs which were obtained mostly by dissections of mature females (cf. Clifford & Boerger, 1974), only in some species some discrepancies were found. The genera *Prosopistoma* (*Prosopistomatidae*) and *Palingenia* (*Palingeniidae*) are in question, where the lowest and the highest fertility in mayflies were found at all. Degrange (1960) states for *Prosopistoma foliaceum* (Fourcr.) the fertility of 174 eggs per female. With regards to the number of ovarioles in this species, which are relatively minute and multiplied in number, the value is too low in my opinion. On the contrary in *Palingenia sublongicauda* Tshern., the value of 12 000 eggs (Kosova, 1967) is too high because ovarioles of species of this genus (*P. longicauda*, *P. fuliginosa*) are provided with relatively small number of growing oocytes. The values calculated after anatomical proportions in these cases are about 300-450 eggs in *Prosopistoma* and 6000-8000 eggs in *Palingenia*. On the other hand, these differences could be explain by the fact that the specimens of the same species originating from different populations remarkably differ in fertility. The differences were observed also in the species having two or several generations a year (cf. Hunt, 1951). Moreover, the fertility depends on some abiotic factors such as temperature etc.

## Relations of mayfly gonads to those of other insect orders having panoistic type of ovarioles

Taking into consideration the results obtained by the study of a great number of mayfly genera from all zoogeographic regions, there is a possibility of precizing the relationships of gonads of the order *Ephemeroptera* to other insect orders with panoistic type of ovarioles. Namely some orders of the class *Entognatha* (*Diplura*) and orders of the *Paleoptera* and *Polyneoptera* are concerned. Even when panoistic ovarioles occur also in other insect groups, phylogenetic relationships of these orders (*Thysanoptera*, (?) *Coleoptera*) to the order *Ephemeroptera* are only very distant. Our considerations concern only the internal reproductive system (testes, ovaries, gonoducts), because a great attention has already been paid to copulatory organs and their appendages (Crampton, 1917, 1918, 1929; Snodgrass, 1931, 1936, 1957).

The anatomical arrangement of mayfly gonads shows relationships both, to some entognathous and apterygotan groups and to some orders of the infraorder *Polyneoptera* and, of course, to the most related order *Odonata* which forms the infraorder *Paleoptera* together with the *Ephemeroptera*.

As far as the entognathous insect orders are concerned, the mayfly gonads are more related to those of the order *Diplura* as in other groups (*Colembolla*, *Protura*) a considerable specialization of gonads occurs (laterally deposited germarium in *Colembolla*, testis without follicles etc.). In *Diplura* the gonads are deposited similarly to mayflies along the alimentary canal, even their persisting metamery can be observed (species of the family *Japygidae* have 7 metameric ovarioles, in other families the ovary is not differentiated into ovarioles at all). Contrary to the situation in mayflies, the gonoducts (both seminal ducts and oviducts) are joined to form the common duct in the last abdominal segments. The paired openings of ducts can be found only in the order *Protura*, where, however, considerable secondary simplification of the ovary occurs (ovary consists of only a single ovariole).

The gonads of the subclass *Apterygota* (containing the only recent order *Thysanura*) are closely related to mayfly gonads especially as their ducts and duct openings are concerned. Ovaries of the order *Thysanura* as well as those of the *Ephemeroptera* possess paired openings. Ovarioles, although no more metamERICALLY arranged, remind still the number indicating the initial metamery (there are 7 ovarioles in the suborder *Microcoryphia*; 5 ovarioles in the suborder *Zygentoma*). The testis has, contrary to that of mayflies, a secondarily complicated structure. There is a small number of testicular follicles, mostly 3

(2-7 in different families), the initial metamery of testis is completely reduced. Vas deferens is usually doubled by several transversal anastomoses which can serve as a seminal vesicle. Otherwise the ducts and gonopores are of the similar type as those of mayflies. The openings of gonoducts are mostly paired and also paired penis lobes can occur in many genera. The reproduction of *Thysanura* is very simple: there is no copulation and strongly modified, two-flagellate spermatozoa forming a spermatophore are laid by males to a substrat and then collected by females. No spermatophore is formed in mayflies but it cannot be simply stated that the lack of spermatophore represents a derived characters. On the other hand, the transfer of spermatozoa during the copulation represents an apparently derived situation in the *Ephemeroptera*.

The gonads of *Ephemeroptera* possess relatively very little common characters with the order *Odonata*, the most phylogenetically related order to mayflies. The only common character is the multiplication of the number of testicular follicles of testes and ovariole of ovaries from originally several metamERICALLY arranged follicles till several hundreds. This multiplication is more expressive with regards to a considerably greater fertility in mayflies than that in dragonflies. The gonoporus of the *Odonata* is unpaired, gonoducts are mutually connected forming the common ducts and the copulatory organs are unpaired as well. While any accessoric reproductive organs are not developed, those organs (both ectadenia and mesadenia) are present in the *Odonata* and they appear already in some groups of the class *Entognatha* and subclass *Apterygota*. Their presence undoubtedly represents a derived character as far as the anagenesis of the insect gonads is concerned. Also the copulatory organs of the *Odonata* are remarkably modified in comparison with those of the *Ephemeroptera*. In females of the most families a short ovopositor is developed (especially in species laying the eggs into plant tissues) and in males there is a secondary copulatory apparatus present on the second abdominal segment which represents a very unique phenomenon within the insects. Although there is no formation of the spermatophore in *Odonata* and the transfer of mature spermatozoa is realized through true copulation (with assistance of male accessoric copulatory organ), the spermatozoa are associated to form spermatozeugmats in the most families.

The gonads of polyneopterous insect orders (i.e. *Plecoptera*, *Embioptera*, *Mantodea*, *Blattaria*, *Isoptera*, *Phasmida*, *Orthoptera*, *Grylloblattodea*, *Zoraptera*, and *Dermaptera*) and those of mayflies have little common characters as well. The multiplication of testicular follicles and ovarioles is again the only common character, even when the number

follicle in the *Ephemeroptera* is mostly higher with the exception of the female of termites which have a very high fertility, too. While there are only slight differences between the testes and ovaries of mayflies in their structure (the gonads of younger larvae can be distinguished only by its openings or their anlagen), the gonads of the insect orders mentioned above are usually comby, shrubby or clustered, testes and ovaries are of the different shape. The gonads of polyneopterous insect orders are mostly situated only in the last abdominal segments and the accessoric reproductive organs are nearly universally present in both males and females. With the exception of some families of the order *Dermaptera* and the *Diploglossata*, there are always the posterior portions of ducts fused to form a common duct so that the openings of gonads are always unpaired. The copulatory organs of males are also unpaired and those of females possess fully developed or at least a reduced ovipositor which is absent only quite exceptionally (*Zoraptera*).

In the orders *Dermaptera* and *Diploglossata* there is a rather different situation in the anatomical arrangement of gonads and their gonoducts. The ovary consists of 8-12 ovarioles connected with the oviduct and the testis is formed by two or more testicular follicles which are closely contiguous. Most probably a secondary reduction of the number of follicles is in question. The gonoporus is unpaired in females (usually paired in mayflies) but it can be paired in adult males. Penis is either formed by a pair of lobes (one of them can be sometimes nonfunctional - *Labiduridae*) or consisting of a single lobe (*Forficulidae*, *Arixeniidae*, *Hemimerus*). Despite of the arrangement of duct openings, these groups are evidently in no close relations to the gonads of mayflies. The paired openings of male gonads in the *Dermaptera* represent undoubtedly only a secondary situation because of the arrangement of ductus ejaculatorius which enters penis as a single stem branching near the apex of the penis lobes. In mayflies even the ectodermal portions of gonoducts are not connected, similarly as in the order *Thysanura*. Moreover, the ovarioles of the *Dermaptera* and *Diploglossata* are of the meroistic polytrophic type having at least one nutritive cell distinctly developed. This type of polytrophic ovarioles represents the most primitive situation and intermediary type between the panoistic (*Thysanura*, *Paleoptera*, *Polyneoptera* except *Dermaptera* and *Diploglossata*) and the meroistic (*Paraneoptera*, *Oligoneoptera*) ovarioles.

The ovaries of *Cloeon dipterum* (L.) are modified in the same way as in the groups having a pseudoplacental viviparity (some *Blattodea* and *Dermaptera*) or ovoviviparity. In ovoviviparous species of polyneo-



pteran order also only a single oocyte matures in the vitellarium of ovariole. In mayflies (*Cloeon*, *Callibaetis*) rarely 2-3 oocytes can develop.

Contrary to the insect order mentioned above, the anatomical arrangement of mayfly gonads enables extremely high fecundity of females which is, except some social insects (*Isoptera*, *Hymenoptera*), the highest within the insects in general. While the testes and ovaries are practically indistinguishable in younger larvae, there are distinct differences in shape of gonads between males and females in older larvae and adults though the gonads are deposited identically along the alimentary canal. These differences are determined only by the relative size of male and female gametes (spermatozoa, eggs). The shape and length of testes do not substantially change during the larval development but a volume increasing of the ovaries is due to longitudinal growth of ovarioles which are connected with the forming of vitellarium. Relatively very small size of mature eggs enables simultaneous maturation and ovulation of several oocytes in vitellarium. This phenomenon together with irreversible degeneration of follicles of gonads before the subimaginal moulting is also unique within the insects.

The surprisingly high fecundity of mayflies is undoubtedly connected with larval ecology and especially life cycles. The loss of offspring caused by both abiotic (temperature, oxygen consumption, downstream drift etc.) and biotic (predation, feeding conditions etc.) factors, is extremely high in the *Ephemeroptera*. The species with relatively long-lived larvae (one generation during 1-2 years) show higher fecundity (2000-8000 eggs per female) than those with several generations a year (500-3000 eggs). Respective differences were observed also in the arrangement of gonads (especially of the ovaries - position to the body segmentation, multiplication of ovarioles etc.).

## Anagenetic trends in forming of internal reproductive organs of the order *Ephemeroptera*

Considering individual phylogenetic (anagenetic) tendencies applied in the forming of internal reproductive system, at first it is necessary to consider which characters are distinctly plesiomorphic (primitive) and which apomorphic (derived) so that it would be possible to identify individual phyletic features by taking into account changes of these characters.

In spite of the fact that no direct palaeontological data exist,

the hypothesis of metameric origin of the insect gonads is generally accepted at present. Ancestral insect forms are assumed to have 10 pairs of metamerically arranged follicles (testicular follicles or ovarioles) entirely independent on one another in the production of gametes and mutually anatomically not connected. Coelomoducts, in this case in function of gonoducts communicated with the outside environment by quite separated openings. The arrangement of gonads with separated follicles was not preserved in recent insect representatives. The connection of segmentally metamerically arranged gonads appeared later by means of lateral, mesodermal ducts which, however, mutually did not communicate. At the same time the reduction of follicles in some abdominal segments and eventually their modifications occurred. The follicles in the last abdominal segments modificate into mesademia (accessoric glands of the mesodermal origin) in males and into paragenital glands and spermatheca in females. Gonads of this type are to be found in the order *Thysanura*. Later secondary multiplication of testicular follicles and especially ovarioles and also various modifications of mesodermal and ectodermal portion of gonoducts (seminal vesicles etc.) occur (the gonads of polyneopterous insect orders, mayflies, dragonflies).

From the above data it is obvious how to evaluate individual characters obtained during the comparative study of mayfly gonads. With regard to the original position of gonads only in ten abdominal segments it is apparent that the shift of gonads to the thorax is secondary. It agrees with the demand of prolongation of gonads with regard to insuring production of higher number of gametes. So the situation when gonads reach till the thorax or even the head (ovary in the genus *Caelen*) is to be considered as derived, gonads reaching to thorax as apomorphic character. On the other hand also the lack of gonads in the first abdominal segments (shifting of gonads caudad) is an apomorphic character as well (lack of gonads in the segments VII-IX is a synapomorphic character). As far as the character discussed here is concerned, it is worth to notice that in the most of families studied the ovaries are shifted to the head more than the testes, and so the ovary seems to be "phylogenetically more derived" in comparison to the testis. This circumstance is probably connected with the differences in size between eggs and spermatozoa and, consequently with the need of space for growing oocytes.

It is more difficult to decide which type of position of gonads to the alimentary canal is plesiomorphic and which is apomorphic. Even when there are no data concerning the position of gonad in insect ancestors, it is presumable that dorsal position was original, that is the position of gonads above the ventral tracheal trunk. Shifting of gonads to dor-

solateral, lateral or even to ventrolateral position occurred probably in connection with the gradual transformation of larval body from the "swimming" to the "crawling" or "burrowing" body type. On the basis of paleontological data it may be assumed that the original type of mayfly larvae was the swimming type in which the dorsal position of gonads is still conserved.

The shape of testis or ovary and the shape of apical part corresponds with the shifting of gonads ventrally and cranially, to the ventrolateral position and to the head (gradual bilateral flattening). Pointing and producing of apical portion of gonad depend undoubtedly on prolongation of gonads to the head and also on a limited space in thorax which is due to development of sizeable thoracic muscles in older larvae.

Another important character is the number and arrangement of follicles of gonads. Taking in account the original presumption of 10 metamerically arranged follicles, then the multiplication on the number of follicles (both testicular follicles and ovarioles) in mayflies is a synapomorphic character having for evaluation of the anagenesis of individual organ systems only a limited value. On the other hand, it is possible to distinguish the differences in total number of follicle even without their counting. Nevertheless it is possible to use this characters for the comparative study, mostly as far as the testis is concerned. In some groups (*Siphonurinae*, *Ametropodinae*) and others large, rounded and nearly spherical follicles can be observed. Even the differences in size of testicular follicles, which are sometimes very remarkable, were observed in some genera (*Ameletus*, *Parameletus*, *Ametropus*, *Pseudiron* and others). This arrangement of follicles probably represents a stage of multiplication of testicular follicles by dividing of several original metameric organs. This type of follicles is unique within the insects in general. The situation when testicular follicles are of different size is supposed to be plesiomorphic (synplesiomorphic within the subfamily *Siphonurinae*). Follicles different in size are always less numerous and arranged into irregular longitudinal rows in dorsal view. The most primitive situation is to be found in the genus *Ametropus* (family *Ametropodidae*) where only several tens of nearly spherical follicles are arranged into the only longitudinal row and where there are remarkable differences in size of follicles (some follicles 2-3 times larger). In some genera only slight differences in size of follicle occur (*Atalophlebia*, *Jappa*, *Ephemerella*-subgenus *Timpanoga* and others). Another type of the arrangement of follicles is manifested by follicles equal in size, relatively large, cylindrical or nearly spherical; their number is about 150-300. An apomorphic situation

in the follicles arrangement is represented by small, elongated and relatively numerous follicles which are arranged into several regular longitudinal rows apparent in dorsal view; their number is higher than 200-300 follicles (*Caenidae*, *Tricorythidae*, *Neoephemeridae* and others).

Contrary to testicular follicles, there are no conspicuous differences in the arrangement of ovarioles as far as their size and number is concerned. All ovarioles are always equal in size and again represent a greater "phylogenetic derivation" of ovary. This fact could be explicable by that, that all mature eggs are to be approximately of the same size and shape so that ovarioles must be of the same size and length as well. Certain differences in number and size of ovarioles among some families, which usually correspond to differences in arrangement of testicular follicles, were observed, too. Shorter, cylindrical and sizeable ovarioles are of plesiomorphic character and elongated, smaller and numerous ones are of apomorphic character.

As concerns the position of testicular follicles or ovarioles to a seminal duct or oviduct, the situation, when the single ovariole or even testicular follicle is so produced to reach even to the previous body segment, is to be considered, with regard to original metameric arrangement of follicles, apparently apomorphic. Originally, in metameric disposing of follicles they undoubtedly stood at the right angle to duct and to one follicle belonged only one body segment. With some exceptions, testicular follicles of mayflies are nearly always deposited perpendicularly to seminal duct because they are relatively short. On the contrary, ovarioles are mostly oblique to the oviduct, as, after the formation of vitellarium they are much longer than testicular follicles. In some genera they are even conspicuously oblique to the oviduct (*Caenidae*, *Leptophlebiidae* and others). In this case the position of ovarioles is the result of an effort for more perfect usage of the body cavity. In the thorax, where in older larvae the greater part of space is filled up by growing flying muscles of pharate adult, ovarioles are oblique almost in all species. As pointed out above, strongly oblique ovarioles are considered to be very derived.

The presence of the mesodermal seminal vesicle itself represents a synapomorphic character within the order *Ephemeroptera*. Nevertheless, even in the arrangement of the seminal vesicle it is possible to recognize certain developmental tendencies. Moreover, the seminal vesicle is apparent already in older larvae much before the first spermatozoa descend into seminal ducts. Originally, the spermatozoa were undoubtedly stored only in a not expanded elongated seminal ducts in the abdominal segments VII-IX so that inconspicuously expanded seminal duct is the plesiomorphic type of the seminal vesicle. It is possible to derive

from this basic type the spindle-shaped or subcylindrical seminal vesicle formed by a gradually expanded seminal duct and after another modification even a cylindrical seminal vesicle formed by a seminal duct suddenly expanded. The rounded seminal vesicle is that of an apomorphic type. The plesiomorphic type of position of the seminal vesicle to body segmentation is that in the abdominal segments VII-IX. An apomorphic type of seminal vesicle position is in the segment IX only. A transient type is represented by position of the seminal vesicle in the segments VIII-IX. This type is common in the most of families.

The separation of seminal ducts as well as oviducts lengthwise and the paired openings of the gonoducts in mayflies is the synplesiomorphic character having nearly no significance for the determining of main phyletic lines.

Several phylogenetic trends, which are to be applied during the anagenesis of gonads within the order *Ephemeroptera* are obvious from the considerations mentioned above. The following tendencies are especially in question:

(i) The tendency of shifting of gonads from the dorsal position ventrally to the dorsolateral, lateral or ventrolateral position to the alimentary canal.

(ii) The tendency of producing of gonads cranially to the thorax or even to the head. In some genera also another shift of gonads was observed especially in those with remarkably shortened abdomen. The gonads can be shifted to the abdominal segments VII or even VIII and need not occur in the first two or three abdominal segments.

(iii) The tendency to shape changes of both testes and ovaries. Originally cylindrical or subcylindrical gonads gradually change to bilaterally flattened or tongue-shaped ones. These changes are apparent especially in the anatomical arrangement of ovaries and are connected with shifting of gonads ventrally.

(iv) The tendency to multiplication of the number of testicular follicles and ovarioles, in the case of the testis also a tendency to diminishing of follicles of the same size and length. With the exception of ovoviviparous species and species of the family *Behningiidae* the ovarioles tend to decreasing of their size as well.

(v) The tendency of slanting of testicular follicles and ovarioles from perpendicular to oblique position to the seminal duct or oviduct. Ovarioles tend to further elongation of vitellarium with growing oocytes.

(vi) The tendency to forming of a specialized, rounded and nearly spherical seminal vesicles from the original type of vesicle represented by only inconspicuously expanded seminal duct in the last abdominal

segments. There is also the tendency to shift the seminal vesicle from the abdominal segments VII-IX only to segment IX.

## Hypothetical scheme of anagenesis of internal reproductive system of the order *Ephemeroptera*

According to the arrangement of internal reproductive organs recent mayflies may be divided into three main developmental lines which are well characterized by the characters found on gonads. Hypothetical scheme of anagenesis of gonads (testes and ovaries) of mayfly families investigated is apparent from Fig. 261. It has to be emphasized here that this scheme is based solely on the anatomical arrangement of gonads not taking into account the other organ system or external morphology so that it represents only the anagenesis of gonads and, consequently, cannot perform the mayfly phylogeny in general.

The first line (1) evidently corresponds with the most primitive situation. It is characterized mostly by a smaller number of testicular follicles and ovarioles (testicular follicles can be of different size). Follicles are always placed perpendicularly to seminal duct, ovarioles perpendicularly or slightly obliquely to oviduct. This developmental line is also characterized by the dorsal position of gonads which is characteristic for the larvae of the swimming type. The subfamilies *Siphonurinae*, *Acanthametropodinae* and *Rallidentinae* (*Siphonuridae*) originate in the beginning of the line. The subfamily *Ametropodinae* also belongs to this group having the most primitive type of testis arrangement within mayflies at all (only one row of follicles of different size). The gonads of the subfamily *Pseudironinae* (*Heptageniidae*) are related to this type of gonads as well but they distinctly differ by their dorsolateral position to the alimentary canal. With regard to the position of gonads, also the subfamily *Metretopodinae* (*Ametropodidae*) and the genus *Chiloporter* (*Ameletopsinae*, *Siphonuridae*) belong to this evolutionary line but they differ in the arrangement of follicles from the *Siphonurinae*. The family *Siphlaenigmatidae* (one New Zealand genus), which represents morphological interstage between the families *Siphonuridae* and *Baetidae*, is undoubtedly contained in this line. The derived type of this evolutionary line (1) is manifested by the family *Baetidae*, where gonads are still placed dorsally, but the follicles are of the same size and in some genera (*Baetodes*, *Pseudocloeon*, *Baetis*) changes in the position of gonads to the body

segmentation occur. There are also modifications of the arrangement of ovary which are due to ovoviviparity.

The second evolutionary line (2 - see Fig. 261) representing the intermediary type between the plesiomorphic and apomorphic arrangement of gonads is characterized by the shift to the dorsolateral position. This group involves the subfamilies *Oniscigastrinae* and *Ameletopsinae* (except the genus *Chiloporter*)(*Siphonuridae*) where gonads are mostly of the same shape as those of the subfamily *Siphonurinae* and the subfamilies *Isonychiinae* (*Siphonuridae*) and *Oligoneuriinae* (*Oligoneuriidae*, *Chromareyinae* not investigated) with related anatomical schemes. Testicular follicles of this group equal in length and size but yet they are not evidently multiplied. Ovarioles can be deposited obliquely or very obliquely to oviduct (*Isonychiinae*) and the ovary can be bilaterally flattened.

The third evolutionary line (3 - see Fig. 261) consisting of the most of recent mayfly groups is characterized by the shift of gonads to the lateral position to the alimentary canal. Two principal lineages (3a, 3b) are contained in this evolutionary line as far as the arrangement of the reproductive system is concerned. The first lineage (3a) is characterized by a relatively small number of testicular follicles and ovarioles. The follicles are large, cylindrical or nearly spherical arranged into regular longitudinal rows, the ovarioles are placed mostly perpendicularly or slightly obliquely. The gonads reach usually only to the metathorax or rarely to the mesothorax. This subgroup includes the subfamily *Heptageniinae* comprising two groups of genera of which one is plesiomorphic and the other apomorphic, and the subfamily *Anepeorinae* with nearly identical anatomical schema as that of the *Heptageniinae* (plesiomorphic group of genera). The subfamily *Arthropleinae* also contained in the subgroup shows close relationships to the apomorphic group of genera of the *Heptageniidae* which itself indicates certain affinity to advanced evolutionary lineage (3b). With regard to the lateral position of gonads and the arrangement of ovary, the subfamily *Coloburiscinae* (*Siphonuridae*) is placed to this subgroup. However, considerably derived arrangement of testis (long and narrowly cylindrical follicles which are oblique to seminal ducts) singles it out from the *Heptageniidae* as well as the *Siphonuridae*.

The second lineage (3b) is characterized by further shifting of gonads cranially. The gonads usually extend from prothorax or mesothorax to the abdominal segment VI (or VII in some genera of the *Ephemerebellidae*). Testicular follicles and ovarioles are apparently more numerous and smaller, always equal in size and usually (ovarioles) oblique or strongly oblique to oviduct. In some families, however, some

genera with very plesiomorphic anatomical schemes were observed (*Leptophlebiidae*, *Ephemerellidae*) but, nevertheless, these families are quite homogeneous from the evolutionary point of view comprising, on the other hand, highly derived genera as well. These genera indicate certain relationships of this group (3b) to the groups of families (1) and (2) and, of course, to subgroup (3a). The remarkable shifting of gonads occurs especially in the families *Caenidae* and *Neophemeridae*, the apomorphic arrangement of gonads was found also in the families *Baetiscidae* and *Prosopistomatidae*. The family *Tricorythidae* (*Machadorythinae* and *Ephemerythinae* not investigated) represents an intermediary type between the *Ephemerellidae* and the *Caenidae* with *Neophemeridae*. While the subfamily *Leptohyphinae* and probably also the *Dicercomyzinae* show relationships to the *Ephemerellidae*, the subfamily *Tricorythinae* is related rather to the *Caenidae* and *Neophemeridae*.

The evolutionary line (3) characterized by the lateral position of gonads includes also the families *Potamanthidae* and *Behningiidae* (3c). These families are characterized above all by the bilateral flattening of both testes and ovaries which is characteristic mainly for the fourth evolutionary line (4 - see Fig. 261). Despite the lateral position of gonad these families show affinity to the other families of the *Ephemeroidea* forming an intermediary group between the evolutionary lines (3) and (4). Owing to some common characters with the family *Leptophlebiidae* (3b), there is no doubt that the differentiation of these families must have occurred a very long time ago.

The last evolutionary line (4) is characterized mainly by the shift of gonads to the ventrolateral position and by the bilateral flattening of the testis and the ovary. The testicular follicles are cylindrical, equal in size, sometimes oblique to seminal duct, the ovarioles are mostly multiplicated, sometimes strongly oblique to oviduct. This evolutionary group is differentiated into two subgroups. The first subgroup (plesiomorphic) consists of the families *Euthyplociidae*, *Palingeniidae* and *Polymitarciidae* (all the subfamilies) and is characterized by the gonads reaching at most to the metathorax or the first abdominal segment. Ovarioles are either perpendicular or slightly oblique to oviduct. The second subgroup comprises the family *Ephemeridae* where the gonads reach to the meso- or metathorax and ovarioles are mostly strongly oblique to oviduct (apomorphic group of genera) forming considerably bilaterally flattened ovary. This family represents an apomorphic subgroup within the group (4).

The evolutionary lines as recognised by the study of gonads and presented above, agree, to a certain extent, with evolutionary lines constructed on the basis of comparative study of copulatory organs.



Nevertheless, there are some contradictions as far as both male and female copulatory organs are concerned.

The plesiomorphic type of the arrangement of male copulatory organs can be found in the families of the superfamily *Ephemeroidea* (*Ephemeridae*, *Palingeniidae*, *Euthyplociidae*, *Polymitarciidae*, *Potamanthidae*, and *Behningiidae*) where the penis lobes are mostly distinctly separated and a great number of the forceps segments is conserved (till 7 in the *Palingeniidae*). The ovaries and the testes of this group are, however, of the apomorphic type. On the other hand in the family *Baetidae*, where the male copulatory organs are very derived (the progressive reduction of the penis and that of segments of the forceps), the gonads possess a lot of evidently plesiomorphic characters. Despite of these exceptions and some further minor departures it can be supposed that in the most of recent families the evolutionary tendencies forming the arrangement of the testis and the ovary correspond to those appearing at the forming of the male copulatory organs (the reduction of forceps segments, the tendency to fusion of the penis lobes, the tendency to the shift of gonoporus etc.).

The similar situation occurs also as to female copulatory organs. The most primitive type of the openings of ducts, unmodified paired gonopores can be found not only in the family *Baetidae*, where the gonads are apparently plesiomorphic but also in the families of the superfamily *Ephemeroidea*, where the gonads are apomorphic in comparison with those of the *Baetidae*. The most derived type of the female copulatory organs (the posterior margin of the seventh abdominal segment produced analogously to the "orthopteroid" ovipositor, the ectodermal portion of oviducts fused) are those of the family *Leptophlebiidae* (some genera). Between these two extreme situations there is a number of intermediary types of arrangement of female gonopores (e.g. the families *Siphonuridae*, *Heptageniidae* and *Oligoneuriidae*). From the evolutionary point of view the arrangement of the copulatory organs of females corresponds only roughly to that of the internal reproductive system. This is the contrary to the arrangement of the copulatory organs of males.

Very similar conclusions were obtained by Koss (1968, 1973) on basis of the study of the chorionic structures of mature eggs and by Landa (1969, 1973) who studied the comparative anatomy of the tracheal system, ventral nerve cord and malpighian tubules. It has been shown that as far as the presence of the ventral anastomoses, the simplification of the visceral tracheal branches and the arrangement of the malpighian tubules are concerned, the families of the superfamily *Ephemeroidea* are much more derived than the *Baetidae* and the *Siphonuridae*. The same contradictions appear as far as the testes and ovaries are

concerned. The arrangement of gonads corresponds much more to that of the tracheal system, central nerve system and malpighian tubules than to the arrangement of external copulatory organs, which, together with the gonads and ducts are the part of the reproductive system despite their ectodermal origin.

This contradiction is explicable especially by the fact that the organ systems conserved their original characters during the phylogenesis while the organs of ectodermal origin (especially those of integument) adapted more quickly to the changes of habitats and met the ecological demands. That is why at present we could find genera (e.g. *Baetis*, *Cloeon* etc.) which, despite their extreme morphological specialization and considerable variability and their specific diversity, conserved their very plesiomorphically arranged organ systems. On the other hand, there are genera (*Ephemera*, *Ephoron*, *Potamanthus* and others) which despite clearly plesiomorphic external morphological characters (hind wings, eyes, paracercus etc.), are undoubtedly derived from the internal anatomy point of view. According to a mosaic distribution of characters also some plesiomorphic characters occurring in anatomically derived families as far as the reproductive system is concerned. For instance, it is relatively very high fecundity within the superfamily *Ephmeroidea* (8000 till 12000 in the genus *Palingenia*). High fecundity (here considered as an plesiomorphic character) is above all conditioned by the multiplication of the ovarioles which is, of course, a derived character. However, as mentioned above we have to take into account that the number of laid eggs is directly proportional to the size of the body because the eggs of the most of species are approximately equal in size. From this example it is obvious that the evaluation of fertility from phylogenetical point of view is very difficult.

With regard to a considerably high diversity in the arrangement of mayfly gonads it may be supposed that the separation of the above evolutionary lines occurred very soon, probably already in the Proterozoic. Landa (1969a) presumes on the basis of the study of the tracheal system that groups being at present well characterized by the arrangement of the thoracic and abdominal tracheal system existed already in the Permian. This presumption is supportable even by the paleontological data especially as the number and the shape of the tracheal gills and their subsequent reduction and specialization, which are closely connected with forming of internal tracheae, are concerned.

## Interfamilial and intrafamilial relationships within the order based on comparative anatomy of gonads

The study of the comparative anatomy of the tracheal system, central nerve system and malpighian tubules in a large number of mayfly genera (Landa, 1959, 1973) and the results obtained may be successfully used in solving of some of a higher classification of the order. Of course I am aware of the fact that neither the evolutionary lines nor the higher classification cannot be constructed solely according a few characters provided by the arrangement of gonad, however carefully studied. It is obvious that different results could be obtained by investigating of other organ systems because all stages and all parts of the organism as a whole evolved at different rates.

As noticed already by Spieth (1933) some older systems insufficiently consider phylogenetic relationships among individual groups (Eaton, 1883-1888; Lameere, 1917; Ulmer, 1920 and others). In correlation with the data known till now, the results obtained by the study of comparative anatomy of gonads can contribute to solve some questions concerning the higher classification. In the following paragraphs the relationships among the families or subfamilies within the order *Ephemeroptera* are discussed. Using the classification by Edmunds, Allen & Peters (1963) as a starting point, the families and subfamilies are arranged according to this system.

The family *Siphonuridae* sensu Edmund et al. (1963) includes very heterogeneous groups as it has been indicated above. As far as gonads are concerned, the division of this family into subgroups results from the anatomical schemes of the individual subfamilies. The subfamilies *Isonychiinae*, *Ameletopsinae*, and *Oniscigastrinae* differ by the dorso-lateral position of gonads. Also Landa (1973) separates the *Ameletopsinae* (except the Neotropical genus *Chiloporter*) into a separated family emphasizing the relations to the family *Baetidae* on the basis of the study of tracheal system. Riek (1973) is of the same opinion, too. The genus *Chiloporter*, which has not only unique arrangement of the tracheal system but also unique forming of the gonads (both testes and ovaries), occupies a quite isolated position among remaining genera of the subfamily *Ameletopsinae*. Especially, as the position of gonads is concerned, the genus *Chiloporter* shows certain relationships to the subfamily *Siphonuridae* or the *Acanthametropodinae* and *Rallidentinae*. According to Landa (1969, 1973) not only the genus *Chiloporter* but the whole subfamily *Oniscigastrinae* are necessary to be excluded from the *Siphonuridae*. For the genus *Chiloporter* Landa (1973) establishes

a separate family *Chilopoteridae*. Also Edmunds (1973b) agrees with this opinion though Riek (1973) leaves the genus *Chiloporter* in the family *Ameletopsinae* and the subfamily *Oniscigastriinae* in the family *Siphonuridae*. According to the arrangement of gonads, the *Ameletopsinae* and the *Oniscigastriinae* represent a separate group which shows relationships partly to the family *Baetidae*, partly to the subfamilies *Isonychiinae* and *Oligoneuriinae*.

By its arrangement of gonads the subfamily *Isonychiinae* is very resembling to the scheme of the subfamily *Oligoneuriinae*. The morphological as well as the anatomical differences of the single genus *Isonychia* (especially those of larvae) lead some authors to isolating of the subfamily and to the separation from the family *Siphonuridae* (Edmunds & Traver, 1954; Landa, 1969a, 1969b). Though Edmunds (1970, 1973b) mentions some elements of affinity to the family *Oligoneuriidae* he classifies the *Isonychiidae* as a part of the family *Siphonuridae*. Riek (1973) considers this subfamily as a part of the family *Oligoneuriidae*, on the basis of external morphological characters of larvae. The anatomical arrangement of gonads would mostly correspond to this opinion. Demoulin (1958) considers the genus *Isonychia* as an independent family having close relationships to the family *Oligoneuriidae*. Landa (1973) shows close affinities of these groups in the arrangement of tracheal system (tracheization of accessoric gills).

The subfamily *Coloburiscinae* differs markedly by its position of gonads from the scheme of the subfamily *Siphonurinae* as well. The lateral position of gonads indicates certain relationships to the family *Heptageniidae* (*Heptageniinae*) from which, however, it differs by the very modified arrangement of the testis. Landa (1973) considers this group as a separate family and places it near to the *Isonychiinae* and *Oligoneuriidae*. Riek (1973) classifies this subfamily directly as a part of the family *Oligoneuriidae*. The arrangement of tracheal system (accessoric gill) and ovaries conform this opinion. Koss & Edmunds (1974) although pointing out apparent relationships to the *Isonychiinae* consider the *Coloburiscinae* as a part of the *Siphonuridae*.

The subfamily *Rallidentinae* (the only genus *Rallidens* from New Zealand) does not substantially differ from scheme of the subfamily *Siphonurinae*. Landa (1973) considers it as a separate family with relations to the families *Ameletopsidae* and *Baetidae*. Demoulin is of a similar opinion as well (Demoulin, 1969). The other authors do not separate it from the subfamily *Siphonurinae* (Riek, 1973; Penniket, 1966). In a similar way also the subfamily *Acanthametropodinae* is classified, the gonads of which are also coincident to those of the *Siphonurinae*. Demoulin (1974), Edmunds (1947, 1970) and others consider it as

a part of the family *Siphonuridae*. The gonads of the Nearctic genus *Analetris*, which is sometimes separated to an independent subfamily, were not investigated.

Tshernova (1974) and Koss & Edmunds (1974) consider the family *Siphonuridae* as defined by Edmunds, Allen & Peters (1963) but they point out relatively great diversity of subfamilies included and the fact that the subfamily *Siphonurinae* itself involves several groups of genera. These are the *Siphonurus* complex, the *Metamonius*-complex and the *Ameletus*-complex. The gonads of genera involved in the *Metamonius* complex were not studied but the gonads of the both other complexes differ in several respects. Similar differences were observed in the arrangement of chorionic structures (Koss & Edmunds, 1974). Riek (1973) forms for several genera of this subfamily an independent subfamily *Nesameletinae* having certain relationships to the subfamily *Rallidentinae*. There is no doubt that some genera (e.g. *Ameletus*) represent generic complexes requiring further taxonomic examinations.

Although the gonads of the family *Siphlaenigmatidae* were not studied they are probably of the analogous type as those of the family *Baetidae*. Penniket (1962), Koss (1973) and Tshernova (1970) consider the single genus *Siphlaenigma* as a separate family, Demoulin (1968) and Riek (1973) consider this group only as a subfamily of the family *Baetidae*. Preliminary results of the study of internal organs (Landa, pers.comm.) indicate that this genus is closely related to some genera of the *Baetidae*.

The family *Baetidae* sensu Edmunds et al. (1963) is accepted by all the authors. From the anatomical point of view (the tracheal system, central nerve system, and malpighian tubules - see Landa, 1969a; the gonads) the family is quite homogeneous; it is possible to observe interstages in the arrangement of internal organ systems. As far as the position of gonads is concerned the genera of the *Baetidae* may be divided into two groups. It is possible to observe the cranial shift of gonads in genera living in running water habitats. Kazlauskas (1969) separates the genera *Cloeon*, *Procloeon* and some others to the subfamily *Cloeoninae*, Riek (1973) practically the same genera to the subfamily *Callibaetinae* so that the family *Baetidae* would consist of two group-shaving the value of subfamilies if we do not take into a consideration the New Zealand genus *Siphlaenigma*. These group would correspond to those formed on the basis of the study of gonads. However it would be very difficult to range the genus *Baetis* where some species represent intermediate forms. Moreover, there are at least ten undescribed genera and therefore it would be better to wait with final division of the family. Especially some carnivorous genera (not investigated here)

markedly differ in both external morphological and anatomical characters. The family *Baetidae* shows clear relationships to the *Siphonuridae* (*Siphonurinae*, *Acanthametropodinae*, *Rallidentinae*) especially as far as the dorsal position of gonads is concerned.

The family *Oligoneuriidae* is characterizable after the arrangement of gonads only on the basis of the study of genera of the subfamily *Oligoneuriinae*, the material of the genus *Chromarcys* separated to a subfamily (Demoulin, 1953; Edmunds, Allen & Peters, 1963) or to a separate family (Tshernova, 1970) is lacking. This family is well characterized by the arrangement of gonads, it forms an interstage type to the family *Heptageniidae*. Riek (1973) involves also the subfamilies *Isonychiinae* and *Coloburiscinae* to the *Oligoneuriidae*.

The family *Heptageniidae* sensu Edmunds et al. (1963) includes heterogeneous subfamilies. As necessitates from the anatomical schemes of subfamilies included the subfamily *Pseudironinae*, where gonads are deposited dorsoventrally and the testicular follicles are of different size, markedly differ from the subfamilies *Heptageniinae* and *Anepeorinae* which have nearly identical scheme. The anatomical peculiarities approach the *Pseudironinae* to the family *Siphonuridae* (*Siphonurinae*) though, gonads are placed dorsolaterally and not dorsally in this case. Riek (1973) who classifies the subfamily *Pseudironinae* directly as a part of the *Siphonuridae* namely to the proximity of the subfamilies *Acanthametropodinae* and *Ametropodinae*, came to a similar result on the basis of the study of the external morphology of larvae and adults. On the other hand Edmunds (1970), Edmunds & Jensen (1973) and Tshernova (1970) defend the hitherto position of the subfamily in the family *Heptageniidae*. The investigation of remaining organ systems is urgently needed to definitively clarify this question.

The continuity of the gonads of the subfamily *Arthropleinae* with those of the subfamilies *Heptageniinae* and *Anepeorinae* is obvious even when there are some differences. As far as the gonads are concerned the genus *Arthroplea* is in the relation to the more derived group of genera of the subfamily *Heptageniidae*. Some authors (Balthasar, 1937; Landa, 1969a, 1969b, 1973) consider this group as a separate family. It is surely possible to separate the genus *Arthroplea* from the family *Heptageniidae* but as the differences are much smaller than e.g. between the *Heptageniidae* and the *Oligoneuriidae* or *Coloburiscinae*, I think the status of the subfamily is quite suitable. Edmunds (1970), Edmunds & Jensen (1973), Riek (1973) and Tshernova (1970) are of the same opinion.

The subfamily *Heptageniinae* is evolutionarily homogeneous though we can find two anatomically well defined groups here of which one is more primitive and the other more derived from the gonads comparative

anatomy point of view. These groups are identical with those defined by Landa (1969a, 1973) on the basis of the arrangement of tracheal system, central nerve system and malpighian tubules. These groups essentially consent also with the evolutionary lines in the frame of the subfamily suggested by Edmunds & Jensen (1973) who, however, consider the genus *Epeorus* (subgenera *Ironopsis*, *Ironodes*) as more derived. They divide the group of more plesiomorphic genera into two subgroups so that there are three main evolutionary lines within the subfamily *Heptageniinae*.

From the arrangement of gonads point of view the family *Heptageniidae* (except *Pseudironinae*) represents a group quite diverse from the family *Baetidae* and other related families. This group differs especially by the lateral position of gonads and this character indicates certain affinity to families *Leptophlebiidae* or even to the *Ephemerebellidae*. Also Riek (1973) and Landa (1969b), who exclude this family from the superfamily *Baetoidea*, are of the same opinion. Riek (1973) establishes a separated superfamily *Heptagenioidea* for this family.

The family *Ametropodidae* in the original sense by Bengtsson (1917) was often discussed by many authors. Like this it is accepted also by Edmunds, Allen & Peters (1963). According to the arrangement of gonads it is obvious that the family consists of two distinct groups - *Ametropodidae* and *Metretopodinae*. The differences found on gonads are not so considerable as those found by Landa (1969a, 1973) in the forming of the tracheal system, central nerve system and malpighian tubules. This author also refers to some elements of the relationships between the family *Heptageniidae* and the *Ametropodinae*. Burks (1953) ranges to the family *Ametropodidae* also the *Pseudironinae* on the basis of some common external morphological characters. The gonads of the only genus *Ametropus* are almost of the same structure as those of the *Siphonurinae* (the testis is even of a more primitive arrangement). Also the gonads of the subfamily *Metretopodinae* (*Metretopus*, *Siphloplecton*) do not substantially differ from the anatomical scheme of *Siphonurinae*. That is why both the subfamilies *Ametropodinae* and *Metretopodinae* can be ranged to the family *Siphonuridae*. Riek (1973) classifies the *Ametropodinae* as close to the *Acanthametropodinae* and the *Metretopodinae* as close to the *Siphonurinae* though the situation would be quite opposite according to the arrangement of gonads. Both these subfamilies are ranged to the *Siphonuridae* also by Demoulin (1955b), Tshernova (1970) and Edmunds (1973b). Landa (1973) and some other authors regard this groups as an independent families.

The family *Leptophlebiidae* represents the most variable group of mayflies from the anatomical point of view although it is quite homogeneous evolutionarily because there is an apparent succession of in-

terstage forms. The groups of genera presented above cohere with those defined by Landa (1969a, 1973) on the basis of the study of the tracheal system, nerve cord and malpighian tubules. The family *Leptophlebiidae* is considerably extensive having a great number of genera in all the zoogeographical regions (as many as 200 genera at least - Peters, pers. comm.). Therefore the anatomical knowing of this family will require a further extensive study. It is obvious, after dissecting of several genera, that a very considerable anatomical diversity exists in scope of this family.

The family *Ephemerellidae* is accepted in the sense of Edmunds, Allen & Peters (1963) by all the authors. A considerable morphological diversity of the largest genus *Ephemerella* especially that of larvae (Edmunds, 1959) is reflected even in a considerable diversity in the anatomical arrangement of gonads. It may be possible to suppose that each subgenus of the genus *Ephemerella* represents a true genus because the differences in anatomical as well as morphological characters are much greater than those among remaining genera (some authors divide the family *Ephemerellidae* into as many as 20 genera). Allen (1965) separates the genera *Ephemerellina*, *Austremerella*, *Teloganella* and *Teloganodes* to the subfamily *Teloganodinae*. As far as the gonads are concerned these genera form anatomically well characterized groups with subgenera of the genus *Ephemerella* so that some subgenera of the *Ephemerella* would have to belong to this subfamily from the anatomical point of view. On the other hand Landa (1969a) emphasizes a considerable anatomical difference between *Ephemerellina* and remaining genera. The groups of genera defined by this author agree with those constructed on the basis of the arrangement of gonads. The most primitive are subgenera *Timpanoga* and *Attenella*.

The family *Tricorythidae* probably includes somewhat heterogeneous groups. The subfamily *Tricorythinae* differs substantially from the subfamilies *Leptohyphinae* and *Dicercomyzinae* especially in the position of gonads to body segmentation (as far as may be judged from insufficiently preserved material). Landa (1969a) arrived to the same conclusion on the basis of the arrangement of the tracheal system, central nerve system and malpighian tubules. This author (Landa, 1973) classifies the latter subfamilies as family *Leptohyphinae* while the former one he leaves in the family *Tricorythinae*. It is probable that after a more detailed study of some tropical genera and of other subfamilies *Ephemerithinae* and *Machadorhythinae* further classification of this family will be published.

The families of the superfamily *Caenoidea* sensu Edmunds, Allen & Peters (1963) i.e. *Caenidae*, *Neoephemeridae*, *Baetiscidae* and *Proso-*



*pistomatidae* are accepted by all the systems of classification. These families are well characterized by the arrangement of gonads as well as that of the tracheal system, digestive system, central nerve system and malpighian tubules (cf. Landa, 1969a, 1973) and their interrelations are apparent. According to Demoulin (1955a, 1956) especially the family *Baetiscidae* shows close relationships to the extinct family *Paedephe-meridae* and, consequently, also to the recent family *Isonychiidae* (wing venation). These conclusions were not confirmed by the study of internal organs although there are some palaeontological evidence. Tshernova (1970) classifies the family *Baetiscidae* as closely related to the families *Ephemerellidae* and *Tricorythidae* on the basis of palaeontological material. However, these groups cohere anatomically only distantly. Some authors classify the families *Baetiscidae* and *Prosopistomatidae* into a separated superfamily.

The families of the superfamily *Ephemeroidea* sensu Edmunds et al. (1963) i.e. *Behningiidae*, *Potamanthidae*, *Palingeniidae*, *Euthyplociidae*, *Polymitarciidae*, and *Ephemeridae* are also accepted by all the authors dealing with the higher classification of the order *Ephemeroptera*. The families *Potamanthidae* and *Behningiidae* differ from the remaining families of this group by the position of gonads (testes and ovaries deposited laterally). Also Landa (1973) considers the family *Behningiidae* constituting a separate evolutionary line which shows certain relationships to the family *Leptophlebiidae*. The family *Behningiidae* is also considerably specialized morphologically (Edmunds & Traver, 1959; Demoulin, 1952, 1961). Contrary to the arrangement of gonads, the family *Potamanthidae* does not substantially differ from other families of the superfamily according to the arrangement of the tracheal system. Riek (1973) classifies both the *Behningiidae* and *Potamanthidae* as members of the *Ephemeroidea*, the *Behningiidae* showing relationship to the family *Ephemeridae*. As far as other families are concerned they can be distinguished into two closely related groups of which the first consists of the *Polymitarciidae*, *Euthyplociidae* and *Palingeniidae*, the second of the family *Ephemeridae*. The superfamily *Ephemeroidea* is similarly divided by Landa (1973) who emphasizes the relationships between the *Ephemeridae* and the *Potamanthidae* which are apparent in the arrangement of tracheal system and malpighian tubules (cf. Landa, 1969a).

Demoulin (1957, 1958) separates the New Zealand genus *Ichthybotus* into a separated family. Although the gonads of this genus were not investigated it can be supposed that they do not markedly differ from those of *Ephemer* (cf. Landa, 1969a, 1973). The family *Ichthybotidae* is accepted also by Tshernova (1970). McCafferty (1972) isolates the Ne-arctic genus *Pentagenia* into a separated family which is reclassified

by McCafferty & Edmunds (1976) as a subfamily of the family *Palingeniidae* on the basis of a newly postulated rule that a derived group would be classified with its more apomorphic ally.

The grouping of recent families into higher taxonomic groups is very unstabilized at present. As an example the family *Baetiscidae* can serve which is classified into the superfamily *Caenoidea* by Edmunds, Allen & Peters (1963), into the superfamily *Prosopistomatoidea* by Riek (1973), into the *Oligoneurioidea* by Demoulin (1958), into the *Ephemeroidea* by Tshernova (1970), and into the *Leptophlebioidea* by Landa (1973, 1969a). This is the reason we avoid the discussion of this question on the basis of comparative anatomy of internal organs. The families would be tentatively divided into higher groups on the basis of position of gonads to the alimentary canal; some groups (e.g. *Ephemeroidea*, *Caenoidea*) are well defined.

## SUMMARY

1. The internal reproductive system (testes, ovaries and gonoducts) of 164 species from 94 genera was investigated. With the exception of monotypic Australasian family *Siphlaenigmatidae* the gonads of all known families and nearly all subfamilies were studied. The older larvae (the differentiation of gonads is completely finished and the changes connected with descent of mature spermatozoa and eggs do not occur yet) were used for anatomical study.

2. The testes are deposited along the alimentary canal and consist of a large number of testicular follicles which envelop the seminal duct from above and from the sides. The follicles are connected with ducts directly. The seminal ducts are formed by a simple tube extending from the apex of testis to the 9th abdominal segment. The seminal vesicle is formed in the last segments of expanding of seminal duct. The most important characters of testes from the comparative anatomy point of view are as follows: (A) position of testes to the alimentary canal (dorsal, dorsolateral, lateral, ventrolateral); (B) position of testes to the body segmentation (testis can be produced to the prothorax); (C) shape of testis and shape of its apical portion (cylindrical, subcylindrical, bilaterally flattened, bent or s-curved); (D) size and arrangement of testicular follicles equal or different in size, (spherical, cylindrical, produced); (E) position of follicles to seminal duct (follicles perpendicular or oblique); (F) shape of seminal vesicle and (G) position of seminal vesicle to body segmentation.

3. The ovaries are deposited similarly to the testes and consist of a large number of ovarioles enveloping the oviduct from above and from the sides. The oviduct is simple and tubiform extending from the apex of ovary to the posterior margin of the 7th segment. The following characters are supposed to be the most important for comparative anatomy purposes: (H) position of ovaries to the alimentary canal; (J) position of ovaries to the body segmentation (similar to that of testes); (K) shape of ovary and shape of its apical portion (cylindrical, moderately flattened, strongly flattened - tongue-shaped); (L) position of ovarioles (ovarioles perpendicular, slightly oblique, strongly oblique to oviduct).

4. Taking into consideration the hypothesis about 10 pairs of

metamerically arranged gonads of insect ancestor which did not communicate one another, the plesiomorphic characters are as follows: different size of testicular follicles, gonads deposited dorsally and only in abdomen, testicular follicles or ovarioles perpendicular to gonoducts and cylindrical seminal vesicle deposited in segments VII-IX. Apomorphic characters are as follows: follicles multiplied and equal in size and length, gonads produced into the thorax and deposited ventrally and ventrolaterally, testicular follicles or ovarioles oblique to ducts, seminal vesicle spherical in segment IX. The following evolutionary tendencies were observed: the shift of gonads to ventrolateral position and cranially to the thorax, multiplication of follicles and its oblique position, bilateral flattening and producing of gonad, shift of seminal vesicle caudad.

5. Based on the study of the most recent subfamilies several evolutionary lines were recognized: (1) gonads deposited dorsally, extending from meta- or mesothorax to segment VI, ovarioles perpendicular or slightly oblique to oviduct, testicular follicles sometimes different in size (*Siphonurinae*). This line consists of the *Siphonurinae*, *Ametropodinae*, *Acanthametropodinae*, *Rallidentinae*, *Chiloporter*, *Pseudironinae*, *Baetidae* and probably also *Siphlaenigmatidae*. The *Ameletopsinae*, *Oniscigastrinae*, *Isonychiinae* and *Oligoneuriidae* form an intermediary group between the first and the second evolutionary line characterized by the dorsolateral position of gonads. (2) gonads deposited laterally, testicular follicles usually multiplied, equal in size, ovarioles sometimes oblique or strongly oblique. This line includes three lineages: (a) *Heptageniidae* (*Heptageniinae*, *Arthropleinae*, *Anepeorinae*), *Coloburiscinae*; (b) *Leptophlebiidae*, *Ephemerellidae*, *Tricorythidae*, *Neophemeridae*, *Caenidae*, *Prosopistomatidae*, *Baetiscidae*. In some families the gonads are remarkably shifted into thorax (into the head in the genus *Caenis*; (c) *Behningiidae*, *Potamanthidae* - these families form an interstage between the groups (1) and (2) (gonads deposited laterally but bilaterally flattened). (3) gonads deposited ventrolaterally, considerably bilaterally flattened. This line includes the *Euthyplociidae*, *Polymitarciidae*, *Palingeniidae*, and *Ephemeridae*.

6. The interfamilial and intrafamilial relationships are discussed on the basis of the arrangement of internal reproductive system. The results are compared with those obtained by Edmunds, Allen & Peters (1963), Landa (1969, 1973), Tshernova (1970), Riek (1973) and others. The relationships between mayfly gonads and gonads of insect order with panoistic ovarioles are also discussed.

# ZUSAMMENFASSUNG

1. Die inneren Geschlechtsorgane (Hoden, Ovarien und Geschlechtswege) wurden bei 164 Arten von 94 Gattungen der Eintagsfliegen studiert. Mit Ausnahme der australischen Familie *Siphlaenigmatidae* wurden alle bekannte Familien und fast alle Unterfamilien untersucht. Für das Gonadenstudium wurden ältere Larven benutzt, bei welchen schon die Differenzierung der Geschlechtsorgane beendet wurde und welche noch keine, mit dem Abstieg der reifen Spermien in den Samenleiter und der reifen Eier in den Eileiter verbundene Veränderungen aufwiesen.

2. Die Hoden sind längs der Verdauungsröhre gelegt und setzen sich aus grosser Menge von Follikeln, die den Samenleiter beiderseits und von oben umhüllen. Die Follikeln münden direkt in den Samenleiter. Der Samenleiter bildet eine enge vom Apikalteil des Hodens bis zum Abdominalsegment IX durchgehende Röhre. In den letzten Abdominalsegmenten verbreitet sich der Samenleiter in die Samenblase. Vom Sichtpunkt der vergleichenden Anatomie sind folgende Merkmale am bedeutendsten: (A) die Lage des Hodens in bezug zur Verdauungsröhre (dorsal, dorsolateral, lateral, ventrolateral); (B) die Lage in bezug zur Körpergliederung (der Hode kann bis in den Prothorax eingreifen); (C) Gesamtform des Hodens und seines Apikalteils (zylinderförmig, verflacht, Hoden median gebogen); (D) Grösse und Anordnung der Follikeln (gleiche oder verschiedene Grösse, kugelförmig, zylinderförmig, länglich); (E) die Lage der Follikeln in bezug zum Samenleiter (senkrecht oder schief); (F) Form der Samenblase und (G) die Lage der Samenblase in bezug zur Körpergliederung.

3. Die Ovarien sind gleichartig wie die Hoden gelegt und von grosser Menge von Ovarioles gebildet, die den Eileiter von oben und zu beiden Seiten umhüllen. Bei älteren Larven ist schon das Vitellarium gebildet. Der Eileiter bildet einfache, vom Apikalteil des Ovars zur Intersegmentalmembran zwischen den Abdominalsegmenten VII und VIII auslaufende Röhre. Vom Sichtpunkt der vergleichenden Anatomie sind folgende Merkmale am wichtigsten: (H) die Ovarlage in bezug zum Verdauungssystem; (J) die Ovarlage in bezug zur Körpergliederung (die Ovarlage analog wie beim Hoden); (K) Gesamtform des Ovars und seines Apikalteiles (zylinderförmig, mässig verflacht, stark verflacht - zungenförmig); (L) die Lage

der Ovarioles in bezug zum Eileiter (senkrecht-, mässig schief- und stark schiefstehende Ovariolen).

4. Nimmt man die Hypothese von 10 wechselseitig nicht kommunizierten segmentan angeordneten Gonaden des Insektenurahns in Betracht, zeigen sich als plesiomorphe Merkmale vor allem: ungleiche Grösse der Testikeln, die nur im Abdomen lokalisierten Gonaden in der Dorsallage, senkrecht stehende Testikeln und Ovariolen und die Samenblase in den Segmenten VII - IX. Apomorphe Merkmale sind: gleiche Grösse und Vermehrung der Testikeln, in den Thorax eingreifende Gonaden, laterale und ventrolaterale Gonadenlage in bezug zum Verdauungssystem, schiefstehende Testikeln und Ovariolen, kugelförmige Samenblase nur im segment IX. Bei den Eintagsfliegen machen sich folgende Tendenzen sichtbar: die Verschiebung der Gonaden in die Ventrolateral- und Laterallage und ihre Verschiebung in den Thorax, Vermehrung der Testikeln und Ovariolen, Verflachung und Verlängerung des Hodens und des Ovars, Verschiebung der Samenblase kaudal.

5. Auf Grunde des Studiums fast aller rezenten Eintagsfliegen- gruppen kann man diese Entwicklungslinien charakterisieren: (1) Gonaden dorsal gelegt, greifen bis in Meso- und Metathorax ein, Ovariolen senkrecht oder mässig schief gestellt, Testikeln können von ungleicher Grösse sein (*Siphonurinae*). Zu dieser Linie gehören *Siphonurinae*, *Ametropodidae*, *Acanthametropodinae*, *Rallidentinae*, *Chiloporter*, *Pseudironinae*, *Baetidae* und wahrscheinlich auch *Siphlaenigmatidae*. Ein Übergangstyp zwischen der ersten und der zweiten Entwicklungslinie ist die Gruppe mit dorsolateral Gonadenlage, repräsentiert von den Unterfamilien *Ameletopsinae*, *Oniscigastriinae*, *Isonychiinae* und *Oligoneuriinae*; (2) Gonaden lateral gelegt, Testikeln können vermehrt sein, gleicher Grösse, Ovariolen können auch stark verschiefte sein. Diese Entwicklungslinie setzt sich aus drei Gruppen zusammen: a) *Heptageniidae* (*Heptageniinae*, *Arthropleinae*, *Anepeorinae*), *Coloburiscinae*; b) *Leptophlebiidae*, *Ephemere-rellidae*, *Tricorythidae*, *Caenidae*, *Neophemeridae*, *Baetiscidae*, *Proso- pistomatidae*. Bei dieser Linie kam es zur deutlichen Verschiebung der Gonaden in den Thorax (bei der Gattung *Caenis* greift das Ovar in den Kopf ein). c) *Behningiidae*, *Potamanthidae*; diese Familien bilden Übergang zur dritten Gruppe. Die Gonaden sind noch lateral gelegt, aber bilateral verflacht. (3) Gonaden in ventrolateral Lage, Ovarien und Hoden können bilateral verflacht sein. Zu dieser Linie gehören Familien *Euthyplociidae*, *Polymitarciidae*, *Palingeniidae* und *Ephemeridae*.

6. Die Beziehungen zwischen den Familien und Unterfamilien eventuell auch zwischen einigen Gattungen werden diskutiert. Die durch das Gonadenstudium eroberte Angaben mit Ergebnissen folgender Autoren verglichen (Edmunds, Allen & Peters, 1963; Landa, 1969, 1973; Tshernova,

1970; Riek, 1973 und andere). Die Beziehungen der Eintagsfliegengonaden zu den Gonaden anderer Insektengruppen mit panoistischen Ovariolen werden auch diskutiert.

# SOUHRN

1. Vnitřní reprodukční systém (varlata, vaječníky a gonodukty) byl studován u 94 rodů (164 druhů) jepic. S výjimkou monotypické australské čeledi *Siphlaenigmatidae* byly studovány všechny známé čeledi a téměř všechny podčeledi. Pro studium gonád bylo použito starších larev, u kterých je již dokončena diferenciace pohlavních orgánů a u kterých dosud nenastaly změny související se sestupem zralých spermií do chámovodu a zralých vajíček do vejcovodu.

2. Varlata jsou uložena podél trávicí trubice a skládají se z velkého množství folikulů, které obalují chámovod shora a ze stran. Folikuly jsou připojeny přímo k chámovodu. Chámovod je tvořen jednoduchou úzkou trubicí, probíhající od apikální části varlete až do abdominálního segmentu IX. V posledních zadečkových segmentech se chámovod rozšiřuje v semenný váček. Z hlediska srovnávací anatomie jsou nejdůležitější tyto znaky: a) uložení varlete vzhledem k trávicí trubicí (dorsální, dorsolaterální, laterální, ventrolaterální); b) uložení vzhledem k tělní segmentaci (varle může zasahovat až do předohrudi); c) celkový tvar varlete a jeho apikální části (válcovitý, zploštělý, varle prohnuté mediálně); d) velikost a uspořádání folikulů (stejně či rozdílné velikosti, kulovité, válcovité, protažené); e) postavení folikulů vzhledem k chámovodu (postaveny kolmo či šikmo); f) tvar semenného váčku; g) uložení semenného váčku vzhledem k segmentaci.

3. Vaječníky jsou uloženy obdobně jako varlata a tvořeny velkým množstvím ovariol, které obalují vejcovod shora a ze stran. U starších larev je již vytvořeno vitellarium. Vejcovod tvoří jednoduchá trubice, probíhající od apikální části vaječníku k intersegmentální membráně mezi abdominálními segmenty VII a VIII. Z hlediska srovnávací anatomie jsou nejdůležitější tyto znaky: h) uložení vaječníku vzhledem k trávicí soustavě; j) uložení vaječníku vzhledem k tělní segmentaci (uložení vaječníků obdobně jako uložení varlat); k) celkový tvar vaječníku a jeho apikální části (válcovitý, mírně zploštělý, silně zploštělý - jazykovitý); l) postavení ovariol vzhledem k vejcovodu (ovarioly postaveny kolmo až mírně šikmo nebo silně šikmo).

4. Vezmeme-li v úvahu hypotézu o 10 párech vzájemně nekomunikujících gonád hmyzího předka, které byly segmentálně uspořádány, potom plesiomorfními znaky jsou zejména: nestejná velikost testikul, uložení



gonád dorsální a pouze v abdomenu, kolmo postavené testikuly či ovario-ly, semenný váček válcovitý, uložený v segmentech VII-IX. Apomorfními znaky jsou: stejná velikost a zmnožení testikul, gonády zasahující do hrudi, uložené laterálně či ventrolaterálně vzhledem k trávicí soustavě, šikmo postavené testikuly či ovario-ly, semenný váček kulovitý, uložený v segmentu IX. U jepic se projevují tyto vývojové tendence: přesunutí gonád do ventrolaterální či laterální polohy a jejich posunutí do hrudi, zmnožení a zešikmení ovariol a testikul, zploštění a protažení varlete i vaječníku, posun semenného váčku kaudálně.

5. Na základě studia téměř všech recentních skupin jepic je možno charakterizovat tyto vývojové linie: (1) Gonády uložené dorsálně zasahující do zado- či středohrudi, ovario-ly postavené kolmo nebo mírně šikmo, testikuly mohou být nestejně velikosti (*Siphonurinae*). Do této linie patří *Siphonurinae*, *Ametropodidae*, *Acanthametropodinae*, *Rallidentinae*, *Chiloporter*, *Pseudironinae*, *Baetidae* a pravděpodobně i *Siphonurinae*. Přechodným typem mezi první a druhou vývojovou linií je skupina s dorsolaterálním uložením gonád, reprezentovaná podčeledmi *Ameletopsinae*, *Oniscigastrinae* a *Isonychiinae* (čeleď *Siphonuridae*) a čeledí *Oligoneuriidae*. (2) Gonády uloženy laterálně, testikuly mohou být zmnožené, stejné velikosti, ovario-ly mohou být i silně sešikmeny. Tato vývojová linie se skládá ze tří skupin: a) *Heptageniidae* (*Heptageniinae*, *Arthropleinae*, *Anepeorinae*), *Coloburiscinae*; b) *Leptophlebiidae*, *Ephemerellidae*, *Tricorythidae*, *Neoephemeridae*, *Caenidae*, *Prosoptomatidae*, *Baetiscidae*. U této skupiny došlo k výraznému posunutí gonád do hrudi (u rodu *Caenis* zasahuje vaječník do hlavy); c) *Behningiidae*, *Potamanthidae*. Tyto čeledi tvoří přechod ke třetí skupině. Gonády jsou uloženy dosud laterálně, ale jsou bilaterálně zploštělé. (3) Gonády jsou ve ventrolaterální poloze, vaječník i varle mohou být bilaterálně zploštělé. Do této linie patří *Euthyplociidae*, *Polymitarcidae*, *Palingeniidae* a *Ephemeridae*.

6. Vztahy mezi čeledmi i podčeledmi, popřípadě i mezi některými rody, jsou prodiskutovány. Údaje získané studiem gonád jsou srovnány s výsledky následujících autorů: Edmunds, Allen & Peters (1963), Landa (1969, 1973), Tshernova (1970), Riek (1973) aj. Diskutují se i vztahy pohlavních orgánů jepic k pohlavním orgánům ostatních skupin hmyzu s panoistickými ovariolami.

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