Comparative anatomy of the internal reproductive organs of mayflies (*Ephemeroptera*)
Comparative anatomy of the internal reproductive organs of mayflies (*Ephemeroptera*)
Scientific Editor
Corresp. member of ČSAV Jaroslav Weiser, DrSc.

Scientific Adviser
Corresp. member of ČSAV Ludovit Weisman, DrSc.
Comparative anatomy of the internal reproductive organs of mayflies

(Ephemeroptera)
CONTENTS

Introduction ........................................... 7
Survey of literature .................................. 9
Material and methods .................................. 16
Structure and basic types of arrangement of testis
and seminal vesicle .................................... 26
Structure and basic types of arrangement of ovary ........................................... 34
Anatomical schemes of internal reproductive system of families,
subfamilies and genera of the order Ephemeroptera ........................................... 38
Discussion .............................................. 81
    Comparison of results with literary data ........................................... 81
    Relations of mayfly gonads to those of other insect
orders having panoistic type of ovarioles ........................................... 84
Anagenetic trends in forming of internal reproductive
organisms of the order Ephemeroptera ........................................... 87
Hypothetical scheme of anagenesis of internal repro-
ductive system of the order Ephemeroptera ........................................... 92
Interfamilial and intrafamilial relationships within
the order based on comparative anatomy of gonads ........................................... 97
Summary ................................................. 105
Zusammenfassung ......................................... 107
Souhrn ................................................. 110
References ............................................. 112
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 Palaeartic 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 Palaeartic 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-Baznosa- nu, 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, Polynoptera). 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.

Acknowledgements

I should like to thank to Dr. Vladimír Landa DrSc., corresponding member of ČSAV and director of Institute of Entomology, Praha, for providing me with the material and for the careful and critical reading of manuscript. My thanks are also due to Prof. G. P. Edmunds of University of Utah, Salt Lake City, Utah; Prof. W.L.Peters of Florida Agricultural and Mechanical University, Tallahassee, Florida; Dr. E.F. Riek of CSIRO, Canberra, Australia; Dr. P. Štys of Department of Systematic Zoology, Charles University, Praha and to others who kindly provided me with material from other zoogeographic regions.
We find the first reference concerning the reproductive system of *Ephemeroptera* in Schwammerdam’s work *Ephemeris vita* (1975), where besides other organ systems also gonads of *Palinchna longicauda* (Oliv.) are described and illustrated. As he was studying testes especially in adults, he came to many incorrect 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 accessory 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 *Palinchna longicauda* (Oliv.), *Ephorom 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 *Eudonurus* and *Rhithrogena* (as *Heptagenia*), *Oligoneuriella* (as *Oligoneuria*), *Caenis*, *Palinchna*, *Potamanthus* and *Ephorom* (as *Polymitarays*) 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 *Ephorom*, 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 Siphlonurus lacustris Etn., Heiner (1914) deals with anatomy of Cloeon dipterus (L.), Baetis fuscatus (L.) and Habrophlebia fusca (Curt.), Vayssière (1882,1890) deals in details with the anatomy of Procopistoma and later (Vayssière, 1934, 1937) describes the gonads of Baetisca carolina Traver, B. obesa Say and Proboecidoplocia 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 monograph on biology and taxonomy of Nearctic mayflies. As to the male reproductive system, the main attention was given to changes of gonads after moulding of larva into sub-imago 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 (larvule), placement of gonopores and inervation 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 Siphlonurus, Parameletus, 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 *Eddyonurus lateralis* (Curt.) and *Rhithrogena semiaolorata* (Curt.) is introduced by Codreanu (1939) who studies the effects of ectoparasite *Symbioaladius 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)—Palaearctic 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 fundamentals 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 phylogensis 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 Polymitarcyidae). 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 mechanismus assisting the transfer of spermatozoa in Habroplebia 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 recognizable 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 chamber with a sac-shaped seminal receptacle which may serve as copulatory pouches. Grandi (1947, 1955) describes female copulatory organs of European species of genera Siphlonurus, Cloeon, Centroptilum, Baetis, Rhithrogena, Epeorus, Heptagenia, Ecdyonurus, Ephemerella, Caenis, Para-leptophlebia, Choroterpes, Habroleptoides, Habrophlebia, and Ephemerella. 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 Lepto-phlebiidae, 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 ovipositor of orthopteroid insects. Copulatory organs of adults in the genus Campururus are described by Morgan (1913), and Needham & Murphy (1924). The development of ovipositor and copulatory organs in male larvae was dealt with by Quadri (1940). There are only slight differences between subimagos and imagos. 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, Siphlonurus, Baetis, Centroptilum, Cloeon (oviparous species), Metretopus, Arthrolea, Heptagenia, Ecdyonurus, Ephemeraella, Caenis, Leptophlebia, and Ephemera 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 nonfibrilar adhesive layer, funnelform 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, Hemiptera), 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.

Siphlonuridae

Siphlonurinae

A - Ameletoides locusalbinus Tillyard, Hedley Creek, New South Wales, Australia, 9.11.1966 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♂, 6♀); NA - Ameletus velox Dodds, Mill Creek, Salt Lake Co., Utah, USA, 3.vi.1965 leg.V.Landa (2♂, 1♀); NT - Siphlonella sp., Rio Illapel, Coquimbo Prov., Caren., Chile 15.xi.1963 leg. G.F. Edmunds (3♂, 1♀); P - Notreletus goethhebueri Lest., brook, Dobřiš, 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 - Siphlonurus aestivalis Eaton, Smutná, Bechyně, South Bohemia, Czechoslovakia, 16.v.1974 leg. T. Soldán (4♂, 7♀); P - Siphlonurus lacustris Eaton, Mumlava, Kořenov, North Bohemia, Czechoslovakia, 4.ix.1973 leg. T. Soldán (11♂, 9♀); P - Siphlonurus armatus Eaton, pools near Lužnice Riv., Sezimovo Ústí, South Bohemia, Czechoslovakia, 10.v.1973 leg. T. Soldán (4♂, 5♀); NT - Siphlonurus (Siphilurella) occidentalis Eaton, Mill Creek, Salt Lake Co., Utah, USA, 3.vi.1965 leg. V. Landa (2♂, 1♀).
Acanthometropodinae
P - Acanthometropus nikolskyi Tshernova, Amur riv., USSR, v.1956 leg.O. A.Tshernova (1♂); NA - Acanthometropus sp., Savannah riv., Georgia, USA, leg. G. F. Edmunds (coll. Landa) (1♀).

Oniscigastriinae

Ameletopsinae

Isonychiinae

Coloburisinae

Rallidentinae

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

Oligoneuriidae

Oligoneuriinae


Heptageniidae

Heptageniinae

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

Anepeorinae

Arthropleinae
Pseudironinae

Ametropodidae

Ametropodinae

Metretopodinae

Leptophlebiidae

**Ephemerellidae**

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

**Tricorythidae**

**Tricorythinae**


**Leptohyphinae**


**Dicerocomyzinae**


**Behningiidae**


**Potamanthidae**

Euthyplociidae


Ephemeridae


Polymitarcidae

Polymitarinae


Campsurinae


Asthenopodinae

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

**Palingeniidae**


**Neoephemeridae**


**Caenidae**


**Baetiscidae**

Prosopistomatidae


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 subimagoes and adults. Similarly, the ovaries of mature larvae, subimagoes 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 (gerarium 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 methylene 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 membranous 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 Siphlonurinae, 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 Amelotopinae, Ontiscostrinae, 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, Arthropelinae, Anepeorinae, Leptophlebiidae, Ephemerellidae, Tricorythidae, Behningiidae, Potamanthidae, Neoperiodidae, Caenidae, Baetiscidae, and Prosoptistomatidae. 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 Ephemeraidae, Polymitarcyidae, Euthysicosidae, 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 (Cinygmulina, Rhithrogena, Epeorus - subgenera Epeorus, Iron, Ironodes), Leptophlebiidae (pleiomorphic group of genera), Ephemerellidae, Behningiidae, Euthyplociidae, Asthenopodinae, Campsuriinae, and Palingeniidae; testes extend from metathorax to the sixth abdominal segment in Siphlonurinae, Acanthametropodinae, Amelotopinae (Ameletopsis, Mirawara), Rallidentinae, Baetidae (Callibaetis, Centropilum, Cloeon, Procloeon, Baetis - some species, Baetopus), Heptageniinae (Afronurus, Eodyonurus, Heptagenia,
Stenacron, Stenonema, Thalerosphyrus), Anepeorinae, Arthrolepinae, Ame
tropodinae, Metretopodinae, Leptohybliidae (some genera), Ephemer
dellidae (some genera), Leptophlebiidae, Diacycoylinae, Potaman
thidae, Ephemeridae (Ephemera), Polymitarcinidae.

(Bb) testes extend either from mesothorax or from prothorax; suspen
sory ligament can occur even in head to the sixth abdominal seg
ment. Testes are produced into mesothorax in Pseudioninae, Ephemer
dellidae (Telogonidae), Ephemeridae (Hexagenia, Lutobrancha, Pen
tagenia), Caenidae (Brachycercus), Prospistomatidae; testes are pro
duced to prothorax in Leptohybliidae (Paraleptophlebia - some species, Hagenulus, Traverella), Caenidae (Caenis, Caenomedea, Ta
smanoceenis), Baetiscidae, Neoephemeraidae.

(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 Ephemerdellidae (Ephemera - subgenera Drummell and Eurylo
drilla: PT-V or PT-IV).

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

(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: Siphlonurinae, Acanta
metropodinae, Oniscostraginae, Ameleopinae (Chiloporter), Ralli
dentinae, Metretopodinae.

(Cb) testis is cylindrical or subcylindrical, straight, with apical part rounded or slightly pointed: Ameleopinae (Ameleopsis, Mi
rawara), Isonychiinae, Coloburiscinae, Baetidae, Oligoneuridae, Heptageniinae, Anepeorinae, Pseudioninae, Arthrolepinae, Ame

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

(Cd) testis is slightly or apparently bilaterally flattened, straight: Behningiidae, Potamanthidae, Ephemideridae, Polymitarcidiae, Palinge
niidae, Euthyplociidae; slightly dorsolaterally flattened in Baeti
tiscidae.
(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: Siphlonurinae (Ameletoides, Ameletus, Metreletus, Parameletus), Acanthametropodinae, Ameletopsisinae (Chiloporter), Rallidentinae, Pseudironinae, Ametropodinae, Metretropodinae, 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:

(Db1) follicles relatively large, short and cylindrical (rarely spherical), each testis consists of approx. 100-250 follicles (follicles arranged at most into four longitudinal rows): Siphlonurinae (Siphlonurus), Oniscigastrinae, Ameletopsisinae (Ameletopsis, Mirawara), Isonychiinae, Coloburiscinae, Baetidae, Oligoneuriinae, Heptageniinae, Anepeorinae, Arthropleinae, Leptophebidae (Atalophelia, Atalomicria, Atalopheboides, Jappa, Kirrara), Ephemerellidae (Ephemerella - subgenera Attenna, Drunella - some species), Behningiidae, Potamanthidae, Ephemeridae, Euthyploeciidae, Polymitarcidae, and Palingeniidae.

(Db2) 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): Leptophebidae (Paraleptophelia, Leptophelia, Habrophelia, Habroleptoiodes, Hagenulus, Traverella, Thraulus), Ephemerellidae (Ephemerella - subgenera Ephemerella, Torleya, Chitonophora), Tricorythidae, Neoephemeredae, Caenidae, Baetisoidae, Prospistomatidae.

(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): Siphlonurinae, Acanthametropodinae, Oniscigastrinae, Ameletopsisinae (Ameletopsis, Mirawara, Chiloporter), Isonychiinae, Rallidentinae, Oligoneuriinae, Heptageniinae, Ametropodinae, Metretropodinae, Leptophebidae (Atalomicria, Atalophebia, Jappa), Ephemerellidae (Ephemerella - subgenera Timpanoga, Attenna, Ephemerella; Teloganodes, Ephemerellina), Leptohypinae, Dicercomysinae, Behningiidae, Potamanthidae, Ephemeridae, Polymitarcinae, Asthenopodinae, Palingeniidae, Euthyploeciidae, Neoephemeredae, Caenidae, Baetisoidae, Prospistomatidae.

(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, Leptophelibidae (Hagenulus, Trave-
rella, Thraulius, Choroterpes), Tricorythinae, Leptothyphinae (Tri-
corythodes), Campsurinae.

(F) shape of seminal vesicle:

(Fa) seminal vesicle is inconspicuous, seminal duct only slightly
extended: Coloburisinae, Oligoneuriinae, Leptophlebiidae (Atalo-
micria, Atalophebia, Jappa), Ephemereillidae (Teloganodes), Tri-
corythidae (Leptothyphinae, Diceroomysinae), Behngiidae, Neopehe-
meridae, Caenidae, Prosopistomatidae.

(Fb) seminal vesicle is apparent, seminal duct extended gradually
caudal; vesicle usually cylindrical or elongated: Oniscoigastrinae,
Ameletopsinae (Ameletopsis, Mirawara, Chiloporter), Baetidae, Hept-
geninae (Stenonema, Steniacron), Arthropleinae, Leptophlebiidae
(Leptophlebia, Pataleptophlebia, Kimminula, Kurrara), Ephemereilli-
da (Ephemereillina, Ephemereilla - subgenera Ephemereilla, Drunella,
Eurylophella, Torleya, Chitonophora), Ephemeredae, Euthyplociidae,
Polymitarcinae, Campsurinae, Palingeniidae.

(Fc) seminal vesicle conspicuous, seminal ducts extended suddenly;
seminal vesicle cylindrical, funneliform or spindle-shaped, only
slightly diminished caudal: Siphlonurinae, Isonychiinae, Ralliden-
tinae, Heptageniidae (Cinygmula, Rhithrogena, Epeorus - subgenera
Epeorus and Iron; Afronurus, Eodyonurus, Heptagenia), Anepeorinae,
Pseudironinae, Ametropodinae, Metretopodinae, Leptophlebiidae, Epe-
merellidae (Ephemereda - subgenera Attenella and Timpanoga), Pota-
manthidae, Aethenopodinae, Baetidae.

(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), Coloburisinae, Oligo-
neuriinae, Arthropleinae, Ephemereillidae (Teloganodes, Ephemereilla
- subgenus Timpanoga), Leptothyphinae, Behngiidae (Behningia),
Neopehmeridae (Potamanthellus), Caenidae (Caenis, Caenomedeua,
Tasmanocoonis), 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: Siphlonurinae (Ameletua, Siphlonella,
Metreletus, Parameletus, Siphlonurus), Acanthametropodinae, Onisco-
gastrinae, Ameletopsinae (Ameletopsis, Mirawara), Isonychiinae
(Isonychia - some species), Baetidae (Callibaetis, Baetis - some species, Baeotopus, Centroptilum, Cloeon, Procloeon), Heptageniinae, Anaperoinae, Pseudironinae, Leptophlebiidae (Atalophlebia, Alasomia, Jappa), Ephemerellidae (Ephemerellina, Ephemerefall - sub-genera Attenella, Drunella, Eurylophella, Chitonophora, Torleya, Ephemerefall), Tricorythinae, Diceroomysinae, Behningiidae (Dolania), Potamanthidae, Ephemeridae, Euthyplociidae, Palingeniidae, Neophe-meridae (Neophephora), 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: Siphlonurinae (Ameletoides), Isonychiinae (Isonychia - some species), Hallidentinae, Baetidae (Baetodes, Pseudocloeon, Baetis - some species), Ametropodinae, Metretopodinae, Leptophlebiidae (Lepto- phlebia, Habrophlebia, Habroleptoides, Thraulus).
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 membraneous 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 oogonia 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 Siphlonurinae, Acanthametopodinae, 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, Oligonsuriinae, 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 Coloburiscoinae, Heptageniinae, Anepeorinae, Arthropleinae, Leptophlebiidae, Ephemerellidae (the anterior part of ovary can be dorsolateral), Triocorythidae, Behningiidae, Potamantidae, Neophemeridae, Caenidae, Baetiscidae, Prosopistomatidae.

(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: Coloburiscoinae, Heptageniinae (Cinygmla, Epeorus - subgenera Epeorus, Iron, Ironopsis), Leptophlebiidae (Atalomicria, Atalphlebia, Atalphlebiodes, Jappa), Ephemeroellidae (Ephemerella), Euthyplociidae (Euthyplocia), Aethenopodinae, Campsuriinae.

(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 (Chiloporter), Isonychiinae, Oligonesurinae (Oligoneuriella, Laochlania), Heptageniinae (Epeorus - subgenus Ironodes), Anepeorinae, Leptophlebiidae (some genera), Behningiidae (Behningia), Potamantidae (Rhoenanopsis), Ephemeridae (Ephemera), Euthyplociidae (Campylocia), Palingeniidae; ovaries are produced into mesothorax in Siphlonurinae (Ameletoides, Amele-
tus, Siphlonella, Metreletus, Parameletus, Acanthometropodinae, Ameletopsinae (Ameletopsis, Mirawara), Rallidentinae, Baetidae (Callibaetis, Baetodes, Cloeon, Proclioneon, Centropilum, Baetis - some species), Oligoneuriinae (Homoeoneuria, Oligoneuriusca), Heptamerinae (Stenonema, Stenaaron), Ametropodinae, Metretopodinae, Leptophlebiidae (Paraleptophlebia - some species, Leptophlebia, Habrophlebia, Habroleptoidae), Ephemereillidae (Ephemereilla - subgenera Ephemereilla, Torleya, Chitonophora), Tricorythinae, Leptothyphinae, Potamanthidae (Potamanthus, Potamanthodes), Ephemereidae (Hexagenia, Litobrancha, Pentagenia), Prosoptistomatidae.

(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 Siphlonurinae (Siphlonurus), Oniscigastrinae, Heptageniinae (Afronurus, Edyonurus, Heptagenia - some species), Pseudironinae, Leptophlebiidae (Pareleptophlebia - some species, Traverella, Hagenulus), Ephemereillidae (Ephemereilla, Teloganodes), Neoephemeridae, Caenidae (Brachycerus), Baetisidae; ovaries are produced into head in some genera of the family Caenidae (Caenis, Caenomeda, Tasmanocoenis).

(Jd) ovaries are deposited in thorax and abdominal segments but not reaching segment VI: Baetidae (Baetodes, Pseudoclaeon, Baetis - some species: PT or MST - IV-V), Leptophlebiidae (some genera), Ephemereillidae (Ephemereilla - 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-cruved, apical part bluntly pointed or rounded: Siphlonurinae, Acanthometropodinae, Rallidentinae, Oniscigastrinae, Coloburiscinae, Metretopodinae.

(Kb) ovary is cylindrical or subcylindrical, only slightly bilaterally flattened, straight, apical part bluntly pointed or rounded: Ameletopsinae (Chiloper thor) Ameletopsis, Mirawara, Isonychiinae, Baetidae, Oligoneuriinae, Aneporinae, Arthrolepineae, Pseudironinae, Ameletopadinae, Leptophlebiidae (Atalomicria, Atalophlebia, Jappa, Atalophlebioidae), Ephemereillidae (Ephemereilla - subgenera Attenella, Timpanoga, Drunella, Ephemereilla, Torleya), Tricorythidae, Leptothyphinae, Caenidae.

(Kc) ovary is tongue-shaped, mostly bilaterally flattened, bluntly pointed or produced into a narrow point: Leptophlebiidae (Leptophlebia, Paraleptophlebia, Habrophlebia, Habroleptoides, Traverella, Hagenulus, Thraulus), Potamanthidae, Ephemeridae, Euthyplociidae,
Polymitarcidae, Palingeniidae, Neopheomeridae, Baetiscidae, Prosopistomatidae.

(L) position of ovarioles to oviducts:

(1a) Ovarioles are perpendicular or slightly oblique to oviducts (the angle between axis of ovariole and axis of oviduct is about 70°-90°): Siphlonurinae, Acanthametropodinae, Oniscigastrinae, Ameletopsinae (Ameletopsis, Mirawara, Chiloporter), Coloburiscinae, Rallidentinae, Baetidae, Oligoneuriinae, Heptageniidae (nearly all genera investigated), Anepeorinae, Arthropleinae, Ametropodinae, Metretopodinae, Leptophlebiidae (Atalomicia, Atalophlebia, Jappa), Ephemerrellidae (Ephemrella - subgenera Attenella, Timpanoga), Triorythinae, Behningiidae, Potamantidae, Ephemeredidae (Ephemera), Euthyplociidae, Palingeniidae, Caenidae (Brachycercus). Ovarioles are usually cylindrical, straight and not produced.

(1b) Ovarioles are apparently oblique to oviducts (the angle between axis of ovariole and axis of oviduct is about 30°-60°): Isonychiinae, Leptophlebiidae (Leptophlebia, Paraleptophlebia, Habrophlebia, Habroleptoides, Traverella, Hagenulus), Ephemerrellidae (Teloganodes, Ephemarella - subgenera Ephemarella, Chitonophora, Torleya), Leptophyphinae, Ephemeredidae (Hexagenia, Litobrancha, Pentagenia), Neopheomeridae, Caenidae (Caenis, Caenomedia, Tasmanooenois), 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 - metathorax; I, II, III, IV, I, 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).

Siphlonuridae

Siphlonurinae
(Figs. 14-27)

Testis: deposited dorsally (Aa); MTT, I, II, III, IV, V, VI (Ba); cylindrical and bent medially (Ameletus, Ameletoides, Paramaletus) or arcuately (Siphlonella) in abdominal segments, s-curved in Siphlonurus (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, Siphlonella, Siphlonurus) (Gb).

Ovary: deposited dorsally (Ha); MTT, 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 (Siphlonella, Paramaletus) or slightly oblique (Ameletoides, Ameletus, Metreletus) (La).

The subfamily Siphlonurinae is quite homogeneous. Basic anatomical characters are the same in all genera investigated with the exception of Holarctic genus Siphlonurus 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:
16,17,20,22 - Siphlonella sp. 24 - Ameletus alexandriae. 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 Siphlonuridae (subfamilies Acanthometropodinae, Oniscigastriinae and Coloburiscinae). 28,35 - Acanthometropus nikolskyi. 29,32,34 - Tasmanophlebia nigrescens. 30,31,36,38 - Coloburiscoides sp. 33,37 - Acanthometropus 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 incospicuous), 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 (Pb); 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 (Pb), anatomical scheme of the subfamily Acanthametropodinae does not differ from that of the Siphlonurinae.

Oniscigastriinae
(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 (Db₁), cylindrical, perpendicular to VD (Ea); VS elongated, narrow, VD extended gradually (Pb), 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 Siphlonurinae. It differs from this subfamily especially in position of gonads (Ab, Hb, Bb, Jc).

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

Ameletoes, 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 (Db₁), perpendicular to VD (Ea); seminal vesicle formed by gradually extended VD, elongated (Pb), deposited in VIII and IX (Gb).

Ovary: deposited dorsolaterally (Hb); MTT, MTT, I,II,III,IV,V,VI (Jb); cylindrical, straight, not bent, bluntly pointed in thorax (Mirawara) or rounded at apex (Ameletoes) (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 Amelotopsis and Australian genus Mirawara are similar in their arrangement of gonads but quite different from the subfamily Siphlonurinae (the Neotropical genus Chaquiwa is probably also contained in this group). The second group consists of the Neotropical genus Chiloporter with anatomical scheme similar to the subfamily Siphlonurinae.

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), large and cylindrical, at the right angle to VD (Ea); VS cylindrical, VD expanded suddenly (Fc), deposited in IX (Isonychia ignota) (Ga) 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 OI (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 Siphlonuridae. 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), 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 Siphlonuridae (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 Siphlonuridae (subfamily Rallidentinae) and Ame-
tropodidae. 51,53,59,61,62 - Ametopus albrighti. 54, 55, 57 - Siphlo-
plecton 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 Siphlonuridae 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 Siphlonuridae in arrangement of gonads; the genus Rallidens corresponds to the Australian genus Ameletoidea.

The family Siphlonuridae 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) Siphlonurinae, Acanthametropodinae, Rallidentinae
(b) Ameletopsia, Mirawara (+ Chaquihua) (i.e. Ameletopsinae excluding the genus Chiloporter)
(c) Chiloporter
(d) Ontoegastrinae
(e) Isonychiinae
(f) Coloburiscinae

If the scheme of gonads arrangement of subfamilies Siphlonurinae, Acanthametropodinae and Rallidentinae is considered to be the basic scheme for the Siphlonuridae, 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 pennadatum. 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 Siphlonuridae or to advanced group of genera of Neptagenitidae.

The subfamily Oniscigastrinae is characterized by the shift of gonads into prothorax (Jc) but both testes and ovaries remain deposited dorsolaterally. While in the subfamily Oniscigastrinae certain elements of affinity with the family Baetidae may be seen, the subfamily Coloburiscinae differs from the Siphlonurinae 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, Bactopus, 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 (Db₁), 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 (Db₁), 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, Bactopus, 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 rhennama. 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 (Siphlonuridae). 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, (Db₁), 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 Palaeartic 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 (Siphlonurinae); 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 (Db₁), perpendicular
Figs. 104-118:
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, Eodyonurus, Heptagenia, Stenacon, 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 (Db₁), 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 *Rhistrogena*—gonads only in abdomen, testicular follicles large, ovarioles nearly perpendicular to OL. The specialized group (b) includes genera *Afronurus, Eodyonurus, Stenacon, 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 (Db₁), 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, 127,1128 - 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 (Db₁), 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 VII-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 *Siphlonurinae* and *Acanthometropodinae* (*Siphlonuridae*).

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 Siphlonuridae.

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 *Siphlonurinae* 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 *Siphlonurinae* (*Siphlonuridae*) 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, Atalophebia, Atalophebioides, 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, Atalophebia*), cylindrical, arranged into regular longitudinal rows (Db₁), perpendicular to VD (Ea); VS spindle shaped (Pb) or inconspicuous (*Atalomicria*) (Fa), deposited in VIII-IX (Gb).

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

*Leptophlebia, Paraleptophlebia, Habrophlebia, Habroleptoidea:*

Testis: deposited laterally (Ac); MST, 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 (Db₁), 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, 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 gutta-cta. 161, 165, 169, 172 - Choroterpes (Choroterpes) picteti. 162, 168 - Nabrophlebia 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, Hagenuius:

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, Atalomiceria, and Jappa) is more plesiomorphic, the third group (Choroterpes, Thraulus, Hagenuius, 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, MT, I, II, III, IV, V (VI) (Jb); subcylindrical, slightly flattened, bluntly pointed in thorax (Kb); ovarioles perpendicular or slightly oblique to VD (La).

(b) Ephemera (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) Ephemera (subgenera Ephemera, Torleya, Chitonophora), Ephemereillina, 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 (Ephemereillina)(La) or oblique to OL (Lb).

The group (a) represents the most pleisiomorphic types within the family. The gonads of subgenera Timpanoga and Attanella 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 Ephemeraldidae 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:
Conads of the family Ephemerellidae. 174, 178, 186, 187 - Ephemerellina picts. 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.

62
Figs. 189-202:
Gonads of the family Ephemereellidae. 189,193,195,198,199 - Ephemeraella (Drunella) conestee.190,192,196,200,201 - Ephemeraella (Timpanoga) hecuba. 191,194,197,202 - Ephemeraella (Ephemeraella) 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 Cinaticostella: Db₁, 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 (Db²); 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 (Db₂); perpendicular or slightly oblique to VD *Tricorythodes* (Ba, Eb); VS formed by gradually expanded (Fa), deposited in VII-IX (Ga).

Ovary: deposited laterally (Hc); MTT, 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 *Dicerocomyzinae.*
Figs. 203-218:
Figs. 219-233:
Diceromyszinae
(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 (Db₂), 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 Diceromyszinae 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 Macropharythinae and Ephemerythinae not investigated) comprises two rather heterogeneous groups. While the subfamilies Leptohyphinae and Diceroymyzinae seem to be related to the family Ephemeroellidae (apomorphic group of genera), the subfamily Tricorythinae shows closer affinities to the families Caenidae and Neopephemeridae (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 (Db₁), 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 Leptophilebiidae 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 (Rheeanthopsis); testicular follicles equal in length and size, arranged into regular longitudinal rows (Db₁), 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 Rheeanthopsis 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 (Db₁), 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, Lithobrancha 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 (Db₁), 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 *Ioathybotus* 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 *Ephemeroidea* (especially to the *Palingeniidae*).

**Euthyplociidae**

*Euthyplociinae*  
(Figs. 234, 238, 243)

Testis: deposited ventrolaterally (Ad), I, II, III, IV, V, VI (Ba); subcylindrical, slightly flattened, rounded or bluntly pointed (*Euthyplocia*) in I (Cd); testicular follicles shortly cylindrical, equal in size, in regular longitudinal rows (Db₁); VS formed by gradually expanded VD (Pb), 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 *Campylacia* 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 (Db₁), perpendicular to VD (Ea); VS formed by gradually expanded VD (Pb), 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 Polymitarciinae 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) sub-cylindrical, slightly flattened, bluntly pointed in I and II (Cd); testicular follicles numerous, equal in size and length, arranged into regular longitudinal rows (Db1), 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 Polymitarciidae 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 (Db1), 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 Polymitarciidae includes two closely related groups of subfamilies. The first group consists of the subfamily Polymitarciinae (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:
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 (Db₁), 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 Polymitarcidae and Euthyplociidae and also to the family Ephemeridae.

Neoephemeredae

Neoephemerenae
(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 (Neoephemera) in thorax (Cb); testicular follicles minute, elongated and cylindrical, equal in size and length, arranged into regular longitudinal rows (Db₂); perpendicular to VD (Ea); VS inconspicuous, formed by gradually expanded VD (Fa), deposited in VII-IX (Potamanthellus) (Ga) or in VIII-IX (Neoephemera) (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 Neoephemeredae 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 (Db₂), 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 Brachyceorus 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 foreward, the ovaries are produced to head in several genera (Caenis, Caenomedeæ, Tasmanooelenis). The family is evolutionarily quite homogeneous, despite these exceptions. The family Caenidae shows close affinity to the Neoephemeredidae 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 (Db₂), 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 Neoephemeredidae 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 (Db₂); 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 Batisoa. There are certain affinities to the families Neosphemeridae and Caenidae as well.
Tab. 1

A tabular summary of the anatomical arrangement of gonads in *Ephemerella*.

<table>
<thead>
<tr>
<th>Family (subfamily, genus)</th>
<th>Position of gonads (A, H)</th>
<th>Position of testes to segments (B)</th>
<th>Position of ovaries to segments (J)</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Siphlonurinae</em></td>
<td>Aa, Ha</td>
<td>Ba</td>
<td>Jb (Jc)</td>
</tr>
<tr>
<td><em>Acanthometropodinae</em></td>
<td>Aa, Ha</td>
<td>Ba</td>
<td>Jb</td>
</tr>
<tr>
<td><em>Oniscigastriinae</em></td>
<td>Ab, Hb</td>
<td>Bb</td>
<td>Jc</td>
</tr>
<tr>
<td><em>Ameletopsis, Mirawara</em></td>
<td>Ab, Hb</td>
<td>Ba</td>
<td>Jb</td>
</tr>
<tr>
<td><em>Chiloporter</em></td>
<td>Aa, Ha</td>
<td>Bd</td>
<td>Jb</td>
</tr>
<tr>
<td><em>Isonychiinae</em></td>
<td>Ab, Hb</td>
<td>Ba</td>
<td>Jb</td>
</tr>
<tr>
<td><em>Coloburiscinae</em></td>
<td>Ac, Hc</td>
<td>Bd</td>
<td>Ja</td>
</tr>
<tr>
<td><em>Rallidentinae</em></td>
<td>Aa, Ha</td>
<td>Ba</td>
<td>Jb</td>
</tr>
<tr>
<td><em>Callibaetis, Baetopus, Centroptilum, Cloeon, Procloeon</em></td>
<td>Aa, Ha</td>
<td>Ba</td>
<td>Jb</td>
</tr>
<tr>
<td><em>Baetodes, Pseudocloeon</em></td>
<td>Aa, Ha</td>
<td>Bc</td>
<td>Jd</td>
</tr>
<tr>
<td><em>Oligoneuriinae</em></td>
<td>Ab, Hb</td>
<td>Ba</td>
<td>Jb (Jc)</td>
</tr>
<tr>
<td><em>Cinygnula, Epeorus, Rhithrogena</em></td>
<td>Ac, Hc</td>
<td>Ba</td>
<td>Ja, Jb</td>
</tr>
<tr>
<td><em>Afronurus, Ecdyonurus, Heptagenia, Stenacron, Stenonema</em></td>
<td>Ac, Hc</td>
<td>Ba</td>
<td>Jb, Jc</td>
</tr>
<tr>
<td><em>Anepeorinae</em></td>
<td>Ac, Hc</td>
<td>Ba</td>
<td>Jb</td>
</tr>
<tr>
<td><em>Arthrolepinae</em></td>
<td>Ac, Hc</td>
<td>Ba</td>
<td>Jb</td>
</tr>
<tr>
<td><em>Pseudironinae</em></td>
<td>Ab, Hb</td>
<td>Bb</td>
<td>Jc</td>
</tr>
<tr>
<td><em>Ametropodinae</em></td>
<td>Ab, Hb</td>
<td>Ba</td>
<td>Jb</td>
</tr>
<tr>
<td><em>Metretopodinae</em></td>
<td>Aa, Ha</td>
<td>Ba</td>
<td>Jb</td>
</tr>
<tr>
<td><em>Atalomicria, Atalophlebia, Atalophlebiodes, Jappa</em></td>
<td>Ac, Hc</td>
<td>Ba</td>
<td>Ja</td>
</tr>
<tr>
<td><em>Leptophlebia, Habroleptodes, Habrophlebia, Kirrara</em></td>
<td>Ac, Hc</td>
<td>Ba</td>
<td>Jb</td>
</tr>
<tr>
<td><em>Kimminsula, Para- leptophlebia</em></td>
<td>Ac, Hc</td>
<td>Bb</td>
<td>Jc</td>
</tr>
<tr>
<td><em>Hagenulus, Traverella, Thraulus, Choroterpes</em></td>
<td>Ac, Hc</td>
<td>Bd</td>
<td>Jd</td>
</tr>
<tr>
<td><em>Attenella, Timpanoga</em></td>
<td>Ac, Hc</td>
<td>Ba</td>
<td>Ja</td>
</tr>
<tr>
<td><em>Drunella, Eurylophella</em></td>
<td>Ac, Hc</td>
<td>Bc</td>
<td>Jd</td>
</tr>
<tr>
<td><em>Ephemeralina, Ephemerella, Teloganodes</em></td>
<td>Ac, Hc</td>
<td>Ba</td>
<td>Jb</td>
</tr>
<tr>
<td>Shape of testis</td>
<td>Shape of ovary</td>
<td>Position of follicles</td>
<td>Position of follicles</td>
</tr>
<tr>
<td>----------------</td>
<td>----------------</td>
<td>----------------------</td>
<td>----------------------</td>
</tr>
<tr>
<td>Ca</td>
<td>Ka</td>
<td>Da (Db)</td>
<td>Ea</td>
</tr>
<tr>
<td>Ca</td>
<td>Ka</td>
<td>Da</td>
<td>Ea</td>
</tr>
<tr>
<td>Ca</td>
<td>Ka</td>
<td>Db₁</td>
<td>Ea</td>
</tr>
<tr>
<td>Cb</td>
<td>Kb</td>
<td>Db₁</td>
<td>Ea</td>
</tr>
<tr>
<td>Ca</td>
<td>Kb</td>
<td>Da</td>
<td>Ea</td>
</tr>
<tr>
<td>Cb</td>
<td>Kb</td>
<td>Db₁</td>
<td>Ea</td>
</tr>
<tr>
<td>Cb</td>
<td>Ka</td>
<td>Db₁</td>
<td>Eb</td>
</tr>
<tr>
<td>Cb</td>
<td>Kb</td>
<td>Db₁</td>
<td>Ea</td>
</tr>
<tr>
<td>Cb</td>
<td>Kb</td>
<td>Db₁</td>
<td>Ea</td>
</tr>
<tr>
<td>Cb</td>
<td>Kb</td>
<td>Da</td>
<td>Ea</td>
</tr>
<tr>
<td>Cb</td>
<td>Kb</td>
<td>Da</td>
<td>Ea</td>
</tr>
<tr>
<td>Cb</td>
<td>Kb</td>
<td>Da</td>
<td>Ea</td>
</tr>
<tr>
<td>Cb</td>
<td>Kb</td>
<td>Da</td>
<td>Ea</td>
</tr>
<tr>
<td>Cb</td>
<td>Kb</td>
<td>Db</td>
<td>Ea</td>
</tr>
<tr>
<td>Cb</td>
<td>Kc</td>
<td>Db₂</td>
<td>Eb</td>
</tr>
<tr>
<td>Cc</td>
<td>Kc</td>
<td>Db₂</td>
<td>Ea</td>
</tr>
<tr>
<td>Cc</td>
<td>Kc</td>
<td>Db₂</td>
<td>Eb</td>
</tr>
<tr>
<td>Cb</td>
<td>Kb</td>
<td>Db₁</td>
<td>Ea</td>
</tr>
<tr>
<td>Cb</td>
<td>Kb</td>
<td>Db₁</td>
<td>Ea</td>
</tr>
<tr>
<td>Cb</td>
<td>Kb</td>
<td>Db₁</td>
<td>Ea</td>
</tr>
<tr>
<td>Family (subfamily, genus)</td>
<td>Position of gonads (A, H)</td>
<td>Position of testes to segments (B)</td>
<td>Position of ovaries to segments (J)</td>
</tr>
<tr>
<td>--------------------------</td>
<td>--------------------------</td>
<td>-----------------------------------</td>
<td>-----------------------------------</td>
</tr>
<tr>
<td>Tricorythinae</td>
<td>Ac, Hc</td>
<td>Bb</td>
<td>Jc</td>
</tr>
<tr>
<td>Leptohyphinae</td>
<td>Ac, Hc</td>
<td>Ba</td>
<td>Jb</td>
</tr>
<tr>
<td>Dicercomyzinae</td>
<td>Ac</td>
<td>Ba</td>
<td>-</td>
</tr>
<tr>
<td>Behningiidae</td>
<td>Ac, Hc</td>
<td>Ba</td>
<td>Jb</td>
</tr>
<tr>
<td>Potamanthidae</td>
<td>Ac, Hc</td>
<td>Ba</td>
<td>Jb</td>
</tr>
<tr>
<td>Ephemerida</td>
<td>Ad, Hd</td>
<td>Ba</td>
<td>Jb</td>
</tr>
<tr>
<td>Hexagenia, Litobrancha,</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pentagenia</td>
<td>Ad, Hd</td>
<td>Bb</td>
<td>Jb</td>
</tr>
<tr>
<td>Euthyplociidae</td>
<td>Ad, Hd</td>
<td>Ba</td>
<td>Ja, Jb</td>
</tr>
<tr>
<td>Polymitarcinae</td>
<td>Ad, Hd</td>
<td>Ba</td>
<td>Jb</td>
</tr>
<tr>
<td>Asthenopodinae</td>
<td>Ad, Hd</td>
<td>Ba</td>
<td>Ja</td>
</tr>
<tr>
<td>Campsurinae</td>
<td>Ad, Hd</td>
<td>Ba</td>
<td>Ja</td>
</tr>
<tr>
<td>Palingeniidae</td>
<td>Ad, Hd</td>
<td>Ba</td>
<td>Jb</td>
</tr>
<tr>
<td>Neoephemeridae</td>
<td>Ac, Hc</td>
<td>Bb</td>
<td>Jc</td>
</tr>
<tr>
<td>Caenidae</td>
<td>Ac, Hc</td>
<td>Bb</td>
<td>Jc</td>
</tr>
<tr>
<td>Baetiscidae</td>
<td>Ac, Hc</td>
<td>Bb</td>
<td>Jc</td>
</tr>
<tr>
<td>Prosopistomatidae</td>
<td>Ac, Hc</td>
<td>Bb</td>
<td>Jb</td>
</tr>
<tr>
<td>Shape of testis</td>
<td>Shape of ovary</td>
<td>Arrangement of follicles</td>
<td>Position of follicles</td>
</tr>
<tr>
<td>----------------</td>
<td>----------------</td>
<td>--------------------------</td>
<td>-----------------------</td>
</tr>
<tr>
<td>(C)</td>
<td>(K)</td>
<td>(D)</td>
<td>(E)</td>
</tr>
<tr>
<td>Cb</td>
<td>Kb</td>
<td>Db₂</td>
<td>Eb</td>
</tr>
<tr>
<td>Cb</td>
<td>Kb</td>
<td>Db₂</td>
<td>Ea, Eb</td>
</tr>
<tr>
<td>Cb</td>
<td>-</td>
<td>Db₂</td>
<td>Ea</td>
</tr>
<tr>
<td>Cd</td>
<td>Kc</td>
<td>Db₁</td>
<td>Ea</td>
</tr>
<tr>
<td>Cd</td>
<td>Kc</td>
<td>Db₁</td>
<td>Ea</td>
</tr>
<tr>
<td>Cd</td>
<td>Kc</td>
<td>Db₁</td>
<td>Ea, Eb</td>
</tr>
<tr>
<td>Cd</td>
<td>Kc</td>
<td>Db₁</td>
<td>Ea</td>
</tr>
<tr>
<td>Cd</td>
<td>Kc</td>
<td>Db₁</td>
<td>Ea</td>
</tr>
<tr>
<td>Cd</td>
<td>Kc</td>
<td>Db₁</td>
<td>Ea, Eb</td>
</tr>
<tr>
<td>Cd</td>
<td>Kc</td>
<td>Db₁</td>
<td>Ea</td>
</tr>
<tr>
<td>Cs</td>
<td>Kc</td>
<td>Db₁</td>
<td>Ea</td>
</tr>
<tr>
<td>Cs</td>
<td>Kc</td>
<td>Db₁</td>
<td>Ea</td>
</tr>
<tr>
<td>Cs</td>
<td>Kc</td>
<td>Db₁</td>
<td>Ea</td>
</tr>
</tbody>
</table>
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 Siphlonurus which is s-curved in the thorax or in the first abdominal segments and which is characteristic for the whole subfamily Siphlonurinae (family Siphlonuridae). However, on the basis of examination of several species of the genus Siphlonurus, 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

81
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. sauvignyi, Ephoron sp. - Thailand) nor in any other genus of the family Polymitarcidae. Similar anastomosis is mentioned and figured by Codreanu (1939) in the genera Eadyonurus (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, Siphlonuridae) 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 Prospistoma (Prospistomatidae) and Palingenia (Palingeniidae) are in question, where the lowest and the highest fertility in mayflies were found at all. Degrange (1960) states for Prospistoma 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 Prospistoma 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, gonducts), 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 gonducts (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 metamereically 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 gonducts 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, gonducts are mutually connected forming the common ducts and the copulatory organs are unpaired as well. While any accessorific 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 accessorific copulatory organ), the spermatozoa are associated to form spermatozeugmats in the most families.

The gonads of polynoeopterous insect orders (i.e. *Plecoptera, Ephemeroptera, Mantodea, Blattaria, Isoptera, Phasmida, Orthoptera, Grylloblat-todea, 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

85
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 anlages), 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 polynoeopterous 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 (*Porticulidae*, *Arizeniidae*, *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*, *Polynoeoptera except Dermaptera* and *Diploglossata*) and the meroistic (*Paraneoptera*, *Oligoneoptera*) ovarioles.

The ovaries of *Cloeon dipterus* (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 gamets (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 molting 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, down-stream 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 gonducts 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 gonducts (seminal vesicles etc.) occur (the gonads of polynoeopterous 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 gamets. So the situation when gonads reach till the thorax or even the head (ovary in the genus Cae-

nis) 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 (Siphlonurinae, 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 Siphlonurinae). 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, Ephemereilla-subgenus Timpomoga 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, Tricoptera, Neophasmatodea 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 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 vitellarian 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 spermatозoa descend into seminal ducts. Originally, the spermatозoa 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 gonducts in mayflies is the synpleiomorphic 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:

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

2. 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.

3. 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.

4. 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 Behnningiiidae the ovarioles tend to decreasing of their size as well.

5. 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.

6. 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 *Siphlonurinae*, *Acanthametropodinae* and *Rallidentinae* (*Siphlonuridae*) 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*, *Siphlonuridae*) belong to this evolutionary line but they differ in the arrangement of follicles from the *Siphlonurinae*. The family *Siphlaenigmatidae* (one New Zealand genus), which represents morphological interstage between the families *Siphlonuridae* 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, Pseudoaloeon, 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 pleisiomorphic and apomorphic arrangement of gonads is characterized by the shift to the dorsolateral position. This group involves the subfamilies Onisigastriinae and Ameletopsinae (except the genus Chiloporter) (Siphlonuridae) where gonads are mostly of the same shape as those of the subfamily Siphlonurinae and the subfamilies Isonychiinae (Siphlonuridae) and Oligoneuriidae (Oligoneuridae, Chromarcyinae not investigated) with related anatomical schemes. Testicular follicles of this group equal in length and size but yet they are not evidently multiplicitated. 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 pleisiomorphic and the other apomorphic, and the subfamily Anepeorinae with nearly identical anatomical schema as that of the Heptageniinae (pleisiomorphic 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 (Siphlonuridae) 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 Siphlonuridae.

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 Ephemerellidae). 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, Ephemerrillidae) 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 Neopehemeraidae, the apomorphic arrangement of gonads was found also in the families Baetisidae and Prosopistomatidae. The family Tricorythidae (Machadorythinae and Ephemerythrinae not investigated) represents an intermediary type between the Ephemerrillidae and the Caenidae with Neopehemeraidae. While the subfamily Leptohyphinae and probably also the Diceromyzinae show relationships to the Ephemerrillidae, the subfamily Tricorythinae is related rather to the Caenidae and Neopehemeraidae.

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 Ephemeroida 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 Euthyplocoidae, Palingentidae and Polymitarcidae (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 Ephemeroidae (Ephemeridae, Palingeniidae, Euthyplociidae, Polymitarcidae, 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 gonoporous 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 Ephemeroidae, 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 Siphlonuridae, 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 Ephemeroidae are much more derived than the Baetidae and the Siphlonuridae. 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, Potamantus* 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 *Ephemeroida* (8000 till 12000 in the genus *Palingenia*). High fecundity (here considered as a 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; Lamere, 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 Siphlonuridae 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 Siphlonuridae 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 Siphlonuridae. For the genus Chiloporter Landa (1973) establishes
a separate family Chilopoteridae. Also Edmunds (1973b) agrees with this opinion though Riek (1973) leaves the genus Chilopotera in the family Ameletopsidae and the subfamily Oniscigastriinae in the family Siphlonuridae. According to the arrangement of gonads, the Ameletopsidae and the Oniscigastriinae represent a separate group which shows relationships partly to the family Baelidae, partly to the subfamilies Isonychiinae and Oligoneuriinae.

By its arrangement of gonads the subfamily Isonychiinae is very ressembling 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 Siphlonuridae (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 Siphlonuridae. 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 accessorision gills).

The subfamily Coloburiscinae differs markedly by its position of gonads from the scheme of the subfamily Siphlonurinae 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 (accessorision 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 Siphlonuridae.

The subfamily Rallidentinae (the only genus Rallidens from New Zealand) does not substantially differ from scheme of the subfamily Siphlonurinae. Landa (1973) considers it as a separate family with relations to the families Ameletopsidae and Baelidae. Demoulin is of a similar opinion as well (Demoulin, 1969). The other authors do not separate it from the subfamily Siphlonurinae (Riek, 1973; Penniket, 1966). In a similar way also the subfamily Acanthametopodinae is classified, the gonads of which are also coincident to those of the Siphlonurinae. Demoulin (1974), Edmunds (1947,1970) and others consider it as
a part of the family Siphlonuridae. 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 Siphlonuridae as defined by Edmunds, Allen & Peters (1963) but they point out relatively great diversity of subfamilies included and the fact that the subfamily Siphlonurinae itself involves several groups of genera. These are the Siphlonurus 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 Rallidentiinae. 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 Bae- tidae. 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 Bae- tidae. Preliminary results of the study of internal organs (Landa, pers.comm.) indicate that this genus is closely related to some genera of the Bae- tidae.

The family Bae- tidae 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 Bae- tidae 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 Bae- tidae would consist of two groups having 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 Bae- tis 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 *Siphlonuridae* (*Siphlonurinae, 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 *Chromarcoys* 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 *Isomychiinae* and *Coloburiiscinae* 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 *Heptagininae* and *Aneperoinae* which have nearly identical scheme. The anatomical peculiarities approach the *Pseudironinae* to the family *Siphlonuridae* (*Siphlonurinae*) though, gonads are placed dorsolaterally and not dorsally in this case. Riek (1973) who classifies the subfamily *Pseudironinae* directly as a part of the *Siphlonuridae* namely to the approximation 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 *Arthrolepinae* with those of the subfamilies *Heptagininae* and *Aneperoinae* is obvious even when there are some differences. As far as the gonads are concerned the genus *Arthrolepis* 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 *Arthrolepis* from the family *Heptageniidae* but as the differences are much smaller than e.g. between the *Heptageniidae* and the *Oligoneuriidae* or *Coloburiiscinae*, 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 *Heptagininae* 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 Ephemerellidae. Also Riek (1973) and Landa (1969b), who exclude this family from the superfamily Baetotidae, 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 Siphlonurinae (the testis is even of a more primitive arrangement). Also the gonads of the subfamily Metretopodinae (Metretopus, Siphopleston) do not substantially differ from the anatomical scheme of Siphlonurinae. That is why both the subfamilies Ametropodinae and Metretopodinae can be ranged to the family Siphlonuridae. Riek (1973) classifies the Ametropodinae as close to the Acanthometropodinae and the Metretopodinae as close to the Siphlonurinae though the situation would be quite opposite according to the arrangement of gonads. Both these subfamilies are ranged to the Siphlonuridae 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 Teloganodininae. 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 Diceroomyzinae 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 Ephemeromyrthinae and Machadorhynthinae 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 Ephemerrilliidae 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, Polymitaridae, 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 Ephemeroidae, 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 Polymitaridae, Euthyplociidae and Palingeniidae, the second of the family Ephemeridae. The superfamily Ephemeroidae 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 Ephemera (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 *Baetisidae* can serve which is classified into the superfamily *Caenoidea* by Edmunds, Allen & Peters (1963), into the superfamily *Prosopistomatoidea* by Riek (1973), into the *Oligoneurioida* 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 gohads 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 gonducts 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 caudally.

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 (Siphlonurinae). This line consists of the Siphlonurinae, Ametropodinae, Acanthametropodinae, Rallidentinae, Chiloporter, Pseudironinae, Baetidae and probably also Siphlaenigmatidae. The Ameletopsinae, Oniscigastriinae, Isonychitinae 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, Arthrolepinae, Aneporinae), Coloburisoniinae; (b) Leptophlebiidae, Ephemeraliidae, Triorythidae, Neogomphidae, 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, Polymitarcidae, 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


2. Die Hoden sind längs der Verdauungsrohr 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 Abdome- nalsegment IX durchgehende Rohr. In den letzten Abdominalsegmenten verbreitet sich der Samenleiter in die Samenblase. Vom Sichpunkt der vergleichenden Anatomie sind folgende Merkmale am bedeutendsten: (A) die Lage des Hodens in bezug zur Verdauungsrohr (dorsal, dorsolateral, lateral, ventrolateral); (B) die Lage in bezug zur Körpergliederung (der Hoden kann bis in den Prothorax eingreifen); (C) Gesamtform des Hodens und seines Apikalteils (zyllinderförmig, verflacht, Hoden median gebogen); (D) Grösse und Anordnung der Follikeln (gleiche oder verschiedene Grösse, kugelförmig, zylinderförmig, länglich); (E) die Lage der Pollikeln 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 Rohr. Vom Sichpunkt 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 (zyllinderförmig, mässig verflacht, stark verflacht - zungenförmig); (L) die Lage
der Ovarioles in bezug zum Eileiter (senkrecht-, mässig schief- und stark schiefstehende Ovariolen).


1. Vnitřní reproduktivní 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 lařev, u kterých je již dokončena diferenciaci 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 skladají 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 abdonálního 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 trubici (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 lařev je již vytvořeno vitellarium. Vejcovod tvoří jednoduchá trubice, probíhající od apikální části vaječníku k intersegmentální membráně mezi abdonálními segmenty VII a VIII. Z hlediska srovnávací anatomie jsou nejdůležitější tyto znaky: h) uložení vaječníku vzhledem k trávicí soustavě; i) uložení vaječníku vzhledem k tělní segmentaci (uložení vaječníku 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 hypotезu o 10 párech vzájemně nekomunikujících gonád hmyzího předka, které byly segmentálně uspořádány, potom plesiomorfními znaky jsou zejména: nestejná velikost testikut, uložení

110
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 sousta-
vě, šikmo postavené testikuly či ovarioly, semenný váček kulovitý, ulo-
žený v segmentu IX. U jepic se projevuje tyto vývojové tendence: přesu-
nutí 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 zasa-
hující do zadní či středohrudi, ovarioly postavené kolmo nebo mírně
šikmo, testikuly mohou být nestejně velikosti (Siphlonurinae). Do této
linie patří Siphlonurinae, Ametropodidae, Acanthometropodinae, Rall-
dentinae, Chiloporter, Pseudironinae, Baetidae a pravděpodobně i Siphla-
enigmatidae. Přechodným typem mezi první a druhou vývojovou linii je
skupina s dorsolaterálním uložením gonád, representovaná podčeleďemi
Ameletopeinae, Oniscagastriinae a Isonychiinae (čeleď Siphlonuridae)
a čeledi Oligoneuriidae. (2) Gonády uloženy laterálně, testikuly mohou
být zmnožené, stejně velikosti, ovarioly mohou být i silně sešíkmeny.
Tato vývojová linie se skládá ze tří skupin: a) Heptageniidae (Heptage-
niinae, Arthropletinae, Aneporinae), Coloburiscinae; b) Leptophlebi-
dae, Ephemerellidae, Tricorythidae, Neoeperheteridae, Caenidae, Proso-
pistomatidae, Baeticidae. U této skupiny došlo k výrazněmu posunutí
gonád do hrudi (u rodu Caenis zasahuje vaječník do hlavy); c) Behningi-
idae, 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, Polymitaroidae, Palinge-
niidae a Ephemeridae.

6. Vztahy mezi čeleďemi i podčeleďemi, popřípadě i mezi některými
rody, jsou prodiskutovány. Údaje získané studiem gonády jsou srovnány
s výsledky následujících autorů: Edmunds, Allen & Peters (1963), Landa
pohlavních orgánů jepic k pohlavním orgánům ostatních skupin hmyzu
s panoistickými ovariolami.
REFERENCES


Demoulin C., 1957: Remarques critiques sur la position systématique des


114


Jensen S.L. & Edmunds G.F., 1973: Some phylogenetic relationships within


Landa V., 1973: A contribution to the evolution of the order Ephemero-


118
Comparative anatomy of the internal reproductive organs of mayflies (*Ephemeroptera*)

Vydala Academia
nakladatelství Československé akademie věd
Praha 1981

Obálku navrhl Josef Tyrš
Redaktorka publikace RNDr. Eva Hrubá
Technický redaktor Oldřich Müller

Vydání 1. - 120 stran
8,08 AA - 8,25 VA
Náklad 300 výtisků - 03/16 - 4566
Vytiskla Polygrafie n. p., závod 6, Praha 8 - Libeň

21 - 022 - 81
Cena brož. výtisku 38,- Kčs
509 - 21 - 827
The Publishing House Academia is preparing for you:

M. Skuhrová, V. Skuhrový
Die Gallmücken /Cecidomyiidae, Diptera/ des Schilfes /Phragmites communis Trin./

Paper covers - approx. 18,- Kčs

V. Skuhrový et al.
Invertebrates and vertebrates attacking common reed stands /Phragmites communis/ in Czechoslovakia

Paper covers - approx 16,- Kčs

J. Prokopíč, S. Bílý
Coleoptera as Intermediate Hosts of Helminths
Studie ČSAV / Studies of Czechoslovak Academy of Sciences/

Paper covers - approx. 20,- Kčs

ACADEMIA
Publishing House of the Czechoslovak Academy of Sciences
Vodičkova 40
112 29 Praha 1 – Nové Město

Tem. skup. 03/16
21 - 022 - 81
Cena brož. výt. 38,- Kčs
509 - 21 - 827