

## COMPARATIVE ANATOMY OF MAYFLY LARVAE (EPHEMEROPTERA)

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Our knowledge of the comparative anatomy of mayflies is very fragmentary. Truly comparative work has been done by PALMÉN (1877) — tracheal system, 12 genera, 16 species; CAZAL (1948) — endocrines, 2 genera, 2 species; ARVY & GABE (1953) — endocrines, 10 genera, 12 species; GRANDI (1950) — digestive system, 6 genera, 6 species; GRANDI (1955) — ducts of female reproductive organs, 17 genera, 30 species; BRINCK (1957) — reproductive organs, 8 genera; GRANDI (1962) — abdominal muscles, 13 genera, 14 species. Other papers give anatomical data on individual species: DRENKELFORT (1910) — *Siphonurus lacustris* ETN.; HEINER (1914) — *Cloeon dipterum* L.; VAYSSIÈRE (1934) — *Baetisca obesa* SAY; VAYSSIÈRE (1937) — *Euthyplocia sikorai* VAYSSIÈRE. MARSHALL (1927) studied the histology of Malpighian tubes. Older data on the anatomy of mayflies are summarized in respective chapters of compendia (SCHRÖDER, 1925, 1928, 1929; WEBER, 1933; NEEDHAM, TRAVER & HSU, 1953, and others).

A detailed topography of the tracheal system and data on the Malpighian tubes and nerve band, based on the study of larvae of Central European mayflies, was published by LANDA (1948). It has been found that the tracheal system, Malpighian tubes and nerve band are formed by considerably different evolutionary processes. Hence these differences might be applied to classification and phylogeny of this order (LANDA, 1959).

In the years 1964–68 I had an opportunity to study — in collaboration with Prof. G. F. Edmunds — live as well as specially fixed material of larvae of most genera from all zoogeographic regions and data on 127 species of 94 genera were obtained. The results are given in the present paper. The application of the study of comparative anatomy to the classification and phylogeny of the order *Ephemeroptera* will be dealt with in other papers.

My thanks are due to Prof. G. F. Edmunds (University of Utah, Salt Lake City), who enabled me to a great extent to carry out the study. I wish to thank also Prof. W. L. Peters (Florida A & M University, Tallahassee), Dr. F. P. Ide (University of Toronto), Prof. L. Berner (University of Florida, Gainesville) and others who offered their valuable advice and material.

### MATERIAL AND METHODS

Older larvae, i.e. those from about the Xth instar to the last instar — the nymph, with all larval characters fully developed, were used for the study of comparative anatomy. The tracheal system, formation of Malpighian tubes and nerve bands, i.e. organs displaying the utmost diversity, were investigated. The larvae were dissected in a Petri dish of paraffin stained red with Sudan III for a greater contrast. The subjects were opened dorsally, eiaes were pinned with

minutiae. Tracheae and other organs were loosened with a thin trickle of water, Pringle solution or alcohol. Important parts of the tracheal system, nerve band and Malpighian tubes were mounted in Canada balsam with Cellosolve. The tracheae were sometimes stained with light green or chlorazol black. Injection with paraffin, asphalt (Lehmann), Berlin blue (Tichomirov), olive oil stained with Sudan III (Gabler) and cobalt naphthenate (Wigglesworth) did not prove useful.

Preferably fresh material was examined whenever available. Genera from regions which I have not visited myself were studied on material fixed with Carnoy and preserved in 75% alcohol or on larval material in alcohol from collections.

The species are arranged according to the classification by EDMUNDS, ALLEN & PETERS (1963); see this publication also for the authors of genera, subfamilies and families. The following genera and species were studied:

### Siphonuridae

*Siphonurinae*: P\* — *Ameletus inopinatus* EAT., Teplá Vltava, Borová Lada, ČSSR, 6.63\*\*, Landa\*\*\*; NA — *Ameletus velox* DODDS, Mill Creek, Salt Lake Co., Utah, USA, 6.65, Landa; NT — *Metamonius* sp., Est. Huemul, Lago Gualletus, Prov. Malleco, Chile, 12. 63, G. F. Edmunds; NA — *Parameletus columbiae* McDUNN, Big Cottonwood Creek, Brighton, Utah, USA, 6.65, Landa; P — *Siphonurus aestivalis* EAT., Ostružná, Sušice, ČSSR, 7. 66, Landa; NA — *Siphonurus lacustris* EAT., Studená Vltava, Stožec, ČSSR, 6. 59, Landa; NA — *Siphonurus occidentalis* EAT., Mill Creek, Salt Lake Co., Utah, USA, 7. 66, Landa. — *Acanthametropodinae*: NA — *Acanthametropus* sp., Savannah River, Georgia, USA, G. F. Edmunds. — *Oniscigaster* sp., Taranaki Co., Taranaki Prov., New Zealand, 2. 58, McFarlane; NT — *Siphonella* sp., Rio Illapel, Caren., Prov. Coquimbo, Chile, 11. 63, G. F. Edmunds. — *Ameletopsinae*: A — *Ameletopsis* sp., Taranaki Co., Taranaki Prov., New Zealand, 2. 58, McFarlane; NT — *Chiloporter* sp., Rio Biobio, Prov. Malleco, Chile, 12. 63, G. F. Edmunds; A — *Mirawara* sp., Coomera River, Lamington, Queensland, Australia, 1. 44, Edmunds. — *Isonychiinae*: NA — *Isonychia* sp., Collasaja River, Macon Co., North Carolina, USA, 7. 66, Landa. — *Coloburiscinae*: A — *Coloburiscoides* sp., Roch Creek, Mt. Kosciuszko, Australia, 2. 46, R. J. Tillyard; A — *Coloburiscus* sp., Huatoki stream, Taranaki Co., Taranaki Prov., New Zealand, 11. 56, A. Hirsch; NT — *Murphyella* sp., Est. Victoria, Marimenuco, Prov. Malleco, Chile, 12. 63, G. F. Edmunds.

### Baetidae

NA — *Baetis* sp., Santa Fe River, Alachua Co., Florida, USA, 6. 65, Landa; P — *Baetis bioculatus* L., Ostružná, Sušice, ČSSR, 9. 59, Landa; P — *Baetis rhodani* (PICT.), Židova strouha, Bechyň, ČSSR, 5. 66, Landa; NA — *Baetis tricaudatus* DODDS, East Canyon Creek, Summit Co., Utah, USA, 6. 65, Landa; NT — *Baetodes* sp., Rio Huallaga, Tingo Maria, Huanuco Prov., Peru, 8. 63, W. L. Peters; NA — *Callibaetis coloradensis* BANKS, Mill Creek, Salt Lake Co., Utah, USA, 6. 65, Landa; P — *Centroptilum luteolum* (MÜLL.), Židova strouha, Bechyň, ČSSR, 5. 66, Landa; NA — *Centroptilum rubropictum* McDUNN, Nantahala Riv., Nantahala, N. Carolina, USA, 7. 65, Landa; P — *Cloeon dipterum* L., Pálenec, Pole, nr Strakonice, ČSSR, 6. 64, Landa; P — *Procloeon pseudorufulum* KIMM., Mže, Milíkov, ČSSR, 6. 66, Landa; NA — *Pseudocloeon* sp., Cullasaja Riv., Macon Co., N. Carolina, USA, 7. 65, Landa; NT — *Baetidae* gen. n., sp. n., San José, Costa Rica, 7. 62, G. G. Musser:

### Oligoneuriidae

*Chromarcyinae*: O — *Chromarcys* sp., Mae Ping, n. of Chiangmai, Chiangmai Prov., Thailand, 11. 64, W. L. Peters. — *Oligoneurinae*: E — *Elassoneuria candida* EAT., Afram Riv., Mankrong, Gold Coast, 9. 50, L. Berner; NA — *Homoneuria* sp., Homochitto Riv., Franklin Co., Mississippi, USA, 6. 56, Berner & Hynes; NT — *Lachlania* sp., Rio Huallaga, Tingo Maria, Huanuco Prov., Peru, 7. 63, W. L. Peters; NT — *Oligoneuria* sp., mountain stream nr. Rio Marauia, NW Taparuarua, Brazil, 1. 63, E. J. Fittkau; P — *Oligoneuriella rhenana* (IMHOFF), Ostružná, Sušice, ČSSR, 7. 66, Landa.

### Heptageniidae

*Heptageniinae*: NA — *Cinygna* sp., Berry Cr., N. Corvallis, Benton Co., Oregon, USA, 5. 59, G. F. Edmunds; O — *Cinygmna* sp., stream, Doi Sutep, w. of Chiangmai, Chiangmai Prov.,

\* P — Palearctic region, NA — Nearctic region, NT — neotropical region, E — Ethiopian region, O — Oriental region, A — Australian region.

\*\* June, 1963.

\*\*\* Collected by. (Collection of).

Thailand, 11. 64, W. L. Peters; NA — *Cinygmula par* EAT., Mill Creek, Salt Lake Co., Utah, USA, 6. 65, Landa; P — *Ecdyonurus dispar* (CURT.), Smutná, Bechyně, ČSSR, 5. 66, Landa; P — *Ecdyonurus torrentis* KIMM., Židova strouha, Bechyně, ČSSR, 5. 66, Landa; P — *Epeorus assimilis* EAT., Otava, Sušice, ČSSR, 5. 63, Landa; NA — *Epeorus (Iron) longimanus* EAT., Mill Creek, Salt Lake Co., Utah, USA, 6. 65, Landa; P — *Epeorus (Iron)* sp., stream nr Borjomi, Caucasus, USSR, 9. 66, Landa; O — *Epeorus (Ironodes)* sp., stream, Doi Sutep, w. of Chiangmai, Chiangmai Prov., Thailand, 11. 64, W. L. Peters; NA — *Epeorus (Ironopsis) grandis* McDUNN, Wolf Creek, Lake Co., Montana, USA, 7. 65, R. K. Allen; P — *Heptagenia flava* ROST., Lužnice, Bechyně, ČSSR, 6. 64, Landa; P — *Heptagenia lateralis* CURT., Křemelná, Černkova Pila, ČSSR, 8. 59, Landa; NA — *Heptagenia simplicioides* McDUNN, Green Riv., Dinos. Nat. Mon., Utah, USA, 6. 65, Landa; P — *Heptagenia sulphurea* (MÜLL.), Smutná, Bechyně, ČSSR, 5. 66, Landa; P — *Rhithrogena aurantiaca* (BURM.), Ostružná, Sušice, ČSSR, 7. 66, Landa; P — *Rhithrogena germanica* EAT., Mže, Milčkov, ČSSR, 4. 67, Landa; NA — *Rhithrogena robusta* DODDS, Grove Creek, Utah Co., Utah, USA, 6. 65, Landa; P — *Rhithrogena semicolorata* CURT., Libušský p. Modřany, ČSSR, 6. 64, Landa; NA — *Stenonema interpunctatum* SAY, River Mile, Old Hickory Dock, Cumberland R., Tennessee, USA, 7. 65, J. W. Richardson; NA — *Stenonema pudicum* HAGEN, Cullasaja Riv., Macon Co., N. Carolina, 7. 65, Landa; NA — *Stenonema smithae* TRAVER, Hogtown Creek, Gainesville, Florida, USA, 6. 65, Landa; P — *Thalerosphyrus* sp., Mouche River, Nahr Besri vic. Deir mash, Lebanon, 7. 52, K. Christiansen. — *Arthropleinae*: P — *Arthroplea congener* BENGTS., Krčový, Kadov, nr Strakonice, ČSSR, 5. 62, Landa.

#### Ametropodidae

*Ametropodinae*: NA — *Ametropus albrighti* TRAVER, Green Riv., Jensen, Utah, USA, 5. 63, G. F. Edmunds. — *Metropodinae*: P — *Metropus norvegicus* EAT., Ly Ipm, Vindelälven, Sverige, A & S. Ulfstrand.

#### Leptophlebiidae

E — *Adenophlebia* sp., Berg Riv., Groot Drakenston, W. Cape Prov., S. Africa, 6. 50, (Edmunds); NT — *Atalophlebia (chilensis type)* sp., Alto de Vilches, Prov. Talca, Chile, 1. 64, L. Peña; NT — *Atalophlebia (anastomosis type)* sp., Colliguay, Prov. Valparaiso, Chile, 11. 63, G. F. Edmunds; P — *Choroterpes picteti* (EAT.), Želivka, Švihov, ČSSR, 7. 67, Landa; O — *Choroterpes* sp., Koratty Riv., Erumeli, Kerala St., India, 2. 65, W. L. & J. G. Peters; O — *Choroterpes (Euthraulius)* sp., Kaveriocriss Riv., Canvery, Madras St., India, 1. 65, W. L. & J. G. Peters; O — *Choroterpides* sp., Mae Ping, Chiangmai, Chiangmai Prov., Thailand, 11. 64, W. L. & J. G. Peters; P — *Habroleptoides modesta* (HAGEN), Mže, Milčkov, ČSSR, 4. 67, Landa; P — *Habroleptoides modesta* (Hagen), Lissuraga, Sare, Pyrenée, France, 10. 66, Landa; P — *Habrophlebia lauta* EAT., Smutná, Bechyně, ČSSR, 5. 66, Landa; NA — *Habrophlebia vibrans* NEEDH., Creek, Lake Raveland, Highlands, N. Carolina, USA, 7. 65, Landa; P — *Indiaphlebia* sp., Koratty Riv., Erumeli, Kerala St., India, 2. 65, W. L. & J. G. Peters; NT — *Hagenulus* sp., Creek, Piñares de Viñales, Pinal del Rio, Cuba, 10. 64, Landa; O — *Kimminsula* sp., Sabaragamuwa, n. of Balangoda, Prov. Maratenua, Ceylon, 2. 62, W. L. Peters; NA — *Leptophlebia (Blasturus) gravastella* EAT., Green Riv., Jensen, Utah, USA, 6. 65, Landa; P — *Leptophlebia marginata* (L.), Velká Kuš, Vrbno, nr Strakonice, ČSSR, 5. 62, Landa; NT — *Massartellopsis* sp., Rio Blanco, Prov. Aconcagua, Chile, 11. 63, G. F. Edmunds; NA — *Paraleptophlebia bicornuta* McDUNN, Little Salmon Riv., Adams Co., Idaho, USA, 9. 63, S. L. Jensen; NA — *Paraleptophlebia guttata* McDUNN, Creek, Lake Raveland, Highlands, N. Carolina, USA, 7. 65, Landa; NA — *Paraleptophlebia pallipes* HAGEN, Mill Creek, Salt Lake Co., Utah, USA, 6. 65, Landa; P — *Paraleptophlebia submarginata* (STEPH.), Smutná, Bechyně, ČSSR, 5. 66, Landa; A — *Thraulius* sp., Bulolo Riv., Wan, New Guinea, 10. 64, W. L. & J. G. Peters; NT — *Traverella* sp., Rio Tulumayo, Tingo Maria, San Martin Prov., Peru, 7. 63, W. L. Peters.

#### Ephemerellidae

*Ephemerellinae*: NA — *Ephemerella (Attenuatella) simplex* McDunn, French Broad Riv., Transylvania Co., N. Carolina, USA, 7. 65, Landa; NA — *Ephemerella (Attenuatella) margarita* NEEDH., Boise Riv., Boise, Ada Co., Idaho, USA, 8. 63, S. L. Jensen; P — *Ephemerella (Chitonophora) krieghoffi* (ULMER), Šur, Jur pri Bratislave, ČSSR, 4. 67, Landa; NA — *Ephemerella (Drunella) conestee* TRAVER, French Broad Riv., Transylvania Co., N. Carolina, USA, 7. 65, Landa; NA — *Ephemerella (Drunella) grandis* EAT., Mill Creek, Salt Lake Co., Utah, USA, 6. 65, Landa; P — *Ephemerella ignita* (PODA), Smutná, Bechyně, ČSSR, 6. 66, Landa; NA — *Ephemerella (Ephemerella) inermis* EAT., Provo Riv., Wasatch Co., Utah, USA, 6. 65, Landa; NA — *Ephemerella (Barylophella) trilineata* BERNER, Hatchet Creek, Alachua Co., Florida, USA,

6. 65, Landa; NA — *Ephemerella (Timpanoga) hecuba* EAT., Trout Creek, Summerland, British Columbia, Canada, 8. 64, G. F. Edmunds; P — *Ephemerella (Torleya) major* KLAP., Ostružná, Sušice, ČSSR, 6. 66, Landa; E — *Ephemerellina* sp., Great Berg Riv., French Hoek Forest Reserve, South Africa, 11. 50, A. D. Harrison.

#### Tricorythidae

*Tricorythinae*: O — *Tricorythus* sp., Kattur Riv., Varadapalyam, Andhra Pradesh, India, 12. 64, W. L. & J. G. Peters. — *Leptohyphinae*: NA — *Tricorythodes albalineatus* BERNER, Santa Fe Riv., Alachua Co., Florida, USA, 6. 65, Landa; NA — *Tricorythodes* sp., stream, Salt Lake City, Salt Lake Co., Utah, USA, 6. 54, Landa. — *Dicercomyzinae*: E — *Dicercomyzon costale* KIM., Days Riv., Gold Coast, 8. 50, L. Berner.

#### Behningiidae

P — *Behningia ulmeri* LEST., Warta, Kuczki, Polska, 6. 58, M. Keffermüller.

#### Potamanthidae

O — *Potamanthodes* sp., Mae Ping, Chiangmai, Chiangmai Prov., Thailand, 11. 64, W. L. & J. G. Peters; P — *Potamanthus luteus* (L.), Smutná, Bechyně, ČSSR, 6. 66, Landa; O — *Rhoenantsopsis* sp., Mae Ping, Chiangmai, Chiangmai Prov., Thailand, 11. 64, W. L. + J. G. Peters.

#### Euthyplociidae

NT — *Campylocia* sp., mountain stream, Rio Marauia, NW Taparuarua, Brazil, 1. 63, E. J. Fittkau; NT — *Euthyplocia* sp., Rio Pendescia, Tulumayo Valley, San Martin Prov., Peru, 6. 63, W. L. Peters.

#### Ephemeridae

O — *Eatogenia* sp., Bhavani River, India, without exact data, (G. F. Edmunds); P — *Ephemera danica* MÜLL., Smutná, Bechyně, ČSSR, 5. 66, Landa; NA — *Ephemera simulans* WALKER, Cullasaja River, Macon Co., N. Carolina, USA, 6. 65, Landa; NA — *Hexagenia munda* EAT., Hogtown Creek, Gainesville, Florida, USA, 6. 65, Landa; NA — *Hexagenia recurvata* MORGAN, Michigan Hollow, near Attica, New York, USA, 5. 16, (G. F. Edmunds); A — *Ichthybotus* sp., Wainui-O-matu, New Zealand, 4. 19, G. F. Edmunds; NA — *Pentagenia vittigera* WALSH, Guadalupe River, s. of Victoria, Texas, USA, 4. 50, T. Dolan.

#### Polymitarcidae

*Polymitarcinae*: P — *Ephoron virgo* (OLIV.), Sázava, Kácov, ČSSR, 7. 66, Landa. — *Campsurinae*: NT — *Campsurus* sp., Ariranha Riv., Nova Teutonia, Brazil, 11. 61, F. Plaumann; NA — *Tortopus* sp., Cozad, Nebraska, USA, 9. 50, R. B. Selander. — *Asthenopodinae*: NT — *Asthenopus* sp., Rio Luna Acu at junc. with Rio Petro Acu, nr. Rio Madeira, Brazil, 9. 60, E. J. Fittkau; E — *Povilla adusta* NAVAS, Lake Kivu, Wahu Island, Congo, 4. 53, G. Demoulin.

#### Palingeniidae

P — *Palingenia longicauda* (OLIV.), Latorica, Leles, ČSSR, 7. 61, Landa.

#### Neophemeridae

NA — *Neophemera (Oreianthus) purpurea* TRAVER, Nantahala Riv., Nantahala, N. Carolina, USA, 7. 65, Landa.

#### Caenidae

P — *Brachycercus harrisella* CURT., Ostružná, Sušice, ČSSR, 6. 66, Landa; NA — *Brachycercus nitidus* TRAVER, Cullasaja Riv., Macon Co., N. Carolina, USA, 7. 65, Landa; NA — *Caenis diminiuta* WALK., Hatchet Creek, Alachua Co., Florida, USA, 6. 65, Landa; P — *Caenis horaria* L., Pálenec, Pole, nr. Strakonice, ČSSR, 5. 64, Landa; P — *Caenis macrura* STEPH., Smutná, Bechyně, ČSSR, 5. 66, Landa; P — *Caenis robusta* EAT., Pálenec, Vrbno, nr. Strakonice, ČSSR, 5. 66, Landa.

### *Baetiscidae*

NA — *Baetisca rogersi* BERNER, Little Escambia Creek, Escambia Co., Alabama, USA, 4. 56, L. Berner.

### *Prosopistomatidae*

P — *Prosopistoma foliaceum* FOURKROY, Maros, Szeged, Hungary, 5. 57, Straškraba.

## ANATOMICAL SCHEMES OF LARVAE OF THE FAMILIES, SUBFAMILIES AND GENERA OF THE ORDER EPHEMEROPTERA

Classification by LANDA (1948) has been used for the tracheal system. The main differences among the tracheal systems of mayfly larvae are in the formation of visceral tracheae and in the presence of ventral anastomoses. The visceral tracheae are indicated by the abbreviation TV (trachea visceralis). Numbers following the abbreviation indicate the future imaginal spiracle, in the ring of which the trachea starts. The spiracle 1 is in the mesonotum, 2 in the metanotum, 3–10 in the abdominal segments I–VIII. The anastomoses are indicated in a similar way — TAV (trachea anastomotica ventralis). All the tracheation of the segments VIII–X is based on the spiracle 10. However, since an anastomosis may appear even at the place of the original stigma 11 in the segment IX, both anastomoses are distinguished by figures indicating the segment (TAV 10 (VIII), TAV 10 (IX)). The following abbreviations are used to show the location of ganglia: PT — prothorax, MST — mesothorax, MTT — metathorax, I–VIII — abdominal segments. Letters in parentheses, e. g. (Aa) (Ba $\beta$ ) indicate the type of the type of the tracheal system, Malpighian tubes or nerve band, as given in the following chapter.

### *Siphonuridae*

#### *Siphonurinae* (Fig. 1, SL; Fig. 12, SL)

Tracheal system: TV2, TV4, TV5, TV6, TV7, TV8, TV9, TV10 (Cb) TAV10 (IX) (Aa).

Malpighian tubes: Tubules coiled, entering individually a band on the digestive tube (Aa).

Nerve band: Distribution of ganglia: PT, MST, MTT, II, III, IV, V, VI, VII, VIII. Connectives fused (Ba $\beta$ )

Subfamily homogeneous.

#### *Oniscigastriinae* (Fig. 1, SI)

Tracheal system: TV2, TV3, TV4, TV5, TV6, TV7, TV8, TV9, TV10 (Ca); TAV6, TAV7, TAV8, TAV9, TAV10 (VIII), TAV10 (IX) (Ba).

Malpighian tubes: Tubules coiled, leading individually into a band on the digestive tube (*Oniscigaster*) (Aa) or into low buds (*Siphonella*) (B).

Nerve band: PT, MST, MTT, II, III, IV, V, VI, VII (2 ganglia). Connectives joined at some places (*Oniscigaster*) or completely fused (*Siphonella*) (Ca $\beta$ ).

Subfamily quite homogeneous. Minor details in the formation of Malpighian tubes and in the fusion of the connectives conform to the evolutionary tendencies of the group.

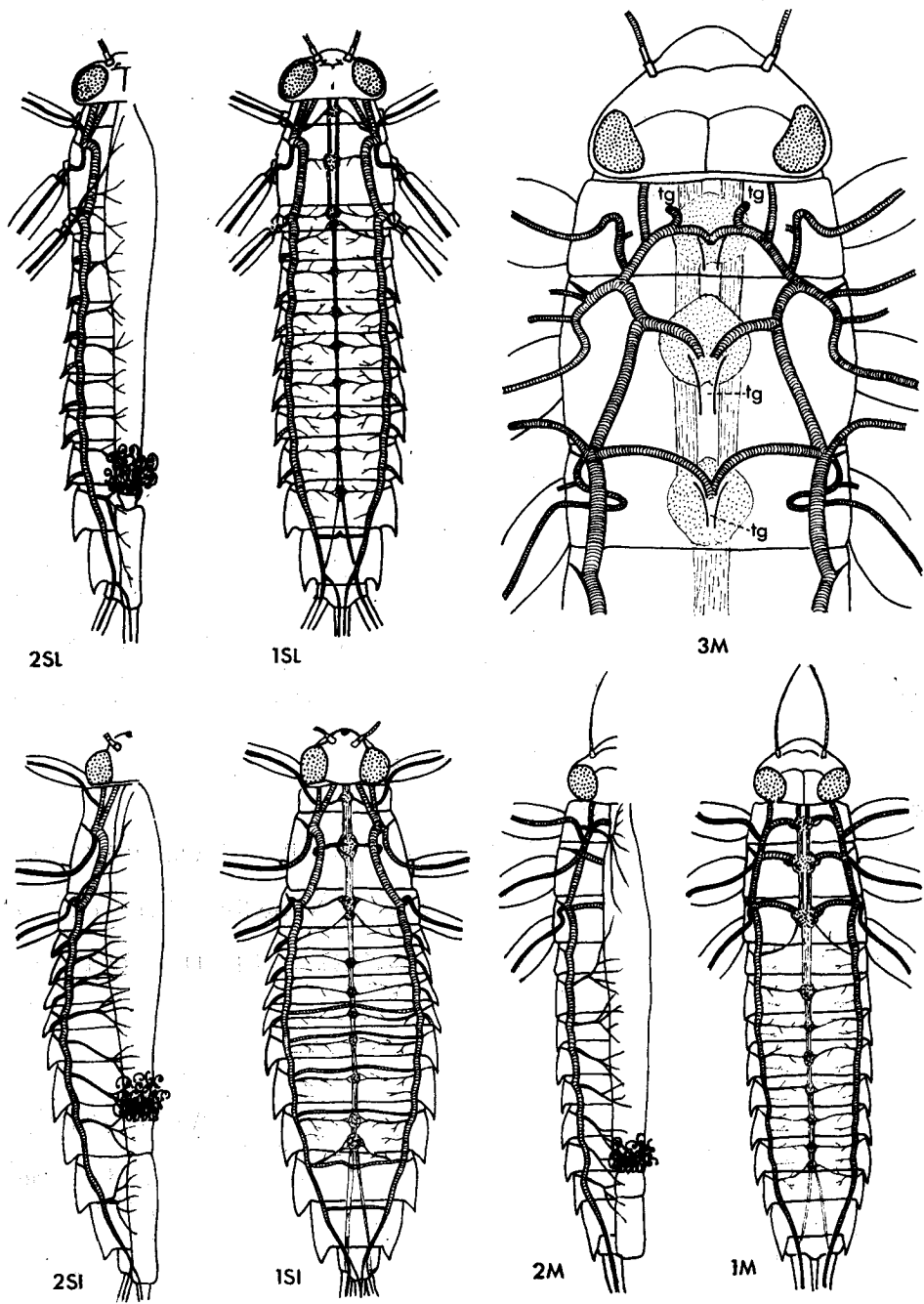


Fig. 1: 1 - ventral part of the body, 2 - visceral tracheae, 3 - tracheae in the thorax. M - *Murphyella* sp., SI - *Siphonella* sp., SL - *Siphonurus lacustris*, tg - tracheal gills.

## *Ameletopsinae*

### *Ameletopsis, Mirawara*

Tracheal system: TV4, TV5, TV6, TV7, TV8, TV9, TV10 (Da); TAV10 (VIII) (Ab). In *Mirawara* TAV was not found (Ca).

Malpighian tubes: Tubules straight (*Ameletopsis*) (Aa) or slightly curved (*Mirawara*) (Ab), individually entering a band on the digestive tube.

Nerve band: PT, MST, MTT, II, III, IV, V, VI, VII (2 ganglia). In *Ameletopsis* the two ganglia are practically fused, similarly as in the family *Baetidae*. Connectives separated, doubled (Ca).

### *Chaquihua*

Basic anatomical characters are the same, except the fact that the visceral branch TV2 is present in the mesothorax (Cb). This situation probably occurs in connection with the excessively developed proximal part of the digestive tube — the crop, which reaches as far as the distal part of the thorax.

### *Chiloporter*

Tracheal system: TV4, TV5 (TV5 is strong, leading up to the head), TV6, TV7, TV8, TV9, TV10 (Da), TAV4, TAV5, TAV6, TAV7, TAV8, TAV9, TAV10 (VIII); TAV10 (IX) (Bb).

Malpighian tubes: Tubules straight, individually entering a band on the digestive tube (Ab).

Nerve band: PT, MST, MTT, II, III, IV, V, VI, VII (2 ganglia). Connectives separated, doubled (Ca).

Both the New Zealand genus *Ameletopsis* and the Australian genus *Mirawara* are similar in their anatomical structure. The presence of the trachea TV2, the genus *Chaquihua* may also be affiliated to this group. The genus *Chiloporter*, however, must be excluded owing to the absolutely different structure of its tracheal system and tracheal gills.

## *Isonychiinae* (Fig. 2, I)

Tracheal system: TV1, TV2, TV3, TV4, TV5, TV6, TV7, TV8, TV9, TV10 (A); TAV10 (IX) (Aa).

Malpighian tubes: Tubules coiled, distally thickened at the outlets and bent outwards. They lead into 8 narrow trunks with thin branches (Cb).

Nerve band: PT, MST, MTT, II, III, IV, V, VI, VII, VIII. Connectives separated, doubled (Ba).

The anatomical characters of this subfamily containing only one genus are very marked; they distinguish this group from the others and relate it to the family *Oligoneuriidae*.

## *Coloburiscinae* (Fig. 1, M)

### *Coloburiscoides, Coloburiscus*

Tracheal system: TV4, TV5, TV6, TV7, TV8, TV9, TV10 (Ca).

Malpighian tubes: Tubules coiled, singly entering a band on the digestive tube (Aa).

Nerve band: PT, MST, MTT, II, III, IV, V, VI, VII (2 ganglia). Connectives fused into one cord (Ca).

## *Murphyella*

The basic anatomical characters are the same as in *Coloburiscus*, with the addition, however, of TV1 (Ba). Neither TAV 10 (VIII) nor TAV 10 (IX) were ascertained (C $\alpha$ ). Their presence, however, cannot be excluded. The tracheal system is maximally affected by the absence of tracheal gills and by the transfer of the respiratory function into the auxiliary tracheal gills on the head and thorax. The tubules of the Malpighian tubes enter low buds (B). The subfamily, despite the extreme changes in the genus *Murphyella*, is homogeneous. The existing changes occur within the scope of the evolutionary tendencies of this group.

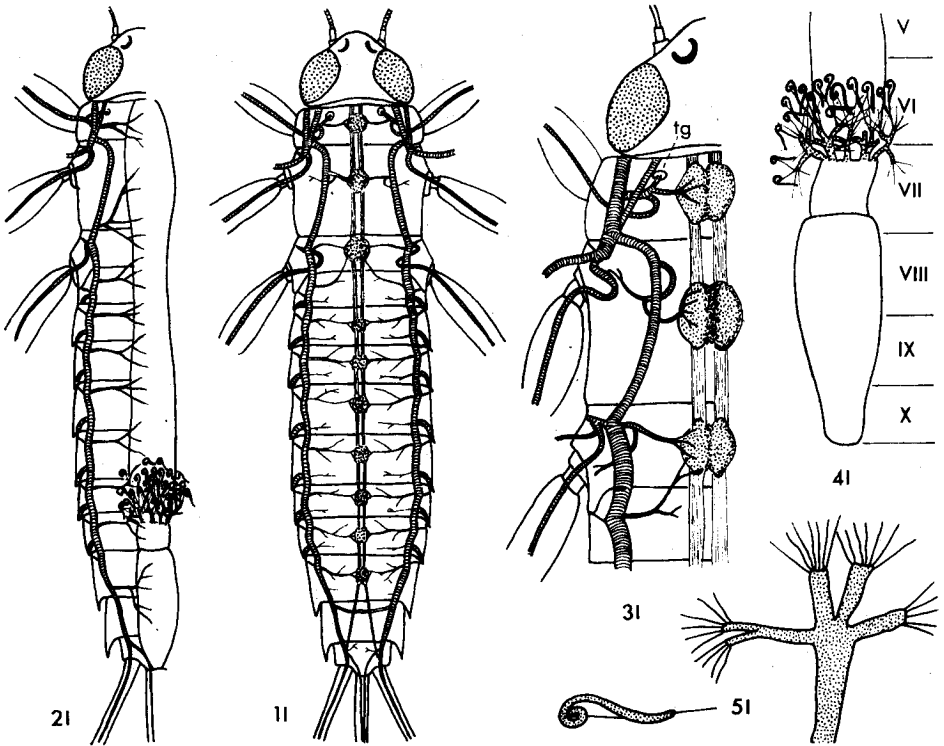


Fig. 2: 1 — ventral part of the body, 2 — visceral tracheae, 3 — tracheae in the thorax, 4 — digestive system with Malpighian tubes, 5 — trunk of Malpighian tubes and a tubule. I — *Isonychia* sp., tg — tracheal gills.

## *Rallidentinae*

Tracheal system: TV2, TV4, TV5, TV6, TV7, TV8, TV9, TV10 (Cb).

Malpighian tubes: Tubules straight, narrowly bent at the outlets, singly entering a band on the digestive tube.

Nerve band: PT, MST, MTT, II, III, IV, V, VI, VII, VIII. Ganglia elongate, oval, connected by a simple band as in *Baetidae*.

Anatomical characters of this subfamily containing only one genus are very marked. They distinguish this subfamily from the others and relate it to *Baetidae*.



The family *Siphonuridae* includes subfamilies with very heterogeneous anatomical characters. The division into the following groups results from their examination:

- (a) *Siphonurinae*
- (b) *Ameletopsinae* (excluding the genus *Chiloporter*), *Coloburiscinae*
- (c) *Rallidentinae*
- (d) *Isonychiinae*
- (e) *Oniscigastrinae*, genus *Chiloporter*

The group (e) (*Oniscigastrinae* and the genus *Chiloporter*) diametrically differs from the basic scheme of the family due to the formation of anastomoses in the abdominal segments and hence it must be excluded. It is necessary also to exclude the subfamily *Isonychiinae* whose scheme is the same as that of the family *Oligoneuriidae*. If the scheme of the related subfamily *Siphonurinae* is considered to be the basic scheme of anatomical characters, then it might be possible to deduce some relatively more recent and more specialized forms of the subfamily *Ameletopsinae* and *Coloburiscinae* (disappearance of the visceral tracheae in the thorax and the shift of the last abdominal ganglion into segment VIII), but the differences are greater than, for example, those between *Siphonurinae* and *Baetidae*, *Oligoneuriinae*, etc. In the subfamily *Ameletopsinae*, and particularly in the *Rallidentinae* certain elements of affinity with the family *Baetidae* may be seen.

#### *Baetidae*

(Fig. 3, B, C; Fig. 12, BR)

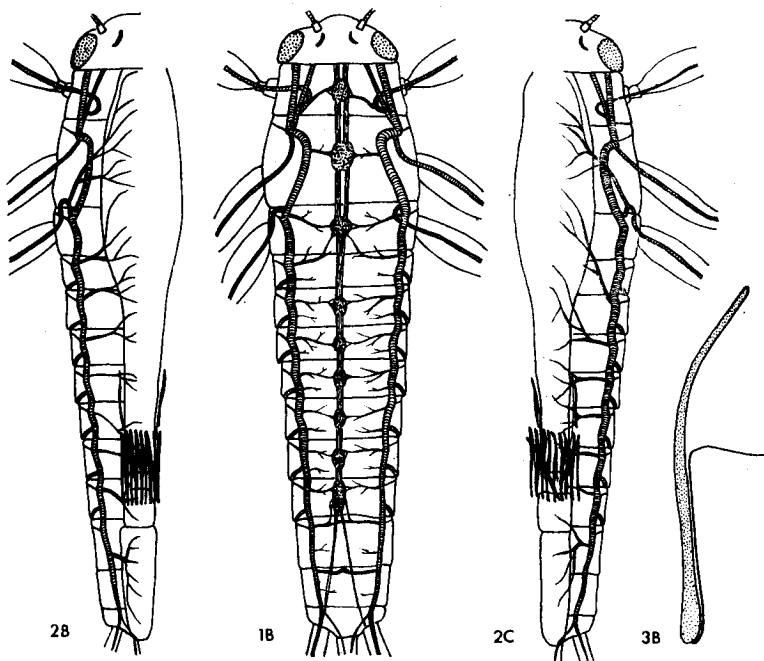


Fig. 3: 1 — ventral part of the body, 2 — visceral tracheae, 3 — tubule of the Malpighian tubes.  
B — *Baetis rhodani*, C — *Callibaetis coloradensis*.

Tracheal system: TV2, TV3, TV4, TV5, TV6, TV7, TV8, TV9, TV10 (Ca), TAV 10 (VIII), TAV10 (IX) (Ac).

Malpighian tubes: Tubules straight, distally club-like, singly entering a band on the digestive tube (Ab).

Nerve band: PT, MST, MTT, II, III, IV, V, VI, VII (2 ganglia). Ganglia in the segment VII merge into one flat body. Connectives joined into a flat band (D).

The Nearctic genus *Callibaetis* and Nearctic species *Centroptilum rubropictum* deviate from the general scheme of anatomical characters, since they lack the visceral trachea in segment I of the abdomen (TV3). In some Nearctic and neotropical genera the median visceral branch in the abdomen is absent (TV5—TV7) (Cb).

In spite of these exceptions, which correspond to the evolutionary tendencies of this group, the family is quite homogeneous.

### *Oligoneuriidae*

#### *Chromarcyinae*

Tracheal system: TV1, TV2, TV3, TV4, TV5, TV6, TV7, TV8, TV9, TV10 (A); TAV 10 (IX) (Aa).

Malpighian tubes: Tubules coiled, entering 8 trunks distally widened and shallowly branched (Ca).

Nerve band: PT, MST, MTT, II, III, IV, V, VI, VII, VIII. Connectives apparently double (Ba $\alpha$ ).

The widened part of the lateral thoracic trunk is elongate, compared with the following subfamily. The present subfamily is close to the following one, with a certain relationship to the subfamily *Isonychiinae*.

#### *Oligoneuriinae* (Fig. 4, O)

Tracheal system: TV1, TV2, TV3, TV4, TV5, TV6, TV7, TV8, TV9, TV10 (A) TAV 10 (IX) (Aa).

Malpighian tubes: Tubules coiled, entering 8 trunks distally widened and shallowly branched (Ca).

Nerve band: PT, MST, MTT, II, III, IV, V, VI, VII, VIII. Connective doubled (Ba $\alpha$ ).

There is a slight deviation from the general scheme in the genus *Homoeoneuria*, where the last abdominal ganglion is shifted to the frontal edge of segment VIII and the connectives merge into a band (Ba $\beta$ ). This specialization corresponds to the evolutionary trend.

The family is quite homogeneous.

### *Heptageniidae*

#### *Heptageniinae* (Fig. 4, E, R; Fig. 12, HS)

The genera of the subfamily *Heptageniinae* may be divided into two groups. Group (a) covers all the genera that are more plesiomorphic from the evolutionary aspect: *Cinygmula*, *Rhithrogena*, *Epeorus* — subgenera *Epeorus*, *Iron* and *Ironodes*. This is the scheme of the group:

Tracheal system: TV2, TV4, TV5, TV6, TV7, TV8, TV9, TV10 (Cb); TAV 10 (IX) (Aa).

Malpighian tubes: Tubules coiled at both ends or bent outwards at their loose ends, entering 8 low buds or short trunks. In the subgenus *Ironodes* the lateral trunks are longer than dorsal and ventral ones (Ca).

Nerve band: PT, MST, MTT, II, III, IV, V, VI, VII, VIII. Connectives separated, doubled (Ba $\alpha$ ).

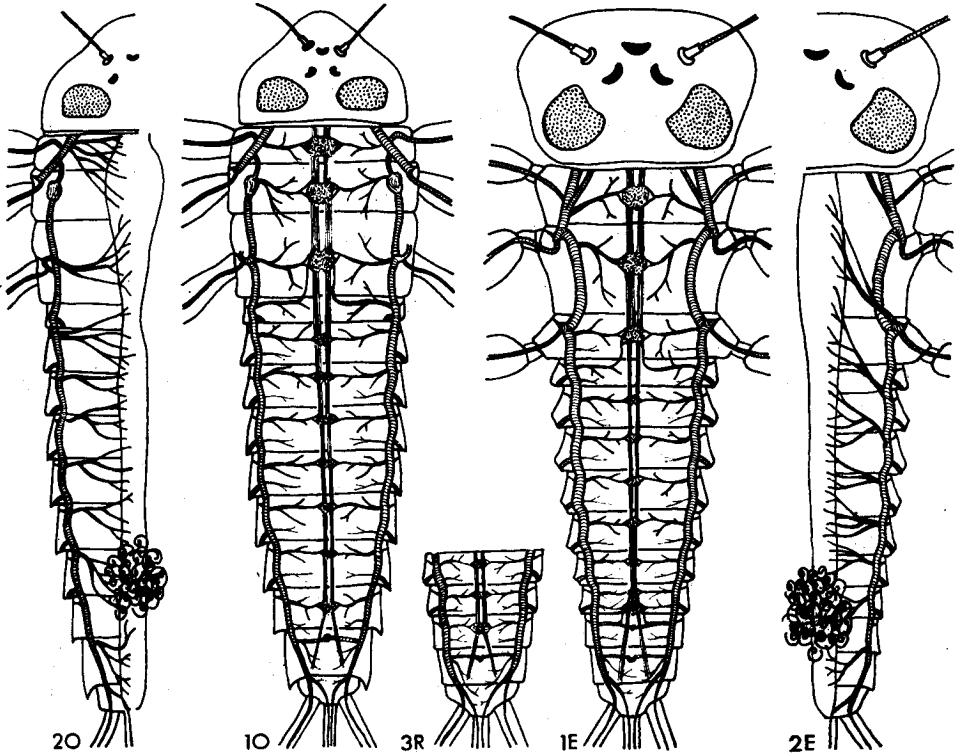


Fig. 4: 1 - ventral part of the body, 2 - visceral tracheae, 3 - ventral part of abdominal segments VIII, IX and X. E - *Ecdyonurus torrentis*, O - *Oligoneuriella rhenana*, R - *Rhithrogena semicolorata*.

Group (b) covers genera that are advanced, more specialized: *Afronurus*, *Ecdyonurus*, *Heptagenia*, *Stenonema*, *Thalerosphyrus*. This is the scheme of the group:

Tracheal system: TV2, TV4, TV5, TV6, TV7, TV8, TV9, TV10 (Cb); TAV 10 (VIII), TAV 10 (IX) (Ac).

Malpighian tubes: Tubules coiled, entering 8 trunks distended and branched at their ends (Ca). In the genera *Afronurus*, *Cinygmmina* and *Heptagenia* the trunks are split to their base, in the genus *Thalerosphyrus* almost undivided.

Nerve band: PT, MST, MTT, II, III, IV, V, VI, VII (2 ganglia). Connectives well discernible, fused between segments V - VII (Ca $\beta$ ).

The Nearctic subgenus *Ironopsis* of the genus *Epeorus* occupies a place in the middle between the above two groups. The last ganglion is shifted to segment VII, TAV 10 (VIII) and develops as late as in the last larval stages; connectives of the nerve band do not merge.

Different stages of evolution may be followed within the framework of the genera of the subfamily *Heptageniinae*. From the aspect of evolution, however, the subfamily *Heptageniinae* is homogeneous.

*Arthropleinae* (Fig. 4, A)

Tracheal system: TV2, TV4, TV5, TV6, TV7, TV8, TV9, TV10 (Cb); TAV 10 (VIII), TAV 10 (IX) (Ac).

Malpighian tubes: Tubules coiled, passing into 8 oval buds which do not branch out (B).

Nerve band: PT, MST, MTT, I, II, IV, V, VI, VII (2 ganglia). Connectives joined into a single cord (Cb $\beta$ ).

The subfamily is well characterized by its anatomical characters.

In general, the family *Heptageniidae* forms a quite homogeneous group. The subfamily *Arthropleinae* differs from the subfamily *Heptageniinae*, due to its anatomic characters.

*Ametropodidae*

*Ametropodinae* (Fig. 5, A)

Tracheal system: TV2, TV4, TV5, TV6, TV7, TV8, TV9, TV10 (Cb); TAV not found (C $\alpha$ ).

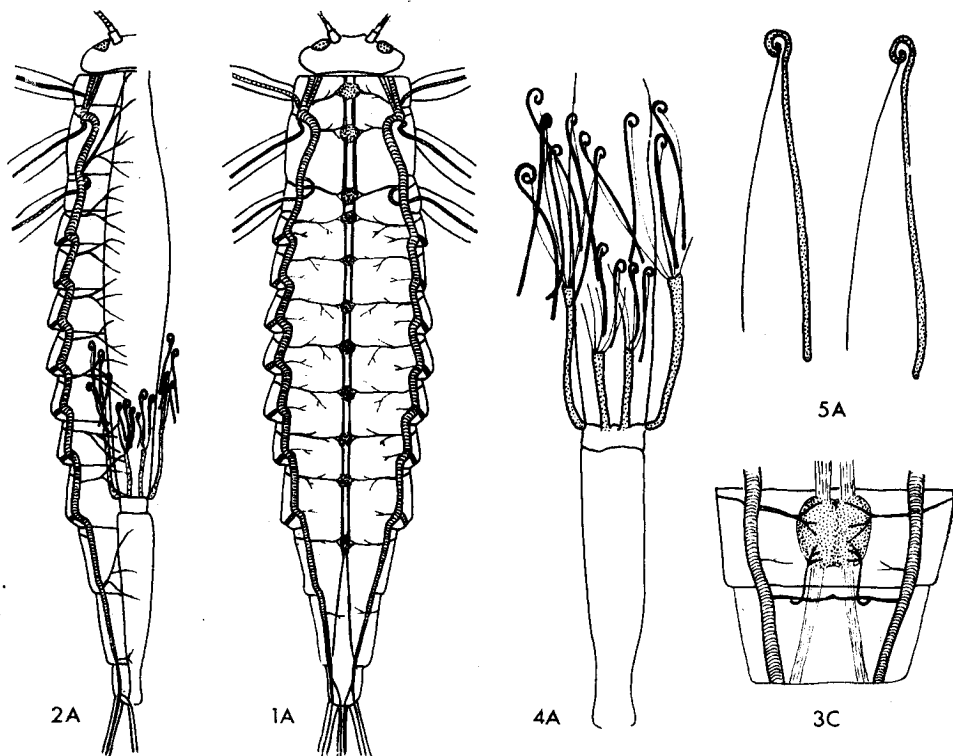


Fig. 5: 1 - ventral part of the body, 2 - visceral tracheae, 3 - ventral part of segments VIII and IX, 4 - digestive tube and Malpighian tubes, 5 - tubules of Malpighian tubes. A - *Ametropus albrighti*. C - *Cinygmula par.*

Malpighian tubes: Tubules long, coiled, entering 6 simple, unbranched trunks. On either side there is one long trunk extending beyond the segment, and two short ones on the upper and lower sides (Db).

Nerve band: PT, MST, MTT, I, II, III, IV, V, VI, VII, VIII. A unique case where the ganglion of abdominal segment I does not merge with that of the metathorax. Connectives loose, separated from each other (A).

### *Metretopodinae*

Tracheal system: TV2, TV4, TV5, TV6, TV7, TV8, TV9, TV10 (Cb); TAV not found (C $\alpha$ ).

Malpighian tubes: Tubules short, coiled, entering 8 short buds (B).

Nerve band: PT, MST, MTT, II, III, IV, V, VI, VII, VIII. Connectives fused (Ba $\beta$ ).

Although the rather poorly preserved material made the study of anastomoses impossible, it is evident from the data acquired so far that the subfamilies *Ametropodinae* and *Metropodinae* are not related in any way, and consequently they cannot remain assigned to the same family. The anatomical characters of the subfamily *Metretopodinae* are in closer affinity with those of the subfamily *Siphonurinae*.

### *Leptophlebiidae*

(Fig. 6, L, P, CH; Fig. 12, PS)

The genera of the family *Leptophlebiidae* may be divided in general into two groups.

Group (a) manifests more original anatomical characters. It has two subgroups, the  $\alpha$  subgroup of plesiomorphic genera and  $\beta$  subgroup of apomorphic ones.

The subgroup  $\alpha\alpha$  includes the genera *Paraleptophlebia*, *Atalophlebia* and *Massartellopsis*. The scheme of the anatomical characters of these genera is the following:

Tracheal system: TV2, TV5, TV6, TV7, TV8, TV9, TV10 (Cc); TAV6, TAV7, TAV8, TAV9, TAV10 (VIII) (Ba).

Malpighian tubes: Tubules curved, entering 8 buds (*Atalophlebia chilensis* type) (B) or 8 longer trunks. The trunks are of the same length and do not branch (Da).

Nerve band: PT, MST, MTT, II, III, IV, V, VI, VII (2 ganglia). Connectives separated, doubled (Ca).

The subgroup  $\alpha\beta$  includes the following genera: *Leptophlebia*, *Adenophlebia*, *Habroleptoides*, *Habrophlebia*. In the genera *Leptophlebia* and *Adenophlebia* further anastomosis TAV5 occurs (Bb). The Malpighian tubes remain of the same type, in *Leptophlebia* they enter buds (B), in *Adenophlebia* 8 longer unbranched trunks (Da). The original scheme of the tracheal system (Cc, Ba) is retained in the genera *Habroleptoides* and *Habrophlebia*, but there is a specialization of the Malpighian tubes, which consist of 8 trunks of different lengths. The lateral trunks become longer (Da).

Group (b) has three subgroups:  $\alpha$  subgroup of plesiomorphic genera and  $\beta$  and  $\gamma$  subgroups of markedly specialized genera.

In the subgroup  $\beta\alpha$  belong the genera *Thraululus* and *Indiaphlebia*. They have the following scheme of anatomical characters:

Tracheal system: TV2, TV6, TV7, TV8, TV9, TV10 (Cd); TAV6, TAV7 TAV8, TAV9, TAV10 (VIII), TAV10 (IX) (Ba).

Malpighian tubes: Tubules coiled, entering 6 unbranched trunks of the same length (Db).

Nerve band: PT, MST, MTT, II, III, IV, V, VI, VII (2 ganglia). Connectives separated, doubled (Ca $\alpha$ ).

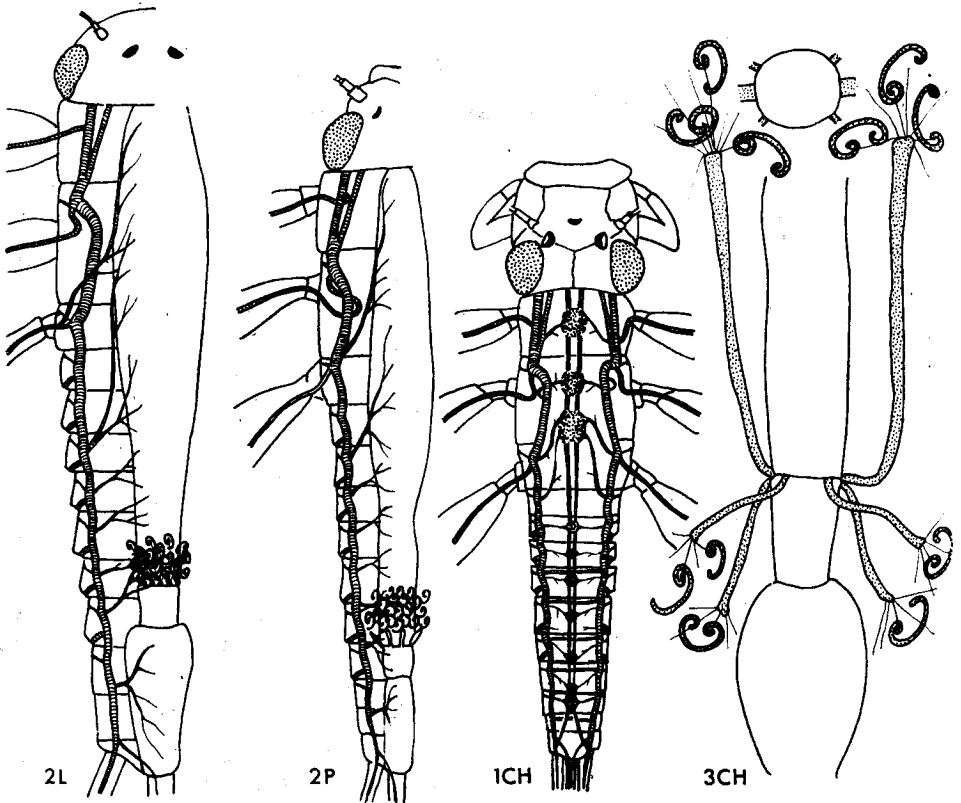


Fig. 6: 1 — ventral part of the body, 2 — visceral tracheae, 3 — digestive system with Malpighian tubes. CH — *Choroterpes* sp., L — *Leptophlebia marginata*, P — *Paraleptophlebia submarginata*.

The genus *Indiaphlebia* is more specialized and it also possesses TAV5 (Bb).

The subgroup b $\beta$  includes the genera of the Oriental region *Choroterpes* and *Choroterpides* (*Choroterpes* also occurs in the Palearctic region). This is the scheme of this subgroup's anatomical characters:

Tracheal system: TV2, TV6, TV7, TV8, TV9, TV10 (Cd); TAV6, TAV7, TAV8, TAV9, TAV10 (VIII), TAV10 (IX) (Ba).

Malpighian tubes: Tubules curved, entering 2 long lateral trunks directed forward and two dorsal trunks and other 2 ventral ones, directed backwards and sideways (6 trunks altogether) (Db).

Nerve band: PT, MST, MTT, II, III, IV, V, VI, VIII (2 ganglia). Connectives separated, doubled (Bb).

The subgroup by contains for the present the neotropical genus *Hagenulus*. This is the scheme of its characters:

Tracheal system: TV2, TV5, TV6, TV7, TV8, TV9, TV10 (Cc); TAV6, TAV7, TAV8, TAV9, TAV10 (VIII), TAV10 (IX) (Ba).

Malpighian tubes: Tubules coiled, entering two relatively long tracheal trunks (Fb $\alpha$ ).

Nerve band: PT, MST, MTT, II, III, IV, V, VI, VII (2 ganglia). Connectives separated (Ca $\alpha$ ).

The family *Leptophlebiidae* is extremely numerous with genera extraordinarily adapted to various environments. In spite of the differences between the two groups, their generic affinity is evident, and hence the family *Leptophlebiidae* may be considered a natural one.

### *Ephemerellidae*

*Ephemerellinae* (Fig. 7, E; Fig. 12, EI)

The genus *Ephemerella* has very heterogeneous anatomical characters. Practically all the subgenera established so far have different characteristics. Generally, the subgenera may be divided into two groups. The group (a) may be considered plesiomorphic, the group (b) derived or apomorphic.

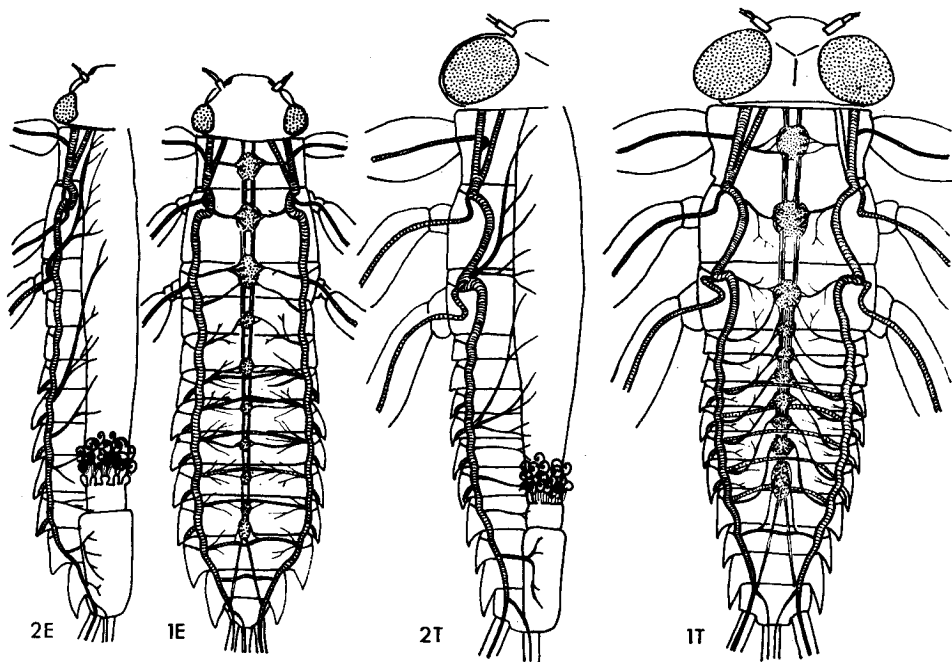


Fig. 7: 1 — ventral part of the body, 2 — visceral tracheae. E — *Ephemerella (Drunella)* sp., T — *Tricorythodes albalineatus*.

In the group (a) belong the subgenera *Attenuatella* and *Timpanoga*. The scheme of the subgenus *Attenuatella* is the following:

Tracheal system: TV2, TV3 (or TV4), TV5, TV6, TV7, TV8, TV9, TV10 (Ca); TAV6, TAV7, TAV8, TAV9, TAV10 (VIII) (Ba).

Malpighian tubes: Tubules coiled, entering 8 low buds which occasionally are only indistinct (B).

Nerve band: PT, MST, MTT, II, III, IV, V, VI (at the boundary line of segments VI and VII), VII, VIII (at the boundary line of segments VII and VIII). Connectives separated, doubled (Bb).

The scheme of the subgenus *Timpanoga* is similar, but the nerve ganglia are shifted forward, and the buds of the Malpighian tubes are somewhat higher.

The group (b) consists of the subgenera *Drunella*, *Ephemerella* s. str., *Torleya* and *Chitonophora*. The subgenus *Drunella* has the following scheme: Tracheal system: TV2, TV6, TV7, TV8, TV9, TV10 (Cd); TAV6, TAV7, TAV8, TAV9, TAV10 (VIII), TAV10 (IX) (Ba).

Malpighian tubes: Tubules coiled, entering buds about twice as long as their width (B).

Nerve band: PT, MST, MTT, I, II, III (boundary line III, IV), V, VI, VII (2 ganglia). Connectives separated, doubled (Cb $\alpha$ ).

The Nearctic species of the subgenus *Ephemerella* s. str. — *Ephemerella inermis* — exhibits a similar scheme. The Palearctic species *Ephemerella ignita* is more advanced. It lacks TV7 and, on the contrary, TAV5 is developed (Bb). A similar scheme is seen also in the Palearctic subgenus *Torleya*. In the Palearctic area the subgenus *Chitonophora* seems to be more derivative; it, too, lacks TV7 and there are anastomoses up to the first abdominal segment (TAV4, TAV5 . . .) (Bb). The nerve ganglia are concentrated within segments I — VI.

The genus *Ephemerellina* has the following scheme:

Tracheal system: TV2, TV5, TV6, TV7, TV8, TV9, TV10 (Cc); TAV6, TAV7, TAV8, TAV9, TAV10 (VIII), TAV10 (IX) (Ba).

Malpighian tubes: Tubules coiled, entering not very distinct buds, practically a band on the digestive tube (B, Aa).

Nerve band: PT, MST, MTT, I, II, III, IV, V, VI, VII. Connectives separated, doubled (Ea).

The genus *Ephemerellina* may be placed in the very variable scheme of the subfamily *Ephemerellinae*. It has, however, distinct relations with and may be quite close to the subfamily *Leptohyphinae*.

The subfamily *Ephemerellinae*, except for the above mentioned genus *Ephemerellina*, undoubtedly represents an evolutionarily homogeneous group. The unstable, fluctuating and widely distributed characters provide material for the study of the evolution of a number of organs of *Ephemeroptera*.

### *Tricorythidae*

#### *Tricorythinae*

Tracheal system: TV2, TV6, TV7, TV8, TV9, TV10 (Cd); TAV6, TAV7, TAV8, TAV9, TAV10 (VIII) (Ba).

Malpighian tubes: Tubules coiled, entering 4 long trunks reaching as far as segment III. Between each of them there is one short trunk on either side (Fa).

Nerve band: PT, MST, MTT, I, II, III, (at the boundary line between III and IV), V, VI, VII (2 ganglia). Connectives separated, doubled (Cb $\alpha$ ).



*Leptohyphinae* (Fig. 7, T):

Tracheal system: TV2, TV6, TV7, TV8, TV9, TV10 (Cd); TAV5, TAV6, TAV7, TAV8, TAV9, TAV10 (VIII) (Bb).

Malpighian tubes: Tubules coiled, singly entering a band on the digestive tube (Aa).

Nerve band: PT, MST, MTT, I, II, III, IV, V, VI, VII. Connectives separated, doubled (Ea).

*Dicercomyzinae*

Tracheal system: TV2, TV6, TV7, TV8, TV9, TV10 (Cd); TAV6, TAV7, TAV8, TAV9, TAV10 (VIII) (Ba).

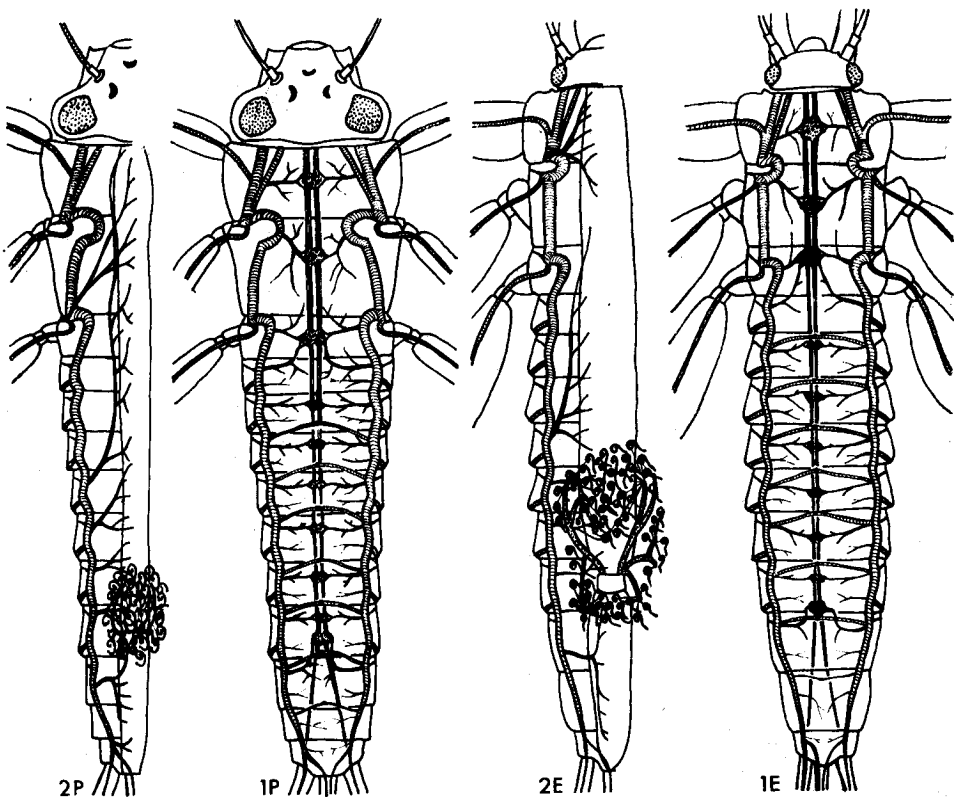


Fig. 8: 1 - ventral part of the body, 2 - visceral tracheae. E - *Euthyplocia* sp., P - *Potamanthus luteus*.

Malpighian tubes: Tubules coiled, singly entering a band on the digestive tube (Aa).

Nerve band: PT, MST, MTT, I, II, III, IV, V, VI (2 ganglia). Connectives separated, doubled (Eb).

The family *Tricorythidae* does not form a homogeneous whole. The anatomical characters of the subfamily *Tricorythinae* on the one hand, and those of the subfamilies *Leptohyphinae* and *Dicercomyzinae* on the other hand,

greatly differ. The former exhibits some relationship to the family *Caenidae*, and, on the contrary, the latter two subfamilies to the family *Ephemerellidae*.

### *Behningiidae*

Tracheal system: TV2, TV6, TV7, TV8, TV9, TV10 (Cd); TAV5, TAV6, TAV7, TAV8, TAV9, TAV10 (VIII), TAV10 (IX) (Bb).

Malpighian tubes: Tubules coiled, entering 8 egg-shaped buds (B).

Nerve band: PT, MST, MTT, II, III, IV, V, VI, VII (2 ganglia). Connectives fused into a shallow band (Ca $\beta$ ).

The family is well characterized by its anatomical features. It manifests a relationship to the family *Leptophlebiidae* as well as to the *Potamanthidae*.

### *Potamanthidae*

(Fig. 8, P)

Tracheal system: TV2, TV6, TV7, TV8, TV9, TV10 (Bd); TAV5, TAV6, TAV7, TAV8, TAV9, TAV10 (VIII), TAV10 (IX) (Bb).

Malpighian tubes: Tubules coiled, entering by their ducts 6 trunks branching out bush-like. There is one long trunk on either side, two short ones on the dorsal and ventral side (Ea).

Nerve band: PT, MST, MTT, II, III, IV, V, VI, VII (2 ganglia) (Ca $\alpha$ ).

The family is quite homogeneous and well characterized by its anatomical features.

### *Euthyplociidae*

(Fig. 8, E)

Tracheal system: TV1, TV6, TV7, TV8, TV9, TV10 (Bb); TAV4, TAV5, TAV6, TAV7, TAV8, TAV9, TAV10 (VIII), TAV10 (IX) (Bb).

Malpighian tubes: Tubules coiled at their ducts, distally nearly straight. They enter 4 trunks with bush-like branching (Eb).

Nerve band: PT, MST, MTT, II, III, IV, V, VI, VII (2 ganglia). The last ganglion at the beginning of segment VIII. Connectives separated (Ca $\alpha$ ).

Owing to its anatomical characters the family is quite homogeneous. It exhibits a close relationship to the plesiomorphic family *Polymitarciidae*.

### *Ephemeridae*

(Fig. 9, H, ED; Fig. 12, ED)

The genera of the family may be divided into two groups. The group (a) is more primitive and includes the genera *Ephemera* and *Ichthybotus*. Its scheme is the following:

Tracheal system: TV2, TV6, TV7, TV8, TV9, TV10 (Cd); (TAV4) TAV5, TAV6, TAV7, TAV8, TAV9, TAV10 (VIII), TAV10 (IX) (Bb).

Malpighian tubes: Tubules coiled, their free ends practically straight, entering by their ducts 6 trunks branching out bush-wise (Ea).

Nerve band: PT, MST, MTT, II, III, IV, V, VI, VII, VIII. Connectives separated (Ba $\alpha$ ).

The genus *Hexagenia* belongs in the specialized group (b). TV6 and TV7 are extraordinarily strongly developed, TV9 is lacking. There are anastomoses in all the segments, hence also in TAV3, TAV4 . . . (Bb). Connectives between II—VII are fused.

Despite markedly different characters of the two groups, the family *Ephemeridae* may be considered evolutionarily homogeneous. The *Ephemeridae* show close relationships to the family *Palingeniidae*.

### *Polymitarciidae*

#### *Polymitarcinae* (Fig. 9, EV)

Tracheal system: TV1, TV6, TV7, TV8, TV9, TV10 (Bb); TAV4, TAV5, TAV6, TAV7, TAV8, TAV9, TAV10 (VIII), TAV10 (IX) (Bb). In the head there are tracheal sacs.

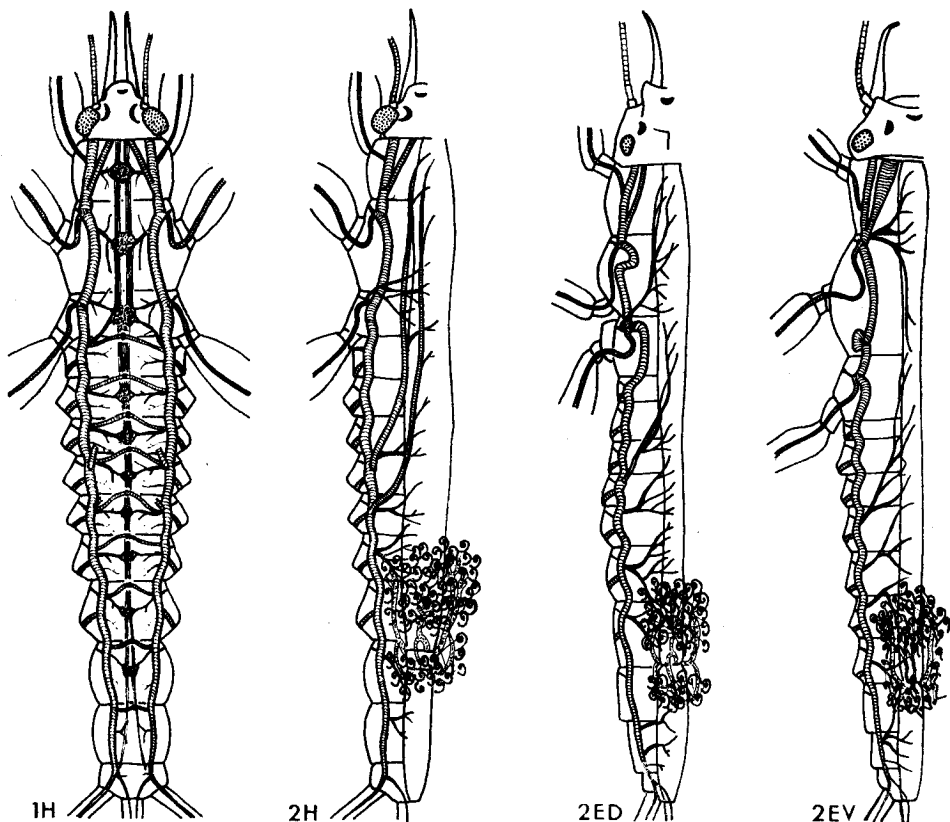


Fig. 9: 1 - ventral part of the body, 2 - visceral tracheae. ED - *Ephemera danica*, EV - *Ephoron virgo*, H - *Hexagenia munda*.

Malpighian tubes: Tubules coiled, entering 6 trunks with bush-like branches (Ea).

Nerve band: PT, MST, MTT, II, III, IV, V, VI, VII, VIII. Connectives separated (Ba $\alpha$ ).

#### *Campsurinae*

Tracheal system: TV1, TV6, TV7, TV8, TV9, TV10 (Bb); TAV4, TAV5, TAV6, TAV7, TAV8, TAV9, TAV10 (VIII), TAV10 (IX) (Bb). There are

tracheal sacs in the head of the genus *Campsurus*, but they are lacking in the genus *Tortopus*.

Malpighian tubes: Tubules coiled, entering 4 trunks branching out bush-like (Eb).

Nerve band: PT, MST, MTT, II, III, IV, V, VI, VII, VIII. Connectives separated (Ba $\alpha$ ).

#### *Asthenopodinae*

Tracheal system: TV1, TV6, TV7, TV8, TV9, TV10 (Bb); (TAV4), TAV5, TAV6, TAV7, TAV8, TAV9, TAV10 (VIII), TAV10 (IX) (Bb). In the genus *Asthenopus* there are tracheal sacs in the head, but they are absent in the genus *Fovilla*.

Malpighian tubes: Tubules coiled, leading into 4 trunks with bush-like branches (Eb).

Nerve band: PT, MST, MTT, II, III, IV, V, VI, VII, VIII. Connectives separated (Ba $\alpha$ ).

The family is homogeneous. The deviations among the subfamilies correspond to the developmental tendencies of this group. In the heads of larvae of most genera belonging to this family there are tracheal sacs, never found in any of the other families. *Polymitarcidae* show a relationship to the family *Euthyplociidae*.

#### *Palingeniidae*

Tracheal system: TV2, TV6, TV7, TV8, TV9, TV10 (Cd); TAV4, TAV5, TAV6, TAV7, TAV8, TAV9, TAV10 (VIII), TAV10 (IX) (Bb).

Malpighian tubes: Tubules coiled entering through its ducts 6 trunks branched out bush-like.

Nerve band: PT, MST, MTT, II, III, IV, V, VI, VII, VIII. Connectives separated (Ba $\alpha$ ).

The family is anatomically almost identical with the more primitive group of *Ephemeridae*.

#### *Neophemeridae*

(Fig. 10, N; Fig. 12, NP)

Tracheal system: TV6, TV7, TV8, TV9, TV10 (Db); TAV4, TAV5, TAV6, TAV7, TAV8, TAV9, TAV10 (VIII), TAV10 (IX) (Bb).

Malpighian tubes: Tubules coiled, passing into 2 long trunks which reach as far as segment II. The tubules reach still farther forwards. On the inner side of the trunks there are 3 processes directed to the centre (Fb $\beta$ ).

Nerve band: PT, MST, MTT, II, III, IV, V, VI, VII (2 ganglia). Connectives separated (Ca $\alpha$ ).

The family is well characterized by its anatomical features. It manifests rather distant relationships to the family *Tricorythidae* (subfamily *Tricorythinae*), and close relationships to the families *Caenidae*, *Prosopistomatidae* and particularly to *Baetiscidae*.

#### *Caenidae*

(Fig. 10, C; Fig. 12, CR, BH)

Tracheal system: TV6, TV7, TV8, TV9, TV10 (Db); TAV were not observed, fine branches in the median line contact each other.

Malpighian tubes: Tubules coiled, entering 2 long trunks which reach as far as segment III. The tubules reach still farther forwards. The hind gut protrudes, forming a flat sack that is laterally extended into 2 lobes. In the genus *Brachycercus* a blind unpaired sac is formed, situated on the dorsal side and extending up to segment IV (Fb $\alpha$ ).

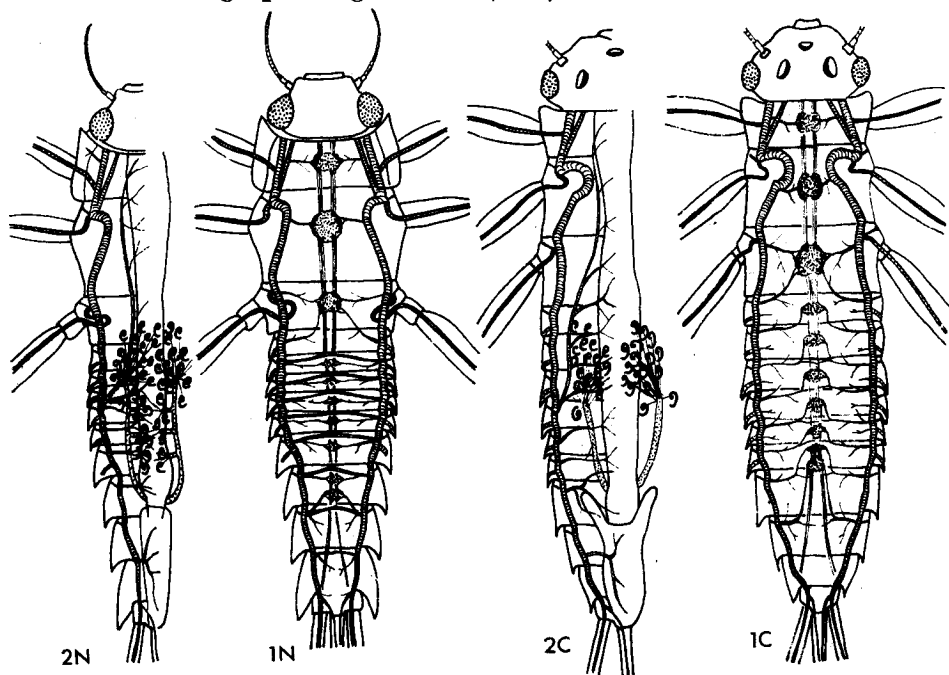


Fig. 10: 1 — ventral part of the body. 2 — visceral tracheae. C — *Caenis diminuta*, N — *Neophemera purpurea*.

Nerve band: PT, MST, MTT, I, II, III, IV, V, VI (7 abdominal ganglia are accumulated in segments I—VI). Connectives are separated (Eb).

The family *Caenidae* is homogeneous. It distantly resembles the family *Tricorythidae* (subfamily *Tricorythinae*), is more closely related to the family *Neophemeridae* and quite close to the families *Baetiscidae* and *Prosopistomatidae*. The genus *Caenis*, however, is more closely related to the genus *Prosopistoma*, and the genus *Brachycercus* to the genus *Baetisca*.

#### *Baetiscidae* (Fig. 11, B)

Tracheal system: TV1, TV4, TV5, TV6, TV7, TV8, TV10 (Ba); TAV were not found, but cannot be excluded. In segments IV—IX strong branches grow out of the trunks and extend to the abdominal muscles where they form thick fasciae.

Malpighian tubes: Tubules coiled at their ducts, almost straight at their loose ends. They enter 2 long trunks which reach as far as the thorax. On their inner side there are 3 blunt processes (Fb $\beta$ ).

Nerve band: All the ganglia accumulate into a formation shaped as a flat deltoid which is situated in the thorax (F).

The family is well characterized by its anatomical features. It also shows some relationships to the families *Neoephemeridae*, *Caenidae* and *Prosopistomatidae*.

*Prosopistomatidae*

(Fig. 11, P)

Tracheal system: TV1, TV4, TV5, TV6, TV7, TV8, TV9, TV10 (Ba); TAV5, TAV6, TAV7, TAV8, TAV9, TAV10 (VIII), TAV10 (IX) (Bb).

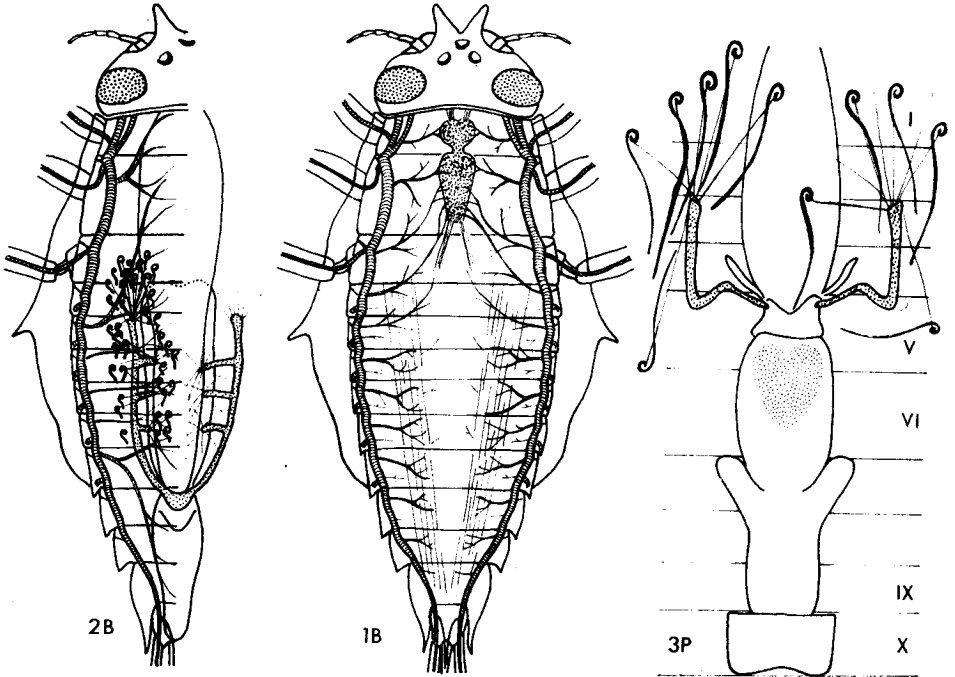


Fig. 11: 1 — ventral part of the body, 2 — visceral tracheae, 3 — digestive tube with Malpighian tubes. B — *Baetisca rogersi*, P — *Prosopistoma foliaceum*.

Malpighian tubes: Tubules unusually long, coiled at their ducts, straight at their free ends. They enter 2 not very long trunks, which are flexed. The proximal part of the hind gut is greatly developed (Fbβ).

Nerve band: All the ganglia are accumulated into a formation shaped as a flat deltoid, which is situated in the thorax (F).

The family is well characterized by its anatomical features. There is a close relationship to the families *Caenidae* and *Baetiscidae*.

COMPARATIVE ANATOMY OF THE TRACHEAL SYSTEM,  
MALPIGHIAN TUBES AND NERVE BANDS

Tracheal system

For comparative anatomy the tracheation of the abdomen and thorax is of the utmost significance. The tracheation of head is rather complicated for this purpose, and its adaptation to the differently formed mouth parts and the shape of the head obscures the basic scheme.

The main feature of the tracheal system is the formation of anastomoses on the ventral side of the abdomen (TAV) and the scheme of visceral tracheae (TV) leading into the digestive tube. The following cases may occur:

Scheme of the anastomoses in the abdomen:

A — Anastomoses appear only in segments VIII and IX, or in one of them.

Aa — Anastomosis occurs only in segment IX (TAV 10, IX). This is possible only in genera where the last ganglion lies in segment VIII (Fig. 1, 1SL; Fig. 2, 3I; Fig. 4, 1O; Fig. 4, 3R; Fig. 5, 3C): *Siphonurinae*, *Isonychia*, *Chromarcyinae*, *Oligoneuriinae*, *Cinygmula*, *Epeorus*, *Rhithrogena*.

Ab — Anastomosis is to be found only in segment VIII (TAV10, VIII). This is possible only in genera where the last ganglion is shifted forwards to segment VII: *Ameletopsis*, *Chaquihua*.

Ac — Two anastomoses occur at the end of the abdomen in segments VIII and IX (TAV10, VIII; TAV10, IX). This is possible in genera where the last ganglion is shifted forward to segment VII (Fig. 3, 1B; Fig. 4, 1E): *Coloburiscinae*, *Baetidae*, *Ecdyonurus*, *Heptagenia*, *Stenonema*, *Arthroplea*.

B — Anastomoses occur in other segments of the abdomen.

Ba — Anastomoses occur in segments IV—VIII or IV—IX (TAV6, TAV7, TAV8, TAV9, TAV10—VIII, TAV10—IX), (Fig. 1, 1SI; Fig. 6, 1CH): *Noticigastriinae*, *Atalophlebia*, *Choroterpes*, *Choroterpides*, *Habroleptoides*, *Habrophlebia*, *Massartellopsis*, *Hagenulus*, *Paraleptophlebia*, *Thraululus*, *Ephemera*, *Ephemerella* — subgenera *Attenuatella*, *Drunella*, *Ephemerella* s. str., *Timpanoga*; *Ephemerellina*, *Tricorythus*, *Dicercomyzon*.

Bb — Anastomoses occur in segments I—VIII or I—IX, II—VIII or II—IX, III—VIII or III—IX (TAV3, TAV4, TAV5, TAV6, TAV7, TAV8, TAV9, TAV10, VIII, TAV10, IX) (Fig. 7, 1E, 1T; Fig. 8, 1P, 1E; Fig. 9, 1H; Fig. 10, 1N): *Chiloporter* (II—IX), *Adenophlebia* (III—IX), *Indiaphlebia* (III—IX), *Leptophlebia* (III—VIII), *Ephemerella* — subgenera *Chitonophora* (I—IX), *Ephemerella* s. str. (III—IX), *Eurylophella* (II—IX), *Torleya* (III—IX), *Tricorythodes* (III—VIII), *Behningia* (III—IX), *Potamanthidae* (III—IX), *Euthyplociidae* (II—IX), *Ephemerella* (II, III—IX), *Ichthyobotus* (III—IX), *Hexagenia* (I—IX), *Pentagenia* (I—IX), *Ephoron* (II—IX), *Campsurus* (II—IX), *Tortopus* (II—IX), *Asthenopus* (III—IX), *Povilla* (III—IX), *Palingenia* (II—IX), *Neoephemerella* (II—IX), *Prosopistoma* (II—IX).

C — Anastomoses are absent.

Ca — Thin branches of nerve tracheae (TN = trachea neuralis) do not fuse in the median line: *Mirawara*, *Murphyella*, *Ametropus*, *Metretopus*.

Cb — Thin branches of nerve tracheae (TN) join irregularly in the median line (Fig. 10, 1C): *Caenidae*.

Scheme of visceral tracheae:

A — Visceral tracheae are present in all segments in which there are future spiracles of the imago, i.e. in the mesothorax, metathorax and in segments I—VII of the abdomen (TV1, TV2, TV3, TV4, TV5, TV6, TV7, TV8, TV9, TV10) (Fig. 2, 2I; Fig. 4, 2O): *Isonychia*, *Chromarcyinae*, *Oligoneuriinae*.

B — Visceral tracheae are present only in the mesothorax and in the abdominal segments.

Ba — Visceral tracheae are present in the mesothorax and in segments II—VIII of the abdomen (TV1, TV4, TV5, TV6, TV7, TV8, TV9, TV10) (Fig. 1, 2M; Fig. 11, 2B): *Murphyella*, *Baetisca*, *Prosopistoma*.

Bb — Visceral tracheae are present in the mesothorax and in segments IV—VIII of the abdomen (TV1, TV6, TV7, TV8, TV9, TV10) (Fig. 8, 2E; Fig. 9, 2EV): *Euthyplociidae*, *Polymitarciidae*.

C — Visceral tracheae are present in the metathorax and in the abdominal segments.

Ca — Visceral tracheae are present in the metathorax and in segments I—VIII of the abdomen (TV2, TV3, TV4, TV5, TV6, TV7, TV8, TV9, TV10). In some cases some of the tracheae in segments III—V, TV5, TV6, TV7 may be reduced or absent (Fig. 1, 2SL; Fig. 3, 2B; Fig. 5, 2A): *Oniscigastrinae*, *Baetidae* excepting *Callibaetis* and *Centroptilum rubropictum*, *Ametropus*, *Ephemerella* — subgenus *Attenuatella*.

Cb — Visceral tracheae are present in the metathorax and in abdominal segments II—VIII (TV2, TV4, TV5, TV6, TV7, TV8, TV9, TV10). Occasionally some of the tracheae in segments IV—VI, TV6, TV7, TV8 may be reduced or absent (Fig. 1, 2SR; Fig. 3, 2C; Fig. 4, 2E): *Siphonurinae*, *Chaquihua*, *Rallidentinae*, *Baetidae* — *Callibaetis*, *Centroptilum rubropictum*, *Heptageniidae*, *Ephemerella* — subgenera *Eurylophella*, *Timpanoga*, *Metretopus*, *Traverella*.

Cc — Visceral tracheae are present in the metathorax and in segments III—VIII of the abdomen (TV2, TV5, TV6, TV7, TV8, TV9, TV10) (Fig. 6, 2L, 2P): *Adenophlebia*, *Atalophlebia*, *Habroleptoides*, *Habrophlebia*, *Hagenulus*, *Leptophlebia*, *Massartelopsis*, *Paraleptophlebia*, *Ephemerellina*.

Cd — Visceral tracheae are present in the metathorax and in abdominal segments IV—VIII (TV2, TV6, TV7, TV8, TV9, TV10) (Fig. 7, 2E; Fig. 8, 2P; Fig. 9, 2ED): *Choroterpes*, *Choroterpides*, *Ephemerella* — subgenera *Chitonophora*, *Drunella*, *Ephemerella*, *Torleya*; *Tricorythodes*, *Behningia*, *Potamanthidae*, *Ephemeridae*, *Palingeniidae*.

D — Visceral tracheae in the thorax are absent. They are present only in the abdomen. The frontal ones run along the digestive tube up to the prothorax.

Da — Visceral tracheae are present in abdominal segments II—VIII (TV4, TV5, TV6, TV7, TV8, TV9, TV10): *Ameletopsis*, *Chiloporter*, *Mirawara*, *Coloburiscoides*, *Coloburiscus*.

Db — Visceral tracheae are present in abdominal segments IV—VIII (TV6, TV7, TV8, TV9, TV10) (Fig. 10, 2N, 2C): *Neophemera*, *Caenidae*.

### Malpighian tubes

The following cases may occur in the formation of Malpighian tubes:

A — Numerous tubules singly enter the band on the digestive tube.

Aa — Tubules are spirally coiled at both ends (Fig. 12, SL): *Siphonurinae*, *Oniscigaster*, *Mirawara* (tubules are only slightly coiled), *Coloburiscoides*, *Coloburiscus*, *Tricorythodes*, *Dicercomyzon*.

Ab — Tubules are straight, club-like, enlarged on the proximal end (Fig. 12, BR; Fig. 3, 3B): *Ameletopsis*, *Chaquihua*, *Chiloporter*, *Baetidae*.

B — Tubules are spirally coiled, entering 8 low flat buds on the digestive tube (Fig. 12 EI): *Siphonella*, *Murphyella*, *Cinygmula*, *Arthroplea*, *Metretopus*, and of the subfamily *Leptophlebiidae* the genera *Atalophlebia* (*anastomosis* type), *Leptophlebia*; *Ephemerellinae*, *Behningia*.

\* C — Tubules are spirally coiled, entering 8 distally enlarged and branching trunks.



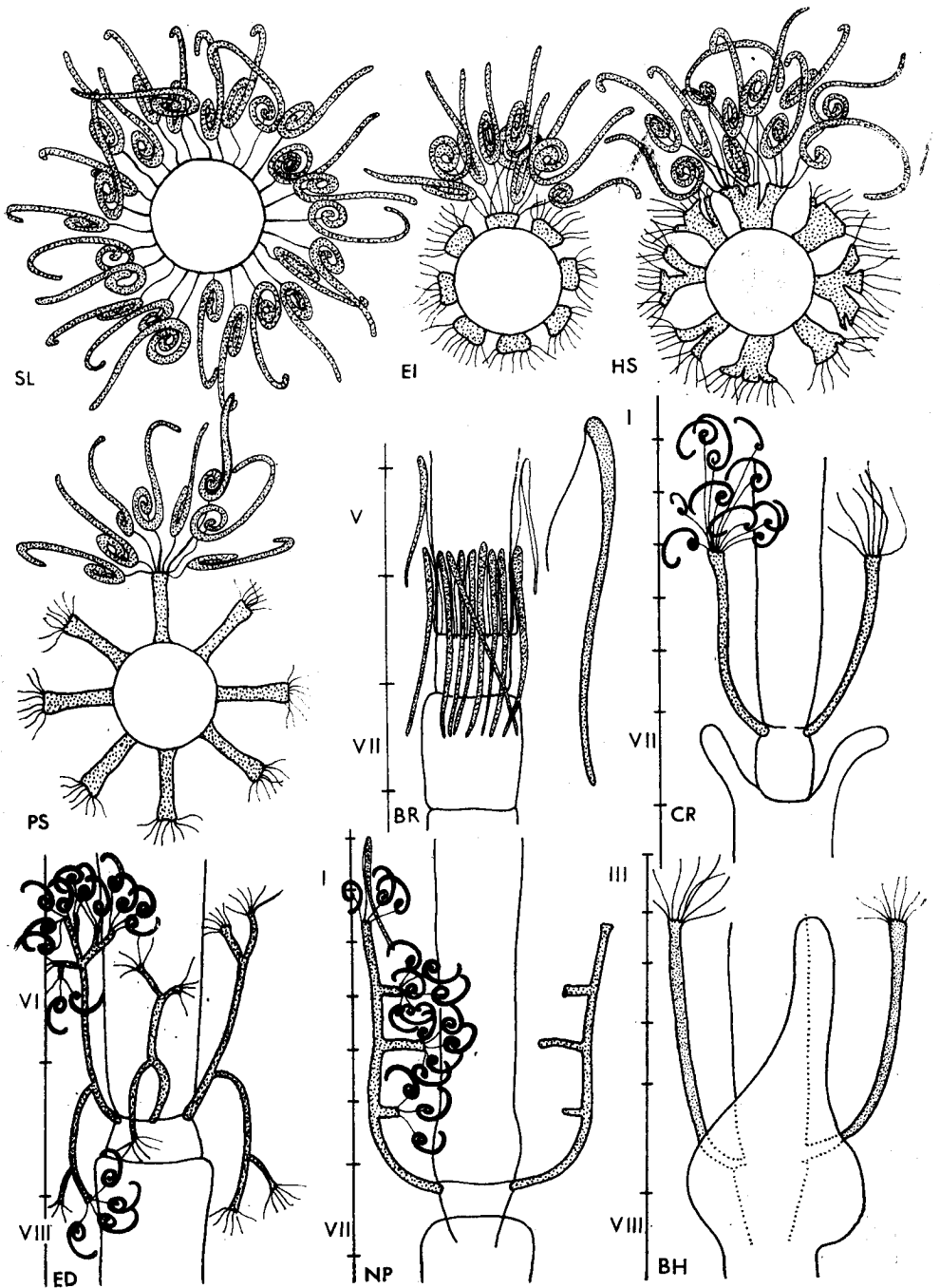


Fig. 12: Malpighian tube. BH - *Brachycercus harrisella*, BR - *Baetis rhodani*, CR - *Coenis robusta*, ED - *Ephemerella danica*, EI - *Ephemerella ignita*, HS - *Heptagenia sulphurea*, NP - *Neoephemerella purpurea*, PS - *Paraleptophlebia submarginata*, SL - *Siphonurus lacustris*. I-VIII - abdominal segments.

Ca — Trunks are short, with only slight branching (Fig. 12, HS): *Chromarcyinae*, *Oligoneuriinae*, *Heptageniidae* except *Cinygmula* and *Arthroplea*.

Cb — Trunks are long, narrow, forming thin branches (Fig. 2, 4I, 5I): *Isonychia*.

D — Tubules are spirally coiled, entering simple unbranched trunks. The trunks are of varying length, generally club-like, enlarged at their distal ends.

Da — 8 trunks are present. They are either  $\alpha$ ) of the same length (Fig. 12, PS): *Adenophlebia*, *Atalophlebia* (*chilensis* type), *Massartellopsis*, *Paraleptophlebia*, *Traverella*, or  $\beta$ ) of different lengths: *Habroleptoides*, *Habrophlebia*.

Db — 6 trunks are present. They are either  $\alpha$ ) of the same length: *Indiaphlebia*, *Thraululus*, or  $\beta$ ) of different lengths (Fig. 6, 3CH; Fig. 5, 4A, 5A): *Choroterpes*, *Choroterpides*, *Ametropus* (tubules bent).

Dc — Only 2 trunks are present: *Hagenulus*.

E — Tubules are spirally coiled, entering trunks with bush-like branching.

Ea — 6 trunks of various lengths are present (Fig. 12, ED): *Potamanthidae*, *Ephemeridae*, *Ephoron*, *Palingenia*.

Eb — 4 trunks are present, 2 long and 2 short ones: *Euthyplociidae*, *Campsurus*, *Tortopus*, *Asthenopus*, *Povilla*.

F — Tubules are spirally coiled, entering trunks which reach as far as segment IV (sometimes as far as III or II); the tubules extend even farther forwards.

Fa — 6 trunks are present, 2 of them are shorter: *Tricorythus*.

Fb — Only 2 trunks are present. They are either  $\alpha$ ) simple (Fig. 11, 3P; Fig. 12, CR, BH): *Caenidae*, *Prosopistomatidae* (tubules are bent), *Hagenulus*, or  $\beta$ ) with 3 unbranched processes extending to the digestive tube (Fig. 12, NP): *Neophemeridae*, *Baetiscidae*. In the genera *Brachycercus* and *Baetisca* the hind gut forms a blind sac reaching as far as segment IV. In the genus *Prosopistoma* the proximal section of the hind gut is extraordinarily well developed.

#### Nerve band

The following types in the formation of nerve bands may be observed:

A — The nerve ganglia are present in all the segments of the thorax (prothorax, mesothorax and metathorax) and in segments I—VIII of the abdomen. Connectives are separated, doubled (Fig. 5, 1A): *Ametropus*.

B — Nerve ganglion of segment I merges with that of the metathorax. Abdominal ganglia are present in segments II—VIII.

Ba — Abdominal ganglia are regularly distributed in the segments.  $\alpha$ ) connectives are separated, doubled (Fig. 1, 1SL; Fig. 2, 1I; Fig. 4, 1O; Fig. 4, 3R; Fig. 5, 3C): *Siphonurinae*, *Isonychia*, *Chromarcyinae*, *Oligoneuriinae* except *Homoeoneuria*, *Cinygmula*, *Epeorus* — subgenera *Epeorus*, *Iron*; *Rhithrogena*, *Ephemera*, *Ichthybotus*, *Pentagenia*, *Polymitarcinae*, *Palingenia*.  $\beta$ ) Connectives are joined (Fig. 9, 1H): *Hexagenia*, *Homoeoneuria*, *Metretopus*.

Bb — Ganglia are irregularly distributed over the abdomen; their distribution does not correspond to the segments. Connectives are separated, doubled (Fig. 6, 1CH): *Choroterpes*, *Choroterpides*, *Ephemerella* — subgenus *Attenuatella*.

C — Nerve ganglion in abdominal segment I merges with that in the metathorax. The last abdominal ganglion is shifted to the segment VII, where consequently there are 2 separate ganglia.

Ca — Ganglia in segments II — VI of the abdomen are regularly distributed throughout the segments. Segment I is without a ganglion.  $\alpha$ ) connectives are separated, doubled (Fig. 8, 1P, 1E; Fig. 10, 1N): *Acanthametropus*, *Ameleptosis* (ganglia in segment VII almost merge, transition to point D), *Chaquihua*, *Chiloporter*, *Mirawara*, *Epeorus* — subgenus *Ironopsis* — *Adenophlebia*, *Atalophlebia*, *Habroleptoides*, *Habrophlebia*, *Indiaphlebia*, *Hagenulus*, *Leptophlebia*, *Massartellopsis*, *Paraleptophlebia*, *Thraulius*, *Traverella*, *Potamanthidae*, *Euthyplociidae*, *Neoephemera*.  $\beta$ ) connectives are fused (Fig. 1, 1SI; Fig. 4, 1E): *Oniscigastriinae*, *Coloburiscinae*, *Ecdyonurus*, *Heptagenia*, *Stenonema*, *Behningia* (connectives are fused into a flat band).

Cb — Ganglia in the abdominal segments are irregularly distributed, their distribution does not correspond to the individual segments. The ganglion of segment II is shifted to I.  $\alpha$ ) connectives are separated, doubled (Fig. 7, 1E): *Ephemerella* — subgenera *Chitonophora*, *Drunella*, *Timpanoga*, *Ephemerella* s. str.; *Tricorythus*.  $\beta$ ) connectives are joined into a band: *Arthroplea*.

D — Nerve ganglion of segment I merges with that of the metathorax. The last abdominal ganglion is shifted forward to segment VII, where it fuses with that of segment VII into a single oval form. Connectives merge into a flat band (Fig. 3, 1B): *Baetidae*.

E — Nerve ganglion of segment I fuses with that of the metathorax. All the abdominal ganglia of segments II — VIII are shifted forward. Connectives are separated, doubled.

Ea — Abdominal ganglia are more or less regularly distributed in segments I — VII (Fig. 7, 1T): *Ephemerella* — subgenus *Torleya*; *Ephemerellina*, *Tricorythodes*.

Eb — Ganglia of abdominal segments II — VIII are more or less regularly concentrated in segments I — VI. Connectives are separated, doubled (Fig. 10, 1C): *Ephemerella* — subgenera *Eurylophella*, *Torleya*; *Dicercomyzon*, *Caenidae*.

F — All the thoracic and abdominal ganglia fuse into one single form of a delta shape, situated ventrally on the thorax (Fig. 11, 1B): *Baetisca*, *Prosopistoma*.

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