

GENERAL PART

Chapter I

Systematic position of Ephemeroptera

Comprehensive discussion on various opinions concerning the systematic position of mayflies among other insects, and the position of insects within arthropods is given in the book "Modern Systematics of Insects" (Kluge 2000).

Here is a brief account of selected subordinated taxa mentioned in this book:

1. **Gnathopoda** Lankester 1881, or **Arthropoda s.l.** Circumscriptional synonyms: **Lobopoda** Snodgrass 1938, **Podophora** Waggoner 1996, **Panarthropoda** Zrzavy & Stys 1997, **Antennopoda** De-Haro 1998. Hierarchical name: **Araneus/fg6** (²sine *Spongia*; ³sine *Fasciola*, *Medusa* et al.; ⁴sine *Homo*; ⁵sine *Limax*; ⁶sine *Lumbricus*; incl. *Peripatus*, *Macrobotus*, *Linguatula*). Holophyly of this taxon is proven by autapomorphies – reduction of coelome, opened blood system, presence of chitin-containing cuticle, and others. An opposite idea about polyphyletic origin of different arthropod groups from different annelids in course of independent "arthropodization" is not grounded. Particularly, absence of coelomic sacs in all arthropods and their presence in all annelids, vertebrates, et al., can be explained neither by their function, nor by animal's mode of life, as each this group contains extremely diverse animals.

Gnathopoda are divided into **Onychophora** Grube 1853 (or **Peripatus/fg1**), **Linguatula/fg1**, **Tardigrada** Spallanzani 1776 (or **Macrobotus/fg1** [nomen oblitum: **Arctiscon/fg1**]), and **Euarthropoda**.

1.1. **Euarthropoda** Lankester 1904, or **Arthropoda s. str.** Hierarchical name: **Araneus/fg7** (sine *Peripatus* et al.; incl. *Calymene*, *Scarabaeus*). Holophyly of this taxon is proven by autapomorphies – presence of sclerites and articulated legs, unique complicate visual system consisting of ocelli and

faceted oculi, unique arthropod setae and others. An opposite idea about polyphyly of this taxon (repeatedly erected in the second half of the XIX century and in 60–70th years of the XX century) is not grounded by any apomorphies.

Euarthropoda are divided into a plesion **Trilobitomorpha** Størmer 1944 (or **Calymene/fg1**) and two holophyletic taxa – **Pseudognatha** Latreille 1821 (or **Araneus/fg8**) and **Mandibulata**.

1.1.1. **Mandibulata** Snodgrass 1935 (non *Mandibulata* Clairville 1798, nec *Mandibulata* Latreille 1825). Circumscriptional synonyms: **Polygnatha** Latreille 1821 (non *Polygnatha* Cuvier 1805), **Cormogradi** Crampton 1928, **Entomomorpha** Lameere 1936. Hierarchical name: **Scarabaeus/fg1** (incl. *Cancer*). Assumed autapomorphies of this taxon are: peculiar structure of ommatidium of faceted eye; mandibles bearing incisor, kinetodontium and mola (see Chapter II); presence of superlinguae (see *ibid.*) and some others. However, these characters are well-expressed in Eucrustacea and Hexapoda, but not in Myriapoda; their absence in Myriapoda can be explained either as a secondary reduction, or as an independent origin of Myriapoda and **Pancrustacea** Zrzavy & Stys 1997 (the taxon uniting Eucrustacea and Hexapoda). The last idea contradicts the assumption about holophyly of Atelocerata.

With some doubt, we accept division of *Mandibulata* into **Eucrustacea** Kingsley 1894 (or **Cancer/fg1**) and **Atelocerata**.

1.1.1.1. **Atelocerata** Heymons 1901. In circumscription matches: **Insecta** SENSU Cuvier 1817 (non Linnaeus 1758), **Tracheata** SENSU Pocock 1893 (non Haeckel 1866). Hierarchical name: **Scarabaeus/fg2** (sine *Cancer*; incl. *Scolopendra*). In favour

of holophyly of this taxon testify reduction of first postoral (tritocerebrum-innervated) limbs, reduction of pretarsal extensor and some other apomorphies.

Atelocerata are divided into holophyletic taxa **Myriapoda** Latreille 1802 (non Myriapodes Latreille 1796) (or **Scolopendra/fg1**) and **Hexapoda**.

1.1.1.1.1. **Hexapoda** Blainville 1816. In circumscription matches: **Insecta** SENSU Leach 1815 (non Linnaeus 1758). Hierarchical name: **Scarabaeus/fg3** (sine *Scolopendra*; incl. *Podura*). Holophyly of this taxon is well-proven by unique autapomorphies, and no one fact is known that would testify against; in spite of this, some authors regard Hexapoda to be polyphyletic, that is a result of confusion provoked by formerly used nomenclature (Kluge 1996c, 1999c, 2000).

Hexapoda are divided into holophyletic taxa **Entognatha** Stummer-Traunfels 1891 (or **Podura/fg1**) and **Amyocerata**.

1.1.1.1.1.1. **Amyocerata** Remington 1954. Circumscriptional synonym: **Ectognathata** Boudreaux 1979; in circumscription also matches: **Ectognatha** SENSU Hennig 1953 (non Stummer-Traunfels 1891), **Insecta** SENSU Handschin 1958 (non Linnaeus 1758). Hierarchical name: **Scarabaeus/fg4** (sine *Podura*, incl. *Lepisma*). Holophyly is proven by peculiar structure of antennae and some other apomorphies.

Amyocerata are divided into **Triplura** and **Pterygota**.

1.1.1.1.1.1-1. **Triplura** Ewing 1942. Circumscriptional synonyms: **Ectotropha** = **Ectotrophi** Grassi 1888, **Ectognatha** Stummer-Traunfels 1891, **Euthysanura** Schepotieff 1909, **Thysanuradelphia** Crampton 1916, **Phanerognatha** Krausse & Wolff 1919, **Panthysanura** Crampton 1928, **Apteren-toma** Chen 1958, **Thysanurata** Bey-Bienko 1962, **Zygoentomata** Brusca & Brusca 1990. In circumscription also matches: **Thysanura** SENSU Lameere 1895 (non Latreille 1796) and **Apterygota** SENSU Scharov 1966 (non Lang 1888). Hierarchical name: **Lepisma/ fg1**.

Triplura unite **Zygentoma** Börner 1904 (or **Lepisma/fg2**) and **Microcoryphia** Verhoeff 1904 (or **Machilis/fg1**). Possibly, **Triplura** is a holophyletic taxon; an opposite idea about holophyly of **Dicondylia** Hennig 1953 (uniting **Pterygota** and **Zygentoma**) is not grounded (Kluge 2000).

1.1.1.1.1.1-2. **Pterygota** Lang 1888. Older circumscriptional synonym: **Pterygogenea** Brauer 1885; younger circumscriptional synonyms: **Eupleo-merentomata** Krausse & Wolff 1919, **Pterentoma** Chen 1958. Hierarchical name: **Scarabaeus/fg5** (sine *Lepisma*; incl. *Ephemer*). Besides wings, which have quite mysterious origin) and undoubtedly evolved once (Kluge 1989a, holophyly of **Pterygota** is proven by some other autapomorphies – integral tentorium, presence of lateral cervical sclerites, characteristic thoracic apodemes and sutures, and others.

Pterygota are divided into **Ephemeroptera** (see Chapters II–III) and **Metapterygota**.

The huge taxon **Metapterygota** Börner 1909 units all winged insects except for mayflies and is regarded to be holophyletic on the basis of the following apomorphies (Kluge 2000).

(1) Only one winged stage is present – imago; i. e. the moult, at which acting wings appear, is the last moult in cycle of development. It is assumed, that the imago of **Metapterygota** corresponds to the subimago of **Ephemeroptera**, which lost ability to moult and got ability to reproduce (Edmunds & McCafferty 1988).

Some authors regard the presence of single winged stage in all **Metapterygota** to be not a synapomorphy, but a convergence; according to their opinion, in different phylogenetic branches of **Pterygota** the primitive representatives had stages of subimago and imago, and during further evolution the stage of subimago was lost. This opinion is based on the fact that for some extinct Palaeozoic representatives of **Palaeodictyoptera** and **Poly-neoptera**, forms regarded to be "subimagoes" were described (Sharov 1957, Sinitshenkova 1979, et al.). These forms have smaller sizes of wings and smaller number of branches of some veins, than in "imago" attributed to the same species. In this respect, they in essence differ from the subimago of **Ephemeroptera**, which wings always have the same size and venation as in imago. If it is assumed that the Palaeozoic long-winged "imagoes" were developed from the short-winged "subimagoes", we would have to admit that during ontogenesis there was disproportionate growth of selected fields of the wing, where new vein branches appeared. However, in ontogenesis of recent insects such does not occur, wing buds grow proportionally, retaining constant arrangement of veins. Most probably, the Palaeozoic short-winged insects are not "subimagoes", but definitive forms. Similar definitive short-winged non-flying forms are present also in many recent groups of insects

(including Ephemeroptera, among which there is one undescribed short-winged species with variable size of wings – FIG.8:E–F). For some Palaeodictyoptera "subimagos" of another kind were described: Their wings have size and venation as in imago, but with tops curved backward, like wing buds of the larvae of the same species (Kukalova-Peck & Peck 1976). In recent insects the similar form of wing is observed in the imago when a wing spreads only partially after moult. Thus, there are no insects, besides Ephemeroptera, where the stage of subimago would be discovered; it permits one to think that the assumption about holophyly of Metapterygota is correct.

(2) Mandible base is diminished; because of this the posterior (lateral) condyle is approximated to the anterior (medial) condyle and located behind it; due to this, mandibles close nearly exactly towards one another. Mandibular-tentorial muscles attached inside the mandibles (i. e. the ventral mandibular muscles) are partly lost (Staniczek 2000), sometimes disappear completely. In this character Metapterygota differ from Ephemeroptera, primary wingless insects, eucrustaceans and myriapods, where the mandible retains well-developed ventral muscles and long basis with the posterior condyle located far from the anterior one.

(3) Superlinguae (initially present in Mandibulata) are lost. Non-unique apomorphy: the superlinguae had also reduced several times in some extremely specialized carnivorous mayfly larvae; they are absent in Zygentoma and Protura. In literature statements are found that some Metapterygota have superlinguae. In these cases processes of hypopharynx for were taken the superlinguae; in contrast to true superlinguae, these processes arise from the hypopharynx itself, but not from ventral wall of the head. Similar processes are present also in some larvae of Ephemeroptera, particularly in majority of Atalophlebia/fg1, where they exist together with the true superlinguae.

(4) Structure of caudalii is simplified: in contrast to Triplura and Ephemeroptera, the paracercus and basi-basal muscles are lost (only muscles going from cerci bases to tergite X, are retained). Besides Metapterygota, reduction of paracercus took place in various groups of Euplectoptera also.

A statement was expressed that the paracercus is retained in some Metapterygota, particularly in larvae of Amphinotic stoneflies Austroperla/fg1; in connection with this, a theory was suggested about common origin of Ephemeroptera and Plecoptera

from Palaeozoic Protephemeroidea (Illies 1960). In this case for the paracercus was taken a secondary gill process. Some other representatives of Metapterygota also have an unpaired caudal process, which has no relation to the paracercus.

(5) Into each wing, branches from two different leg tracheae come, one of which arises from the intersegmental spiracle lying ahead of the wing, and another from the intersegmental spiracle lying behind the wing (in contrast to Ephemeroptera where all wing tracheae arise from the ahead lying spiracle). We can not exclude that this character is not an apomorphy of Metapterygota, but vice versa, an apomorphy of Ephemeroptera (or of Euplectoptera only).

The alternative opinion is to unite Ephemeroptera and **Odonatoptera** Lameere 1900 (or **Odonata** Fabricius 1793 s. l., or **Libellula/fg1**) in a taxon **Subulicornes** Latreille 1807 (circumscriptional synonyms: **Raphiacera** Billberg 1820, **Subulicornia** Burmeister 1839 and **Hydropalaeoptera** Rohdendorf 1968), which in its turn is united with an extinct Palaeozoic taxon **Protorrhynchota** Rohdendorf 1968 (or **Dictyoneura/fg1**) to a taxon **Palaeoptera** Martynov 1923.

The following characters were named as possible apomorphies of Subulicornes or Palaeoptera.

(1) In all Palaeoptera wings are unable to fold on back, thus in rest are either spread by sides or raised upwards. Many authors follow the opinion by Martynov, who regarded this character to be a plesiomorphy. However, some investigators accept another hypothesis about wing evolution, according to which the wings were initially able to fold on the back, but in Ephemeroptera, Odonata and Protorrhynchota this ability was lost in connection with specialization (Rasnitsyn 2002). This opinion can be supported by the fact that Ephemeroptera retain a suture separating the posterior articulatory process of basal plate (FIG.6:APP) from the remaining part of the wing basal plate; this suture is invariably present in all mayflies, but does not enable any mobility or flexibility. Possibly, the posterior articulatory process of Ephemeroptera is homologous to the 3rd axillary sclerite of Neoptera (Brodsky 1974). In Neoptera, the 3rd axillary sclerite is movably articulated with the wing base, and when turning over, makes the wing to fold on back.

(2) In all Palaeoptera longitudinal veins arising from wing base, alternate as concave and convex (while in Neoptera such regular alternation is characteristic only for anteriormost veins – marginal

C, concave Sc, and convex RA). In Subulicornes, besides this, triad principle of vein branching is present, which serves regular alternating of all longitudinal veins, including branches and intercalaries (Fig.7:B); in Ephemeroptera triad principle is expressed in branching of the majority of veins, while in Odonata in branching of RS only. Both in Ephemeroptera and Odonata, the vein RS (which in all Subulicornes except for Protephmeroidea arises not from RA, but from MA) has the same manner of branching: it divides into two concave branches and a convex intercalary between them (RSa, iRS, RSp), and then the anterior branch divides into two concave branches and a convex intercalary between them (RSa₁, iRSa, RSa₂) (FIG.7:C).

(3) It is assumed that the maxillary galea is fused with lacinia: Ephemeroptera have an integral biting lobe and a segmented palp; Odonata have an integral biting lobe and a non-segmented appendage, which can be regarded either as a palp or as a galea. In the

both cases, the biting lobe bears on its inner side two parallel longitudinal rows of denticles and stout setae (FIG.3:E) (while in many other Hexapoda denticles and setae form a single row). Maxillae of Protorrhynchota are highly modified, and their structure is poorly known.

(4) In Subulicornes (but not in Protorrhynchota) imaginal (but not larval) antennae are diminished, with flagellum vestigial. Non-unique apomorphy. Most probably antennae were reduced independently in Ephemeroptera and in Odonata. In Ephemeroptera the antennae retain primitively indeterminate number of segments (FIG.76:B), while in Odonata they are constantly 7-segmented.

(5) Larvae are aquatic and sharply differ from imagoes. Most probably, this feature appeared independently in Ephemeroptera and Odonata, as larvae of these two taxa have no any common morphological characters connected with their aquatic inhabitancy.