

# INTRODUCTION

## A BRIEF HISTORY OF MAYFLY CLASSIFICATION

In the early classifications (Linnaeus 1758, et al.) all mayflies, constituting a single holophyletic genus *Ephemera* Linnaeus 1758 (placed to artificial order Neuroptera), were divided into two groups according to the number of imaginal caudalii – 3 or 2. Each of these groups was actually polyphyletic. The imaginal paracercus is developed in the majority of European Furcatergaliae and vestigial in the majority of European Tridentisetata and Branchitergaliae; thus if one studies superficially the European species only, an impression could appear that this character allows one to divide mayflies into natural groups. However, more detailed examination of mayflies reveals that representatives with 3 and 2 caudalii occur in many evidently holophyletic taxa (see Index of characters [2.3.20]). After Latreille (1802) introduces a rank of family to zoological systematics, it became possible to raise the rank of mayflies from genus to family and to attribute generic ranks to subordinated groups. In the beginning of the XIX century there were attempts to divide mayflies into subordinate groups based of presence or absence of hind wings (Leach 1815, et al.); all mayflies were divided into 4 genera: *Ephemera* (3 caudalii and 4 wings), *Brachycercus* Curtis 1834 (3 caudalii and 2 wings), *Baetis* Leach 1815 (2 caudalii and 4 wings) and *Cloeon* Leach 1815 (2 caudalii and 2 wings). However, the type species of the generic names *Baetis* and *Cloeon* appear to be related (recently both are placed to Turbanoculata), and the genus *Baetis* in such sense appears to be very heterogenous. Later, the number of genera was increased (Pictet 1843–1845, et al.), but the classification remained artificial.

Eaton (1883–1888 et al.) made a comprehensive revision of mayfly species and suggested a new classification. His taxa diagnoses are based on adult characters only and are rather formal; larval structures are excellently illustrated but insufficiently described; for many taxa larvae were unknown or associated wrongly. It is even difficult to understand how such detailed and absolutely correct drawings

of larvae could be made by the investigator, who did not know the taxonomic significance of many characters shown on them. Many supraspecies taxa established by Eaton were natural, although they did not have sufficient diagnoses.

Later (Lestage 1917, et al.) ephemeropterologists paid more and more attention to larval characters rather than to imaginal ones, and established classifications based mainly or solely on larval characters.

Since the artificial Linnaean order Neuroptera was completely divided into smaller natural orders (the process started by Burmeister 1829, and finished by Packard 1886 and Handlirsch 1903), mayflies got ordinal rank and were divided into a number of families and superfamilies, which in large degree corresponded to sections, series and groups proposed by Eaton (1883–1888) to the former family Ephemeridae. Basing mainly on larval characters, authors of new classifications changed many of these taxa to make the classification more natural and suggested different phylogenetic schemes (Ulmer 1920b, Edmunds & Traver 1954, Demoulin 1958, Tshernova 1970, Landa 1969, Riek 1973, et al.). Recently it is usual to accept several superfamilies, approximately from 10 to 40 families and several hundred genera.

Attempts to divide mayflies into highest taxa has undergone the following evolution.

1) McCafferty and Edmunds (1979) divided all mayflies into Pannota and Schistonota, regarding Pannota to be holophyletic, and Schistonota to be paraphyletic. Even if one agrees with the phylogenetic hypothesis of these authors, this classification is not good, because here the paraphyletic taxon is larger than the holophyletic one.

2) Because of this, Kluge (1989), based on the same phylogenetic theory, suggested dividing mayflies into Furcatergalia (which included Pannota and a part of Schistonota) and Costatergalia (which included a part of Schistonota), regarding Furcatergalia to be holophyletic, and Costatergalia to be paraphyletic. In this classification, the two taxa regarded to be holophyletic and paraphyletic have subequal species numbers, which is also not good, but better than the previous classification.

3) The next step was made by McCafferty

(1991), who divided the paraphyletic taxon Costatergalia into two, thus dividing mayflies into three taxa of equal rank – Pisciforma (paraphyletic), Setisura (assumed to be holophyletic) and Rectracheata (subequal to Furcatergalia and assumed to be holophyletic).

4) The next step in this direction was made by Kluge (oral presentation 1992 and publication 1998), who united the taxon Eusetisura (subequal to Setisura) with Furcatergaliae (subequal to Furcatergalia and Rectracheata) to form a large holophyletic taxon Bidentiseta.

Such subsequent change of classification agrees with the general rule, according to which in course of investigation, classification always approximates to the cladistic ideal never reaching it (Kluge 2000).

If one ignores disagreements concerning the systematic position of some small taxa (*Baetisca*, *Prosopistoma*, *Pseudiron* and *Vetulata*) which made us create new circumscriptional names for higher taxa, the change of classification can be shown as following (TABLE 1).

However, the phylogenetic hypotheses on which the classifications by McCafferty & Edmunds (1979), Kluge (1989) and McCafferty (1991) were based, are now regarded to be not quite correct: attributing *Baetisca* and *Prosopistoma* to taxa Pannota, Furca-

tergalia and Rectracheata now is regarded to be wrong (Kluge 1992–1998, McCafferty 1997); attributing *Pseudiron* to Setisura now is also regarded to be wrong (Kluge 1992–1998, Wang & McCafferty 1995); the taxa Ractracheata (uniting *Vetulata* with *Furcatergalia*) and Pannota are polyphyletic.

Taking into account these corrections, a new classification was suggested, where mayflies are divided into Posteritorna and Anteritorna, and the later – to Tridentiseta and Bidentiseta (Kluge 1992–1998). In the present monograph, this classification is accepted.

The general classification of mayflies can be correctly understood only by taking into account particular classifications of subordinate taxa. A lot of papers on systematics of selected mayfly taxa were published; especially useful ones appeared in the last decades. Review of this literature would take too much space; the reader can find references to the most important papers in the Special Part of this book, where references for each taxon under consideration are given. Several taxa that are not recognized in the presented classification, are here also characterized and supplied with references (see divisions "Classifications of ..." and "Systematic position of ..." in the Special Part).

**Table 1.** Simplified version of development of higher mayfly classification from 1979 to 1998. Taxa shown in the same line, do not exactly mach in circumscription, thus they have different circumscriptional names. Names of wittingly paraphyletic taxa are shown by bold. For other explanations see text and alphabetic Index of supraspecies taxa names.

Phylogeny	Ranking names of 6 taxa which include most part of Ephemeroptera	General classification of Ephemeroptera by:			
		McCafferty & Edmunds 1979	Kluge 1989	McCafferty 1991	Kluge 1992–1998
	Baetis/fg	<b>Schistonota</b>	<b>Costatergalia</b>	<b>Pisciforma</b>	<b>Tridentiseta</b>
	Heptagenia/fl=Oligoneuria/g1			Setisura	Bidentiseta
	Leptophlebia/fg1		Pannota	Furcatergalia	
	Ephemera/fg				
	Caenis/fl=Brachycercus/g1				
	Ephemerella/fg1				

## METHODS OF ASSOCIATING LARVAE AND ADULTS

Mayfly systematics is based on a combination of larval, subimaginal and imaginal characters; however, larvae and winged stages (subimago and imago) are so different, that their association represents a special problem. In literature one can find many mistakes, when such association was made wrongly, so that larvae and imagoes of different species were regarded as belonging to the same species, and vice versa, that of the same species were described as different species. Such confusions were made not only on the species level, but on the level of supra-species taxa (genera and families) as well.

Some features of winged stages can be found in the larval stage; this helps to associate them. As in other Pterygota, wing venation is the same in larval wing buds and adult wing (FIGS 37:A; 75:A). Some authors confuse venation with tracheation; tracheation strongly changes during larval development, while venation remains constant. In the larval wing bud venation represents a system of internal hypodermal channels, which can be seen on translucent slide as light lines. For this purpose it is necessary to take such larva, which is not preparing to moult to next instar or to subimago, in other case wing hypodermis with its channels is crumpled under the larval cuticle.

Mature larvae, which are preparing to moult to subimago, can be used to extract and study subimaginal features – thorax sclerotization (FIG.102:A–B), caudalii, sometimes genitals (FIG.84:B–C) and others. Subimaginal wings extracted from mature larva, can be spread after treating by alkali. Structure of subimaginal tarsus with claws can be studied on translucent slide of total larval leg in Canadian balsam; in shortly-moulting mayflies the same slide allows to study structure of imaginal tarsus with claws as well (FIG.98:A–B).

Examination of mature larva allows one to study only selected adult characters, but not all of which are necessary; particularly, in many mayfly species crumpled subimaginal genital buds inside mature larvae differ from imaginal genitals so strongly, that their comparison does not allow the association of larvae and adults correctly.

In most cases exact association of larvae and imagoes can be made by rearing only. The aim of rearing is to get such specimens, each of which has: (1) exuviae of mature larva of last instar, (2) exuviae

of subimago, (3) imago. In order to do this, it is necessary to collect mature larvae, put them in a cage with water, wait until larva moults to subimago, then take its larval exuviae to alcohol and move subimago to another cage without water, than wait until subimago moults to imago and put imago and its subimaginal exuviae in alcohol together with the larval exuviae. Here are given suggestions how to do it successfully.

Some larval mayflies, especially those, which normally inhabit stagnant waters, can be kept in a simple aquarium or a can, until moulting to subimago. But larvae normally inhabiting running waters, especially mountain streams, can not live in stagnant water for a long time. For all species it is best to use special water-cages made of net and put into natural running water (not obligatory to the same stream where these larvae inhabit).

The author uses water-cages of original construction, which can be folded and packed compactly when travelling, and can be used in all kinds of running waters, including mountain streams and greatest rivers, independently of weather and water level. Here are shown two variants of such water-cage: The 1<sup>st</sup> variant (FIG.1:A–B) has 2 frames made of aluminium attached from outside by threads to an integral cube of polyamide (kapron) net, which has 5 equal walls – 4 side walls + bottom. The 2<sup>nd</sup> variant (FIG.1:C–D) has 2 walls made of translucent plastic and 3 walls (2 side walls + bottom) made of an integral band of polyamide net.

In the both cases the net cube (either made of the polyamide net or the polyamide net and translucent plastic) continues above by a tube made of textile. Framework (made of aluminium or translucent plastic) is supplied with 4 floats made of foamy plastic, two of which are attached to the framework, and other two are removable and serve to make the whole construction rigid when ready for work. Removable bracket with a string on its top allows closing the textile part and at the same time supporting it, in order not to allow emerged subimagoes to fly away. A plummet under the water-cage prevents overturning by wind (that is especially likely in rain when the textile above is wet and heavy). A long polyamide cord serves to tie the water-cage to something on the bank.

If there is no necessity to pack water-cages compactly for travelling, the water-cage can have simpler construction. In all cases it must have following details. The water-cage is supplied with floats in such a manner that when floating, a half of

the water-cage is located in the water, and a half above the water, to allow subimagos escape from the water. Water-cage must be not large, about 12 cm high (without the textile part) and 12 cm with: in larger water-cage it is difficult to find larval exuviae of small species, and smaller water-cage does not allow looking into it by both eyes when searching for larval exuviae and emerged adults. Walls (at least partly) are made of fine polyamide (kapron) net (cell 0.4 mm). The bottom is made of the same net, as the walls: the dust brought by water current through the walls must fall down thorough the bottom not accumulating on it. Inside the water-cage, there must be no places where larvae or their exuviae can be hidden; the framework and sutures must be outside, but not inside. No objects (stones, sand, leaves, sticks, etc.) should be putted into the water-cage; the polyamide net is a comfortable substrate for mayfly larvae, and water current brings enough food though the net for that larvae, which are not mature enough to stop feeding. The polyamide part of the water-cage is opened from above and continued by a textile tube, which has the same width as the polyamide part and subequal length. This allows to open and close the water-cage wider or narrower depending on behaviour of the emerged subimagos, not allowing them to fly away. Cotton textile is a comfortable substrate for subimagos. When closed, the textile part should have the form of a high roof to give more space for subimagos, and to protect them from rain. The water-cage floating in running water should be fixed by a cord to something on the bank (tree branch, stone or something other).

Many (up to several dozens) larvae can be placed at once into the same water-cage, but it is better to use several water-cages.

It is preferable to check water-cages often, not less than three times a day, in extreme cases not less than once a day: if larval exuviae stay in water longer than one day, they are destroyed. Emerged subimagos should be removed from the water-cage to an air-cage.

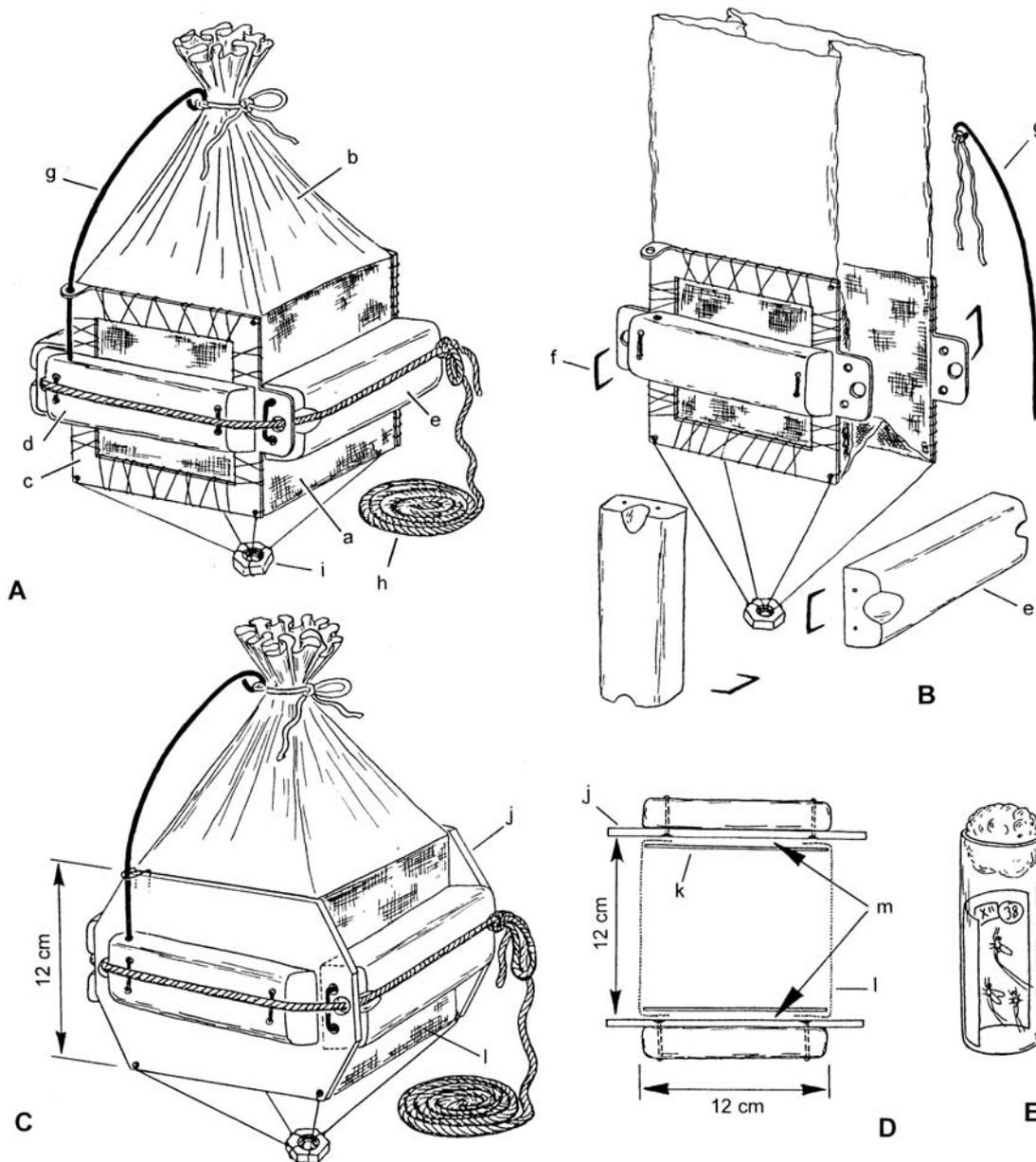
Such air-cage can be a glass tube about 10 cm length and about 2.5-3 cm in diameter, and is closed by cotton-wool (FIG.1:E). Inside the tube it is necessary to put a piece of paper, which is somewhat shorter than the tube and somewhat wider than its diameter; this paper must be immovably pressed to a wall of tube. It has three functions: (1) a comfortable substrate for subimago, that makes it to sit quietly and not to spend energy for flying; (2) water

absorption; (3) label, on which a specimen number is written by pencil (the same number has the tube with alcohol containing larval exuviae of this specimen). It is necessary to move subimagos from the water-cage to the air-cage, not touching them by fingers or pincer. Subimago sitting on the wall of the water-cage, can be covered by the air-cage; subimago sitting on the water surface can be moved with help of thin stick, to which it crawls if place the stick in front of subimago. It is very important to note, that glass air-cage with subimago never should be kept at direct sun light, even for a moment; it must be always in shade or in a box. Most subimagos (apart of shortly-moulting ones) develop in about 24 hours – some times less or some times more, quicker in the warm and longer in the cold.

A usual error made when rearing, is confusing of larval exuviae and adults of externally similar species when several larvae are kept together in the same water-cage. In order to avoid this, it is necessary either to use individual water-cages for each specimen (that is rather difficult), or to take out carefully all emerged subimagos and larval exuviae each time when check the water-cage. For this purpose, it is important not to confuse exuviae of mature larvae from which subimagos emerged, with exuviae of younger larvae, from which larvae of next instar emerged.

All stages of mayflies can be preserved in alcohol of high concentration (75% and higher). As these insects are delicate, it is better to put them into tubes full of alcohol and closed by cotton wool, and to put these tubes into a hermetically closed glass with alcohol: in this case tubes should not contain air bulbs, which could destroy mayflies if shaken.

For examination, it is useful to make slides of all parts of mayflies and their exuviae. Separated parts can be mounted in Canadian balsam; this allows to study not only cuticle, but muscles as well. Delicate translucent cuticular parts – colourless wings, tergalii, subimaginal exuviae and cuticular parts treated by alkali – can be mounted in glycerine to see better their details (in this case cover glass can be glued to the mount by Canadian balsam by sides).



**Figure 1.** Cages for rearing mayflies.

**A-D** – Two different variant of water-cages for rearing subimagoes from larvae: **A-B** – 1<sup>st</sup> variant of water-cage, made of polyamide net with aluminium framework: **A** – in assembled condition ready to use; **B** – in disassembled condition; **C-D** – 2<sup>nd</sup> variant of water-cage, made of polyamide net and translucent plastic: **C** – in assembled condition ready to use; **D** – scheme of horizontal section, to show method of fastening of plastic walls, net walls and non-removable floats. **E** – air-cage for rearing imagoes from subimagoes.

**a** – cube (without upper wall) made of polyamide net; **b** – textile tube; **c** – 2 aluminium frameworks attached to polyamide net by threads; **d** – 2 foamy plastic floats attached to framework; **e** – 2 removable foamy plastic floats; **f** – 4 metallic staples to fix removable foamy plastic floats; **g** – removable metallic bracket with string; **h** – polyamide cord; **i** – plummet; **j** – 2 walls of thick translucent plastic; **k** – 2 square plates of thin translucent plastic; **l** – band of polyamide net forming two walls and bottom; **m** – schematically shown two spaces, where thick and thin plastic plates are glued together by the same translucent plastic dissolved in chloroform.

## PRINCIPLES OF NON-RANKING ZOOLOGICAL NOMENCLATURE

Classification of living organisms always reflects ideas about phylogeny (or "natural system" of older authors), independently which explanation to principles of systematics was given by these or that authors. The main problem in phylogenetic investigation, is a necessity to use a great number of facts concerning characters and their distribution among organisms. There are no direct methods for reconstructing phylogeny; thus we have to use a single known indirect method – cladistic analysis (it can be called also scientific cladistic analysis, in order to avoid confusion with the numerical cladistic analysis). The scientific cladistic analysis, or analysis of apomorphies, never gives a correct final result, but allows an approximation of it; the process of such approximation is endless when more and more characters are taken into account. In this situation strict principles of text layout and nomenclature of taxa become important components of scientific work. C. Linnaeus elaborated such principles for the XVIII century scientific level, and they allowed reaching great success during the subsequent quarter of the millennium. Thanks to this, a great number of facts was accumulated, and phylogenetic theory was elaborated, which, in its turn, made the Linnaean principles out of date.

Particularly, the ranking zoological nomenclature elaborated by Linnaeus (1758) and Latreille (1802) and adopted by the modern International Code of Zoological Nomenclature (2000) in our days is not enough to supply with names all taxa in a serious scientific classification. Working on the present monograph and the book "Modern systematics of insects", the author had to restudy general principles of biological nomenclatures and to elaborate a new system of non-ranking nomenclatures for zoology (Kluge 1999a, 1999b, 1999c).

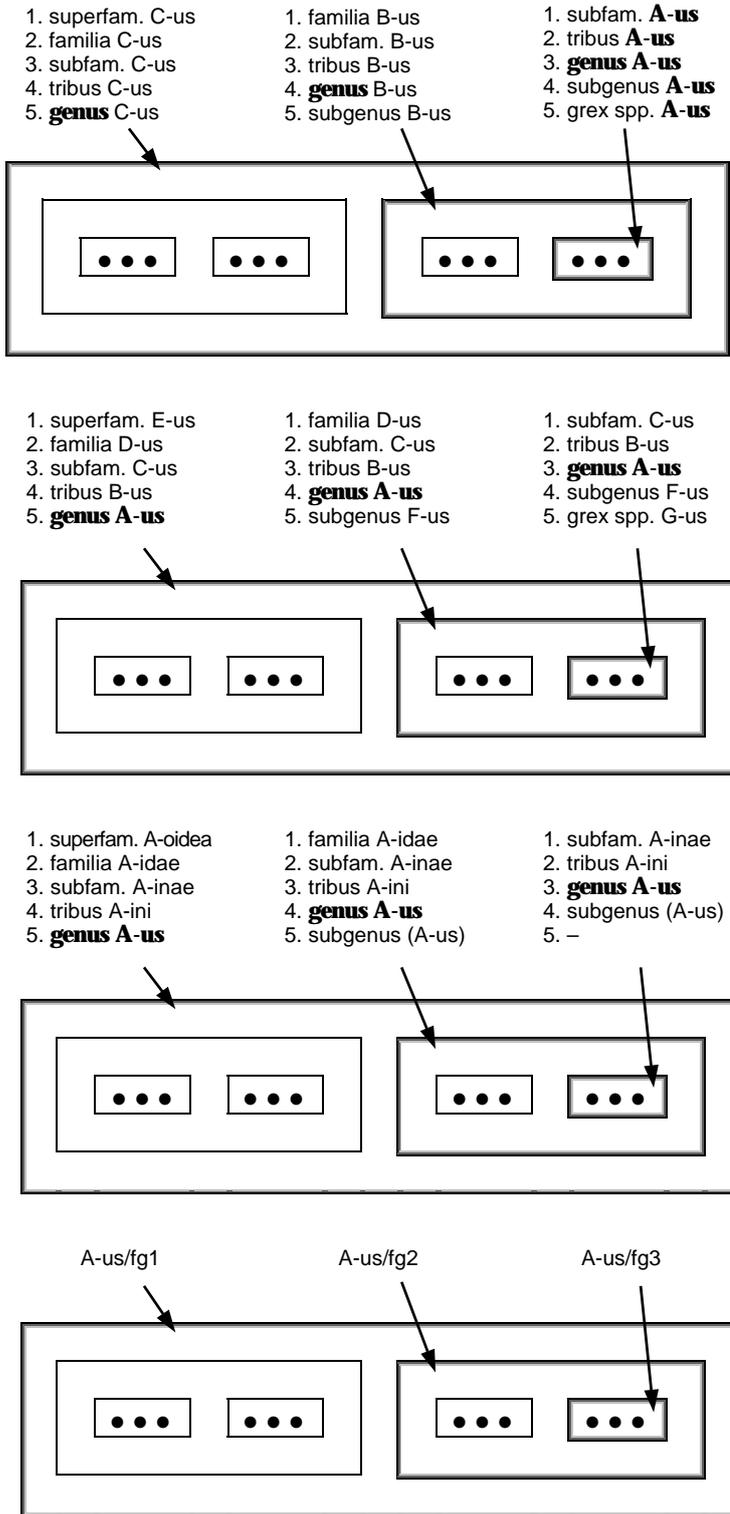
Problems of reconstructing phylogeny, principles of systematics and principles of all zoological nomenclatures are discussed in detail in the book "Modern systematics of insects. Part I" (Kluge 2000); the English translation of the chapter on systematics and nomenclature from this book is available from the Internet, <http://www.bio.pu.ru/win/entomol/KLUGE/sys-ins.htm>. Here are repeated only the most important explanations for the non-ranking nomenclature used in the present book.

### Why do different types of nomenclature coexist?

Classification cannot be permanent; instead, it is subject to incessant change, because it is based on phylogeny, and there is no direct way to reconstruct phylogeny; as all methods of reconstructing phylogeny are indirect and rely on the entire body of biological knowledge, and the latter is continuously growing, the process of adjusting our idea of phylogeny, and hence changing classification, will be endless as well. So there is no hope that a perfect and final classification of living organisms would ever be built. Should a constant classification appear, rules of nomenclature would become redundant, as the names of all taxa in such classification will only need to be validated once and for all. It is the inability to create such a classification that forces us to set universal rules of naming taxa.

All principles of nomenclature pursue a single aim: to have names firmly stick to taxa. Yet any taxon has many different attributes, which include its circumscription, diagnosis, rank, position in the classification, etc. It is impossible to make a name refer to all such attributes at once, because any change of the classification entails changes in these attributes. For example, in different classifications taxa of the same circumscription may have different ranks, different diagnoses or be assigned to different higher taxa; and vice versa, taxa of the same rank can have different circumscriptions, and so on. Nomenclature must support ever-changing classification, which implies that a name can only be associated with just one attribute of a taxon.

Based on the attribute with which a name is associated, several fundamentally different types of nomenclatures can be recognised, viz. rank-based, circumscription-based, description-based, phylogeny-based, hierarchy-based, etc. Among them, only rank-based, hierarchy-based, and circumscription-based ones are meaningful. Their difference is shown in FIG. 2.



### Circumscriptional nomenclature

Five variants of ranks arrangement (1–5) are shown; one rank (**genus**) and one name (**A-us**) are everywhere marked by bold to demonstrate that certain name (**A-us**) always belongs to taxa of the same circumscription (the darkest rectangle), independently of their ranks.

### Ranking non-typified nomenclature

Five variants of ranks arrangement (1–5) are shown; one rank (**genus**) and one name (**A-us**) are everywhere marked by bold to demonstrate that certain name (**A-us**) always belongs to taxa of the same rank (**genus**), while these taxa can have different circumscriptions.

### Ranking typified nomenclature

Five variants of ranks arrangement (1–5) are shown; one rank (**genus**) and one name (**A-us**) are everywhere marked by bold (see above). A-oidae, A-idae, A-inae and A-ini are typified names formed from the generic name A-us; rank-depending endings are given according to ICZN (in different ranking typified nomenclatures different endings are used).

### Hierarchical nomenclature

**Figure 2.** Difference between circumscriptional, ranking and hierarchical nomenclatures. Different nomenclatures are applied here for the same classification of 12 species (black dots) united in 7 hierarchically subordinated supra-species taxa (rectangles) of 3 ranks; names are applied to 3 subordinated supra-species taxa (rectangles with shaded borders), which have 3 different ranks.

### Rank-based (ranking) nomenclatures

In these nomenclatures a name is associated with a certain rank of taxon (such as genus, family, etc.) and is subject to change whenever the rank changes, but remains the same when other attributes (such as circumscription or position) change (FIG.2). The ranking nomenclature still plays a major role in taxonomy, because all international codes, including the International Code of Zoological Nomenclature, are based on this principle. A significant shortcoming of ranking nomenclature is that names are associated with a purely conventional taxon's attribute, i. e. its rank. In different classifications the same ranking name can be assigned to taxa of different circumscription while taxa consisting of the same members (i. e. having identical circumscriptions) should be given different names within the same ranking nomenclature if such taxa have different ranks. As a result, ranking nomenclature may cause confusion (Kluge 1996c, 1999a–c, 2000).

### Hierarchy-based (hierarchical) nomenclatures

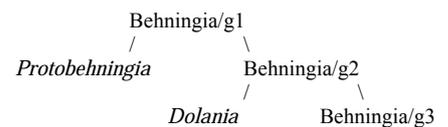
In hierarchy-based nomenclature a name is associated with the taxon's placement within hierarchical classification and does not depend on rank (FIG.2). This nomenclature is based on the recently enacted International Code of Zoological Nomenclature (ICZN), yet overcomes some important flaws of the ICZN's ranking principle.

Generic names, that fall under rules of ICZN and, thus, are rank-based by definition, can be used not only in rank-based nomenclature but to derive hierarchy-based names as well, in which case type species of generic names, authorship, priority and co-ordination all work just as provided by the ICZN. Unlike in the ICZN's nomenclature, in the hierarchy-based nomenclature no name is assigned absolute rank (such as genus, family, etc.), but refers rather to a relative rank indicated by the number of higher hierarchically subordinated taxa. That's why the hierarchy-based nomenclature can be used in non-ranked classification.

The **hierarchy-based**, or **hierarchical name** (NOMEN HIERARCHICUM) consists of an available generic name (or, better, of an available name of genus-group in terms of the ICZN) to which, after a slash, are attached the letter(s) "f" and/or "g" and a number ("1" or higher). Here is the procedure to create a hierarchy-based name: first we pick the oldest generic name within the taxon in question.

Since in our classification we use no ranks and just disregard them, the priority of the generic name can be established based on authorship of either genus-group or family-group names (according to ICZN, they may not be the same). After the slash we insert either a "g" (as in "genus") if the priority gets established based on genus-group names, or an "f" (as in "familia" – family) if we establish it based on family-group names. Number "1" is attached to the taxon, which in our hierarchical classification is the largest (highest) among taxa, for which this generic name is the oldest within the chosen group of names (i. e. within the genus-group for names followed by "g" or within the family-group for names followed by "f"). Subordinated taxa with the same generic name are numbered according to their order of subordination in such a way that the smaller (lower) is the taxon, the higher is the number.

For example, the taxon uniting *Behningia ulmeri*, *Dolania americana* and *Protobehningia asiatica*, in hierarchical nomenclature can be named Behningia/g1. The generic name *Behningia* Lestage 1930 is the oldest among genus-group names whose type species are included into this taxon (i. e. *Dolania* Edmunds & Traver 1959 and *Protobehningia* Tshernova & Bajkova 1960). The number "1" is attributed to this taxon, because this is the highest taxon for which the generic name *Behningia* is the oldest. If we take a higher taxon (in our classification it is Fossoriae), it will include the type species of the older name *Ephemera*, thus its hierarchical name should be formed from "*Ephemera*", but not from "*Behningia*". The taxon subordinated to Behningia/g1 can be named Behningia/g2, and the taxon subordinated to it – Behningia/g3:

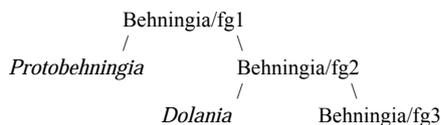


The taxa with the same oldest generic name are numbered from the highest to the lowest, not vice versa, because the highest one can be easily identified based on priority, while taxa splitting can be unlimited.

Based on genus-group priority rules alone, one can assign unique hierarchy-based names to all taxa within a classification. However, as the current Code provides for a separate priority for family-group names, the hierarchy-based names generated under the rules for the genus-group give no idea what should taxa names be in a rank-based nomenclature if

assigned family-group ranks (i. e. if we treat these taxa as tribes, subfamilies, families, or superfamilies). In this book hierarchy-based names are presented in such a format that allows converting them into familiar-looking rank-based names without recurring to any additional information. All we need to make a hierarchy-based name convertible to rank-based one is adding to it, with an "=" in between (no spaces), another hierarchy-based name, this time the one obtained based on family-group priority. In this case the name base is spelled out in its original form (i. e. as a generic name, without family-group endings) followed by a slash and an "f" instead of "g". Both the generic name and the number established based on genus- and family-group rules often match; in such cases we just write down one generic name with the letters "fg" and the number.

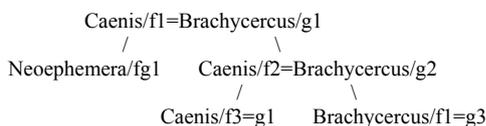
For example, the generic name *Behningia* is a base for family name Behningiidae Motas & Bacesco 1937 and other available family-group names with the same authorship; thus, in the example given above, taxa names can be written as following:



If the generic names are identical but the numbers are not, we insert into the hierarchy-based name both numbers with their respective letters, separated by an "=" without spaces. If the generic names are not identical we write down both generic names (separated by an "=" without spaces) with their respective letters and numbers.

For example, there is a taxon that includes type species of two generic names: *Caenis* Stephens 1835 and *Brachycercus* Curtis 1834, of which the latter is older; however, the oldest family-group name derived from the name *Caenis* – Caenidae Newman 1853 – is older than the oldest family-group name derived from *Brachycercus* – Brachycercidae Lestage 1924. The taxon including both type species will have the hierarchy-based name  $\text{Caenis/f1=Brachycercus/g1}$ . Such spelling means that under ICZN rules, if this taxon is assigned genus-group rank its name will be *Brachycercus*, while if assigned family-group rank its name should be derived from the generic name *Caenis*. One of subordinated taxa within  $\text{Caenis/f1=Brachycercus/g1}$  also includes both type species, and its hierarchy-based name will be  $\text{Caenis/f2=Brachycercus/g2}$ . In rank-based nomenclature this taxon also can be either named

*Brachycercus* or get a typified name derived from *Caenis*, depending on whether we consider it a genus-group or a family-group taxon. This taxon, in turn, contains two taxa: one including the type species of the generic name *Caenis*, and another – the type species of the generic name *Brachycercus*. The hierarchy-based names of these taxa will be  $\text{Caenis/f3=g1}$  and  $\text{Brachycercus/f1=g3}$ , respectively. Hierarchy of these taxa looks as follows:



As classification changes, numbering in hierarchy-based names also shifts, so depending on classification taxa of the same circumscription may have different names, while taxa of different circumscriptions may be named identically. Hierarchy-based and rank-based nomenclature share such disadvantage, only circumscription-based nomenclature (see below) is free of it. The important benefit of hierarchy-based nomenclature is that the names shift only if there are changes in the classification, i. e. if the subordination of taxa is modified, while in rank-based nomenclature names change with any rank shift as well. Unlike rank changes, always purely discretionary, classification changes are always based on evidence and can be discussed.

If a hierarchy-based name is used, it may be helpful to provide details on how taxa are arranged in this classification, as a comment on the name's number. This can be done when the name is first mentioned, listing (in parentheses) generic names of closest excluded taxa (using "**sine**", Latin for "without") and those of directly subordinated taxa (using "**incl.**" – *incluso*, including).

For example:

$\text{Behningia/fg2}$  (*sine Protobehningia*; *incl. Dolania*).

If the name mentioned for the first time has number much larger than "1", it can be helpful to list also excluded generic names of higher taxa.

For example, in this book classification starts with the taxon Gnathopoda Lankester 1881, which hierarchical name is written as  $\text{Araneus/fg6}$  (<sup>2</sup>*sine Spongia*; <sup>3</sup>*sine Fasciola, Medusa* et al.; <sup>4</sup>*sine Homo*; <sup>5</sup>*sine Limax*; <sup>6</sup>*sine Lumbricus*; *incl. Peripatus, Macrobiotus, Linguatula*). This means that the highest taxon, to which the oldest generic name *Araneus* Clerck 1958 can be attributed, is

Araneus/fg1 (incl. *Spongia*) (circumscriptional name – Metazoa Haeckel 1874); its subordinated taxon is Araneus/fg2 (sine *Spongia*; incl. *Fasciola*, *Medusa* et al.) (circumscriptional name – Eumetazoa Bütschli 1910); its subordinated taxon is Araneus/fg3 (sine *Fasciola*, *Medusa* et al.; incl. *Homo*) (in circumscription matches Coelomaria sensu Haeckel 1898); its subordinated taxon is Araneus/fg4 (sine *Homo*; incl. *Limax*) (circumscriptional name – Trochozoa Beklemishev 1944); its subordinated taxon is Araneus/fg5 (sine *Limax*; incl. *Lumbricus*) (circumscriptional name – Polymeria Hadži 1953; widely used name – Articulata auct.); its subordinated taxon is Araneus/fg6 (sine *Lumbricus*; incl. *Peripatus*, *Macrobiotus*, *Linguatula*) (circumscriptional name – Gnathopoda Lankester 1881).

### Circumscription-based (circumscriptional) nomenclatures

Under this approach a name is associated with a certain circumscription of a taxon without regard of its rank or position (FIG.2). Special circumscription-based names have a wider circulation. Such a name can be called either **circumscription-based**, or **circumscriptional** (NOMEN CIRCUMSCRIBENS); in the previous papers this term was translated from Russian as "**volumetric name**" (Kluge 1999a, 1999b). Each circumscription-based name is attached to a taxon of a given circumscription (i. e. a certain set of members included, but not the number of species). Most generally accepted circumscription-based names are those of major taxa, but there were no rules governing their usage until recently, when such rules were suggested (Kluge 1999) based on long established and well-proven custom.

To make a decision on using a circumscription-based name, we assess the name based on three criteria: 1) availability, 2) circumscription match, and 3) validity (rank-based names are assessed by availability and validity only). The key concept of circumscription-based nomenclature is the "admissible membership", based on which one can decide whether several taxa are identical in terms of circumscription. To determine whether taxa match in circumscription, the following parameters have been introduced (Kluge 1996):

**Listed membership:** the set of species, explicitly or implicitly referred to in the publication as members of the taxon.

**Net membership:** listed membership less (1) species whose position is considered uncertain in the

publication, and (2) species erroneously listed as members of the taxon contrary to the diagnosis provided for that taxon in the same publication.

**Excluded membership:** a set of species explicitly or implicitly (see above) referred to in the publication as non-members of the taxon or as members of taxa other than those subordinated to it.

**Net excluded membership:** excluded membership less (1) species whose position is considered uncertain in the publication, and (2) species erroneously listed as members of another taxon contrary to the diagnoses provided in the same publication.

**Admissible membership, or admissible circumscription:** any set containing all species of net membership and no species of net excluded membership.

**Original listed membership, original net membership, original excluded membership, original net excluded membership, and original admissible membership** – all refer to their respective parameters in the context of the publication where the name in question was first published.

**Criteria of availability for circumscription-based names.** Since rank- and circumscription-based nomenclatures are inherently incompatible, it would be helpful to effectively separate rank-based names from circumscription-based ones. We propose to do so using such criteria of availability that would make names available as rank-related unavailable for purposes of circumscription-based nomenclature, and vice versa.

It would be appropriate to consider available for purposes of circumscription-based nomenclature all scientific names published since 1758 other than species-, genus-, and family-group names subject to ICZN, and other than typified names (those derived from type-genera names using only suffixes, endings and/or the stems "-form-" and "-morph-"). In that case all species-, genus-, and family-group names and all typified names (including both family-group names and typified names of higher taxa) would be available only as rank-based ones.

Examples: **Odonata**, **Odonatoidea**, **Odonatoptera** and **Odonatoptera** are available circumscription-based names, as they are derived from "Odonata", which is not a generic name (though some of these names have been first introduced as rank-based). **Ephemeroptera**, **Ephemeroptera** and **Ephemeropteroidea** are available circumscription-based names, as they are derived by adding the stem "-pter-" to the generic name

"*Ephemera*". **Oniscomorpha** may be either an available circumscription-based name if assigned to a taxon within Diplopoda (where there is no genus named *Oniscus*), or a typified rank-based name if assigned to an eucrustacean group containing the genus *Oniscus*.

**Circumscription match.** Depending on how well names match taxa in terms of circumscription, names may be mismatching, non-univocally matching, or exactly matching.

**Mismatching name** is such an available circumscription-based name whose admissible circumscription is inconsistent with the taxon's circumscription. In circumscription-based nomenclature such a name cannot be valid for this taxon by definition.

**Non-univocally matching name** (NOMEN CIRCUMSCRIBENS NON UNIVOCUM) is such an available circumscription-based name whose admissible circumscription is not inconsistent with the circumscriptions of both the taxon in question and another taxon (taxa) within the same classification.

**Exactly matching name** (NOMEN CIRCUMSCRIBENS UNIVOCUM) is such an available circumscription-based name whose admissible circumscription is not inconsistent with the circumscription of the taxon while being inconsistent with the circumscription of any other taxon within the classification.

Example: for the name Plectoptera Packard 1886, the admissible circumscription would be any set including its original listed membership (the family Ephemeridae as it was generally accepted at that time) and not including the original excluded membership (all other insect taxa, which Packard mentioned in the same paper as not belonging to his Plectoptera). Adding new mayfly taxa described thereafter into Plectoptera is not inconsistent with the original admissible circumscription of the name Plectoptera, because Packard, being unaware of them, didn't refer to them as non-members of Plectoptera. Likewise, Packard said nothing on whether *Triplosoba*, *Protereisma* and other extinct Palaeozoic groups remotely related to extant mayflies are part of Plectoptera. This means that if we use a classification where a taxon includes all mayflies and Palaeozoic groups, while its subordinate taxon includes all extant mayflies but no Palaeozoic groups, the name Plectoptera should be considered non-univocally matching either taxon.

The name Agnatha Cuvier 1798, which was used by some authors (Börner 1904, Martynov 1924–1938 and others) for the same taxon as Plectoptera, actually has original admissible

circumscription mismatching circumscription of the taxon under consideration. Originally this name (as "Agnathes" in French spelling) was attributed to a taxon uniting the genus *Phryganea* (i. e. caddisflies – Trichoptera) and the genus *Ephemera* (i. e. mayflies). Because of this, its subsequent attributing to mayflies only was regarded to be wrong (Handlirsch 1904); this decision agrees with recently proposed principle of circumscriptional nomenclature (that can not be said about other Handlirsch's nomenclatural suggestions).

**Circumscription-based synonymy.** Different names matching the same taxon are **circumscription-based synonyms**. Such synonyms may be **exact** (SYNONYMA CIRCUMSCRIBENTIA UNIVOCA) or **non-univocal** (SYNONYMA CIRCUMSCRIBENTIA NON UNIVOCA). Circumscription-based synonymy fundamentally differs from the rank-based synonymy, including synonymy as defined by ICZN; unlike rank-based synonyms, circumscription-based synonyms apply to taxa identical in circumscription, but not necessarily in rank. Therefore, whenever we mean circumscription-based synonyms we should always make it clear. The valid circumscription-based name should be chosen among circumscription-based synonyms, if any.

**Validity of circumscription-based names.** The valid circumscription-based name is the oldest one among exactly or non-univocally matching available names of the taxon. If an exactly matching name is also the oldest, it becomes the only valid name of the taxon; if the oldest name is only non-univocally matching, then the oldest exactly matching name becomes the second valid name of the taxon.

Thus, unlike the rules for rank-based names, those for circumscription-based names allow for more than one valid name for a taxon.

For example, the taxon uniting extant mayflies excluding Palaeozoic groups, has the oldest univocally matching name Euplectoptera Tillyard 1932, and more old non-univocally matching name Plectoptera Packard 1886.

In the circumscription-based nomenclature, exceptions can be made in usage of the principle of priority, but never in usage of the principle of circumscriptional matching. In exceptional cases a younger name can be used instead of the oldest one; reason for this can be homonymy, hemihomonymy, or other inconvenience of the oldest name, or

general acceptance and stability of the younger name.

The name Plecoptera Packard 1932, being not preoccupied, nevertheless has an inconvenient similarity with the name Plecoptera Burmeister 1839 (stoneflies); it was substituted by a younger name Ephemeroptera Hyatt & Arms 1891, which has the same admissible membership and in our days is generally accepted.

Some authors (Demoulin 1956b, Tshernova 1970) adopted the name Plecoptera for mayflies including Permian representatives, but excluding Carboniferous ones, and the name Ephemeroptera – for mayflies in the widest sense, including Permian and Carboniferous representatives. Other authors (Tillyard 1932) used the name Plecoptera for mayflies in the widest sense. According to the principle of circumscriptional nomenclature, the names Plecoptera and Ephemeroptera having the same original admissible membership, can not be arbitrarily used for different taxa of the same classification.

The taxon uniting recent mayflies can be called either Euplecoptera (if it is important to indicate that it does not include the Palaeozoic groups), or Ephemeroptera (= Plecoptera) (in the cases when this is not important, for example in faunistic lists of recent species).

### Combining circumscription-based and hierarchy-based nomenclatures

**Use of different nomenclatures.** Among supraspecific taxa, the hierarchy-based nomenclature based on the natural hierarchy of the phylogenetic tree works better than the rank-based one relying on purely artificial absolute ranks, while on the species level the rank-based nomenclature is adequate because it relies on evidence-based definition of species.

Therefore it would be only appropriate to switch to hierarchy-based nomenclature dealing with supraspecific taxa while retaining the rank-based nomenclature for species-group names. However, circumscription-based nomenclature is better equipped to satisfy taxonomic needs than hierarchy-based nomenclature, so if there is a choice between hierarchy-based and circumscription-based names, the latter should be preferred. Hierarchy-based nomenclature has only one, yet very important advantage over the circumscription-based one: to codify the circumscription-based nomenclature new rules are to be introduced (including homonymy rules – see Kluge 1999),

published names catalogued and many new names created, while to adopt the hierarchy-based nomenclature all we need is current ICZN rules and already available pool of genus-group and family-group names, so we may go ahead converting these rank-based names into hierarchy-based ones using a simple procedure.

**Format of species name in non-rank-based nomenclature.** Rejecting absolute ranks in supraspecific taxa would mean getting rid of the generic rank as well. But under ICZN any species name may only exist as a binomen, i. e. combined with a name of a genus (but not of a taxon of another rank). Specific epithet can not be used unless in such a combination since many epithets are used more than once throughout the nomenclature; it is also impossible to replace generic names in binomina with names of supraspecific taxa of another rank(s) because this would upset homonymy.

In a non-rank-based nomenclature, a species name might have the following format: first goes the specific epithet, then authorship and year (parenthesis is never used: secondary binomina do not exist since there is no binomina whatsoever), then the original generic name in square brackets (whether it reflects currently recognized position of the species or not); if the original combination included a subgeneric name, such name (in parentheses) may follow the generic name in square brackets. This or similar format is widely used in catalogues. The generic name works here as a surname: initially given based on kinship, it is not subject to change and is used for identification purposes no matter how accurately it describes actual relationship.

To indicate current position of the species we may add, before the epithet, a hierarchy-based name of any higher taxon where this species belongs; such names will not be mistaken for generic part of a binomen because of their distinct hierarchy-based format. If the species is a type for the hierarchical name, number in the hierarchical name before such species name can be substituted by asterisk – "\*".

The same species name can be written either as  
Behningia/fg3 *ulmeri* [*Behningia*],  
or:  
Behningia/fg\* *ulmeri* [*Behningia*].

Unlike the original generic name (the one in square brackets) which can never be altered, the hierarchy-based name in front is subject to change to reflect progress in taxonomy.

Such format has obvious advantages over the one currently in use. The generic name within a binomen is charged with two conflicting functions: (1) ensuring the uniqueness of the species name, and (2) reflecting the taxonomist's opinion on the species position. Each of these tasks is difficult in itself, and trying to accomplish both at once is hardly practical. As species position changes, homonyms may emerge or vanish, thus creating the need to replace epithets; this may lead to extremely puzzling situations where the very identity of the species under discussion is not clear and downright confusing. On the other hand, there are cases requiring either more or less details about species position, so generic name alone may not be enough.

For example, in two different papers the names of two obviously different species look like this:

species 1:

*Epeorus znojko* (Tshernova 1938),

species 2:

*Epeorus znojko* (Tshernova 1938).

Such name format sends confusing message on which species is referred to in each case. The following format carries much more information:

species 1:

*nojko* Tshernova 1938 [*Ecdyonurus*],

species 2:

*znojko* Tshernova 1938 [*Iron*].

If our knowledge about these two species would be limited to original descriptions and type specimens (adults only), their respective positions could be presented as follows:

species 1:

Rhithrogena/fg2 *znojko* Tshernova 1938 [*Ecdyonurus*],

species 2:

*Epeorus/g2 znojko* Tshernova 1938 [*Iron*],

since the taxa Rhithrogena/fg2 and Epeorus/g2 are well-defined based on adult stage. In current classification, Rhithrogena/fg2 is divided into Cinygmula/g1 and Rhithrogena/fg3; Cinygmula/g1 and Rhithrogena/fg3 are defined based on larvae only. Epeorus/g2 is divided into Ironodes/g(1) and Epeorus/g3, and the latter into Epeorus/g4, Caucasiron/g(1) and other subordinated taxa; *Ironodes*, Epeorus/f4 and *Caucasiron* are defined based on larvae only. Now that the larvae of both species are known, we may elaborate:

species 1:

Rhithrogena/fg3 *znojko* [*Ecdyonurus*],

species 2:

Caucasiron/g(1) *znojko* [*Iron*];

or in a more detailed way:

Epeorus/g3 Caucasiron/g(1) *znojko* [*I.*].

All these alternative names showing the position of

species 2 are correct and differ only in the amount of details they provide. In contrast, traditional name format makes all but one binomen incorrect, while the only "correct" binomen turns to be different depending on publication.

The traditional binary format is very concise and convenient whenever species taxonomy is not an issue, e. g., in papers on ecology, physiology and other non-taxonomic texts. In papers dealing with species position and status it is advisable to use more elaborate non-rank-based name format.

**New names.** In order to confer availability of a new genus or family group name, this name should be once published satisfying all provisions of availability proposed by the ICZN. Theoretically, it would be not important to indicate rank of the taxon in such publication, but enough to indicate if the new name belongs to the genus group or to the family group, because in all ICZN's rules the original rank is ignored. However, it is not clearly said in the ICZN, if a taxon name originally introduced without a rank, becomes available, or not. In order to avoid confusion, in this book new names are supplied with arbitrary ranks. For example, a new family group name Epeorini is here arbitrarily and temporarily supplied with a tribal rank, in spite of the fact that its highest taxon Epeorus/fg1 is a subordinate taxon inside Rhithrogena/fg1, which in its turn was earlier proposed to be a tribe. In the same manner, new genus group names are here arbitrarily and temporarily supplied with subgeneric ranks, while they can belong to taxa subordinate to traditional subgenera or/and divided into traditional subgenera.

**Sliding binomina and polynomina.** To show the hierarchical subordination concisely, names may be presented as binomina or polynomina. To do so, names of two or more taxa are to be arranged consecutively starting from the highest one; names of circumscription-based, hierarchy-based and/or rank-based nomenclatures may be used. There can be either no punctuation marks between names, just like between elements of binomina in the current nomenclature, or hyphens can be inserted.

For example, names of selected taxa from this book can be written as following:

Ephemeroptera Anteritorna Bidentiseta Branchitergaliae;

Branchitergaliae Heptagennota *Pseudiron*;

Heptagennota Pentamerotarsata;

Pentamerotarsata Radulapalpata Rhithrogena/fg2;

Rhithrogena/fg2 Cinygmula/g1 *cavum* Ulmer 1927 [*Cinygma*];  
 or:  
 Ephemeroptera-Anteritorna-Bidentiseta-Branchitergaliae;  
 Branchitergaliae-Heptagennota-*Pseudiron*;  
 Heptagennota-Pentamerotarsata;  
 Pentamerotarsata-Radulapalata-Rhithrogena/fg2;  
 Rhithrogena/fg2-Cinygmula/g1-*cavum* [*Cinygma*].

**The layout of a taxonomic paper.** Modern taxonomic papers of Linnaean tradition tend to give each taxon a separate diagnosis, a description, and a differential diagnosis (also called comparison or discussion); the diagnosis is supposed to contain a summary of diagnostic characters, the description to provide a detailed characteristics of the taxon, and the differential diagnosis to pinpoint what distinguishes it from other individual taxa. Such reiteration of the same characters is impractical, since description, diagnosis and differential diagnosis are but vaguely special. As a matter of fact, the description is just an elaborate diagnosis, while the latter is nothing but a concise description: both reflect only a part of the taxon's characters (the number of characters of any taxon being infinitely large), and only those of taxonomic importance. Differential diagnosis is believed to be special in that the characters are described in comparison with those of other taxa. However, any character is meaningful only in a comparative context, so the only thing which sets the differential diagnosis aside is that it presents the comparison expressly, while in both the description and diagnosis the comparison is implicit. Yet a scientific paper is no place for implicit statements: its very aim is to expose the author's findings and opinions. That's why it is essential for any taxonomic text (be it a description, a diagnosis, differential diagnosis or whatever you choose to call it) to provide comparison in an explicit form.

Within the Linnaean tradition taxonomic diagnoses usually follow a certain plan whose standard vary depending on rank. For example, if a diagnosis of an order says that fore wings are transformed into elytra, the diagnoses of other orders within the same class will state that the fore-wings are not so transformed, while the diagnoses of superorders may not mention this character. Such an approach makes it easier for the reader to find a character of interest while avoiding redundancy in diagnoses of consecutively subordinated taxa. But in papers following such a plan the diagnoses of taxa would depend on purely artificial absolute ranks, thus inconsistent with the goal of building a natural system where taxa are

supposed to be natural entities.

In this book we use another approach to meet taxonomic requirements. Each supraspecific taxon is characterized following a universal rank-independent scheme allowing to do without assigning absolute ranks to taxa, i. e. to switch to non-rank-based post-Linnaean classification. First the autapomorphies are listed, then the characters of unclear phylogenetic status, then the plesiomorphies; finally, or perhaps among plesiomorphies, variable characters of the taxon may be mentioned (usually referring to lower taxa not discussed here). There is no special paragraph for synapomorphies: all the apomorphies shared with any other taxa are listed under "Autapomorphies" of a higher taxon rather than among characteristics of this one. All doubtful synapomorphies are listed as "Characters of unclear phylogenetic status"; this paragraph may be subdivided as necessary. Each character is not only described but also compared, whenever possible, to other taxa; its unique or otherwise status is indicated. If necessary, references are given [in square brackets] to the description of a more general character in a higher taxon.

All characters are numbered with the only purpose to facilitate looking for similar items in descriptions, not for counting characters. Character counting used in all recent cladistic computer programs deprives such programs of any scientific meaning. One cannot assign numbers to characters unless for the sake of convenience, as we do when we arrange a text into sentences, paragraphs, chapters, etc.; the numbers may not be attributed any biological meaning.

A general "Index of Characters" is attached to the main text (taxa characteristics). In the index, the characters are arranged by structural parts to which they belong; the arrangement of the structural parts follows the usual pattern. Under each character entry, taxon names are listed, each followed by a reference number under which the character is described. To facilitate the search, some characters are mentioned in the index more than once. From the outside, the index may look like the character list and matrix of a cladistic paper, but it is just an index (like a table of contents or an alphabetic index), not a base for conclusions. The index lists all hierarchically subordinated taxa discussed in the text, not only "operational units" to be included into a matrix (the cladistic "operational unit" is rank-related, which makes it artificial and hardly meaningful). The numbers of structural parts used in the index are by

no means a universal character numbering; each character is given a number to refer to the taxon description.

Authorship of each supraspecies taxon name is given just below the corresponding title. In order not to repeat several times the same authorship for hierarchical names based on the same generic name, authorship is everywhere given only for the hierarchical name with number "1". Together with authorship, there are given objective synonyms and those subjective synonyms, which are based on type species regarded to be conspecific.

Other subjective supraspecies synonyms are absent in hierarchical nomenclature. In ranking nomenclature, synonyms are taxa of the same rank. In circumscriptional nomenclature, synonyms are taxa of the same circumscription. In hierarchical nomenclature, name has no fixed rank or circumscription; thus it has no subjective synonyms. Taxa can have one or several genus-group names included (in this book, all these names are listed in the end of the taxon characteristics); these are not synonyms, but names for subordinate taxa which can be established.

**Fonts.** In agreement with recommendation of the ICZN (Supplement B6), all names of genus-group and species-group are given in *Italics*, and all other names, including hierarchical names, are given in normal font; it is not necessary to use Italics for hierarchical names, because the symbol "/g" indicates availability of the genus-group name.

**Citation of authors and dates.** Citation of authors of taxa names used in this book, may seem to be non-traditional. Actually there are no good rules or traditions for such citation. Even in modern literature, we can often see citation of author's name without date, such as "*Ephemera* L.", or "*Ephemera danica* Müller". Such kind of citation comes from tradition existed in the XVIII and beginning of XIX century, when it was well justified: At that time rules of nomenclature did not exist, and there were no concepts of availability, validity, priority, and starting point of nomenclature. Many names came to zoology from ancient Latin and Greek languages, and no one zoologist could be regarded as the author of such name. If different zoologists applied different names for the same animal, or applied the same name for different animals, no one of these zoologists could be regarded to be wrong, and each zoologist

continued to use the same nomenclature in all his publications. So, in order to clarify which animal is understood under the certain name, one had to cite the author after the animal's name. Such author's name was often separated from the animal's name by a comma, and it was referred to the author in whose sense the name was used, but not to the author responsible for the name's availability. In this case date was not important, because the same author often used the same name in all his publications, and it was not important who used this name earlier.

Recently, according to the Code (51.2), when the author is cited after the taxon's name without punctuation mark, this is the author responsible for the name's availability, but not for its current usage. The availability is conferred by a certain publication, which has a certain date. In accordance with principle of priority, validity of an available name is provided by the date of publication, but not by personal services of the author (as it was proposed by Linnaeus). Thus, in fact, the author's name is cited in order to cite the date, and its citation without date is meaningless.

Nevertheless, there are no strict rules for the date citation; it can be written without punctuation mark, but often is separated from author's name by a comma. When a taxon name is used as a part of the sentence (for example, as a subject), such comma inside it can lead to grammatical confusion. The same happens when there are more than two authors of the publication conferring the name availability, and their names are separated by commas.

In order to avoid commas, and at the same time clearly distinguish taxon's name from author's names, and to distinguish names of several authors (which can consist of more than one word each), here date is used without comma, and between all author's names ampersand is inserted: *rubromaculata* You & Wu & Gui & Hsu 1981 [*Cinygmmina*], or Coryphoridae Molineri & Peters & Zuñiga de Cardoso 2001.

### Phylogenetic status of taxon

It is generally accepted to divide all taxa into **holophyletic** [the term introduced by Ashlock (1971) instead of "**monophyletic**" sensu Hennig], **paraphyletic** [the term introduced by Hennig] and **polyphyletic** [the term introduced by Haeckel] ones (for detailed explanation – see Kluge 2000 and English translation of this chapter in Internet, [http://www.bio.pu.ru/win/entomol/KLUGE/syst\\_1\\_2.htm](http://www.bio.pu.ru/win/entomol/KLUGE/syst_1_2.htm)). Phylogenetic (cladistic) principle of systema-

tics declares that all taxa should be holophyletic only, but never polyphyletic or paraphyletic. However, besides evidently holophyletic, paraphyletic and polyphyletic taxa, there are many those which phylogenetic status is not clarified yet, and they exist in all classifications together with holophyletic ones. Some authors call them "plesions", to distinguish from holophyletic taxa; in the preliminary text of this revision, the term "plesion" was also used in this meaning. Dr J.G. Peters paid my attention to the fact that in modern literature the term "plesion" is used in various meanings, and helped to find its original definition.

Indeed, Patterson and Rosen (1977) who introduced the term "**plesion**" (in plural "**plesions**"), applied it for taxa of any phylogenetic status, including holophyletic ones, and used it to represent a phylogenetic tree as a sequence of taxa rather than a hierarchy of taxa: in their classification, several plesions written one after another, mean that this is a pectinate portion of phylogenetic tree, in which each plesion is a sister group of all those that succeed it. In this sense, the term "plesion" indicates systematic

position of the taxon and substitutes traditional Linnaean ranks, but does not characterize the taxon itself. In the ancient Greek, the word "**plesion**" (plural "**plesia**") means neighbour in direct and indirect meanings, that is close to the meaning of the term "plesion" proposed by Patterson and Rosen. In the same paper (Patterson & Rosen 1977:163) it was suggested to put into quotation marks name of a taxon which is "nonmonophyletic, or ... no longer contains its type genus, or both". In order to avoid confusion, it would be better not to use the term "plesion" and quotation marks to signify paraphyletic taxa.

Instead, here is suggested a new term "**plesiomorphon**" (in English plural "**plesiomorphons**", but not Greek "plesiomorpha"): plesiomorphon is a taxon characterized by plesiomorphies only; thus, its holophyly is not proven, and possibly (or probably) this taxon is paraphyletic, but its paraphyly is also not proven yet. Plesiomorphon can be a taxon of any size and systematic position in ranking or non-ranking classification, living or fossil, with any name (ranking, hierarchical, circumscriptional or other).