

A PARADOXICAL PROBLEM IN THE PHYLOGENY OF FURCATERGALIA (EPHEMEROPTERA)

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If all known characters of imagos, subimagos and larvae are taken into account, it would seem that the larvae of Caenidae have originated from Neophemeridae which have originated from Ephemeroidea; but at the same time the winged stages of Caenidae have originated from Tricorythidae which have originated from Ephemerellidae. While this situation is unclear, it is impossible to divide Furcatergalia into superfamilies which could be generally accepted.

INTRODUCTION

The superfamily Ephemeroidea and the families Neophemeridae, Caenidae, Ephemerellidae, Tricorythidae and Leptophlebiidae belong to the infraorder Furcatergalia s. str. (KLUGE, 1993; KLUGE *et al.*, 1994).

Older authors, who paid the most attention to adult structure, regarded Caenidae and Tricorythidae to be closely related, because representatives of these families have a similar general appearance and wing venation in the adults. Thus EATON (1883-1888) united *Tricorythus*, *Leptohyphes* and *Caenis* into «Section 7»; LAMEERE (1917) united these genera into the tribe Caenini; LESTAGE (1917) and NEEDHAM *et al.* (1935) placed the genera which now are placed into Caenidae and Tricorythidae, into the subfamily Caeninae.

In the same way based on imaginal characters, the older authors believed that the Neophemeridae were closely related to Ephemeroidea. Modern authors, however after considerable research, have based their classification and phylogenetic ideas on the structure of larvae. On the basis of larval structure, Tricorythidae are regarded as closely related to Ephemerellidae, but not to Caenidae, and Neophemeridae are regarded as related to Caenidae, but not to Ephemeroidea (e.g. EDMUNDS, 1962; MCCAFFERTY, 1991).

But in studying the larval structures, the modern authors have forgotten the imagos. At the same time mayfly imagos have many interesting features in their pterothorax structure, some of which have an important taxonomic level (KLUGE, 1994). Examination of the imaginal and subimaginal thorax structure proves the ideas of the older authors con-

cerning close the relationship of Caenidae with Tricorythidae (KLUGE, 1992), and Neophemeridae with Ephemeroidea (see below). At the same time the ideas about the relationships between Tricorythidae and Ephemerellidae, and between Neophemeridae and Caenidae, are supported by the excellent synapomorphies in the larval structure (see below). If all known apomorphies are summarized, a paradoxical ring-like figure develops instead a phylogenetic tree (Fig. 1). This strange phylogenetic scheme is proved by the presented synapomorphies.

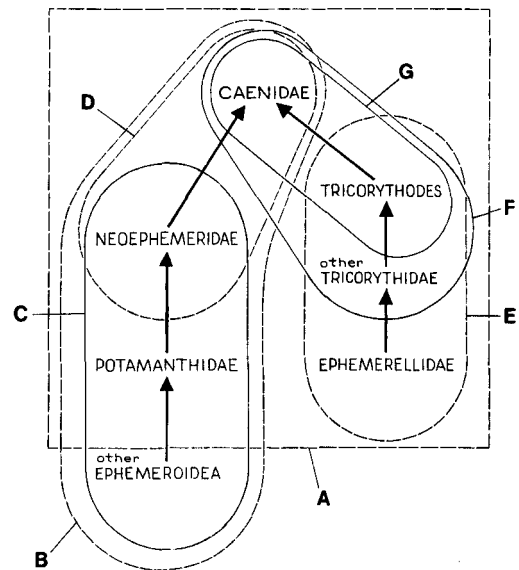


Fig. 1. Synapomorphies of certain groups of Furcatergalia. Integral lines show synapomorphies mainly in adult (imaginal and subimaginal) structure, interrupted lines - synapomorphies in larval structure. Arrows inside the ovals are directed from plesiomorphic to apomorphic condition. Explanation in the text.

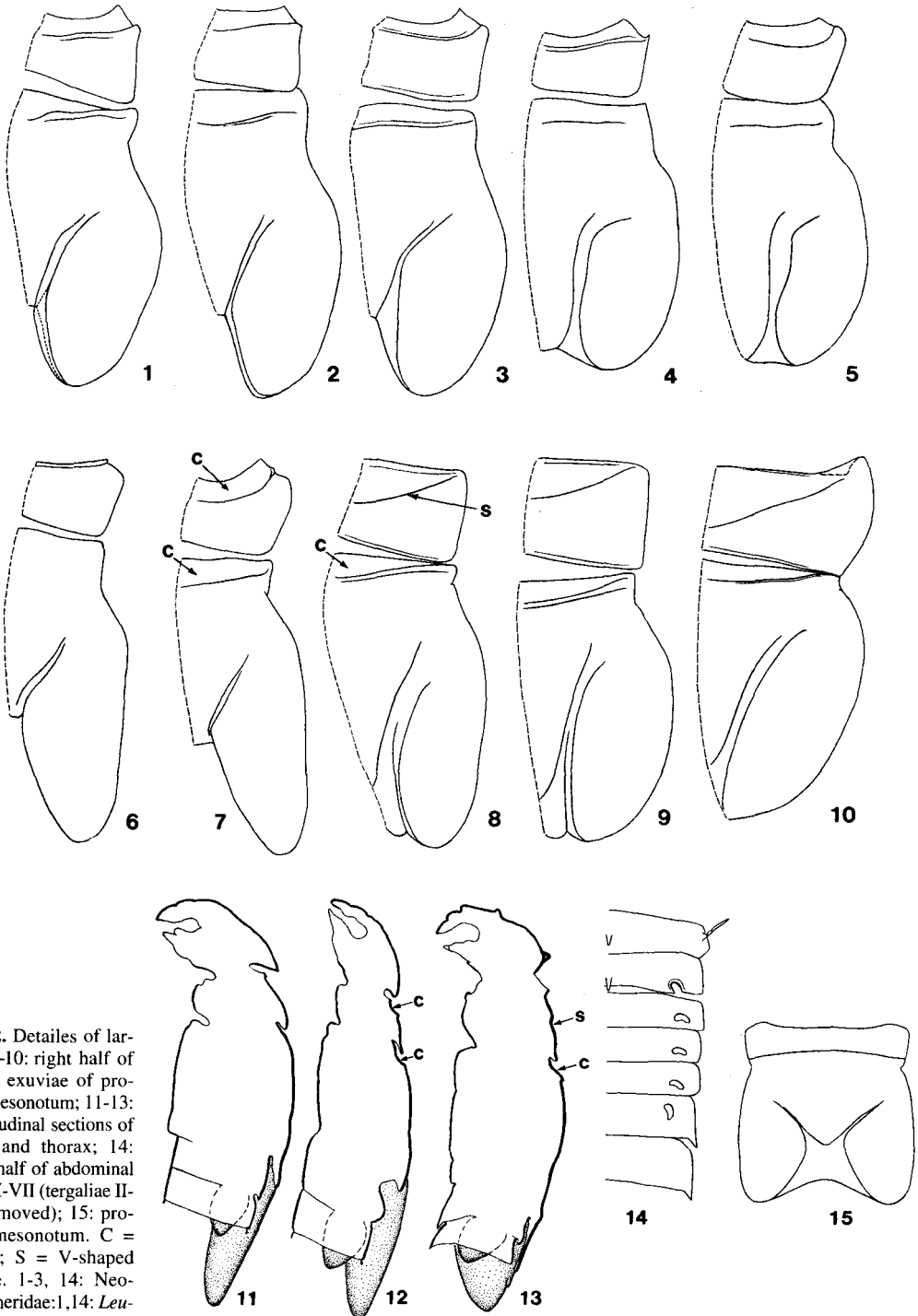


Fig. 2. Details of larvae. 1-10: right half of larval exuviae of pro-and mesonotum; 11-13: longitudinal sections of head and thorax; 14: right half of abdominal terga I-VII (tergalia II-VI removed); 15: pro-and mesonotum. C = collar; S = V-shaped suture. 1-3, 14: *Leucorhoenanthus maximus* (JOLY); 2: *Neophemera tshernovae* KAZL.; 3: *Potamanthellus rarus* TIUN. ET LEV.; 4: *Caenis miliaria* (TSHERN.); 5: *C. macrura* STEPH.; 6, 11: *Leptophlebia chocolata* IMAN.; 7, 12: *Potamanthus luteus* L.; 8: *Ephemerella nuda* TSHERN.; 9: *Tricorythodes cubensis* KLUGE & NAR.; 10: *Tricorythus tinctus* KIMM.; 13: *Ephemerella (Drunella) submontana* BROD.; 15: *Oligoneuriella pallida* HAG.

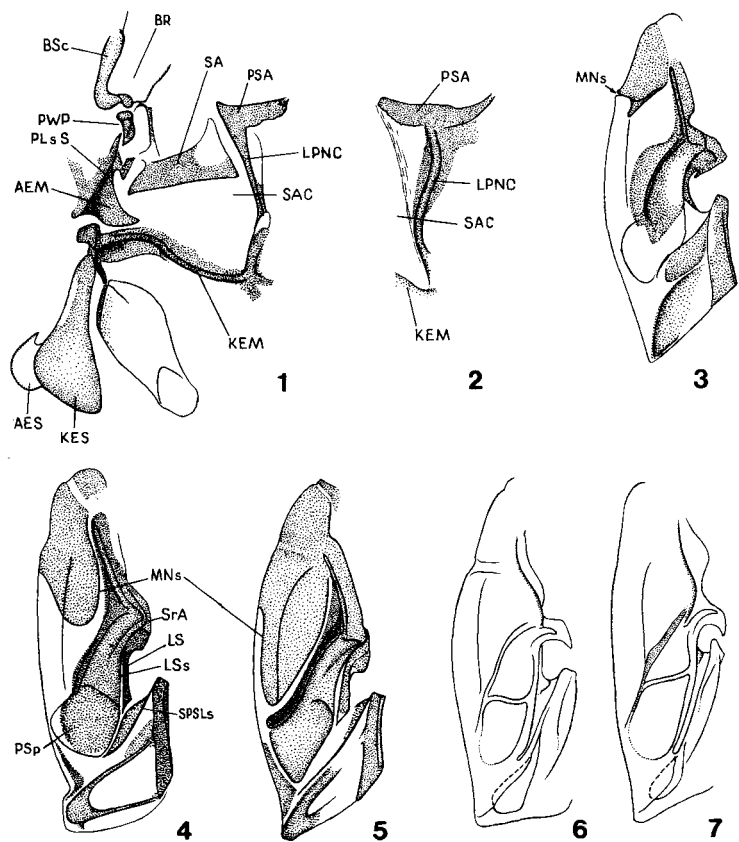


Fig. 3. Details of subimaginal exuviae. 1: mesopleural region; 2: lateropostnotal sclerotization; 3-7: right half of mesonotum. 1, 4: *Ephemera strigata* ETN.; 2, 3: *Ephemera aurivillii* BGTN.; 5: *Leucorhoenanthus maximus*; 6: *Tricorythodes cubensis*; 7: *Caenis macrura*. AEM = anepimeron; AES = anepisternum; BSc = basisubcostale; BR = basiradiale; KEM = katepimeron; KES = katepisternum; LPNC = lateropostnotal crest; LS = lateroscutum; LSs = lateral scutal suture; MNs = mesonotal suture; PLsS = superior pleural suture; PSA = postsubalar sclerite of lateropostnotum; PSp = posterior scutal protuberance; PWP = pleural wing process; SA = subalare; SAC = subalar cavity; SPSLs = scuto-parascutellar suture; SrA = suralare.

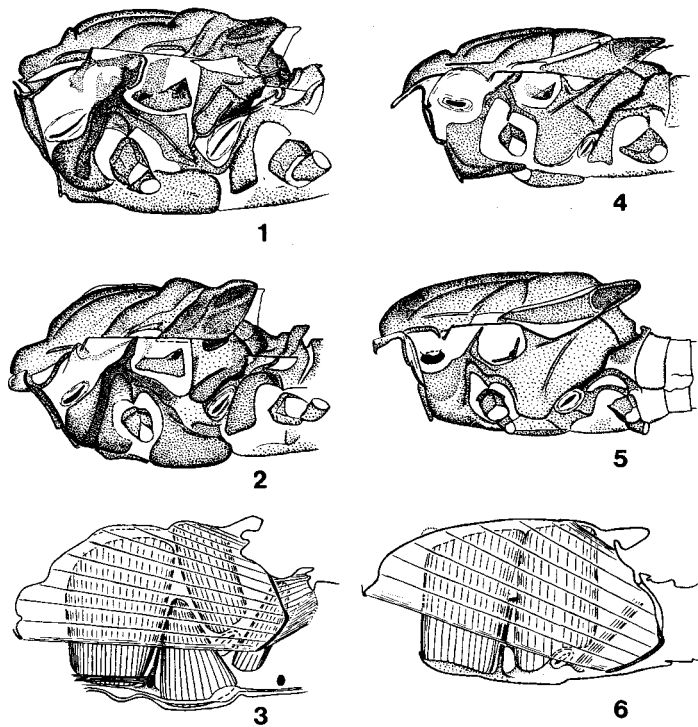


Fig. 4. Pterothorax of male imago. 1, 2, 4, 5: left view; 3, 6: longitudinal section. 1: *Ephemera (Drunella) aculea* ALLEN; 2, 3: *Leucorhoenanthus maximus*; 4: *Tricorythodes cubensis*; 5, 6: *Caenis macrura*.

RESULTS

Synapomorphies of Potamanthidae + Neoephemeridae + Caenidae + Ephemerellidae + Tricorythidae (Fig. 1, A)

(1) Tergaliae (for explanation of the term see KLUGE, 1989; 1996) of the pair one (I) are vestigial, stick-formed, 2-segmented (Fig. 2: 14). Such structure of tergaliae is unique: it is not found in any other mayflies, in spite of the fact that reduction of the tergalia I independently takes place in some taxa. In all Potamanthidae, Neoephemeridae and Caenidae the 2-segmented vestigial tergaliae of the first pair are present, but in the majority of the Ephemerellidae and Tricorythidae they are completely reduced, being preserved only in the tribe Timpanogini and some of Teloganodini.

(2) Larval mesonotum with the collar - the invaginated band bordering the anterior margin, separated from the remainder of mesonotum by the transverse crest (Figs 2: 1-5, 7-10, 12, 13). The same collar is present also in Euthyplociidae.

*Synapomorphies which suggest of Caenidae originate from Ephemeroidea (Fig. 1, B-D)**Synapomorphy of Ephemeroidea + Neoephemeridae + Caenidae (Fig. 1, B).*

(1) Larval pronotum with the collar - the invaginated band bordering the anterior margin (Fig. 2: 1-5, 7, 12). This collar is especially distinctly developed in Potamanthidae, Euthyplociidae, Neoephemeridae, and *Caenis*; generally the larval pronotum in these taxa is not specialized. The representatives of Ephemeroidea and Caenidae with a highly specialized and modified pronotum (*Brachycercus*, and burrowing Ephemeroidea) have a less distinct collar. The presence of the pronotum collar is the unique feature of Ephemeroidea, Neoephemeridae and Caenidae, such a collar is not found in any other mayflies.

Synapomorphies of Ephemeroidea + Neoephemeridae (Fig. 1, C).

(1) In the fore wing veins MP2 and CuA curved near base and strongly divergent from vein MP1 (Fig. 5: 2) (sometimes vein MP2 has lost

its base and arises from vein CuA). Such curvature of these veins is unique and not found in any other Ephemeroptera.

(2) The mesonotal suture (for explanation of the terms in thorax structure - see KLUGE, 1994) it turned backward from the point where it crosses the median suture; in subimago the pigmented area anteriorly to the mesonotal suture is covered by microtrichiae. The mesonotal suture can go very far back, nearly reaching the posterior scutal protuberances, so it looks like two pairs of longitudinal sutures - in *Eatonica* (subfam. Hexageniinae), *Palaeoanthus* (KLUGE, 1993: 1, m), Neoephemeridae (Fig. 3: 5) (its median longitudinal portion was called «additional sutures» in TSHERNOVA *et al.*, 1986). In the majority of examined Ephemeridae and Potamanthidae the mesonotal suture does not go so far back (Fig. 3: 4). In the highly specialized Ephemeroidea (Polymitarcyidae, Euthyplociidae, Behningiidae, Palingeniinae) the mesonotal suture becomes indistinct and disappears. It is absent also in Caenidae. Besides Ephemeroidea and Neoephemeridae, the mesonotal suture is curved backward only in Leptophlebiidae and Baetoidea (Tetramesotarsata). In other mayflies the mesonotal suture, if present, is more or less transverse (Fig. 3: 3 and KLUGE *et al.*, 1995).

(3) The lateral scutal suture (for explanation of this term - see KLUGE, 1994) runs from suralare posteromedially, nearly straight, and reaches the posterior scutal protuberance; the lateral margin of lateroscutum is nearly straight (Fig. 3: 4, 5). Such a structure is found in all examined Neoephemeridae and Ephemeroidea, and differs from other mayflies.

(4) In subimago the lateropostnotal crest arises from the anterior end of the postsubalar sclerite, and runs ventrally along the margin of the subalar cavity (Fig. 3: 1) (for explanation of the terms - see KLUGE, 1994). These sclerites are distinctly visible on subimaginal cuticle with well pigmented pleural sclerites (*Ephemera*, and Neoephemeridae), but poorly visible on pale pleura of Potamanthidae, and not visible on colourless subimaginal cuticle of Palingeniinae and Polymitarcyidae. This shape of the sclerite is unique for Ephemeroidea and Neoephemeridae. In the other mayfly taxa the lateropostnotal crest arises from the postsubalar sclerite far from its anterior end, and runs at

distance from the margin of subalar cavity, so their subimaginal sclerotization of the latero-postnotum has an ax-like shape (Fig. 3: 2).

(5) In the larvae tergaliae of segments II-VI bilamellate, each lamella with numerous pointed processes on both margins (except for the dorsal lamella of the tergaliae II in Neophemeridae, which are operculate). In other respects tergaliae II-VI of Neophemeridae strongly differ from those of Ephemeridae, being more highly specialized and having synapomorphies with those of Caenidae.

In general Neophemeridae have more derived structure of imagos and larvae than the Ephemeroidea. In contrast to Ephemeroidea, most of which have the ventral bases of the subalar-sternal muscles turned together (KLUGE, 1996: Fig. 27) (plesiomorphic character), Neophemeridae have these muscle bases (and corresponding to them furcasternal protuberances - see KLUGE, 1994) widely separated, with the metathoracic nerve ganglion turned between them (KLUGE, 1996: Fig. 28). This feature of Neophemerida is derived, but not unique: the same is found in all other Furcatergalia except Ephemeroidea, and in selected taxa of Pisciforma and Setisura.

Synapomorphies of Neophemeridae + Caenidae (Fig. 1, D).

(1) Tergaliae of pair II operculate, square. Operculate tergaliae may appear independently also in some other mayfly taxa, but usually they have other form.

(2) Tergaliae of pairs III-VI semicircular, with numerous pectinately branched marginal processes (EATON, 1883-1888: Pl. 41: 14-17; 42: 23-26). Form of these tergaliae is just the same in all Neophemeridae and Caenidae, and distinctly differs from that of all other mayflies.

(3) Bases of tergaliae VI strongly turned forward (Fig. 2: 14) (in contrast to Leptohiphinae and Timpanogae, which also have operculate tergaliae).

(4) Tergaliae of pair VII absent. This is not unique: such reduction takes place in several unrelated mayfly groups.

Larvae of Caenidae are more derived in their structure than those of Neophemeridae, having completely reduced ventral leaves of tergaliae II-VI (which are preserved in Neophemeridae as rudiments).

Winged stages of Caenidae are so strongly modified that their structure cannot be compared with those of Neophemeridae: the mesonotal suture is absent, so its initial form is unknown; the subimaginal cuticle lack pigmented and sclerotized areas, and mesonotum is entirely covered by microtrichiae, so the initial form of subimaginal sclerotization and position of microtrichiae are unknown.

Synapomorphies which suggest origination of Caenidae from Ephemerellidae (Fig. 1, E-G)

Synapomorphies of Ephemerellidae + Tricorythidae (Fig. 1, E).

(1) Paraglossae fused with mentum.

(2) Larval pronotum with V-shaped suture (Fig. 2: 8-10, 13).

(3) Tergaliae initially consist of upper and lower portions, the lower portion bifurcate, each of its two lobes with a row of processes (KLUGE, 1992).

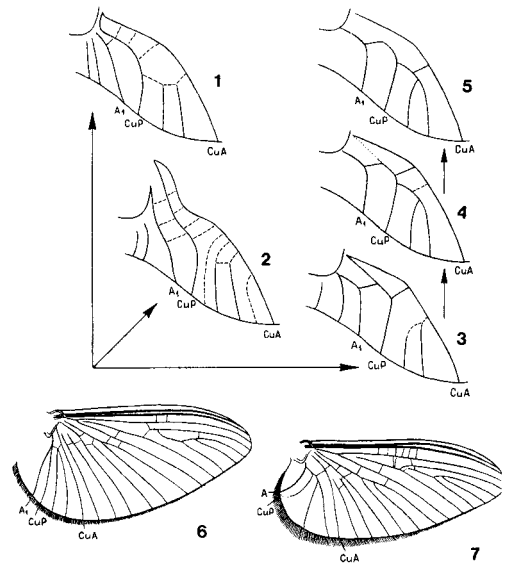


Fig. 5. Fore wing venation. 1-5: scheme of evolution of cubital field venation: 1: Leptophlebiidae; 2: Ephemeroidea and Neophemeridae; 3: Ephemerellidae; 4: *Leptohiphes*, *Tricorythodes*, *Ephemerythus* and *Dicercomyzon*; 5: *Tricorythodes* (the constant veins are shown by integral lines, the variable veins - by interrupted lines). 6: *Caenis macrura*; 7: *Tricorythodes cubensis*.

Synapomorphies of Tricorythidae + Caenidae and Tricorythodes + Caenidae (Fig. 1, F-G)

There are about 10 synapomorphies in the structure of adult pterothorax and wings, which are described in a separate paper (KLUGE, 1992), and the synapomorphy of Tricorythidae (s. l.) with Caenidae in the structure of larval caudal filaments (their bases are thickened in male, but have normal size in female - KLUGE & NARANJO, 1990: Fig. 16).

The pterothorax of Caenidae and Tricorythidae is very strongly specialized (Fig. 3: 6, 7; 4: 4-6) and strongly differs from pterothorax of other Ephemeroptera (Fig. 4: 1-3). The pterothorax structure of Caenidae is extremely specialized and is very constant inside the family (various species of *Caenis*, *Brachycercus* and *Caenopsella* were examined). *Tricorythodes* has a somewhat less specialized structure of the pterothorax, but with many synapomorphies with Caenidae. *Leptoxyphes* and other Tricorythidae have pterothorax structure intermediate between those of *Tricorythodes* and Ephemerellidae. In the same way Caenidae and *Tricorythodes* have synapomorphies: vein CuP arises from vein A1, and bifurcate vein ICu connected basally with veins CuP and CuA (Fig. 5: 6, 7); the wing venation of other Tricorythidae is intermediate between those of *Tricorythodes* and Ephemerellidae (Fig. 5: 3-5).

At the same time larvae of all Tricorythidae, including *Tricorythodes*, have no synapomorphies with larvae of Caenidae (besides the male caudal filaments structure - see above). The external similarity of larvae of *Tricorythodes* (and other Leptoxyphinae) with those of Caenidae is evidently a result of convergence.

CRITICAL DISCUSSION ON THE TAXON «PANNOTA»

MCCAFFERTY & EDMUNDS (1979) and MCCAFFERTY (1991) used the name «Pannota» for the group of mayflies which includes Neophemeridae, Caenidae, Ephemerellidae, Tricorythidae, Baetiscidae and Prosopistomatidae. The only character which unites these families, is a fusion of larval wing buds. But actually such fusion takes place also in Oligoneuriidae

(Fig. 2: 15), Coloburiscidae, and some other taxa which are not placed to «Pannota», while in some of Neophemeridae the fusion is nearly absent (Fig. 2: 1, 2). In Ephemerellidae and Tricorythidae the wing buds are fused one with another (Fig. 2: 8-10) (as in Oligoneuriidae - Fig. 2: 15), but in Neophemeridae and Caenidae wing buds are fused only with the hind margin of the mesonotum (Fig. 2: 1-5). So this character can not be regarded as synapomorphy of all «Pannota». As it is shown in a separate paper (KLUGE, 1997) Baetiscidae and Prosopistomatidae are not related to other «Pannota» and to Furcatergalia in general. The presence of fused wing buds means that Neophemeridae, Caenidae, Tricorythidae and Ephemerellidae cannot be united and separated from other Furcatergalia.

CONCLUSIONS

The combinations of adult and larval characters of Neophemeridae, Caenidae, Tricorythidae and Ephemerellidae do not allow the construction of a phylogenetic tree in which all branches would be directed from the plesiomorphic to the apomorphic states of characters, and each complex of apomorphies would appear only once. Usually this is termed convergence. Here convergence may be supposed to take place between larval structures of Neophemeridae and Caenidae, or between imaginal structures of *Tricorythodes* and Caenidae. In each of these hypotheses, one has to assume that a number of unique compositive characters which have no adaptive role, have appeared independently twice (that is hardly conceivable).

If hypotheses about convergence are not accepted, two different hypotheses can be suggested. The first one - is reversion, the result of which is that the relatively primitive structure of adults of Ephemerellidae (which are similar to that of the majority of other mayflies) originated from highly specialized imaginal structure of Caenidae and Tricorythidae; in this case the structure of larval tergaliae peculiar to Ephemerellidae and Tricorythidae had originated from the more specialized tergaliae structure of Neophemeridae-Caenidae type. Therefore the

evolution had to go in the direction: Neophemeridae - ancestors of Caenidae - Tricorythidae - Ephemerellidae.

The other hypothesis - is that Caenidae originated simultaneously from two ancestors (Neophemeridae and Tricorythidae) with the help of transduction: the main genetic information which regulates the larval development, was inherited by Caenidae from Neophemeridae, while the main part of genetic information responsible for the imaginal structure, was inherited by them from Tricorythidae.

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