A new autapomorphy of the taxon Tricoryptera and redescription of *Ephemerythus*

Новая аутапоморфия таксона *Tricoryptera* и переописание *Ephemerythus*

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ABSTRACT. The taxon Tricoryptera Kluge, 2004 is characterized by unique ontogenesis of hind wing, that is an autapomorphy of this taxon; this character is expressed only in Ephemerythus/fg 1 and some representatives of Leptohyphes/fg 1, while in all other Tricoryptera hind wings are completely lost. System of Ephemerythus/fg 1 is revised, the following subjective synonymy is suggested: *Ephemerythus* (=Tricomeraella = Limnokijara *syn.n.*); *Ephemerythus niger* (= E. (Tricomeraella) *straeleni* *syn.n.* = E. *dissimillimus* *syn.n.*). A new subspecies *Ephemerythus niger ugandanus* *subsp.n.* is described basing on imagoes reared from larvae in the west of Uganda.

ПЕРЕЧИСЛЕНИЕ. Таксон Tricoryptera Kluge, 2004 характеризуется уникальным онтогенезом заднего крыла, что является его аутапоморфией. Этот признак выражен только у Ephemerythus/fg 1 и у некоторых представителей Leptohyphes/fg 1, тогда как у всех прочих Tricoryptera задние крылья полностью утрачены. Пересмотрена система Ephemerythus/fg 1, предложена следующая объективная синонимия: *Ephemerythus* (=Tricomeraella; = Limnokijara *syn.n.*); *Ephemerythus niger* (= E. (Tricomeraella) *straeleni* *syn.n.* = E. *dissimillimus* *syn.n.*). По имаго, выведенным из личинок на западе Уганды, описан новый подвид *Ephemerythus niger ugandanus* *subsp.n.*

Systematic position of Tricoryptera

The taxon TRICORYPTERA Kluge, 2004 belongs to the holophyletic taxon PANTRICORYTHI Kluge, 2004, which belongs to the holophyletic taxon Ephemera/fg 1, which belongs to the holophyletic taxon FURCATERGALIAE Kluge, 1998, belonging to the holophyletic taxon BIDENTISETA Kluge, 1993 in the holophyletic taxon ANTERITORNA Kluge, 1993; holophyly of each of these taxa is proved by unique autapomorphies [Kluge, 2004].

However, some authors accept a taxon PANNOTA McCafferty & Edmunds, 1979, which unites Ephemera/fg 1 with Caenotergaliae (originally — also with Posteritorna); this taxon has no place in phylogenetic systematics. Nobody suggested any diagnosis to Pannota: originally it was characterized only by fusion of larval fore protoptera, but in this respect Ephemera/fg 1 has more similarity with Eusetisura (which was
never attributed to Pannota), than with Caenotergaliae: in Ephemerella/fg1 and Eusetisura fore protoptera are connected by a mesial plate which can give raise to imaginal plumidia (Fig. 6), while in Caenotergaliae fore protoptera are connected only by scutellum [Kluge, 1997, 2004].

Detailed phylogenetic classification is given in the website "Phylogeny of Ephemeroptera" [Kluge, web publication].

Characteristics of Tricoryptera

The taxon TRICORYPTERA Kluge, 2004 is characterized by a unique autapomorphy: reduction of the proximal portion of CuP on fore wing, so that CuP lost its connection with CuA [Kluge, 1997, 2004].

Another autapomorphy, known for Tricoryptera, is reduction of hind wings: in all representatives hind wing is either diminished, with elongate costal projection, or completely lost. This character was regarded to be non-unique, because diminishing and loss of hind wing independently occurs in various non-related mayfly taxa; in many cases diminishing of hind wing is accompanied with elongation of its costal projection. But actually, as it is shown below, modification of hind wing in Tricoryptera has unique features, not found in any other mayflies; so this character represents the second good autapomorphy, which proves holophyly of Tricoryptera.

Besides these two autapomorphies, Tricoryptera have the following characters of unclear phylogenetic status:

- Infrascutellum is reduced, and sculellum is enlarged and modified; this character is in common with Teloganodes/fg1 (which, probably, is a sister group with Tricoryptera) and with Caenoptera (which has non-explainable similarity with Tricoryptera [Kluge, 1997, 2004]).
- Subimaginal cuticle of mesonotum has no relief line separating lateral pigmented area from medial colorless area; this line is initially characteristic for Ephemerella/fg1 [Kluge, 2004]; it is well expressed in all Ephemerella/fg2, Vietnamella/fg1 and some other taxa, but is absent in all Tricoryptera. Formerly, I had no subimagines of Ephemerithys/fg1, so structure of their subimaginal mesonotum was unknown. The newly examined specimens of Ephemerithys niger from Uganda have no this line (Fig. 20), and this allows to conclude that the line is absent in all Tricoryptera. Among Ephemerella/fg1, this line is absent, besides Tricoryptera, also in Teloganodes/fg1.
- Tricoryptera also have non-unique characters common with Teloganodes/fg1 and some other taxa: absence of paired submedian projections on larval abdominal terga, which are characteristic for many other Ephemerella/fg1; loss of stick-like tergali I; reduction of tergali VII.

In the previous diagnosis of Tricoryptera, I gave also one more non-unique character: "adults are shortly-molting..." [Kluge, 2004]. Actually, this character is wrong, because shortly-molting adults are characteristic not for all Tricoryptera, but only for a part of them. As I could observe in Uganda, subimagines of Ephemerithys niger and Diceromyzon costale Kimmins, 1957 develop for a rather long time; unlike Tricorygnatha and Leptohyphes/fg1, whose subimagines and imagines keep wings spread by sides, like Caenoptera, subimagines of Ephemerithys/fg1 and Diceromyzon/fg1 keep their wings raised up, as in most other Ephemeroptera.

Autapomorphy of Tricoryptera — unique modification of hind wing

Hind wing is diminished and has a long, narrow pointed costal projection; at the same time, larval hind protopteron has no costal projection, but retains a shallow rounded convexity on costal margin; when adult hind wing develops inside protopteron, its costal projection locates inside the costal convexity of protopter on, being arched at apical direction (Fig. 2). Such hind wings are present in Ephemerithys/fg1 (which belongs to Tricoryptera-Afrotricorythi), Leptohyphes/fg2 and some other taxa belonging to Tricoryptera-Letothyphes/fg1. Shape of hind protoptera in these taxa is similar, but shape of adult hind wing is different: in Ephemerithys/fg1 costal projection is directed anteriorly, can be straight [Gillies, 1960: Fig. 2; Kluge, 2004: Fig. 99C] or somewhat arched apically (Fig. 2); in representatives of Leptohyphes/fg1, the costal projection is arched proximally (Fig. 8). In other Tricoryptera hind wings and their larval protoptera are completely lost, so this character is not expressed.

By structure and development of hind wing, the taxon Tricoryptera differs from most Ephemeroptera and most insects in general, whose adult wings and protoptera have similar shape and retain evolutionary correlation. Similarly diminished hind wing with enlarged costal projection occurs in many non-related mayfly taxa (particularly, in Teloganodes/fg1, some other Ephemerella/fg1 and in many representatives of Leptophlebia/fg1), but in these cases larval hind protopteron has a costal projection, whose apex corresponds to the apex of costal projection of adult hind wing.

Old-World Tricoryptera

As shown earlier [Kluge, 2004], all Old-World representatives of Tricoryptera constitute a holophyletic taxon AFROTRICORYTHI Kluge, 2004, which is characterized by a unique Y-shaped vein in cubital field (Fig. 1) and is divided into 4 distinctly outlined holophyletic taxa: Ephemerithys/fg1, Diceromyzon/fg1, Machadorythys/fg1 and Tricorygnatha. Characteristic and composition of the taxon Ephemerithys/fg1 are discussed below.

Additions to the general characteristic of Ephemerithys/fg1

To the characteristic of Ephemerithys/fg1 given earlier [Kluge, 2004], the following additions and comments should be given.
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In imago and subimago all claws, including claws of male imaginal fore leg, are ephemeropteroid (that is a plesiomorphy [Kluge, 2004]). In the original description [Gillies, 1960], there was stated that “Male fore leg, claws similar; mid and hind legs, claws dissimilar.” This is a mistake. M.T. Gillies sent me paratypes of *E. kiboensis* (one of the three species described by him in 1960) — 4 male imagos collected by him on Kil-
manjaro 13.X.1958. One of these specimens has a fore leg, and its claws are dissimilar (i.e., ephemeropteroid). All representatives of E. niger (the type species of Ephemerythus), collected by me in Uganda, also have all claws ephemeropteroid.

Larvae are operculate-gilled: anteriormost pair of tergalii (belonging to abdominal segment II), serve as gill opercula, and other tergalii (pairs III–VI) serve as tracheal gills. While morphologically tergalii II only slightly differ from the next ones (Figs 10–14), they strongly differ in their movement. As I could observe in Uganda, when larva of Ephemerythus niger makes respiratory movements, its tergalii II only raise up to allow other tergalii to move, but are unable to make rhythmic respiratory movements themselves. Tergalii of the next pairs make fast rhythmic respiratory movements and provide water current necessary for respiration. By this feature Ephemerythus/fgl well differs from Tricomerella, whose tergalii of all pairs are able to make synchronous, rhythmical, respiratory movements. The same kind of tergalial movements, as in Ephemerythus/fgl, independently evolved in Leptohyphes/fgl, and Caenoptera, unlike Machado­ries, Limnokijara, etc., which were exam­ined by me, hind wings have the same size; nothing is said about difference of their size in literature; according to the original description [Gillies, 1960], in E. pictus “hind wing brownish-purple to base of spur”. The fourth character is also wrong: according to the original description [Gillies, 1960], in E. kiboensis “basal segment with numerous sharp spines on inner surface extending almost to its base”; in specimens received by me from M.T. Gillies, they are really not concentrated distally (Fig. 27), being similar to that of E. niger (Fig. 25). So the “genus Limnokijara” has no any characteristics and should be regarded as a junior synonym of Ephemerythus (= Limnokijara syn.n.).

At the present time only 3 species of Ephemerythus/fgl are described: E. niger (= E. (Tricomerella) straeleni = E. dissimillimus), E. pictus and E. kiboensis. However, among larvae, on which originally [Gillies, 1960] the generic diagnosis of Ephemerythus was based, there were repre-

sentatives of different species. He sent me two larvae, one from Tanzania, another from Cameroon, which belong to two different species, and the both are not conspecific neither with *E. niger*, nor with larva ascribed by Demoulin [1965] to *E. pictus*. This means that there are more than three species of *Ephemerythus*, and at least one of them is not described (Table 1).

**Ephemerythus niger** Gillies, 1960

= *Ephemerythus (Tricomera) straeleni* Demoulin 1964, syn.n.

= *Ephemerythus dissimillimus* Kopelke 1980, syn.n.

Larva is described by Demoulin [1964]. Male and female imagoes are described by Gillies [1960] and Kopelke [1981]. Egg is described by Kopelke [1980]. Distributed in central and eastern Africa: Congo, Tanganyika, west of Uganda. The form which inhabits in Uganda, is described below as a new subspecies *Ephemerythus niger ugandanus* subsp.n.

**Ephemerythus niger ugandanus** Kluge, subsp.n.

Figs 1–26


**Larva.** CUTICULAR COLORATION: Whole cuticle light-brownish, nearly unicolor or with indistinct diffusive maculae only.

**HYPODERMAL COLORATION:** Head and thorax have blackish maculae, variable individually. Each femur has blackish band near apex. Fore protoptera have blackish bases and often (not always) have blackish lines corresponding to convex longitudinal veins; their invisible ventral sides often have blackish lines corresponding to concave longitudinal veins (Fig. 6). Abdomen has blackish maculation as in imago, with the same sexual dimorphism: terga 1–11 and VII–VIII in most

| Table 1. Characters of the known forms belonging to the taxon Ephemerythus/fg1. |
|---------------------------------|-----------------|-----------------|-----------------|-----------------|-----------------|
|                                  | *E. niger* (= *straeleni* = *dissimillimus*) | *E. pictus* | *E. dissimillimus* Demoulin 1964 | *E. pictus* | *E. pictus* |
| **Larva:**                      |                 |                 |                 |                 |                 |
| proximal dentiseta enlarged     | +               | ?               | ?               | ?               | +               |
| pronotum with stretched posterolateral corners | -               | ?               | ?               | -               | +               |
| hypoderm of fore protoptera: membrane dark | ?               | -               | +               | +               | -               |
| transverse setal row on fore femur regular | -               | ?               | ?               | +               | -               |
| homolog of transverse setal row on mid & hind femur | +               | ?               | -               | -               | +               |
| tergalius V with ventral lobe | +               | ?               | ?               | ?               | -               |
| tergalius VI present | +               | ?               | -               | -               | -               |
| **Imago:**                      |                 |                 |                 |                 |                 |
| hind wing proximally dark       | +               | +               | ?               | ?               | +               |
| female hind wings               | ±               | +               | ?               | ?               | ±               |
| male abdominal terga III–V light | +               | +               | ?               | ?               | ±               |
| male abdominal tergum VI light  | +               | -               | ?               | ?               | ±               |
| 1st segment of gonostylus with spines on distal swelling only | +               | -               | ?               | ?               | ±               |
| penes angulate                  | +               | ?               | ?               | ?               | ±               |

+ — present, — absent, ? — undefined.
+ — есть, — нет, ? — не известно.
part dark, tergum IX in most part light; in male terga III–VI in most part light (Fig. 19), in female much darker. Dorsal lamella of tergalius II (gill operculum) has hypoderm blackish in proximal half, colorless in distal half (Fig. 10). Dorsal lamellae of tergalii III–VI and ventral lamellae of tergalii II–V are diffusively darkened in proximal part (Figs 11–14). In proximal part of caudal hypoderm of each segment is blackish distally and colorless proximally; in distal parts of caudal hypoderm is colorless.

SHAPE AND SETATION: As figured by Demoulin [1964: Fig. 1A–I]. Maxilla lacks palp; proximal dentiseta is enlarged, both dentisetae are pectinate; besides dentisetae, biting edge bears a few (about 5–7) large setae (Fig. 24). Pronotum is nearly rectangular, with fore and hind margins nearly straight,
lateral margins slightly convex (Fig. 6). Mesial plate of mesonotum [characteristic for Ephemera/fgl — see Kluge, 2004] nearly reaches apices of fore protopera; in course of transformation to subimaginal, most its hypodermal degenerate and does not give rise to imaginal plumidia (see below). Pronotum and mesonotum, including mesial plate, bear small spatulate setae of variable size and proportions (Fig. 7); fore protopera lack such setae, bear long hair-like setae. Fore legs are the shortest, hind legs the longest. Femora bear large, stout, spatulate, brown setae of variable length and width, arranged as the following: On fore femur, instead of a regular rows characteristic for Pantricorynth [Kluge, 2004], there is a transverse oblique stripe of irregularly situated, long, spathulate setae of variable size; longitudinal row on distal part of outer margin is either absent, or consists of a few irregularly situated, spathulate setae (Fig. 16). On middle and hind legs there are 3 longitudinal stripes of irregularly situated, spathulate setae: (1) a longitudinal stripe of small setae on anterior side near inner margin; (2) a longitudinal stripe of longer setae along middle of anterior side and (3) a longitudinal stripe of long setae on outer margin; at the middle of outer margin this stripe forms a short transverse row, serially homologous to the transverse row on fore femur (Fig. 17). Tibiae bear irregularly situated, pointed, stout, spine-like setae on inner margin and have spathulate setae arranged as the following: on fore tibia one row of small spatulate setae on anterior side (Fig. 16), on middle and hind tibia 2 rows of larger spathulate setae (Fig. 17). Each tarsus bears a row of stout, pointed, spine-like setae on inner margin, lacks spathulate setae. Each claw has 5–7 denticles on inner side and 1–3 subapical denticles on anterior side (Fig. 15). Abdominal segments II–VI lack posterolateral spines. Segments VII–IX have posterolateral spines, which become longer from segment VII to segment IX. Posterior margins of abdominal terga are smooth or with fine serration, long, thin setae. Sternum IX of male is similar to that of female, protogenital stylus is not expressed; protopenis as in Fig. 26. Abdominal segments I–V are adjacent to posterior margins of terga; bases of tergalii VI are small and separated from posterior margin of tergum. Tergalii II are operculate, unable for respiratory vibrations; their ventral bifurcate lobes are well-developed and have numerous processes. Tergalii III–V also with well-developed ventral bifurcate lobes with numerous processes. Tergalii VI are short, without ventral lobes. Tergalii VII are absent. Caudalii have each segment colorless in anterior half, with indistinct unpaired grayish macula near hind margin; sternum VIII–IX in most part are grayish (Fig. 19). On sternum IX, lines of proximal attachment of sternostyliger muscles are widely separated, semicircular; sternostyliger muscles are paired, with proximal bases widely separated (Fig. 25). Styliger has a triangular, median projection. Penis has anulate lateral margins. Styliger, penis and gonostylus are light. Caudalii have each segment colorless in proximal half and blackish in distal half.

Imago, female. Head and thorax are similar to that of male. Legs are darker, dirty ochre-brownish, each femur has a blackish band near apex. Fore wing is slightly tinged with brownish, especially in costal and subcostal fields. Vestige of hind wing is either absent, or has a form of a very small (about 0.1 mm length) papilla (Fig. 5). Abdomen is ochre; blackish maculae on terga I–II and VII–VIII are as in male; tergum IX has blackish maculae a little smaller than on tergum VII; each sternum has a pair of longitudinal, lateral stripes. Secondary ovipositor consists of a short papilla on posterior margin of sternum VII and a longer narrow process arising in posterior direction from anterior margin of sternum VIII (Figs 21–22); cuticle of these formations is colorless, hypodermal blackish. Subanal plate of sternum IX is long and narrowly-triangular.

Egg. Described by Kopelke [1980]. Shape is unusual, long, narrowing toward pole opposite to the cap (Fig. 23). Cap has composite structure, with two layers and additional small cap on apex. Chorion is smooth. The pole opposite to the cap, bears an unusual tube, which terminates by opening surrounded by denticles; this tube bears adhesive threads.

Dimensions. Fore wing length 6–7 mm.

Comparison. The new subspecies differs by the following characters of female: hind wing of female is always absent, and fore wing of female imago is slightly tinged by brownish. According to the original description of E. nigra, its female has “hind wings as in male; sometimes reduced or absent” and “fore wing hyaline except at wing root”. According to the description of E. strenuata, the single known female specimen has “les ailes II ont un calus costal allongé en éperon triangulaire”. According to the description of E. dissimillimus, its “Hinterflügel zu einem winzigen, 0,2 mm langen Stummel reduziert” and “Vorderflügel hyalin”.

Ephemerithys kiboensis Gillies, 1960


Imago, male. Described by Gillies [1960]. Claws of fore leg are ephemeropteroid (in contrast to the original description — see discussion above). Genitals as in Fig. 27.
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**Ephemerythus** sp.T


**Larva.** CUTICULAR COLORATION: Whole cuticle is light-brownish, nearly unicolor or with indistinct diffusive maculae only.

HYPODERMAL COLORATION: All legs are gray in distal part, non-pigmented in proximal part. Hypoderm of fore

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Figs 24-27. 24-26 – *Ephemerythus niger ugandanus* subsp.n., 27 – *E. kiboensis*; 24 – apex of maxilla, ventral view (dentisetae shown by dots; most part of apical setae not shown, area occupied by them shown by dotted line); 25 – genitals of male imago, holotype, ventral view (musculature of left half shown by interrupted lines); 26 – abdominal sternum XI of male larva, dorsal view (hypodermal rudiments of future subimaginal penis and gonostyli shown by interrupted lines). 27 – genitals of male imago, ventral view.

Рис. 24-27. 24-26 – *Ephemerythus niger ugandanus* subsp.n.; 27 – *E. kiboensis*; 24 – вершина максиллы, вентрально (дентисеты показаны пунктировкой; большая часть дистальных щетинок не показана, занимаемая ими область показана точечной линией); 25 – гениталии самца имаго, гениталии вентрально (мускулатура левой половины показана прерывистыми линиями); 26 – X1 стернит брюшка личинки самца, дорсально (гиподермальные зачатки будущего субимагинального пениса и гоностилией показаны прерывистыми линиями); 27 – гениталии самца имаго, вентрально.
wing membrane is uniformly dark brown, veins light. Hypoderm of hind wing membrane is brown, darker in proximal half.

SHAPE AND SETATION: Maxilla has biting edge not shortened, proximal dentiseta is not enlarged, ventral row of setae is not shortened [as in Demoulin, 1965: Fig. 11f]. Femora are wide, with stout spatulate setae arranged typically for Pantricorythidae: on fore femur a regular transverse row near middle is continued distally on outer and inner margins; on middle and hind legs rows run along whole outer and inner margins. Hind proptera are developed, their shape is similar to male hind proptera of *E. niger* (Fig. 3). Abdominal segments I–V lack posterolateral spines, segments VI–IX have posterolateral spines. Bases of tergalii II–IV are adjacent to posterior margins of terga; bases of tergalii V are small and separated from posterior margin of tergum. Tergalii V lack ventral portion; tergalii VI are absent.

**Comparison.** This larva differs from *E. niger* by non-enlarged proximal dentiseta and reduction of hind pairs of tergali. Possibly it is conspecific with larvae described by Demoulin [1965] as "*E. ?kiboensis*". Relation with *E. kiboensis* and *E. pictus* is unknown. Possibly, this larva belongs to the same species which was described and figured by Kimmins [1955] as "nymph of Ephemereellidae (genus uncertain)".

**Ephemerythus** sp.C

**MATERIAL.** Cameroon, Yaoundé, 6.IX.1956, coll. M.T. Gillies: 1 ½ larva.

**Larva.** CUTICULAR COLORATION: Whole cuticle is light-brownish, nearly unicolor or with indistinct diffusive maculae only.

SHAPE AND SETATION: Maxilla has biting edge shortened and directed apically, with proximal dentiseta strongly enlarged and ventral row of setae shortened (similar to Fig. 24). Hind proptera are absent. Abdominal segments I–V lack posterolateral spines; segments VI–IX have posterolateral spines. Bases of tergalii II–IV are adjacent to posterior margins of terga; bases of tergalii V are small and separated from posterior margin of tergum. Tergalii V lack ventral portion; tergalii VI are absent.

**Comparison.** This larva differs from *E. niger* by reduction of hind pairs of tergalii. Its relation with *E. kiboensis* and *E. pictus* is unknown.

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