

CLASSIFICATION AND PHYLOGENY OF THE BAETIDAE (EPHEMEROPTERA) WITH DESCRIPTION OF THE NEW SPECIES FROM THE UPPER CRETACEOUS RESINS OF TAIMYR

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Male and female imagines and subimagines of the extinct Upper Cretaceous species *Palaeocloeon taimyricum* sp. n. are described and placed in the new subfamily Palaeocloeoninae subfam. n. The existent baetid subfamilies are united into the holophyletic group of subfamilies Turbanoculata. Palaeocloeoninae with Turbanoculata form the holophyletic taxon Liberevenata. Liberevenata with Siphlaenigmatidae form the holophyletic taxon Tetramerotarsata. The group of subfamilies Turbanoculata is divided into the subfamily Afrotiptilinae subfam. n. and the subgroup of subfamilies Anteropatellata. Apomorphies and plesiomorphies of all these taxa are discussed, as well as the problems of nomenclature.

INTRODUCTION

Until now, no fossils reliably belonging to Baetidae have been described. The genus *Mesobaetis* BRAUER, REDTENBACHER ET GANGLBAUER, 1889 which is known as larvae from Mesozoic deposits, was initially placed in Baetidae, then erroneously placed in Leptophlebiidae, and now it is regarded as belonging to Siphonuroidea (SINITSHENKOVA, 1985). *Cloeon emmavillensis* RIEK, 1954 is described as larvae from Pliocene of Australia; these fossils can belong either to Baetoidea or to Siphonuroidea.

In the present paper well preserved specimens of Upper Cretaceous Baetidae are described and placed in the new primitive subfamily Palaeocloeoninae. These specimens - inclusions in Taimyrian retinite - were collected by expeditions of the Palaeontological Institute of Russian Academy of Sciences (Moscow). Besides the new species of Baetidae, the mayfly fauna of this retinite contains two species of *Cretonea* (superfamily Siphonuroidea), two species of *Palaeoanthus* (superfamily Ephemeroidea) (KLUGE, 1993) and an undescribed species of the extinct Mesozoic family Hexagenitidae.

REMARKS ON NOMENCLATURE

According to the International Code of Zoological Nomenclature (ICZN), valid names of all taxa which have ranks from subspecies to superfamily, depend only upon the type specimen and the rank. Such a principle of nomenclature would be convenient if the classification was constant, and each combination of type specimen and rank

would belong to a single taxon only. But in the situation when different opinions concerning the classification are present, the unified names of the taxa in some cases can become useless. Different classifications suggested for the same organisms, taxa with quite diverse diagnoses and diversifications can have the same type specimens and the same rank. For example, the name «Baetoidea» (with the type specimen - neotype of *Baetis fuscatus* L. and the rank of superfamily) in different recent papers is accepted as the taxon which includes all Pisciforma + Setisura, as only a part of them, only as Pisciforma, or only as Baetidae s. str. + Siphlaenigma. The name «Baetidae» can be accepted in the narrow sense (without *Siphlaenigma*) or in the wide sense (including *Siphlaenigma*); in the first half of our century this name was used for all Ephemeroptera except Ephemeroidea and Heptageniidae (NEEDHAM *et al.*, 1935). The name «Baetinae» can be used for the mayflies which are more closely related to *Baetis fuscatus* L. than to *Cloeon dipterum* L. (KAZLAUSKAS, 1972; NOVIKOVA & KLUGE, 1987), or to some wider group up to the taxon which is the sister group to *Siphlaenigma* (i.e. the same as «Baetidae» s. str.). In the first half of our century the name «Baetinae» could be used for all Pisciforma together with the primitive representatives of Setisura. The classification will not stop changing, as it is based on phylogeny, and many aspects of phylogeny are still unclear. In order to discuss scientific problems one we must have a name for each scientific concept, thus each proposed taxon (which is characterized by its own diagnosis and diversification and each assumed phylogenetical branch must have the name which would not be mixed with names of other taxa or phylogenetical branches. Even if it is a taxon which can not be generally accepted, or the phylogenetical branch which is assumed by somebody but actually unreal, they must have their own names in order to make criticism possible. In the present paper in the cases when the unified nomenclature is not enough to supply the taxa with their own names, the ununified names are used: Tetramerotarsata, Liberevenata, Turbanoculata, and Anteropatellata. These names are independent of rank, but are attributed to the taxa of certain diversifications. So they do not belong to the family-group taxa names in terms of the ICZN, and rules of the ICZN are not applicable for them, as well as for the names of higher taxa - Ephemeroptera, Anteritorna, Pisciforma. Besides the ununified names, for

each family-group taxon a unified name is used - Baetoidea, Baetidae, and Baetinae - as it is demanded by rules of the ICZN.

PHYLOGENY OF THE BAETIDAE

The suborder Anteritorna KLUGE, 1994 includes the infraorder Pisciforma MCCAFFERTY, 1991 with the

Superfamily Baetoidea or Tetrameroparsata KLUGE, nom. nov.

= Baetoidea: KLUGE *et al.*, 1995

= Baetidae: MCCAFFERTY & EDMUNDS, 1979

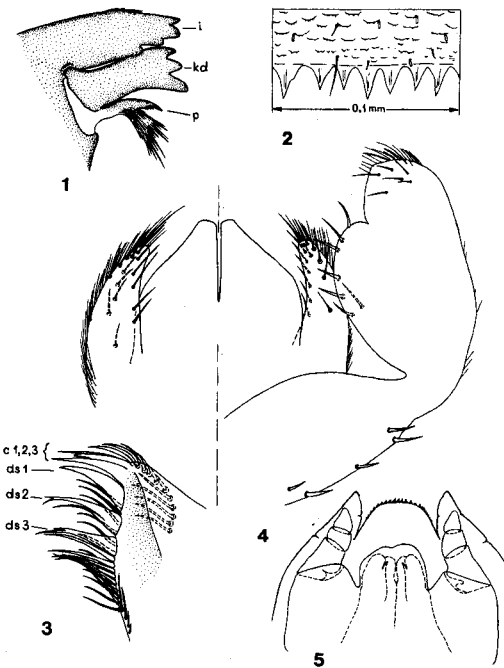
Plesiomorphic characters common for Tetramerotarsata and some other taxa

Winged stages (imago and subimago). (1) Anterior paracoxal suture* (* the names of mayfly

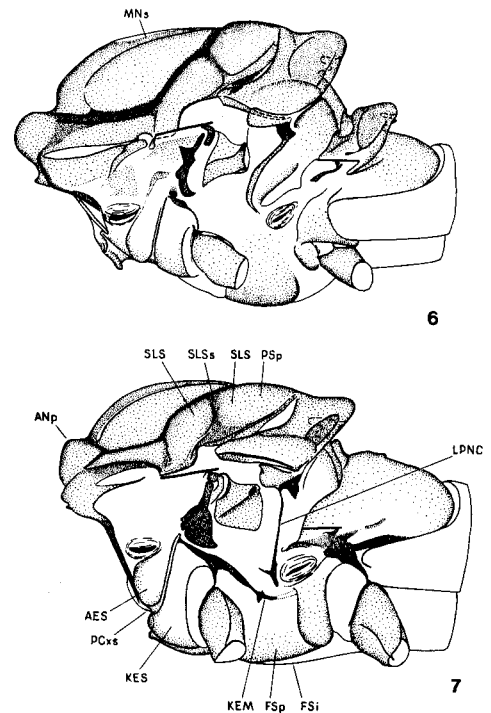
thoracic structures are explained in KLUGE, 1994a) of mesothorax continued on ventral side of episternum (Figs 6, 7). The same character state occurs in majority of other Pisciforma (KLUGE *et al.*, 1995), in the superfamily Oligoneuroidea of the infraorder Setisura (i.e. in Isonychiidae, Coloburiscidae, Oligoneuriidae) and in the suborder Posteritorna.

(2) On all legs, except for the fore legs of male, first tarsal segment fused with tibia (Figs 8, 9, 14). The same character state occurs in majority of Ephemeroptera except for Heptagenioidea.

(3) Claws of all legs dissimilar: posterior one hooked and pointed, anterior one blunt (Figs 8, 9, 11, 14). The same character state occurs in majority of Ephemeroptera; in some groups claws secondarily become similar and hooked (in Siphonuridae s. str., in selected genera of Leptophlebiidae, in selected species of Heptageniidae and others).



Figs 1-5. *Siphlaenigma janae*, mature nymph. 1: apex of left mandible; 2: hind margin of abdominal tergum V; 3: apex of right maxilla; 4: labium (in left half - dorsal view, in right half - ventral view); 5: genitalia of male subimago inside larval cuticle. c1, 2, 3 - three maxillary canines, ds1, ds2, ds3 - dentisetae, i - incisor, kd - kinetodont, p - prostheca.



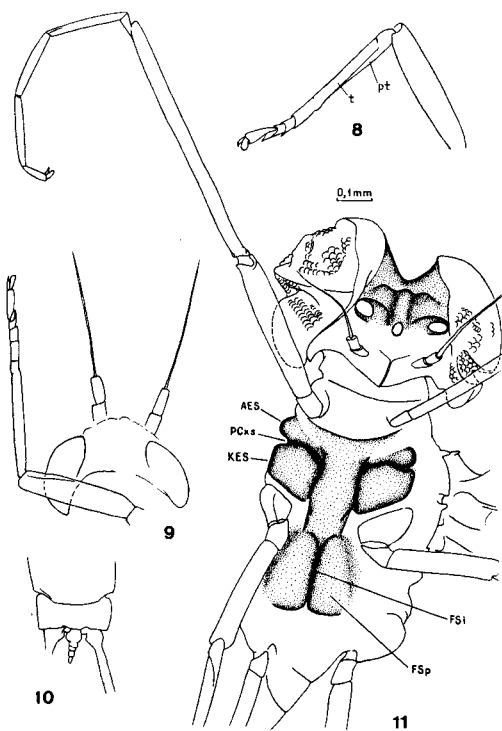
Figs 6, 7. Subimaginal pterothorax dissected from mature male nymph, left view. 6: *Siphlaenigma janae*; 7: *Afroptilum sudafricanum*. AES - anepisternum, ANp - anteronotal protuberance, FSi - furcasternal median impression, FSp - furcasternal protuberance, KEM - katepimeron, KES - katepisternum, LPNC - lateropostnotal crest, MNs - mesonotal suture, PCxs - paracoxal suture, PSp - posterior scutal protuberance, SLS - sublateroscutum, SLSs - sublateroscutal suture.

Larvae. (4) Maxillae with three dentisetae (i.e. specialized thickened setae of the inner-dorsal row) and three apical canines (immobile apical projections). The same character state occurs in the majority of other Pisciforma (KLUGE *et al.*, 1995); in *Posteritorna* the number of dentisetae is more than three, in the infraorders *Setisura* and *Furcatergalia* - usually two.

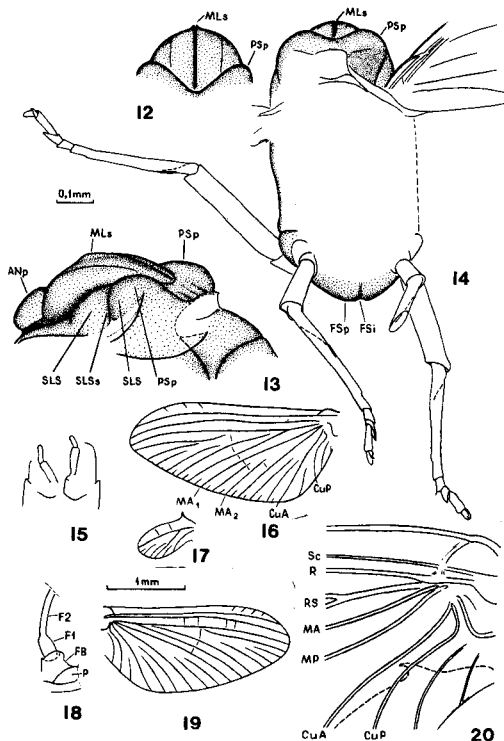
(5) Caudal filaments with primary swimming setae (a row of setae on the inner side of each cercus and a row of setae on each lateral side of paracercus). The same in the order *Pisciforma* (that gives the reason of its name), the same character state occurs in the Palaeozoic sub-order *Permoplectoptera* and in the primitive representatives of *Posteritorna*, *Setisura* and *Furcatergalia*.

Apomorphies of Tetramerotarsata

Winged stages (imago and subimago). (1) mesonotal suture* absent (Figs 6, 7, 13), only in subimago of *Siphlaenigmatidae* rudimentary mesonotal suture represented as a paired longitudinal line - border between smooth light median area and covered with microtrichiae pigmented area of mesoscutum (Fig. 6); in other *Tetramerotarsata* mesoscutum of subimago entirely pigmented and covered with microtrichiae. In the majority of other *Ephemeroptera* the mesonotal suture is distinct in both, the



Figs 8-11. *Palaeocloeon taimyricum*, gen. nov. and sp. nov. 8: male subimago, paratype No. 7, right middle leg; 9, 10: female, paratype No. 3; 9: head and fore leg; 10: apex of abdomen, dorsal view; 11: male imago, holotype, ventral view. AES - anepisternum, FSi - furcasternal median impression, FSp - furcasternal protuberance, KES - katepisternum, PCxs - paracoxal suture, pt - patella, t - tibia.



Figs 12-20. *Palaeocloeon taimyricum*, gen. nov. and sp. nov. 12-14: male imago, holotype; 12: mesonotum, hind view; 13: mesonotum, left-hind view; 14: mesothorax, middle and hind legs, hind view; 15-17: male subimago, paratype No. 2; 15: genitalia; 16-17: fore and hind wings in the same scale; 18-20: male imago, paratype No. 1; 18: fragment of genitalia; 19: fore wing; 20: base of fore wing and costal process of hind wing. ANp - anteronotal protuberance, F1, F2 - segment 1 and 2 of forceps, FB - forceps base of styliger, FSi - furcasternal median impression, Sp - furcasternal protuberance, MLs - median longitudinal suture, P - penis, PSp - posterior scutal protuberance, SLS - sublateroscutum, SLSs - sublateroscutal suture.

imago and subimago, more or less transverse (KLUGE, 1994a; KLUGE *et al.*, 1995); in Leptophlebiidae and some of Ephemeroidea it becomes longitudinal and indistinct, in some Leptophlebiidae it can be similar to that of Tetramerotarsata (KLUGE, 1993: Fig. 5 1, m). So this character of Tetramerotarsata is apomorphic, but not unique.

(2) Mesonotum with a sublateroscutal suture (Figs 6, 7, 13 SLSs) - transverse suture running across sublateroscutum (SLS). This suture is absent in other mayflies. It is similar to the transverse interscutal suture (TIs) of Caenidae and Tricorythidae (PROVONSHA, 1990; KLUGE, 1992c; 1994), but differs in the following characters: TIs separates the posterior scutal protuberance (PSP) which contains the base of the scuto-lateropostnotal muscle (S.LPNm) and from the sublateroscutum which contains bases of the scuto-coxal muscles (S.CmA and S.CmP). The sublateroscutal suture of Tetramerotarsata runs across the sublateroscutum and separates the base of S.CmA from the base of S.CmP, while the posterior scutal protuberance is not separated from the posterior part of the sublateroscutum.

(3) Anterior paracoxal suture* of mesothorax turned anterior, so anepisternum smaller than katepisternum (Figs 6, 7, 11). In other taxa of mayflies the anepisternum can be subequal, or smaller, or larger than the katepisternum.

(4) On fore wing CuP is curved backward in its base (Figs 16, 19, 20) or have lost its connection with CuA (in the group Turbanoculata). This character is apomorphic, but not unique: besides Tetramerotarsata the same takes place in Leptophlebiidae (KLUGE, 1993).

(5) Cubital field of fore wing with one or several intercalaries (Figs 16, 19). In the primitive case (in the majority of the Siphonuroidea) there is a series of veins running from CuA to the hind margin of the wing; these veins are turned into intercalaries independently in various mayfly taxa, including Tetramerotarsata.

(6) At least the tarsi of middle and hind legs of male and all tarsi of female 4-segmented (including first segment fused with tibia) (Figs 8, 9, 14). The name Tetramerotarsata is connected with this character. All Tetramerotarsata have well developed functional legs. In all other mayflies which have functional legs, tarsi are 5-segmented (including the

first segment which can be rudimentary). Only in some mayflies which have rudimentary functionless legs (Oligoneuriidae, some Ephemeroidea), the tarsi have less than five segments.

Larvae. (7) Paraglossa with dorsal and ventral longitudinal rows of setae (Fig. 4). In the majority of Turbanoculata the ventral row is reduced (NOVIKOVA & KLUGE, 1987).

Composition. The superfamily Tetramerotarsata includes two families: Siphlaenigmatidae and Liberevenata. The following branching of the phylogenetic tree is assumed:

- 1. Tetramerotarsata
 - 1.1. Siphlaenigmatidae
 - 1.2. Liberevenata
 - 1.2.1. Palaeocloeoninae
 - 1.2.2. Turbanoculata
 - 1.2.2.1. Afroptilinae
 - 1.2.2.2. Anteropatellata
 - 1.2.2.2.1. Cloeoninae
 - 1.2.2.2.2. Callibaetinae
 - 1.2.2.2.3. Baetinae.

Family Siphlaenigmatidae PENNIKET, 1962

= family Siphlaenigmatidae PENNIKET, 1962;

= subfamily Siphlaenigmatinae: MCCAFFERTY & EDMUNDS, 1979.

Apomorphies of Siphlaenigmatidae

Winged stages (imago and subimago). Eyes of male not separated into dorsal and ventral portions (PENNIKET, 1962: Fig. 2) (as in Palaeocloeoninae). Furcasternal protuberances* of mesothorax contiguous (as in Palaeocloeoninae - see below). In fore wing MA bifurcate to MA1 and MA2 which at the base connected; no marginal intercalaries (PENNIKET, 1962: Fig. 1) (in contrast to Liberevenata). Traces of tibio-patellar suture present on middle and hind legs, but absent on fore legs of both sexes (as in Palaeocloeoninae and Afroptilinae - see below). Fore tarsi of male with 5 long segments, in *Siphlaenigma janae* first segment longest (PENNIKET, 1962: Fig. 9) (in contrast to Liberevenata). Posterior projection of sternum IX (i.e. styliger of male and postgenital plate of female) well developed (Fig. 5; PENNIKET, 1962: Figs 4, 13) (in contrast to Liberevenata). Forceps with two apical segments; penis well developed (Fig. 5; PENNIKET, 1962: Figs 3, 4) (in contrast to Liberevenata). Paracercus long

(PENNIKET, 1962: Fig. 13) (in contrast to *Liberevenata*).

Larvae. Prothecae of both mandibles with short entire proximal part and tuft of bristle-like projections (Fig. 1) (as in majority of Ephemeroptera, but in contrast to *Liberevenata*). Glossae wider than paraglossae, lack setae (Fig. 4) (autapomorphy). Tibio-patellar suture present on middle and hind legs, but absent on fore legs (as in imago; as in Afroptilinae - see below). Forceps buds of mature male larva not shortened (Fig. 5).

Composition. The family Siphlaenigmatidae includes the single genus *Siphlaenigma* PENNIKET, 1962 with the single New Zealand species *S. janae* PENNIKET, 1962.

Material examined. Mature male and female larvae just before molting to subimago, with completely developed subimaginal structures (without labels) (Figs 1-6). 8 larvae, New Zealand, South Isl., Maori Gully Cr., 17.III.1993, A. Staniczek.

Family Baetidae, or Liberevenata KLUGE, nom. nov.

= family Baetidae: PENNIKET, 1962;

= subfamily Baetinae: MCCAFFERTY & EDMUNDS, 1979

Apomorphies in winged stages (imago and subimago)

(1) In fore wing MA2 free, not connected with MA (Figs 16, 19). This is a unique character and not found in any other Ephemeroptera; only in Prosopistomatidae MA is unforked. In all other Ephemeroptera MA furcates to MA1 and MA2, which are connected at the base. The name *Liberevenata* arises from this character and the next one.

(2) Fore wing with free marginal intercalaries (Figs 16, 19). The same character independently appears in some other taxa (e.g. family Ephemerellidae).

(3) First segment of tarsus of male fore leg rudimentary (Fig. 11). A similar character independently appears in the infraorder Furcatergalia, where the first tarsal segment is shortened on all legs of both sexes (KLUGE, 1983; 1984).

(4) Posterior projection of sternum IX (i.e. styliger of male and postgenital plate of female) reduced; in male only lateral portions of styliger, which bear the forceps muscles, well developed, forming a pair of forceps bases

(Fig. 18). The same character independently appears in some other mayfly taxa.

(5) Forceps with one apical segment (Fig. 15). The same reduction of one or both apical segments independently takes place in some other mayfly taxa (e.g. superfamily Ephemerelloidea).

(6) Penis strongly reduced (Fig. 18). This is the unique character of *Liberevenata*.

(7) Paracercus rudimentary (Fig. 10). The same character state occurs in many other mayfly taxa: the majority of Posteritorna, Pisciforma, Setisura and in some of the Furcatergalia.

Composition. *Liberevenata* includes the subfamily Palaeocloeoninae subfam. nov. and the group of subfamilies Turbanoculata.

Subfamily Palaeocloeoninae subfam. nov.

Type genus: Palaeocloeon gen. nov.

Characteristics

Winged stages (imago and subimago). Eyes of male not separated to dorsal and ventral portions (Fig. 11) (same character state in Siphlaenigmatidae). Median longitudinal suture of mesonotum prominent in its anterior part (Fig. 12) (same character state in Afroptilinae and some Cloeoninae, while in other Ephemeroptera this suture is concave). Furcasternal protuberances of mesothorax contiguous (Figs 11, 14) (same character state in Siphlaenigmatidae). On fore wing in each space only one marginal intercalary can be present (Fig. 16) (as in the Afroptilinae and Cloeoninae, but not in Baetinae). Traces of tibio-patellar suture present on middle and hind legs (Figs 8, 14), but absent on fore legs of both sexes (Figs 9, 11) (as in the Siphlaenigmatidae and Afroptilinae).

Larvae. Unknown. As in the winged stages the tibio-patellar suture is visible on middle and hind legs, but absent on fore legs, it may be concluded that larvae also have this suture present on middle and hind legs, but absent on fore legs (as in Siphlaenigmatidae and Afroptilinae - see below). As in subimago second segments of forceps divergent (Fig. 15), it may be concluded that the position of the subimaginal forceps buds inside mature larva is the same as in Cloeoninae (Fig. 31).

Composition. The subfamily Palaeocloeoninae includes the single extinct genus *Palaeocloeon* gen. nov.

Genus Palaeocloeon KLUGE, gen. nov.

Type species: Palaeocloeon taimyricum sp. nov.

Diagnosis. The same as for the subfamily Palaeocloeoninae.

Composition. Monotypic.

Palaeocloeon taimyricum KLUGE, sp. nov.
(Figs 8-20)

Male imago. Head dark, deeply concave between compound eyes. Mesothorax dark, its structure as in Figs 11-14, structure of scutellum and metanotum unknown. Fore wings wide, with posterior margin longer and tornus more distinct than in majority of recent Baetidae. Pterostigma with few oblique cross veins. Hind wing relatively large, with straight (not hooked) acute costal projection. Abdomen colourless. Legs colourless. Forceps with long slender segments.

Female imago. Head wide, eyes widely separated.

Dimensions. One of the smallest representatives of Baetidae, body length little more than 2 mm.

Material. Deposited in the Palaeontological Institute of Russian Acad. Sci. in Moscow. Taimyr, Ust'-Enisey distr., right bank of river Nizhnaya Agapa, 40 km lower its source, lake Lagannakh. Inclusions in retinite. Upper Cretaceous, Cenomanian, Dolgan F. Holotype: ♂ imago with well preserved thorax, head and legs, but without abdomen, its wings are poorly visible inside the stone (Figs 11-14). Paratype No. 1: ♂ imago with preserved ventral part of thorax, legs, left wings, fragment of abdomen (Fig. 18-20) in the same stone as holotype, the impress of fore wing on the slide No. I). Paratype No. 2: ♂ subimago - fragment of thorax, left fore and hind wings, abdomen with genitals (Figs. 15-17) (in two pieces of stone on slide No. II). Paratype No. 3: ♀ (imago or subimago?) - apex of abdomen (Fig. 10) (in the same two pieces of stone as the paratype No. 2 on the slide No. II). Paratypes No. 4 & No. 5 in one stone: No. 4: ♂ imago - head and fore legs; No. 5: ♀ (imago or subimago?) - apex of abdomen. Paratype No.: ♂ (imago or subimago?) - ventral part of head, fore and middle legs (Fig. 9); in the same stone fragments of other specimens. Paratypes No. 7 & No. 8 in one stone: No. 7: ♂ subimago - pterothorax, abdomen, wings, legs (Fig. 8); No. 8: ♂ imago - head, thoracic sterna, fragments of legs. Other paratypes from the same locality: wings and wing fragments of several specimens in the stones with paratype No. 6 and on slides III, IV. Taimyr, Khatanga distr., right bank of river Maimecha, Jantardakh. Inclusions in retinite. Upper Cretaceous, Cognak-Santon, Kheta F. Paratypes: Fragments of 2 ♂ imagoes.

Group of subfamilies Turbanocolata KLUGE, gr. nov.

Apomorphies in winged stages (imago and subimago)

(1) Eyes of male separated into dorsal and ventral portions, dorsal portion (turban eye) highly specialised, with stem lacking facets (only pigment cells of rudimentary ommatidia developed on stem). Besides Turbanocolata turban eyes of similar structure are present only in some Leptophlebiidae.

(2) Furcasternal protuberances widely separated, metathoracic nerve ganglion situated between them (Fig. 7); if furcasternal protuberances contiguous, then only at one point and metathoracic nerve ganglion situated anterior to this point. In the Ephemeroptera which have a primitive structure of the mesothoracic furcasternum - Siphlaenigmatidae, Palaeocloeoninae (see above), North Hemisphere Siphonuroidea (see KLUGE *et al.*, 1995) and some other taxa - the furcasternal protuberances, which contain the base of subalar-sternal muscles* are contiguous over all their length and metathoracic nerve ganglion is situated behind them, in the metathorax or on the boundary between meso- and the metathorax. The moving of this ganglion anteriorly, connected with separation of the bases of the subalar-sternal muscles and furcasternal protuberances is an apomorphy of Turbanocolata. But this apomorphy is not unique, because the same process takes place independently in many other mayfly taxa.

(3) In subimago (but not in imago) sclerotization of lateropostnotal crest* long and straight; the sclerotization of the mesothoracic katepimeron long, narrow, distinct, and turns back up to the end of sclerotization of lateropostnotal crest (Fig. 7). This structure is unique and not found in other Ephemeroptera. As the pattern of the subimaginal pleural sclerotization in *Palaeocloeon* is unknown, it is not clear if this character is an autapomorphy of Turbanocolata or autapomorphy of Liberevenata.

Composition. The group of subfamilies Turbanocolata includes subfamily Afroptilinae subfam. nov. and the subgroup of subfamilies Anteropatellata subgr. nov.

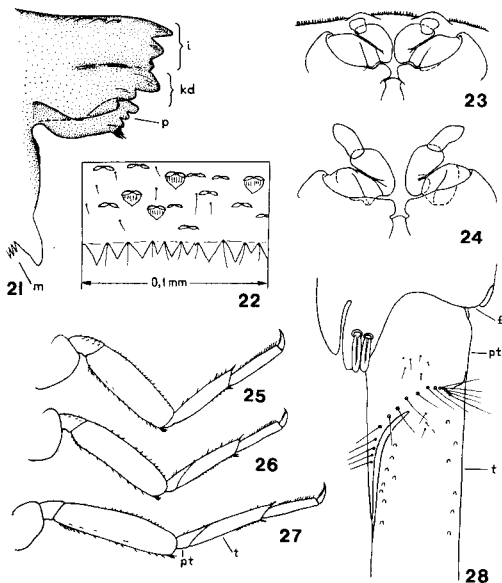
Subfamily Afroptilinae KLUGE, subfam. nov.

Type genus: *Afroptilum* GILLIES, 1990

Apomorphies

Winged stages (imago and subimago). In fore wing in each space only one marginal intercalary can be present (the same in Palaeocloeoninae and Cloeoninae, but not in Baetinae). Traces of tibio-patellar suture present on middle and hind legs, but absent on fore legs of both sexes (same character state in Siphlaenigmatidae and Palaeocloeoninae). Other characters typical for Turbanoculata.

Larvae. Traces of tibio-patellar suture present on middle and hind legs, but absent on fore legs (Figs 25-28). Submarginal forceps buds under cuticle of mature larva (which are examined only for *Afroptilum sudafricanum*) are curved in such a manner, that the first segment is directed medially, second segment - laterally (as in Cloeoninae) and third segment - laterally (in contrast to Cloeoninae).



Figs 21-28. Afroptilinae subfam. nov, mature male nymphs. 21-27: *Afroptilum sudafricanum*; 21: apex of left mandible; 22: hind margin of abdominal tergum V; 23: genitals of male subimago under nymphal cuticle; 24: the same when molting begins; 25-27: right fore, middle and hind legs; 28: *Afroptilum* tarsale, proximal part of patello-tibia of middle left leg, view from outer side. i - incisor, kd - kinetodont, m - mola, p - prostheca, pt - patella, t - tibia.

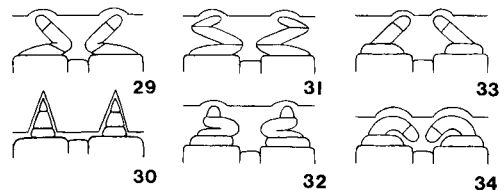
Composition. The subfamily Afroptilinae includes the genus *Afroptilum* GILLIES, 1990 (type species *Centroptilum sudafricanum* LESTAGE, 1924) and related afrotrropical genera.

Material examined. *Afroptilum sudafricanum* (LESTAGE, 1924) - 4 mature ♂ larvae, Kenya, Kitabe, Nairobi distr., 14.X.1988, N. Pacin. *Afroptilum tarsale* Gillies, 1990 - 1 ♂ subimago with larval exuvia, Tanzania, Amani, Dodwe st., C. Goom, 19.II.1991, M.T. Gillies.

Subgroup of subfamilies Anteropatellata KLUGE, subgr. nov.

Apomorphies

Traces of tibio-patellar suture present on all legs of larva, subimago and imago of both sexes. The plesiomorphic state for Ephemeroptera is the absence of these traces on fore legs and their presence on middle and hind legs (as in Siphlaenigmatidae, Palaeocloeoninae, Afroptilinae and the majority of mayflies of all families). In some Ephemeroptera traces of tibio-patellar suture disappears also on the middle legs or on all legs (KLUGE, 1994b). Only in two mayfly taxa - the subgenus *Rhithrogena* (in the family Heptageniidae) and the subgroup of subfamilies Anteropatellata - traces of this suture are present on fore legs. The appearance of this suture on fore legs can be explained only as secondary restoration, which takes place independently in two taxa. Among the examined species only one species - *Cloeon (Centroptilum) kazlauskasi* (KLUGE, 1983) does not agree in its structure with the classification suggested. This species has all the characters of the genus *Cloeon* s. l. and the subgenus *Centroptilum* s. str. (see KLUGE & NOVIKOVA, 1992), but its traces of the tibio-patellar suture are the same as in Afroptilinae.



Figs 29-34. Position of submarginal forceps buds under cuticle of mature nymph (schematised). 29: type of *Afroptilum*; 30: type of *Callibaetis*; 31: type of *Cloeon*; 32: type of *Nigrobaetis*; 33: type of *Baetis*; 34: type of *Labiobaetis*.

Composition. The subgroup Anteropatellata includes the majority of Baetidae and is distributed all over the world. Classification of Anteropatellata is not clear now. The majority of Holarctic species fall into three subfamilies: Baetinae sensu KAZLAUSKAS, 1972, Cloeoninae KAZLAUSKAS, 1972 and Callibaetinae RIEK, 1973. But in tropical regions many representatives of the subfamilies Baetinae and Cloeoninae are not distinctly determined; probably for some tropical genera new subfamilies will be erected. Previously it was difficult to discuss the phylogeny and systematics of Baetidae, because the polarities of many characters were unknown. Now, in connection with the description of the primitive subfamilies - Palaeocloeoninae and Afroptilinae subfam. n. - it becomes possible to discuss polarity of some important characters.

Polarity of some characters in Anteropatellata

(1) Intercalaries of fore wing. The subfamily Cloeoninae is characterized by single intercalaries in each space, the subfamily Baetinae - by double intercalaries and in Callibaetinae intercalaries can be single or double. Single intercalaries is plesiomorphy, as it is a character of Palaeocloeoninae and Afroptilinae.

(2) Structure of scales on abdominal terga of larva. In some groups of Baetinae (*Cloeodes*, *Nigrobaetis*, *Fallceon*, *Caribaetis*, *Americabaetis*, *Labiobaetis*, *Acerpenna* and some others) each scale base has two covers on its corners. This state is plesiomorphic, as the same structure is found in the representative of Afroptilinae (Fig. 22).

(3) Position of the subimaginal forceps buds under cuticle of mature nymph. Several different positional types are found in Anteropatellata: (a) type of *Callibaetis* - Fig. 30 (KLUGE, 1991: Fig. 1.14); (b) type of *Cloeon* - Fig. 31 (found in all Cloeoninae - NOVIKOVA & KLUGE, 1987: Fig. 10; KLUGE & NOVIKOVA, 1992: Figs 4, 5); (c) type of *Nigrobaetis* - Fig. 32 (found in *Nigrobaetis*, *Fallceon*, *Caribaetis*, *Americabaetis*, *Cloeodes* - NOVIKOVA & KLUGE, 1987: Figs 9, 11; KLUGE, 1991: Fig. 1.17; 1992a: Figs 2.10, 11; 3.1; 1992b: Figs 1.18; 3.8; 4.14; NOVIKOVA & KLUGE, 1994: Figs 1-22); (d) type of *Labiobaetis* - Fig. 34 (found in *Labiobaetis* and *Acerpenna* - NOVIKOVA & KLUGE, 1994: Figs 23-35); (e) type

of *Baetis* - Fig. 33 (found in *Baetis* s. str., *Acentrella*, *Baetiella* - NOVIKOVA & KLUGE, 1987: Fig. 12; 1994: Figs 26, 27). The type of *Callibaetis* looks like the most primitive among the named types, because it is similar to the position of the forceps buds in *Siphlaenigma* (Fig. 5), *Siphonuroidea* and the majority of other Ephemeroptera. But the type of *Cloeon* can also be plesiomorphic, because it is similar to the type of *Afroptilum* (Figs 29, 23, 24).

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