

RELATIONSHIPS OF THE GENERA *ACANTHAMETROPUS*, *ANALETTRIS*,
AND *SIPHLURISCUS*, AND RE-EVALUATION OF THEIR HIGHER
CLASSIFICATION (EPHEMEROPTERA: PISCIFORMA)

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ABSTRACT

The historical higher classification of the genera *Acanthametropus* Tshernova, *Analetris* Edmunds, and *Siphuriscus* Ulmer is reviewed. The first comprehensive generic description of *Siphuriscus* is given, and first figures of wings are provided. A cladistic analysis of adult and larval characters of *Acanthametropus* and *Analetris*, and adult characters of *Siphuriscus* reveal a close relationship between the former two genera, which represent a well-defined clade based on five identified synapomorphies; however, *Siphuriscus*, which has been classified with them in the past, does not share any apomorphies with them but instead shares apomorphies with the genera of Siphonuridae *sensu stricto*. *Acanthametropus* and *Analetris* are recombined in the family Acanthametropodidae, suppressing Analetrididae; and *Siphuriscus* is reassigned to the family Siphonuridae *sensu stricto*, although taxon rank for both of these clades is still tentative and awaits comparative cladistic analysis of the entire suborder Pisciforma. The relationship to each other of these clades also remains in doubt. *Stachelbergisca* Tshernova, a fossil genus formerly classified with the three extant genera apparently does not share any of the 11 apomorphies used in this study, and is placed as family *incertae* within the Pisciforma.

The relationships and classification of the pisciform mayflies *Acanthametropus pecatonica* (Burks) from North America, *Acanthametropus nikolskyi* Tshernova from eastern Russia, *Analetris eximia* Edmunds from western North America, and *Siphuriscus chinensis* Ulmer from China have been tentative in the past. We have restudied all known stages of each of these species and are here able to offer a first cladistic analysis of the represented genera within the framework of other pisciform mayflies.

Ulmer (1920) appropriately placed his *Siphuriscus* genus, which was and still is based on alate stages only, in the family Siphonuridae *sensu lato*. Little could be ascertained with respect to its relationships within Siphonuridae at that time.

Tshernova (1948) described *Acanthametropus* from larvae from the Amur Basin and placed it in the family Ametropodidae. Burks (1953) independently discovered larvae of *Acanthametropus* in Illinois, named them *Metreturus* and also believed this taxon was related to other psammophilous mayflies, such as *Ametropus* Albarda. Edmunds and Traver (1954) removed *Metreturus* to Siphonuridae *sensu lato*, and Edmunds and Allen (1957) synonymized

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Metreturus with *Acanthametropus*. Edmunds *et al.* (1963) created a separate subfamily Acanthametropodinae for the genus. Tshernova *et al.* (1986) showed that a previous adult description of *Isonychia polita* Bajkova (1970) was actually of the adult of *Acanthametropus*. We have confirmed this association. McCafferty (1991a) compared larvae in the Eastern and Western Hemispheres and confirmed that there were two distinct species of *Acanthametropus*.

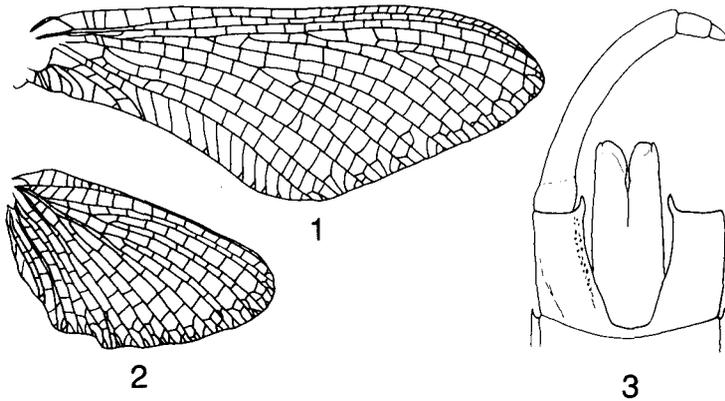
Edmunds in Edmunds and Koss (1972) described *Analetris* based on larvae and placed it in the subfamily Acanthametropodinae. Demoulin (1974) created a separate subfamily Analetridinae for *Analetris*. Lehmkuhl (1976) provided the first adult description of the genus.

Edmunds and Koss (1972) placed *Acanthametropus*, *Analetris*, *Siphuriscus*, and the fossil genus *Stackelbergisca* Tshernova in the subfamily Acanthametropodinae. Demoulin (1974), while recognizing *Acanthametropus* and *Analetris* in separate subfamilies (erecting the subfamily Analetridinae), could not place *Siphuriscus* and *Stackelbergisca* to any subfamily with any certainty. Edmunds *et al.* (1976) restated the broad concept of Acanthametropodinae, and suggested a strong possibility that *Acanthametropus* could prove to represent the larval stage of *Siphuriscus*. This is definitely not the case based on our examination and comparison of *Siphuriscus* adults (see below).

Families of pisciform mayflies have become more restricted in recent years (see e.g. Campbell 1988, McCafferty 1991c), basically recognizing previous subfamilies of Siphonuridae *sensu lato* at the family level. Much of this is related to the hypothesis of McCafferty and Edmunds (1979) that Siphonuridae *sensu lato* is, to a large extent, polyphyletic and that a number of lineages within it share apomorphies with other more derived lineages of Ephemeroptera [although some extreme splitting of families can be traced to Riek (1973)]. This hypothesis has since been corroborated cladistically for certain of these previous subfamilies. For example, Coloburiscidae and Isonychiidae (previous subfamilies of Siphonuridae *sensu lato*) were shown by McCafferty (1991b) to be in sequential ancestral positions of a major lineage including the Oligoneuriidae and Heptageniidae, and Oniscigastridae (another previous subfamily of Siphonuridae *sensu lato*) appears to be at the base of the suborder Rectracheata (see Landa and Soldán 1985, McCafferty 1991b). Edmunds (see e.g. Edmunds 1973) has long realized the close relationship of the Siphlaenigmatidae (another previous subfamily of Siphonuridae *sensu lato*) with the family Baetidae.

McCafferty (1991c), as part of this move to recognize all of the separate lineages represented by Siphonuridae *sensu lato*, provisionally recognized families Acanthametropodidae and Analetrididae among several others in the Pisciforma. This particular classification was based on presumed rather than demonstrated cladistic data. We have now discovered data, however, that allow us to resolve cladistically the relationships among the genera *Acanthametropus*, *Analetris*, and *Siphuriscus*. We are publishing this data and analysis at this time at the prompting of co-workers, such as R. D. Waltz, who are preparing keys and synopses of higher taxa of Ephemeroptera and need to know, for example, if the North American genera *Acanthametropus* and *Analetris* will fall to the same or separate families.

The only existing description of *Siphuriscus* was the original by Ulmer (1920). Unfortunately, it did not include characters that we now know are important for comparative generic and cladistic purposes. The concurrent description of *S. chinensis* Ulmer, the only species known in the genus, was also incomplete. In addition, very important wing venation characteristics were not figured by Ulmer. Therefore we acquired the original, and, to our knowledge, the only material of *Siphuriscus* from the Berlin Museum and give a description of *Siphuriscus* based on characters of use in generic level



Figures 1-3. *Siphuriscus chinensis* male adult type specimen. 1. Forewing. 2. Hindwing. 3. Genitalia, ventral.

delineation. This is followed by a cladistic analysis of the three genera. We conclude with a short discussion of the classificatory implications of our analysis.

Siphuriscus Ulmer
Siphuriscus chinensis Ulmer, 1920

Siphuriscus chinensis Ulmer, 1920:62.

Syntypes, China, Tsayin San (Tsayin Mountains), S. V. Mell. Berlin Museum. Male adult syntype here designated LECTOTYPE (blue label); one male adult and two male subimagos, same data, designated PARALECTOTYPES. A folded brown label accompanying a specimen reads in part "Aug 10." This may be a collecting date, but no year is indicated, and other writing on the labels is indecipherable.

Male Adult. Body length, excluding terminal filaments: ca. 18mm. Forewing length ca. 20mm. Hindwing length ca. 12mm.

Head: Median ocellus with lateral and hind margins elevated. Frontal aspect of head capsule slightly shorter in length than forecoxae. **Thorax:** Pronotum emarginate posteriorly. All sterna lacking spines and spine vestiges. Forewings (Fig. 1) without stigmatic anastomoses, with 10-15 parallel cross-veins directly connecting CuA and hind margin. Anal margin of forewings extending ca. one half the length of the wings. Hindwings (Fig. 2) relatively long (ca. one half length of forewings), with MA and MP forked in basal half of wings (note that the hindwing shown in Fig. 2 is drawn from the pinned type specimen without mounting; the hind margin is actually smooth not scalloped or sinuate as it appears in the drawing—that being an artifact of the dried wing). Forefemora each with two blunt projections at exterior apex and only slightly longer than foretibiae (ratio 17:15). Relative ordered length of foretarsal segments (from longest to shortest): 2-3-1-4-5. Relative ordered length of

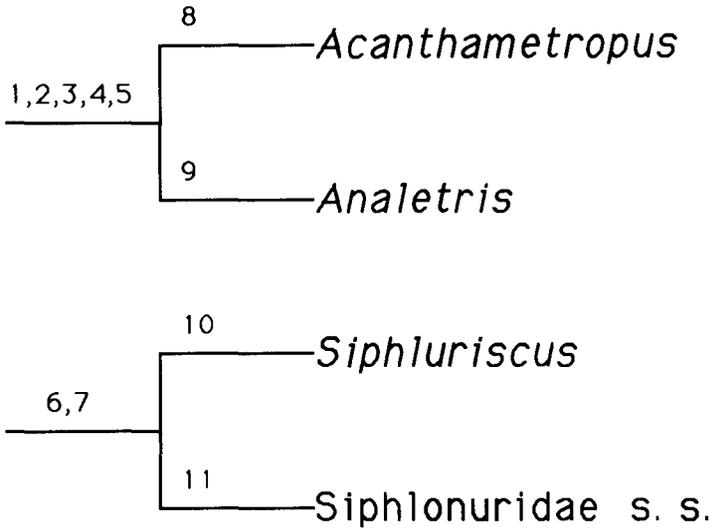


Figure 4. Clades represented by *Acanthametropus*, *Analettris*, and *Siphuriscus*. Numbers represent synapomorphies and autapomorphies of the corresponding characters detailed in Table 1.

hindtarsal segments (from longest to shortest): 1-2-5-3-4; segment 1 partially fused with tibia. Claws all similar and sharp. *Abdomen*: Abdomen lacking dorsal and ventral tubercles, armature, or vestiges of such. Median terminal filament short, but slightly longer than abdominal terga 8, 9, and 10 combined. Genitalia (Fig. 3): Forceps with two short terminal segments. Subgenital plate deeply concave. Penes furcate medially.

Male Subimago (pinned). Similar to adult, except frontal head capsule subequal to forecoxae, ordered length of foretarsal segments 1-2-3-5-4, and genital forceps with only one short terminal segment.

PHYLOGENY

In order to determine the possible relationships of *Acanthametropus*, *Analettris*, and *Siphuriscus*, our OTU's analyzed were *Acanthametropus*, *Analettris*, *Siphuriscus*, and also other genera of Siphonuridae *sensu stricto* lumped together (*Dipteromimus* McLachlan, *Edmundsius* Day, *Parameletus* Bengtsson, *Siphonisca* Needham, and *Siphonurus* Eaton), so that all elements of the problematic higher taxa under consideration were represented. Our outgroup for establishing character state polarity consisted of non-Acanthametropodidae and non-Siphonuridae *sensu stricto* Pisciforma, including all extant genera listed as Baetoidea and Heptagenioidea by Hubbard (1990). These taxa essentially represent all mayflies that have been associated phylogenetically with the OTU's. Details of the numbered characters used for cladistic analysis and appearing on Fig. 4 are given in Table 1, where both the apomorphic and comparative plesiomorphic states are described.

Table 1. Characters used in cladistic analysis of *Acanthametropus*, *Analetris*, and *Siphuriscus* (see Fig. 4).

Apomorphy	Plesiomorphy
1. Prosternum with spine (larva) or spine vestige (adult).	-Prosternum without spine.
2. Claws longer than tibiae (larva)	-Claws shorter than tibiae.
3. Forefemora 2X foretibiae length (male adult).	-Forefemora less than 2X foretibiae length.
4. Penes fused medially.	-Penes more-or-less furcated.
5. Forewings with cubital field short (less than half length of anal margin), with short series of somewhat anastomose veinlets.	-Forewings with cubital field long (one half or more length of anal margin), with long series of simple or forked veinlets.
6. At least mid- and hindclaws similar, sharp (adult).	-All claws dissimilar, one blunt, one sharp.
7. Median terminal filament reduced (adult).	-Median terminal filament well developed.
8. Abdominal terga with tubercles (larva).	-Abdominal terga without tubercles.
9. Clypeus minute and triangular.	-Clypeus transverse.
10. Hindwing with MA forked in basal half of wing.	-Hindwing with MA forked at mid-length or beyond.
11. Forewing with MP stem connected to CuA by one or more crossveins.	-Forewing with MP stem not connected to CuA by crossveins.

Two unconnected clades (Fig. 4) are indicated by our cladistic analysis. Synapomorphies used to deduce these clades within the Pisciforma are indicated as numbers on the stems of the respective clades. Selected autapomorphies are also indicated for informational purposes on the terminal branches. As can be seen, *Acanthametropus* and *Analetris* share at least five significant synapomorphies, including both adult and larval characters. Since these apomorphies are not shared by other Ephemeroptera, they clearly indicate a close relationship between the two genera, as has always been hypothesized on phenetic grounds by Edmunds (see e.g. Edmunds and Koss 1972). *Siphuriscus*, which has been grouped with latter genera in the past, does not share apomorphies with those genera, but instead shares apomorphies with the genera of Siphonuridae *sensu stricto* (see OTU description above).

No apomorphies used in this study connect the two indicated clades, and therefore we have no evidence that they represent sister groups, and we have not arbitrarily connected them in Fig. 4. Only a more exhaustive cladistic analysis of the entire Pisciforma will resolve their exact relationships.

The fossil genus *Stackelbergisca* cannot be placed to either clade based on its available adult and larval characteristics (see Tshernova 1948). Despite our attempts, we were unable to borrow any material of *Stackelbergisca* for comparative analysis. However, based on figured forewing venation and larval legs, it apparently does not share forewing apomorphies (see character 5, Table 1) or larval claw apomorphies (see character 2, Table 1) with the *Acanthametropus-Analetris* clade. It does appear to possess plesiomorphies common in various lineages of the Pisciforma, which are of no aid in cladistic analysis. Unfortunately, it appears from published figures that basal forewing venation is somewhat obscured in the fossil, and thus we cannot decipher whether crossveins are connecting the stem of MP with CuA, a characteristic we propose as an apomorphy that may define at least one branch of the

Siphuriscus-Siphonuridae *sensu stricto* clade (see character 11, Table 1 and Fig. 4). In essence, with respect to *Stackelbergisca*, we cannot find any of the apomorphies indicated in Table 1.

CLASSIFICATION

Based on our phylogenetic findings, we suggest that the genera *Acanthametropus* and *Analetris* be recombined in the family Acanthametropodidae. We also suggest that the genus *Siphuriscus* be replaced in the family Siphonuridae *sensu stricto*. The fossil genus *Stackelbergisca* cannot be placed to any family with any confidence and thus is placed in family *incertae* at this time, although it is without a doubt a member of the Pisciforma.

In addition to not knowing at this time if Acanthametropodidae and Siphonuridae *sensu stricto* share an immediate common ancestor, the taxonomic rank of the clades studied here remains tentative until our cladistic analysis is completed. There is always the possibility that they should be expressed at subfamilial or another level, either within the same family or different families. We would argue, for the time being, that consideration of these clades as families is prudent given the preliminary data before us, most importantly the apotypic cladistic position of the Baetidae, which is appropriate to maintain at the family level (see discussion in McCafferty 1991c). In any case, there are no cladistic data supportive of placing *Siphuriscus* or *Stackelbergisca* in the same supergeneric category with *Acanthametropus* and *Analetris* unless such a taxon is extremely inclusive in scope.

Acanthametropodidae was placed in the proposed infraorder Arenata, and Siphonuridae *sensu stricto* was placed in the proposed infraorder Imprimata by McCafferty (1991c). Arenata included pisciform mayflies whose larvae are adapted more-or-less for psammophilous existence [see review of psammophilous mayflies in McCafferty (1991a)]; however, it appears that such adaptations are subject to homoplasy, bringing such an infraorder classification into question. For example, *Siphonisca*, a member of Siphonuridae *sensu stricto* reported by Edmunds *et al.* (quoting C. P. Alexander) as occurring "along low sandy margins," has independently evolved sternal processes on the thoracic sternum (restricted to meso- and metasternum) paralleling somewhat the sternal processes found more extensively in the Acanthametropodidae, which are also psammophilous. The appropriateness of infraordinal classification of these families should be clarified by further cladistic analysis of the Pisciforma.

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