

Zeitschrift: Mitteilungen der Schweizerischen Entomologischen Gesellschaft = Bulletin de la Société Entomologique Suisse = Journal of the Swiss Entomological Society

Herausgeber: Schweizerische Entomologische Gesellschaft

Band: 68 (1995)

Heft: 1-2

Artikel: A reclassification of Siphonuroidea (Ephemeroptera)

Autor: Kluge, N.J. / Studemann, D. / Landolt, P.

DOI: <https://doi.org/10.5169/seals-402585>

Nutzungsbedingungen

Die ETH-Bibliothek ist die Anbieterin der digitalisierten Zeitschriften auf E-Periodica. Sie besitzt keine Urheberrechte an den Zeitschriften und ist nicht verantwortlich für deren Inhalte. Die Rechte liegen in der Regel bei den Herausgebern beziehungsweise den externen Rechteinhabern. Das Veröffentlichen von Bildern in Print- und Online-Publikationen sowie auf Social Media-Kanälen oder Webseiten ist nur mit vorheriger Genehmigung der Rechteinhaber erlaubt. [Mehr erfahren](#)

Conditions d'utilisation

L'ETH Library est le fournisseur des revues numérisées. Elle ne détient aucun droit d'auteur sur les revues et n'est pas responsable de leur contenu. En règle générale, les droits sont détenus par les éditeurs ou les détenteurs de droits externes. La reproduction d'images dans des publications imprimées ou en ligne ainsi que sur des canaux de médias sociaux ou des sites web n'est autorisée qu'avec l'accord préalable des détenteurs des droits. [En savoir plus](#)

Terms of use

The ETH Library is the provider of the digitised journals. It does not own any copyrights to the journals and is not responsible for their content. The rights usually lie with the publishers or the external rights holders. Publishing images in print and online publications, as well as on social media channels or websites, is only permitted with the prior consent of the rights holders. [Find out more](#)

Download PDF: 11.12.2025

ETH-Bibliothek Zürich, E-Periodica, <https://www.e-periodica.ch>

A reclassification of Siphonuroidea (Ephemeroptera)

N. J. KLUGE¹, D. STUDEMANN^{2*}, P. LANDOLT^{2*} & T. GONSER³

¹Department of Entomology, St. Petersburg State University, St. Petersburg 199034, Russia

²Department of Entomology, Institute of Zoology, Pérolles, CH-1700 Fribourg, Switzerland

³Limnological Research Center, EAWAG, CH-6047 Kastanienbaum, Switzerland

The superfamily Siphonuroidea is proposed, its phylogenetic position discussed and definitive characteristics are presented for all the families contained. New characters of the thorax, the female genitalia, and the egg chorion are used. The Siphonuroidea consist of a Northern Hemisphere group of families (Siphonuridae s. str., Dipteromimidae, Ameletidae, Metretopodidae, Acanthametropodidae and Ametropodidae) and a Southern Hemisphere group of families (Oniscigastridae, Nesameletidae, Rallidentidae, and Ameletopsidae). The family Dipteromimidae and the subfamily Parameletinae are established. The synonymy of *Isonychia polita* and *Acanthametropus nikolskyi* is documented. Fossil Siphonuroidea of uncertain family status are included. The relationships between the families are discussed.

Key words: eggs, Ephemeroptera, morphology, phylogeny, Siphonuridae, Siphonuroidea, systematics.

INTRODUCTION

The taxonomy and the phylogeny of Siphonuroidea or Siphonuridae *sensu lato* are subject to different opinions. The authors that have worked on the rank and composition of this taxon (EDMUNDS, 1972; MCCAFFERTY & EDMUNDS, 1979; LANDA & SOLDAN, 1985; MCCAFFERTY, 1991; TOMKA & ELPERS, 1991; KLUGE, in press, and others) have used the taxon Siphonuridae in different senses. These differences are based on (1) the importance attached to adult versus larval characters, (2) the interpretation of characters as being synapomorphic or symplesiomorphic, (3) the paraphyletic nature of the group, and (4) inadequate diagnoses of many taxa. We describe additional characters for the diagnoses and present a new classification of the Siphonuroidea.

MATERIAL AND METHODS

The species and stages examined are listed in Tab. 1.

The internal genitalia of female imagines (which in Siphonuridae s. str. consist of a sclerotized copulatory pouch inside abdominal segment VII – Figs 9-14) are a very important character for differentiation. For its examination the following procedure was used: The dissected abdomen with an intact sternum VII was boiled in a solution of KOH or NaOH with a concentration of about 10% for several minutes in order to release the cuticula from soft tissues.

*Reprint requests, address for correspondence

Table 1. Species and stages examined. L = larva; S = subimago; I = imago.

| Family, Genus | Species | Stages examined | | | | | | |
|------------------------|---------------------------------------|------------------------------------|-----|-----|-----|-----|-----|---|
| | | L | S ♂ | S ♀ | I ♂ | I ♀ | egg | |
| SIPHLONURIDAE | | | | | | | | |
| <i>Siphlonurus</i> | <i>aestivalis</i> (EATON, 1903) | + | + | + | + | + | + | |
| | <i>alternatus</i> (SAY, 1824) | + | + | + | + | + | + | |
| | <i>armatus</i> EATON, 1870 | + | + | + | + | + | + | |
| | <i>chankae</i> THERNOVA, 1952 | + | + | + | + | + | + | |
| | <i>croaticus</i> ULMER, 1919-20 | + | + | + | + | + | + | |
| | <i>flavidus</i> (PICTET, 1865) | + | + | + | + | + | + | |
| | <i>hispanicus</i> (DEMOULIN, 1958) | + | + | + | + | + | + | |
| | <i>immanis</i> KLUGE, 1985 | + | + | + | + | + | + | |
| | <i>lacustris</i> EATON, 1870 | + | + | + | + | + | + | |
| | <i>lusoensis</i> PUTHZ, 1977 | + | + | + | + | + | + | |
| | <i>montanus</i> STUEDEMANN, 1992 | + | + | + | + | + | + | |
| | <i>occidentalis</i> EATON, 1885 | + | + | + | + | + | + | |
| | <i>palaeartcticus</i> TSHERNOVA, 1930 | + | + | + | + | + | + | |
| | <i>zhelochtsevi</i> TSHERNOVA, 1952 | + | + | + | + | + | + | |
| <i>Parameletus</i> | <i>chelifer</i> BENGTSOON, 1908 | + | + | + | + | + | + | |
| | <i>minor</i> BENGTSOON, 1909 | + | + | + | + | + | + | |
| | sp. | | | | | | + | |
| <i>Siphlonisca</i> | <i>aerodromia</i> NEEDHAM, 1909 | + | + | | + | + | + | |
| DIPTEROMIMIDAE | | | | | | | | |
| <i>Dipteromimus</i> | <i>tipuliformis</i> McLACHLAN, 1875 | + | + | + | + | + | + | |
| AMELETIDAE | | | | | | | | |
| <i>Ameletus</i> | <i>alexandrae</i> BROODSKY, 1930 | + | + | + | + | + | + | |
| | <i>camtschaticus</i> ULMER, 1927 | + | + | + | + | + | + | |
| | <i>cedrensis</i> SINITSHENKOVA, 1977 | + | + | + | + | + | + | |
| | <i>celer</i> McDUNNOUGH, 1934 | | | | | | + | |
| | <i>costalis</i> MATSUMURA, 1931 | + | + | + | + | + | + | |
| | <i>inopinatus</i> EATON, 1887 | + | + | + | + | + | + | |
| | <i>montanus</i> IMANISHI, 1930 | + | + | + | + | + | + | |
| | <i>parvus</i> KLUGE, 1979 | + | + | + | + | + | + | |
| | <i>procerus</i> BAJKOVA, 1976 | + | + | | + | | | |
| | <i>similior</i> McDUNNOUGH, 1928 | | | | | | + | |
| | <i>suffusus</i> McDUNNOUGH, 1936 | | | | | | + | |
| | <i>validus</i> McDUNNOUGH, 1924 | | | | | | + | |
| | <i>Metreletus</i> | <i>balcanicus</i> (ULMER, 1919-20) | + | + | + | + | + | + |
| | METRETOPODIDAE | | | | | | | |
| <i>Metretopus</i> | <i>alter</i> BENGTSOON, 1930 | | | | + | + | + | |
| | <i>borealis</i> (EATON, 1871) | + | + | + | + | + | + | |
| | sp. n. | + | + | + | + | + | + | |
| <i>Siphloplecton</i> | sp. 1 | | | | + | + | + | |
| | sp. 2 | + | | | | | + | |
| ACANTHAMETROPODIDAE | | | | | | | | |
| <i>Acanthametropus</i> | <i>nikolskyi</i> TSHERNOVA, 1948 | + | | | + | | + | |
| <i>Analetris</i> | <i>eximia</i> EDMUNDS, 1972 | + | | | | | | |
| AMETROPODIDAE | | | | | | | | |
| <i>Ametropus</i> | <i>fragilis</i> ALBARDA, 1878 | + | + | + | + | + | + | |
| ONISCIGASTRIDAE | | | | | | | | |
| <i>Oniscigaster</i> | <i>wakefieldi</i> McLACHLAN, 1873 | + | | + | | | + | |
| <i>Siphlonella</i> | sp. | + | | | | | | |
| <i>Tasmanophlebia</i> | <i>nigrescens</i> TILLYARD, 1933 | + | | | | | | |
| NESAMELETIDAE | | | | | | | | |
| <i>Nesameletus</i> | <i>flavitinctus</i> (TILLYARD, 1923) | + | + | + | | + | + | |
| <i>Ameletoides</i> | <i>lacusalbinae</i> TILLYARD, 1933 | + | | | | | | |
| <i>Metamoni</i> | sp. | + | + | | | | | |
| RALLIDENTIDAE | | | | | | | | |
| <i>Rallidens</i> | <i>mcfarlanei</i> PENNIKET, 1966 | + | | | | + | + | |
| AMELETOPSIDAE | | | | | | | | |
| <i>Ameletopsis</i> | <i>perscitus</i> EATON, 1899 | + | | + | | + | + | |
| <i>Chiloporter</i> | sp. | + | | | + | + | + | |
| <i>Mirawara</i> | sp. | + | | | | | | |
| <i>Chaquihua</i> ? | sp. | + | | | | | | |

Eggs were dissected from the abdomen of females (imagines, subimagines, or mature larvae) and transferred to an alcohol solution (80%). The eggs were dehydrated through a stepwise immersion in alcohol (absolute), a mixture of alcohol/acetone (1 : 1) and acetone (100%) and then dried by critical point drying. The mounted eggs were coated with a 75nm Au/Pd layer and examined with a Hitachi H700 scanning electron microscope at 25 kV.

The details of the pterothorax structure described by KLUGE (1994) are marked in the text by one asterisk (*). The details of the maxillary structure, marked in the text by two asterisks (**), are described by KLUGE (in press).

PHYLOGENETIC POSITION AND STATUS OF SIPHLONUROIDEA

According to recent research, the phylogenetic relationships of actual groups of Ephemeroptera seem to be as shown in Fig. 1 (for a detailed discussion – see KLUGE, in press). The taxon regarded here as being the superfamily Siphonuroidea was previously divided into two or three families – Siphonuridae *s. l.*, Ametropodidae, and Metretopodidae (EDMUNDS *et al.*, 1976). The family Siphonuridae *s. l.* thus included all Siphonuroidea except *Ametropus*, *Metretopus*, and *Siphloplecton*. In this wide sense it was characterized primarily by the similar fore wing venation in all of its representatives, which have a series of veins running in the cubital field from CuA to the hind margin (“type S” in the present paper). The larvae of the majority of Siphonuridae *s. l.* have the same swimming specialization, which earlier authors regarded as evidence of the close relationship between members of this

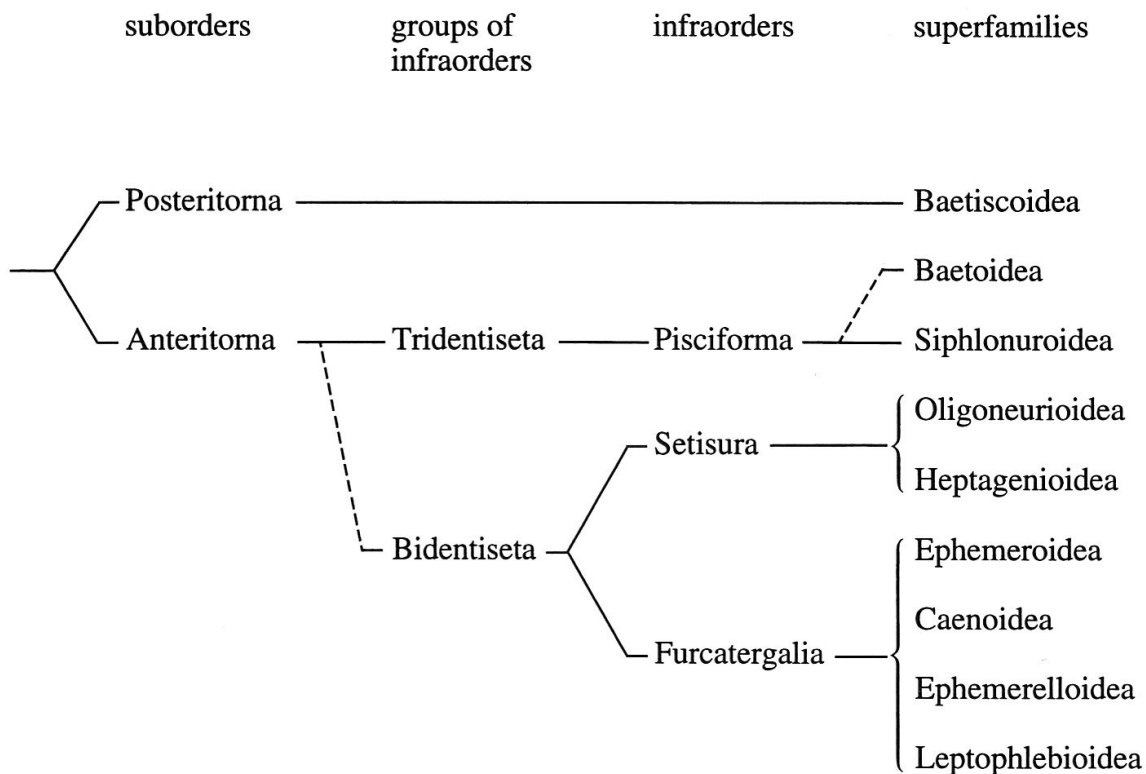


Fig. 1. Phylogeny of recent superfamilies of Ephemeroptera

taxon. According to the majority of recent authors (McCAFFERTY & EDMUNDS, 1979, and others), these characters of Siphonuroidea are plesiomorphic. This opinion is based on (1) the discovery of Palaeozoic (Lower Permian) larvae of *Protereisma americana* (DEMOULIN, 1970) and others, which belong to the family Protereismatidae (suborder Permoplectoptera) and combine the archaic features of this suborder (e. g. homonomous wings, 9 pairs of tergallae) with the swimming specialization of the Siphonuroidea-type (particularly caudal filaments with primary swimming setae on the inner sides of cerci and lateral sides of paracercus) (CARPENTER, 1979); (2) the presence of many different Siphonuroidea-like larvae and imagines in Mesozoic deposits; (3) the occurrence of swimming specializations of larvae in many different groups of Ephemeroptera; many mayfly larvae which have lost this specialization preserve some of its elements (in particular, the ability to make dorsoventral swimming movements with their abdomens, sometimes rudimentary primary swimming setae on caudal filaments) (KLUGE *et al.*, 1984). An alternative opinion is that the Ephemeroidea is the most primitive group of Ephemeroptera. This opinion is based on the description of Lower Permian larvae of the genus *Phtharthus* HANDLIRSCH, 1904. These larvae were described as having caudal filaments and tergallae of the Ephemeroidea-type and wing pads directed backwards (HANDLIRSCH, 1906-1908). The type specimens of *Phtharthus rossicus* HANDLIRSCH, 1904, and *Ph. netschajevi* HANDLIRSCH, 1904, preserved in the Geological-Mineralogical Museum of Kazan University (Tatarstan, Russian Federation), have recently been reexamined by Kluge. HANDLIRSCH's descriptions and figures are incorrect. These larvae have caudal filaments of the Siphonuroidea-type, lamellate tergallae¹, and lack wing pads. Probably the larvae of *Phtharthus* are conspecific with the specimen described as the larva of *Misthodotes sharovi* by TSHERNOVA (1965).

Since the characters of Siphonuridae *s. l.* are now regarded as being sympleiomorphic, this taxon is assumed to be paraphyletic. Therefore, some authors divide it into smaller groups in order to make a system, based on holophyletic taxa. Groups such as the Isonychiinae and the Coloburiscinae, which were initially placed in the Siphonuridae *s. l.*, have been transferred to the superfamily Oligoneurioidea, since their similarity with Siphonuroidea is sympleiomorphic, while their similarity with Oligoneurioidea is synapomorphic (McCAFFERTY & EDMUNDS, 1979). Oniscogastridae, Nesameletidae, Rallidentidae, and Ameletopsidae are regarded as separate families by some authors (McCAFFERTY, 1991), although initially they were placed in the Siphonuridae *s. l.* In recent years the genera *Ameletus* and *Metreletus*, which were formerly placed in Siphonuridae, have been moved to the family Rallidentidae (TOMKA & ELPERS, 1991) or to the family Ameletidae (McCAFFERTY, 1991; STUDEMANN *et al.*, 1994). McCAFFERTY (1991) established the separate family Acanthametropodidae.

Distinct diagnoses have never been given for the families into which the former Siphonuridae *s. l.* have been divided. Each of these families can be characterized by unique features of the larvae, but problems exist with characters of the winged stages. The structures traditionally used to separate taxa (wing venation, leg proportions, and structure of genitalia) are not sufficient for this purpose because wing venation is nearly the same in the majority of Siphonuroidea, and genital

¹ About the usage of the term "tergallae" (as homologous organs) and the term "tracheal gills" (as analogous organs) see KLUGE, 1989

structure demonstrates marked variability between species. Some characters of the thorax (described here for the first time) and egg (examined by scanning electron microscope) are useful for this purpose.

A preliminary classification of Siphonuroidea is given here. We are unable to give complete diagnoses for the winged stages of all the siphonuroid families because the thorax and egg structures of some genera have not been examined as yet. Thorax and egg structures of all Southern Hemisphere genera examined are figured here in order to promote the discovery of common family characters. Some new family characters are described here for the winged stages, eggs, and larvae.

SUPERFAMILY SIPHLONUROIDEA

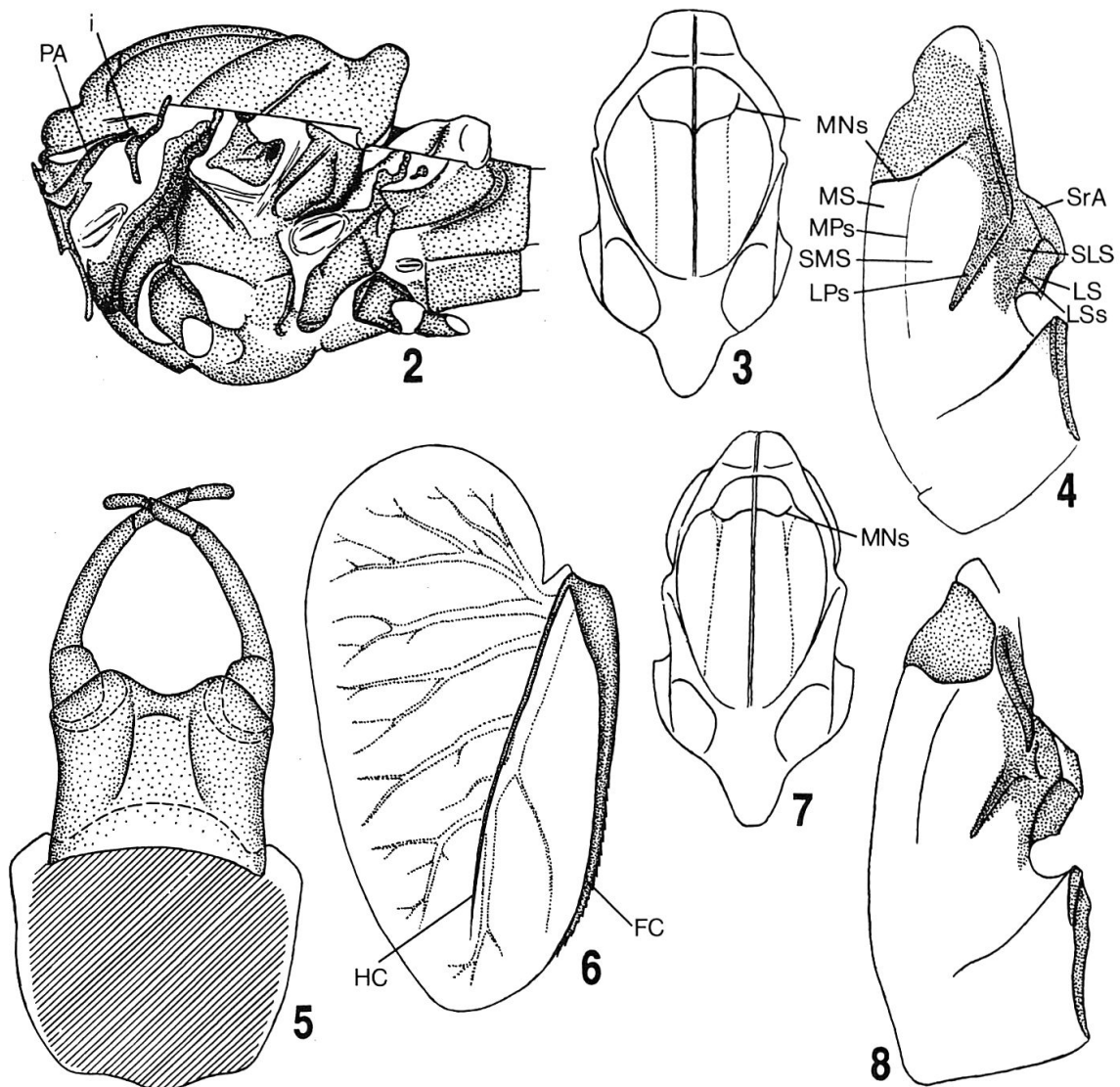
Comparative characteristics. According to KLUGE (in press), Siphonuroidea belong to the suborder Anteritorna (Fig. 1), which differs from the suborder Posteritorna (that includes Baetiscidae and Prosopistomatidae) by having the tornus of the fore wing between the ends of CuA and CuP (Fig. 32).

The infraorder Pisciforma, including Siphonuroidea, can be separated from the two other infraorders (Setisura and Furcatergalia) by the following characters (KLUGE, in press): (1) The larval maxilla usually bears three dentisetae (stout specialized setae in the inner-dorsal row of setae)** (Fig. 39). In a few cases the number of dentisetae is reduced (Figs 20, 21). In the infraorders Setisura and Furcatergalia no more than two dentisetae are present. (2) In contrast to Furcatergalia, the first tarsal segment of the winged stages in Siphonuroidea is not shortened. (3) In contrast to Setisura, the eggs of Siphonuroidea never have anchors consisting of a single spirally coiled thread with apical knob, but anchors of other structures may be present (Figs 62, 66, 70, 76).

Whithin the Pisciforma, the superfamily Siphonuroidea differs from the superfamily Baetoidea (which includes Siphlaenigmatidae and Baetidae) by the following plesiomorphic characters of the winged stages: (1) The mesonotum has a distinct mesonotal suture* which can be transverse (Fig. 7) or curved backwards medially forming an angle (Fig. 3). In Baetoidea the mesonotal suture is very strongly turned backwards laterally or disappears. (2) All tarsi are 5-segmented. In Baetoidea at least tarsi of fore and hind legs are 4-segmented. (3) In the fore wing CuA and CuP are connected basally, forming an acute angle (Fig. 32). In Baetoidea CuP is basally curved or not connected to CuA.

Siphonuroidea is probably paraphyletic and the most primitive group of recent Ephemeroptera, most of its representatives having a complex of plesiomorphies. The larvae are usually of the swimming type and their caudal filaments bear primary swimming setae (i. e., setae arranged in a regular row on each lateral side of the paracercus and on the inner side of each cercus). The tergallae usually consist of a plate with two costae (Fig. 6). The imagines of the majority of Siphonuroidea have a similar fore wing venation: their cubital field is narrow with a series of veins running from CuA to the hind margin of the wing; in a few cases (Metretopodidae, Ametropodidae, *Metreletus* and *Cretoneta*), intercalaries are present between CuA and CuP; Ametropodidae have a distinctive fore wing venation. The paracercus in the imagines can be rudimentary or developed (Tab. 2).

Classification. The Siphonuroidea can be divided into two groups of families: a group of families distributed only in the Northern Hemisphere and a group of families distributed only in the Southern Hemisphere. These two groups differ in the mesosternum structure of the winged stages.



Figs 2-8. Siphonuridae. 2-4 - *Siphonurus aestivalis*, male imago: 2 - pterothorax (lateral view), 3 - mesonotum (dorsal view); 4 - right half of subimaginal skin of mesonotum. 5-6 - *S. palaearticus*: 5 - sternum IX and styliger (dorsal view), 6 - tergite of pair III. 7 - *Parameletus chelifer*, imago, mesonotum (dorsal view); 8 - *Siphonisca aerodromia*, right half of subimaginal skin of mesonotum. FC - fore costa, HC - hind costa, i - incision of scutum, LPs - lateroparapsidal suture, LS - lateroscutum, LSs - lateral scutal suture, MNs - mesonotal suture, MPs - medioparapsidal suture, MS - medioscutum, PA - posterior arm of prealar bridge, SLS - sublateroscutum, SMS - submedioscutum, SrA - suralare.

A) NORTHERN HEMISPHERE GROUP OF FAMILIES

Composition. Siphonuridae s. str., Dipteromimidae, Ameletidae, Metretopodidae, Acanthametropodidae, Ametropodidae.

Characteristics of the imago and subimago. Furcasternal protuberances* of mesothorax contiguous over their entire length (Fig. 31) (plesiomorphic character); paracoxal suture of mesothorax running across the ventral side of the episternum, completely dividing it into an episternum and a katepisternum (Fig. 31); venation of cubital field of fore wing variable (Tab. 2); paracercus rudimentary or as large as cerci (Tab. 2).

Table 2. Characteristics of families from the Northern Hemisphere.

- *¹ similar = on each leg both claws similar, pointed and hooked
 *² dissimilar = on each leg one claw pointed and hooked, the other blunt
 *³ type S = cubital field with a series of veins running from CuA to the hind margin of the wing (Figs 11 a-c in STUDEMANN & TOMKA, 1991)
 *⁴ type M = cubital field with intercalaries (Figs 1-6 in BERNER, 1978)
 *⁵ type A = A1 and CuP terminate close to tornus, cubital field with intercalaries (Fig. 54.8 in TSHERNOVA *et al.*, 1986)
 *⁶ see Figs 53-57 in STUDEMANN *et al.*, 1988
 *⁷ see Figs 60-61 in STUDEMANN *et al.*, 1988
 *⁸ movable tergaliae can make rhythmical respiratory movements
 *⁹ slightly movable tergaliae are unable to make rhythmical respiratory movements

| | subimago and imago | | | | | | larva |
|--------------------------------|---------------------------|--------------------------|----------------------------|----------------------------|--|----------------|--------------------------------|
| | mesonotal suture | claws of legs | cubital field of fore wing | subgenital plate of female | subanal plate of female | paracercus | tergalia |
| Siphonuridae: - Siphonurini | turned backwards (Fig. 3) | similar* ¹ | type S * ³ | small | moderately developed* ⁶ | reduced | movable* ⁸ |
| - Parameletini | transverse (Fig. 7) | similar | type S | small | moderately developed with median process | reduced | movable |
| Dipteromimidae | transverse | similar | type S | well developed | well developed* ⁷ | well developed | ? |
| Ameletidae | turned | dissimilar* ² | types S and M | small | well developed* ⁷ | reduced | slightly movable* ⁹ |
| Metretopodidae | transverse | dissimilar | type M* ⁴ | well developed | moderately developed | reduced | movable |
| Acanthametro-podidae | transverse | dissimilar | type S | small | small | well developed | ? |
| Ametropodidae | transverse | dissimilar | type A* ⁵ | small | absent | well developed | ? |

Family Siphonuridae BANKS, 1900 (*s. str.*)

(Figs 2-14, 61-63)

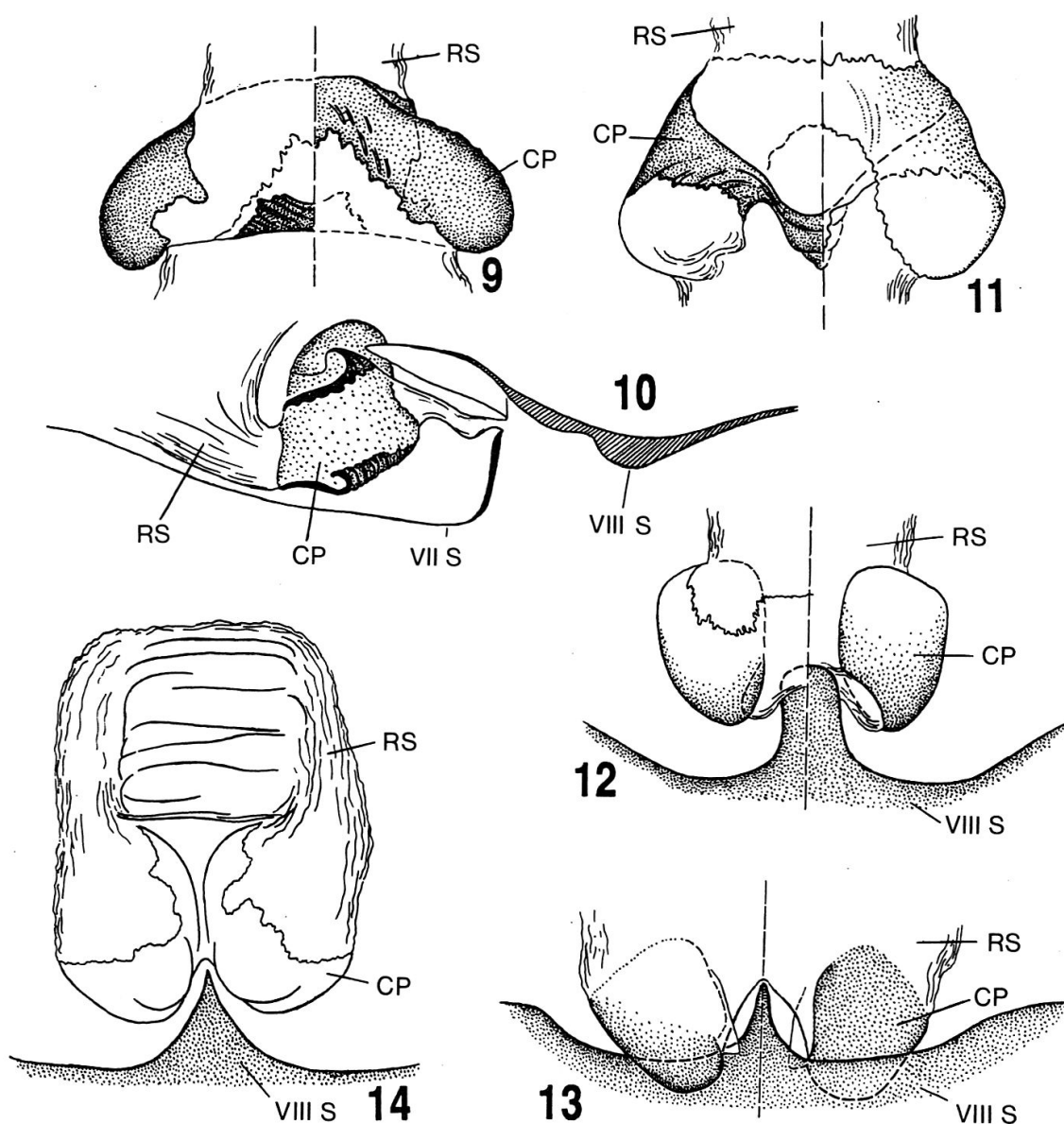
Composition. This family includes the Holarctic genera *Siphonurus* (more than 20 species) and *Parameletus* (6 species), and the Nearctic genera *Edmundsius* (one species) and *Siphonisca* (one species).

Characteristics. Besides the characters listed in Tab. 2, the following distinctive characters are present: (1) in the larva, hind costa of tergalia very far from hind margin and very weak (Fig. 6); (2) in the subimago the lateral sclerotized pigmented area of mesonotum biramous, stretching along lateroparapsidal and lateral scutal sutures* (Figs 4, 8) (as in Oniscigastridae); (3) in the female imago (not in the subimago!) sclerotized copulatory pouch present (Figs 9-14) (found in *Siphonurus*, *Parameletus*, and *Siphonisca*; unique structure, not found in other Ephemeroptera); (4) eggs with convex rough spots formed by the tops of threads closely pressed together; these spots are situated close to the micropyle and dispersed on the egg surface (Figs 61-63; Figs 65-75 in STUDEMANN *et al.*, 1988) (in contrast to other families where, if bundles of threads are present, they are terminated with knobs, Figs 65-76, 79-81).

Classification. We divide this family into two subfamilies – Siphonurinae and Parameletinae *subfam. nov.*

Subfamily Siphonurinae BANKS, 1900

Composition. This subfamily includes *Siphonurus* EATON, 1868 (= *Siphurella* BENGTTSSON, 1909; = *Andromina* NAVAS, 1919) and presumably *Edmundsius* DAY, 1953. According to the description of DAY (1953), *Edmundsius* shows similarities with *Siphonurus* in imaginal and larval structures.



Figs 9-14. Siphonuridae - copulatory pouch of female imago. 9, 10 - *Siphonurus aestivalis*: 9 - dorsal view (in left half) and ventral view (in right half), 10 - longitudinal section. 11 - *S. lacustris* - dorsal view (in left half) and ventral view (in right half). 12 - *Parameletus chelifer* - the same. 13 - *P. minor* - the same. 14 - *Siphonisca aerodromia* - dorsal view. CP - copulatory pouch, RS - receptaculum seminis, VII S, VIII S - sternum VII, VIII.

Characteristics. In the larva at least the first two pairs of tergaliae double; posterior margin of tergites with spines (Fig. 9a in STUDEMANN & TOMKA, 1991). In the female imago copulatory pouch variable (Figs 9-11), but not as in *Parameletini*.

Subfamily Parameletinae subfam. nov.

Composition. This subfamily includes *Parameletus* BENGTSSON, 1908 (= *Siphonuroides* McDUNNOUGH, 1923; = *Palmenia* ARO, 1910; = *Potameis* BENGTSSON, 1909; = *Sparrea* PETERSEN, 1909) and *Siphlonisca* NEEDHAM, 1909.

Characteristics. In the larva all tergaliae simple; posterior margin of tergites without spines (Fig. 9b in STUDEMANN & TOMKA, 1991). In the female imago copulatory pouch with two basal lobes; the pigmented area of sternum VIII has anterior median projection that turns between these lobes (Figs 12-14). Additionally, there are similarities between *Parameletus* and *Siphlonisca* in the form of their tergaliae and penis (Figs 3A - 3D, 4I - 4J in SÖDERSTRÖM & NILSSON, 1986, and Figs 10, 24 in BURIAN & GIBBS, 1988).

Family Dipteromimidae fam. nov.

(Figs 15, 64)

Composition. This family includes the Japanese genus *Dipteromimus* McLACHLAN, 1875 (= *Dipteromimodes* MATSUMURA, 1931) (one species).

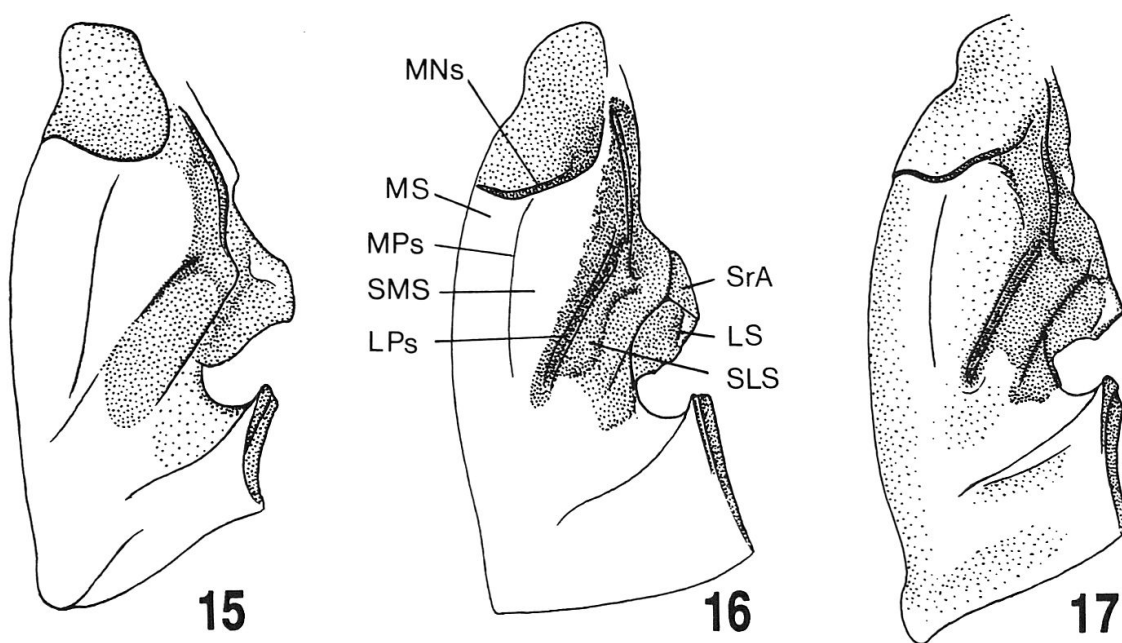
Characteristics. Besides the characters listed in Tab. 2, the following distinctive characters are present: in the larva (1) glossa and paraglossa pedunculated (Fig. 28G in UENO, 1931); (2) maxilla with small galea-lacinia, with big palpus, the second segment of the palpus is the smallest (Fig. 28E in UENO, 1931); (3) in the imago and subimago posterior wing greatly reduced (Fig. 21 in UENO, 1931); (4) in the subimago the pigmented areas on mesonotum as in Fig. 15.

Family Ameletidae McCafferty, 1991

(Figs 18-22, 65, 66)

Composition. This family includes the Holarctic genus *Ameletus* EATON, 1865 (= *Chimura* NAVAS, 1915; = *Palaeoameletus* LESTAGE, 1940) (more than 40 species) and the European genus *Metreletus* DEMOULIN, 1951 (one species).

Characteristics. Besides the characters listed in Tab. 2, the following distinctive characters are present: in the larva (1) the length of the labrum exceeds its width; (2) mandibles elongated with a reduction of the prostheca of the right mandible; (3) maxilla with broadened truncate anterior margin, apical bristles long and pectinate, maxillary canine** reduced, only one dentiseta** present (Figs 20, 21); (4) glossa of labium truncated with wide anterior margin (Pl. 49 in EATON, 1883-1888); in the imago and subimago (5) epimerum of mesothorax with membranous area between anepimerum and katepimerum (Fig. 18) (in contrast to other families – Figs 2, 36, 43, 50, 55); (6) lateroparapsidal suture* of mesonotum elongated (Fig. 22) (as in *Metretopodidae*); (7) in subimago the lateral sclerotized pigmented area of mesonotum very large, occupying submedioscutum* up to the medioparapsidal suture* (Fig. 22); (8) in the male imago styliiger plate with membranous area dorsally (Fig. 19) (in contrast to *Siphonuridae* and other families – Fig. 5); (9) chorion of egg usually with knobs situated inside small cells of reticulation (Figs 65, 66; Figs 76-79 in STUDEMANN *et al.*, 1988) (a similar structure is also present in *Metretopus*, Figs 67, 68).



Figs 15-17. Dipteromimidae and Metretopodidae - right half of subimaginal mesonotum. 15 - *Dipteromimus tipuliformis*, subimago; 16 - *Metretopus* sp. n. (Siberia), subimaginal skin; 17 - *Siphloplecton basale*, subimaginal skin. Labeling terms as in Figs 2-8.

Family Metretopodidae TRAVER, 1935

(Figs 16, 17, 67-71)

= Siphloplectonidae LESTAGE, 1938

Composition. This family includes the Holarctic genus *Metretopus* EATON, 1901 (3 species) and the Nearctic genus *Siphloplecton* CLEMENS, 1915 (5 species).

Characteristics. Besides the characters listed in Tab. 2, the following distinctive characters are present: in the larva (1) claw of foreleg bifid (Figs 43-46 in BERNER, 1978); (2) maxillary palpus with small second segment; (3) labial palpus two-segmented; (4) in the imago and subimago lateroparapsidal suture* elongated (Figs 16, 17) (as in Ameletidae); (5) in the subimago the lateral sclerotized pigmented area of mesonotum long, but not reaching posterior end of lateroparapsidal suture* (Figs 16, 17).

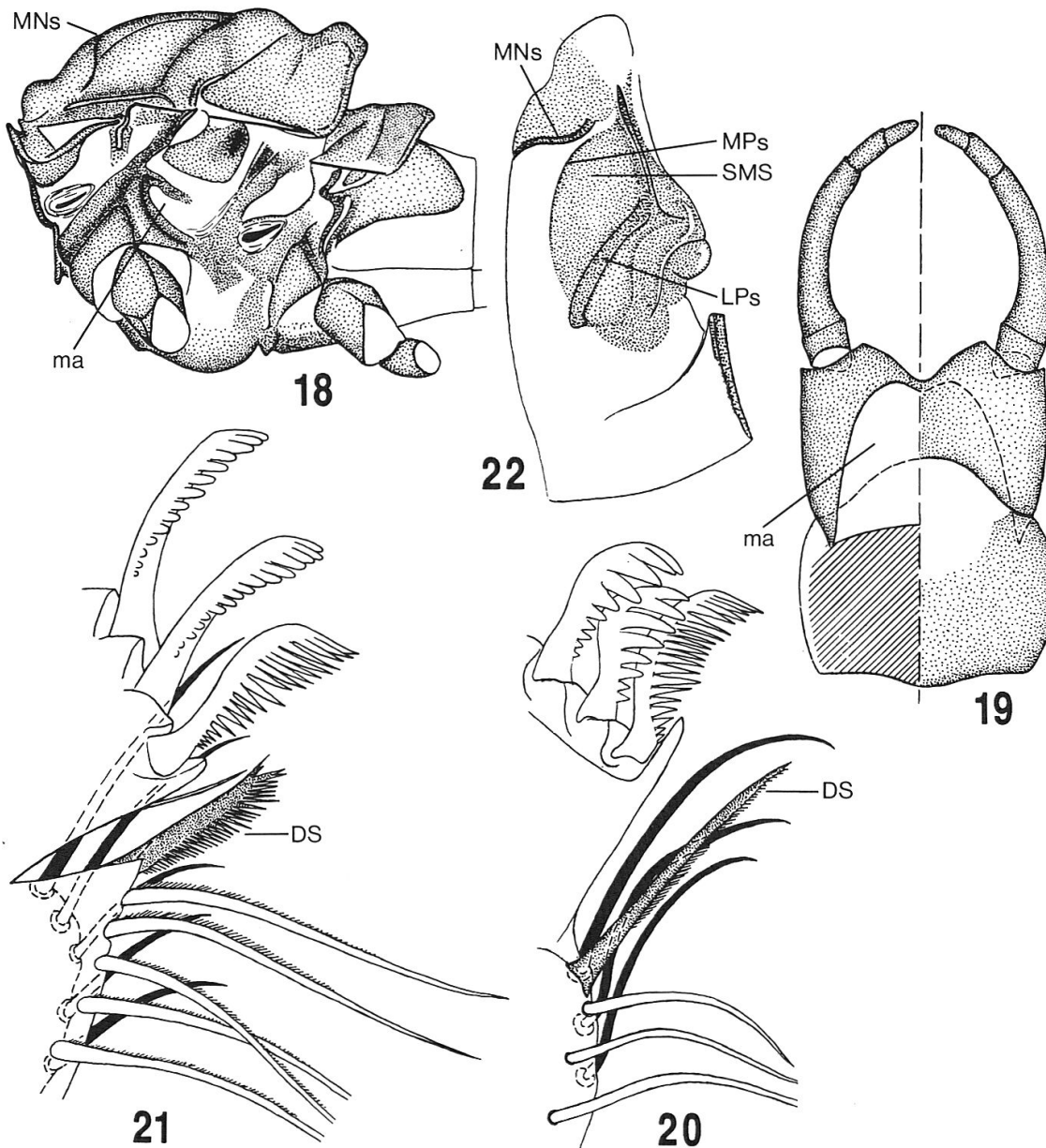
Family Acanthametropodidae EDMUNDS, 1963

(Figs 23-35, 72-75)

= Analetrididae DEMOULIN, 1974

Composition. This family includes the Nearctic and East-Palearctic genus *Acanthametropus* THERNOVA, 1948 (= *Metreturus* BURKS, 1953) (1 or 2 species) and the Nearctic genus *Analettris* EDMUNDS, 1972 (one species).

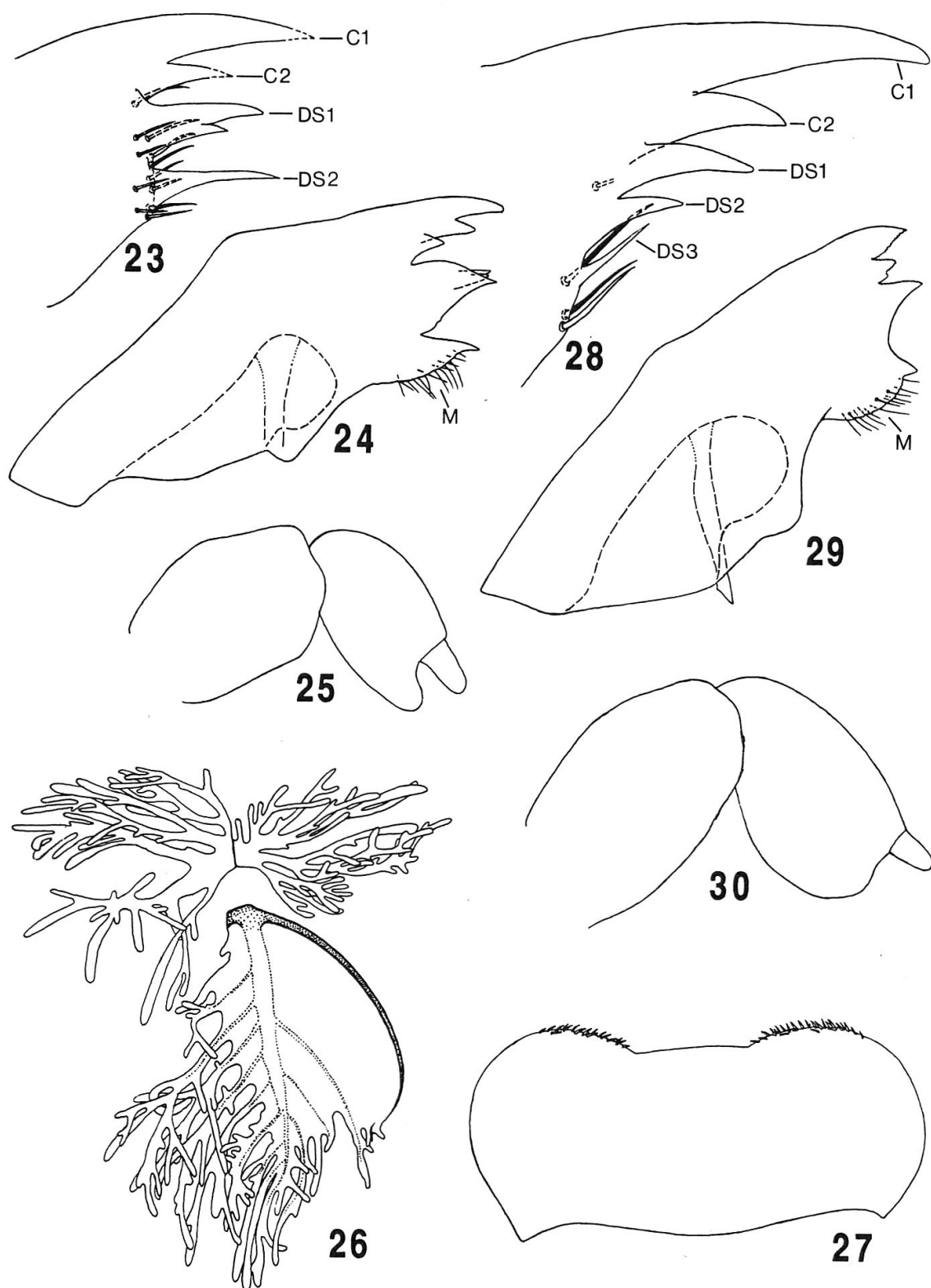
Characteristics. Besides the characters listed in Tab. 2, the following distinctive characters are present: in the larva (1) wide median invagination of labrum (Fig. 27; Fig. 19 in LEHMKUHL, 1976); (2) mandible modified (of carnivorous type), short and wide, lamellous structures on mola reduced (Figs 24, 29); (3) maxilla modified, with canines** and dentisetæ** situated in the same plane; only two canines are present, two dentisetæ are canine-like, third dentisetæ rudimentary or absent (Figs 23, 28);



Figs 18-22. Ameletidae. 18-20 - *Metreletus balcanicus*: 18, 19 - male imago: 18 - pterothorax (lateral view), 19 - sternum IX and styliger - dorsal view (in left half) and ventral view (in right half); 20 - larva, apex of left maxilla. 21 - *Ameletus costalis*, the same. 22 - *A. montanus*, right half of subimaginal skin of mesonotum.

DS - dentiseta, LPs - lateroparapsidal suture, ma - membranous area, MNs mesonotal suture, MPs - medioparapsidal suture, SMS - submedioscutum.

(4) second segment of labial palpus widened (Figs 25, 30); (5) median tubercles present at least on prosternum and mesosternum (Fig. 15 in LEHMKUHL, 1976); (6) femur of fore and middle leg widened, distinctly wider than femur of hind leg (Figs 20-22 in LEHMKUHL, 1976); (7) tarsus much longer than tibia (Figs 20-22 in LEHMKUHL, 1976); (8) tarsal claw of hind leg longer than the others; (9) tergalia with double ventral lamella (Fig. 26; Fig. 9a in LEHMKUHL, 1976); in the imago and subimago (10)



Figs 23-30. Acanthametropodidae, larva. 23-27 - *Acanthametropus nikolskyi*: 23 - apex of left maxilla, 24 - left mandible, 25 - labial palp, 26 - tergalia VI (ventral portion detached and spread), 27 - labrum (24, 25, 27 in the same scale). 28-30 - *Analettris eximia*: 28 - apex of left maxilla, 29 - left mandible, 30 - labial palp (29, 30 in the same scale). C1, C2 - maxillar canines, DS1, DS2, DS3 - dentisetae, M - mola.

prosternum with median projection (Pl. 57 Fig. 15 in TSHERNOVA *et al.*, 1986); (11) on fore wing CuP relatively longer than in most Siphonuridae, veins arising from CuA to the hind margin strongly oblique (Fig. 32, 34; Fig. 3 in LEHMKUHL, 1976); (12) tarsus of middle and hind legs very long, first tarsal segment longer than tibia (Fig. 31).

Family Ametropodidae BENGTSSON, 1913

(Fig. 76)

Composition. This family includes the Holarctic genus *Ametropus* ALBARDA, 1878 (4 or 5 species).

Characteristics. Besides the characters listed in Tab. 2, the following distinctive characters are present: in the larva (1) foreleg reduced, palp-like, with projection on coxa and setae on claw; (2) middle and hind legs with very long claws; (3) tergalia with long marginal setae (Plate II and III in KEFFERMÜLLER, 1959); (4) in the imago and subimago CuP of fore wing terminates close to tornus, A1 is very long, with a series of veins running from it to the hind margin of the wing (Pl. 54 Fig. 8 in TSHERNOVA *et al.*, 1986).

B) SOUTHERN HEMISPHERE GROUP OF FAMILIES

Composition. Oniscigastridae, Nesameletidae, Rallidentidae, Ameletopsidae.

Characteristics of the imago and subimago. Furcasternal protuberances* of mesothorax separated by a median invagination* at least in their posterior portion (Figs 37, 44, 51, 54); paracoxal suture of mesothorax running across ventral side of episternum (Figs 37, 44, 54) or not (Fig. 51). Fore wing of *Siphonurus* type ("type S" = cubital field with a series of veins running from CuA to the hind margin of the wing). Paracercus variable within a family, several times shorter than cerci (Figs 45, 56) or nearly as long as cerci.

Family Oniscigastridae LAMEERE, 1917

(Figs 36-42, 77)

Composition. This family includes the New Zealand genus *Oniscigaster* McLACHLAN, 1873 (3 species), the Neotropical genus *Siphonella* NEEDHAM & MURPHY, 1924 (one species), and the Australian genus *Tasmanophlebia* TILLYARD, 1921 (= *Tasmanophlebiodes* LESTAGE, 1935) (3 species).

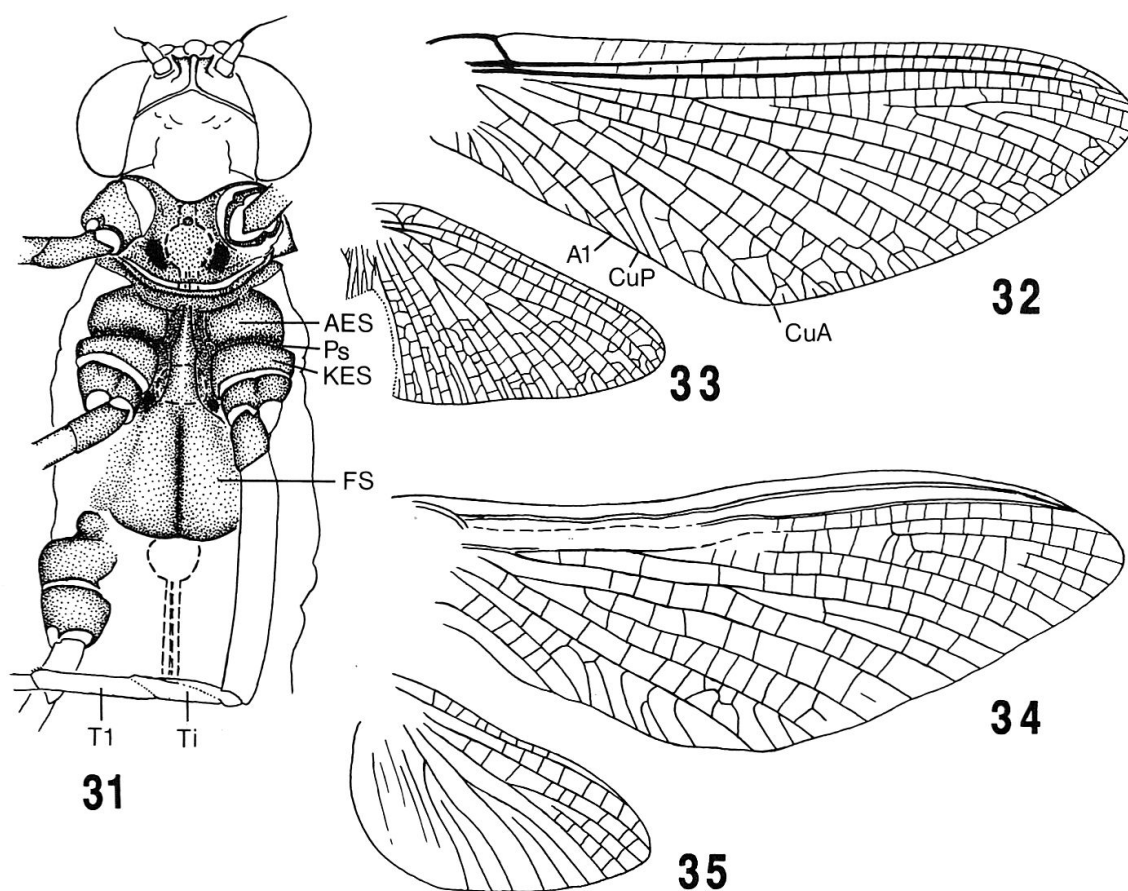
Characteristics. Besides the characters listed in Tab. 3, the following distinctive characters are present: in the larva (1) median protuberance present at least on abdominal terga I-IV; (2) tergaliae disposed dorsally; (3) in the imago and subimago median invagination of furcasternum of mesothorax with parallel sides, not widened posteriorly (Fig. 37); (4) in the subimago the lateral pigmented sclerotized area of mesonotum, if developed, biramous, as it stretches along lateroparapsidal and lateral scutal sutures* (Figs 40, 41) (as in Siphonuridae). Only the thoraci of *Oniscigaster* and *Siphonella* have been examined.

Family Nesameletidae RIEK, 1973

(Figs 43-49, 78)

= Metamoniidae MCCAFFERTY, 1991

Composition. This family includes the New Zealand genus *Nesameletus* TILLYARD, 1933 (one species), the Australian genus *Ameletoides* TILLYARD, 1933 (one species), and the Neotropical genus *Metamoni*us EATON, 1885 (one species).



Figs 31-35. Acanthametropodidae: *Acantahametropus nikolskyi*. 31-33 - male imago (holotypus of *Isonychia polita*): 31 - head and thorax (ventral view, nerve ganglia shown by interrupted lines), 32, 33 - fore and hind wings; 34, 35 - fore and hind wings extracted from mature female larva (the same specimen as in Figs 23-27, 72-75).

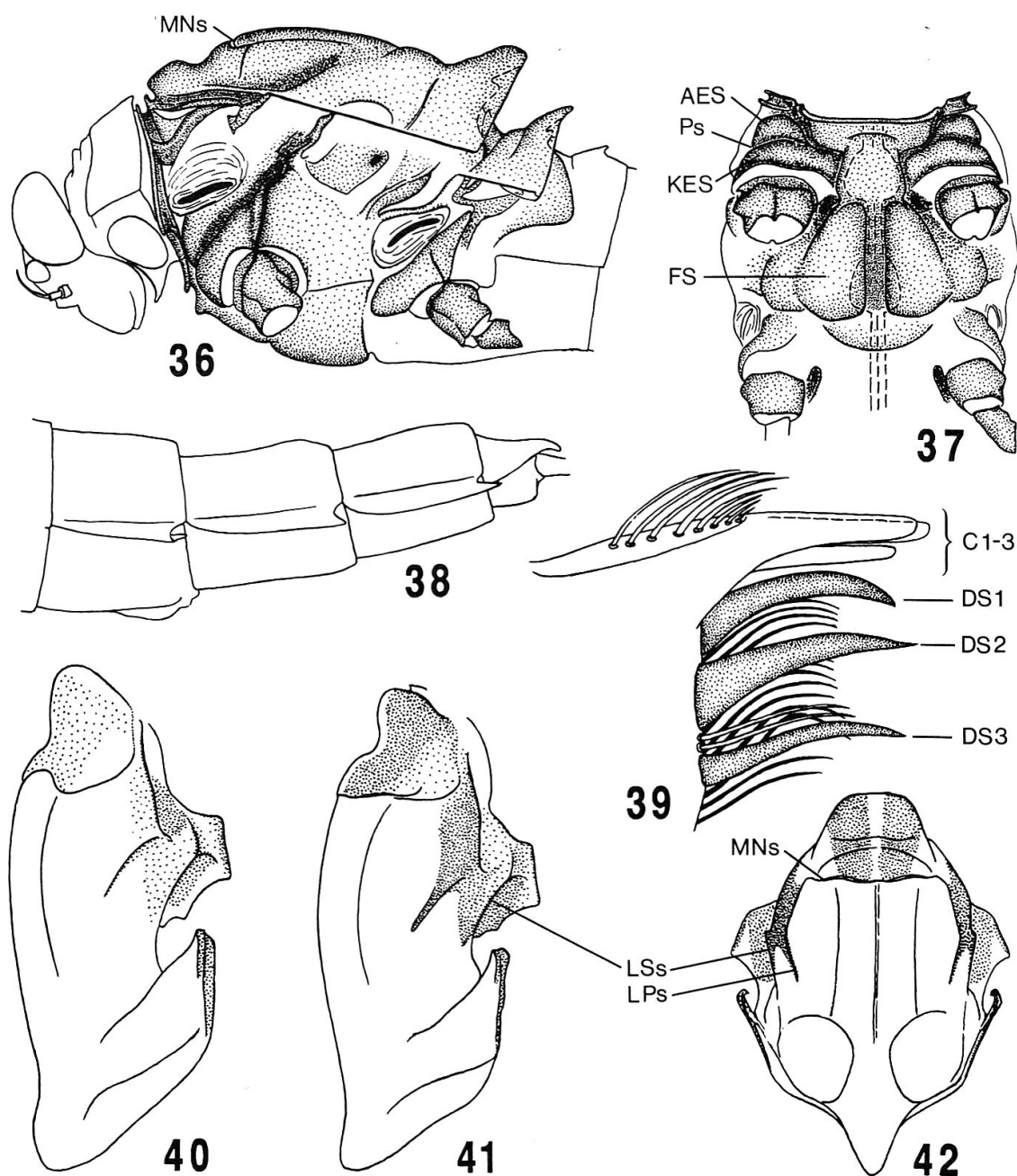
AES - anepisternum, KES - katepisternum, FS - furcasternum, Ps - paracoxal suture, T1 - first tarsal segment, Ti - tibia.

Table 3. Characteristics of the imagines of families from the Southern Hemisphere.

*1 dissimilar = on each leg one claw pointed and hooked, the other blunt

*2 similar = on each leg both claws similar, pointed and hooked

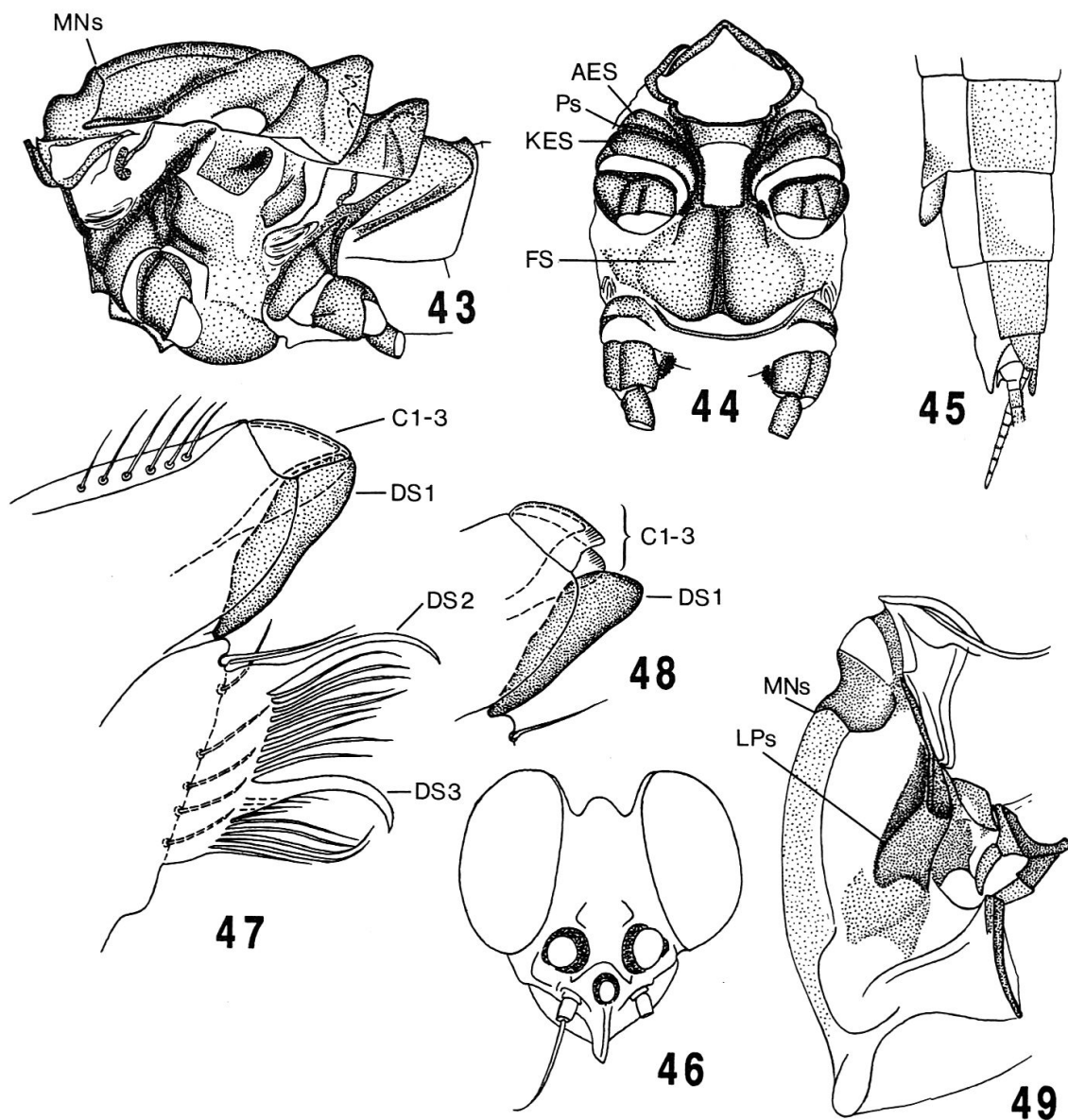
| | claws of legs | subgenital plate of female | subanal plate of female |
|-----------------|---------------|---|---|
| Oniscigastridae | dissimilar *1 | absent (in <i>Oniscigaster</i>) Fig. 38 | absent, Fig. 38 (in all three genera) |
| Nesameletidae | similar *2 | well developed, Fig. 45 (in <i>Nesameletus</i>) | well developed, Fig. 45 (in <i>Nesameletus</i>) |
| Rallidentidae | dissimilar | well developed, Fig. 52 | moderately developed Fig. 52 |
| Ameletopsidae | dissimilar | well developed (in <i>Ameletopsis</i> , <i>Chiloporter</i>), Fig. 56 | well developed (in <i>Ameletopsis</i> , <i>Chiloporter</i>), Fig. 56 |



Figs 36-42. Oniscigastridae. 36-40 - *Oniscigaster* sp. 36-38 - female imago: 36 - head and thorax (lateral view), 37 - pterothotax (ventral view, nerve ganglions shown by interrupted lines), 38 - apex of abdomen (lateral view); 39 - larva, apex of left maxilla; 40 - subimaginal cuticula extracted from mature male larva, right half of mesonotum. 41, 42 - *Siphonella* sp., subimaginal cuticula extracted from mature female larva: 41 - right half of mesonotum, 42 - dorsal view of mesonotum.

AES - anepisternum, C1-3 - three maxillar canines, DS1, DS2, DS3 - dentisetae, FS - furcasternum, KES - katepisternum, LPs - lateroparapsidal suture, LSs - lateral scutal suture, MNs - mesonotal suture, Ps - paracoxal suture.

Characteristics. Besides the characters listed in Tab. 3, the following distinctive characters are present: in the larva (1) mandibles elongated with fused canines (Fig. 61 in PHILLIPS, 1930 and Fig. 6 in TILLYARD, 1933); (2) maxilla with stout and sclerotized first dentiseta** ; second and third dentisetae rudimentary and situated on a common plate (Figs 47, 48); (3) third segment of maxillary palpus short (Fig. 63 in PHILLIPS, 1930, and Fig. 7 in TILLYARD, 1933); (4) labium with long and narrow glos-sae and paraglossae (Fig. 62 in PHILLIPS, 1930, and Fig. 8 in TILLYARD, 1933), glos-sae with stout apical setae (Fig. 64 in PHILLIPS, 1930); in the imago and subimago (5) occiput with unpaired projection (Fig. 46); (6) the mesonotal suture* very close to



Figs 43-49 *Nesameletidae: Nesameletus flavitinctus*. 43-46 - female imago: 43 - pterothorax (lateral view), 44 - the same (ventral view), 45 - apex of abdomen (lateral view), 46 - head; 47, 48 - larva, apex of left maxilla; 49 - right half of subimaginal skin of mesonotum. Labeling terms as in Figs 36-42.

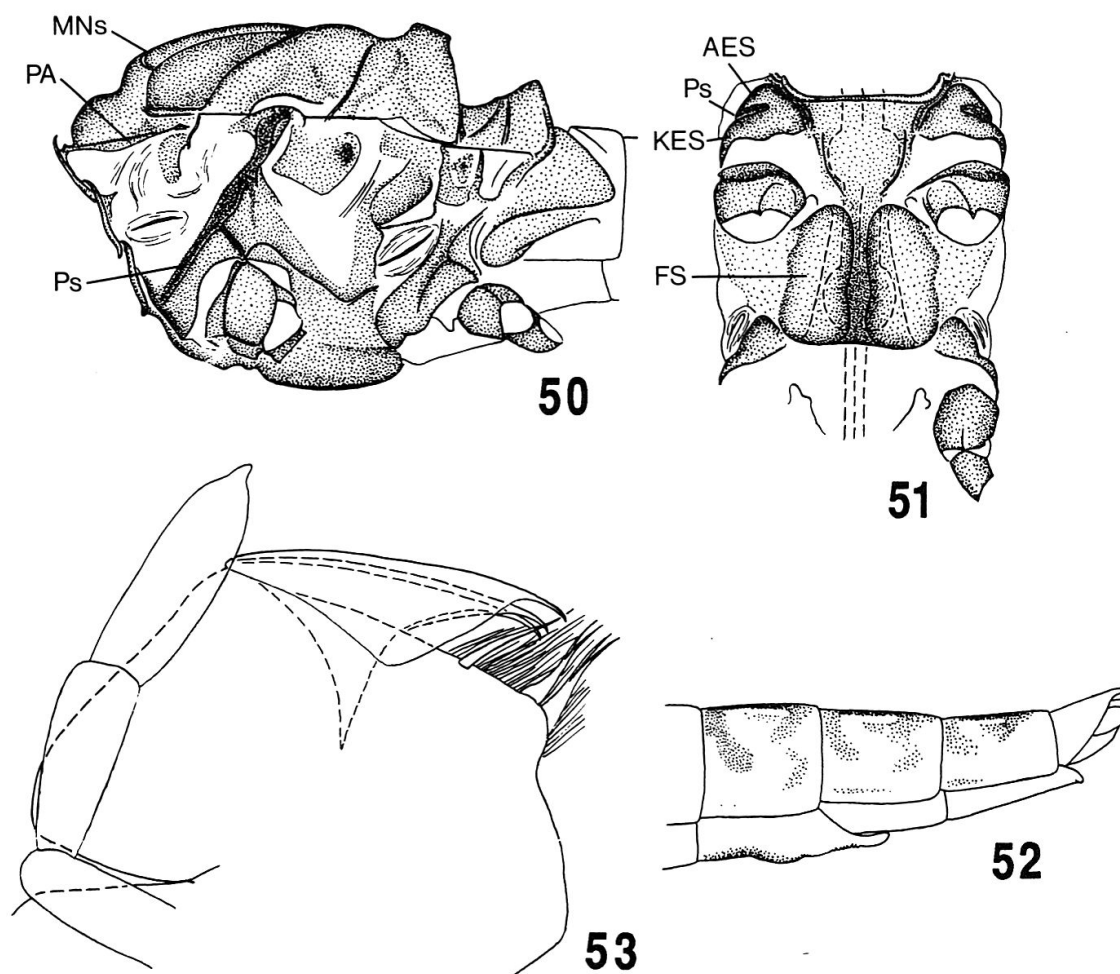
anteronotal transverse impression*, moderately curved backwards medially and laterally, medially forming a distinct angle (Figs 43, 49); (7) in the subimago the lateral sclerotized pigmented area of mesonotum occupies sublateroscutum* between pigmented parts of lateroparapsidal and lateral scutal sutures* (Fig. 49) (as in Ameletopidae). Characters (5) to (7) have been examined in the subimago of *Nesameletus* and the subimaginal parts dissected from mature larvae of *Ameletoides* and *Metamonius*.

Family Rallidentidae PENNIKET, 1966

(Figs 50-53, 79-81)

Composition. This family includes the monospecific New Zealand genus *Rallidens* PENNIKET, 1966.

Characteristics. Besides the characters listed in Tab. 3, the following distinctive characters are present: in the larva (1) mandibles with a broad ridge from which arises a straight series of 10-11 oblique rows of long, strongly curved setae



Figs 50-53. Rallidentidae: *Rallidens mcfarlanei*. 50-52 - female imago: 50 - pterothorax (lateral view), 51 - the same (ventral view, nerve ganglions and inner borders of bases of subalar-sternal muscles shown by interrupted lines), 52 - apex of abdomen; 53 - larva, left maxilla. Labeling terms as in Figs 36-42; PA - posterior arm of prealar bridge.

(Figs 11-15 in PENNIKET, 1966); (2) maxilla very wide and short, maxillary canines** and dentisetæ** strongly modified (Fig. 53); (3) tergallae with ventral fibrillous lamellae (Fig. 16 in PENNIKET, 1966); in the imago and subimago (4) paracoxal suture of mesothorax does not cross ventral side of episternum (Figs 50, 51) (in contrast to other examined Siphonuroidea); (5) on hind wing MP furcates distally; (6) on eggs micropyles situated on convexities of the chorion (Figs 79-81).

Family Ameletopsidae EDMUNDS, 1957

(Figs 54-60, 82, 83)

= Chiloporteridae LANDA, 1973

Composition. This family includes the New Zealand genus *Ameletopsis* PHILLIPS, 1930 (one species), the Australian genus *Mirawara* HARKER, 1954 (3 species), and the Neotropical genera *Chiloporter* LESTAGE, 1931 (2 species), and *Chaquihua* DEMOULIN, 1955 (2 species).

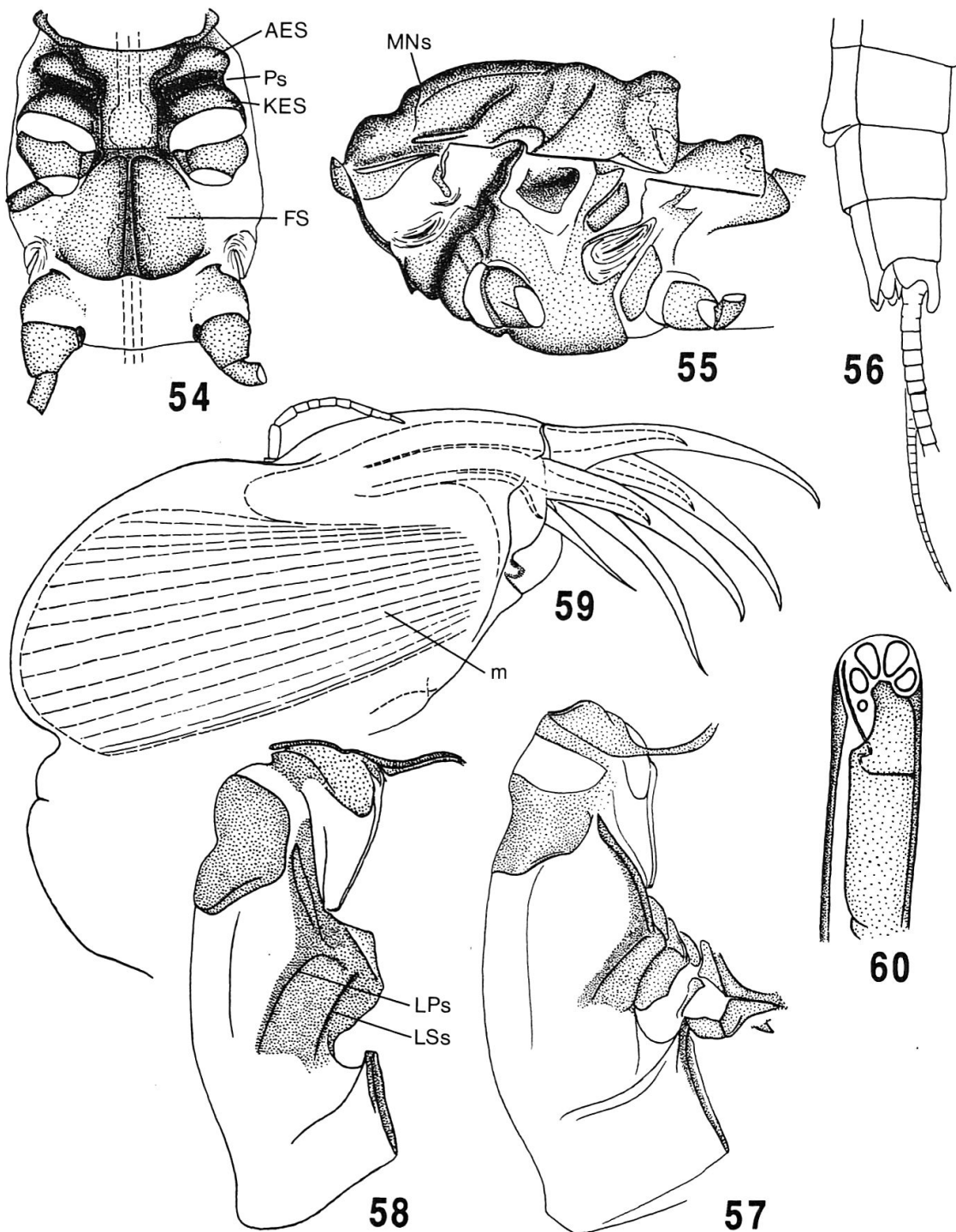
Characteristics. Besides the characters listed in Tab. 3, the following distinctive characters are present: in larva (1) head flattened and large (in contrast to all other Siphonuroidea); (2) mandibles specialized for carnivorous feeding, with very long canines and long molar area; molar area without lamellous structures, protheca absent (Pl. 53 Fig. 4-5 in EATON, 1883-1888); (3) maxilla apically with five movable appendages of unknown origin (in contrast to dentisetæ**, the appendages of the next instar develop inside the old ones) (Figs 59, 60); (4) maxillary and labial palpi with multiple secondary segmentation (Fig. 59; Pl. 53 Figs 7-8 in EATON, 1883-1888); (5) legs with 2- or 3-segmented tarsi (Fig. 74 in PHILLIPS, 1930); (6) tergallae with tufts of fibrillous filaments (in *Chiloporter* and *Mirawara*) or without (in *Ameletopsis*); (7) in the subimago the lateral sclerotized pigmented area of mesonotum occupies sublateroscutum* between the pigmented parts of latero parapsidal and lateral scutal sutures* (Figs 57, 58) (as in Nesameletidae).

C) FOSSIL SIPHLONUROIDEA OF UNCERTAIN FAMILIES

Since the majority of the fossil Siphonuroidea species are known as a single stage or only as details of one stage and the diagnoses of the recent families of Siphonuroidea include character complexes of various stages (larvae, subimagines, imagines, and eggs), the fossils cannot with certainty be attributed to a family.

Winged stages or fragments of winged stages are known of the following Mesozoic (Jurassic and Cretaceous) genera of Siphonuroidea *fam. incert.*: *Stackelbergisca* TSHERNOVA, 1967; *Olgisca* DEMOULIN, 1970; *Cretoneta* TSHERNOVA, 1971 (transferred from Leptophlebiidae and redescribed by KLUGE, 1993); *Proameletus* SINITSHEKOVA, 1976, and of the following Palaeogenic species from Baltic amber: *Baltameletus* DEMOULIN, 1968; *Balticophlebia* DEMOULIN, 1968; *Xenophlebia* DEMOULIN, 1968, which was originally placed in Leptophlebiidae, probably also belongs to the Siphonuroidea.

A number of Mesozoic genera is described from larvae which have a Siphonuroidea-like appearance (swimming specialization of the body and primary swimming setae on caudal filaments). However, these larvae can not be attributed even to the superfamily with certainty since the same larval appearance is also present in other ephemeroteran superfamilies.



Figs 54-60. Ameletopsidae. 54-57 - *Ameletopsis perscitus*: 54, 55 - male imago: 54 - pterothorax (ventral view, nerve ganglions shown by interrupted lines), 55 - the same (lateral view); 56 - female subimago, apex of abdomen; 57 - right half of subimaginal skin of mesonotum. 58-60 - *Chiloporter* sp.: 58 - subimaginal cuticula extracted from mature male larva; 59-60 - left maxilla of larva: 59 - dorsal view (appendages of the next instar inside the old ones shown by interrupted lines), 60 - view from inner-apical side (five movable appendages removed). Labeling terms as in Figs 36-42, m = muscle.

DISCUSSION

Each of the Siphonuroidea families is probably holophyletic, based on the presence of unique characters (see above). Some of these characters may be apomorphic. The phylogenetic relationships of these families remain uncertain.

Relationships of Siphonuroidea with Baetoidea and Heptagenioidea

TOMKA & ELPERS (1991) suggest a phylogenetic tree for Ephemeroptera, in which some Siphonuroidea families are regarded as being more closely related to the Baetoidea and to the Setisura than to other siphonuroid families. This paraphyletic nature of the Siphonuroidea is quite probable. However, some of the positions in the phylogenetic tree and some of the synapomorphies on which this tree is based appear to be doubtful. The Setisura, together with all Pisciforma other than Ametropodidae, are supposed to be a sister group of Ametropodidae on the basis of a single synapomorphy: absence of a nerve ganglion in abdominal segment I (this ganglion is moved to the metathorax and united with the metathoracic ganglion) (character 4 of Fig. 1 in TOMKA & ELPERS, 1991). Ameletopsidae, Acanthametropodidae, and Metretopodidae are assumed to be related to Baetoidea and Setisura on the basis of a single synapomorphy: absence of a nerve ganglion in abdominal segment VIII (character 6 of Fig. 1 in TOMKA & ELPERS, 1991). According to this tree, the same changes (dislocation of nerve ganglions from segments I and VIII) must have taken place independently in the Furcatergalia. Similar changes in the nervous system – the forward relocation of ganglia and their integration with others – have occurred independently in various insect taxa, therefore such characters are not sufficient to prove the monophyly of the group. Metretopodidae are viewed as being related to the Baetoidea and Setisura since they have intercalaries in the cubital field of the forewing (character 10 of Fig. 1 in TOMKA & ELPERS, 1991). However, a similar venation is also present in the genus *Metreletus* of the Ameletidae. On the other hand, in Coloburiscinae (which belong to the Setisura) the venation of the cubital area of the forewing is exactly the same as in the Siphonuridae *s. str.*, in *Ameletus*, and in the Southern Hemisphere Siphonuroidea. The Metretopodidae are assumed to be related to Setisura on the basis of the following synapomorphy: 2-segmented labial palp (i. e., second and third segments of labial palp are fused together; character 14 of Fig. 1 in TOMKA & ELPERS, 1991). However, the same fusion of these segments takes place independently in various other groups of Ephemeroptera (e. g. in *Brachycercus* of the family Caenidae, in *Baetopus* of the family Baetidae). At the same time in some Setisura (e. g. in Coloburiscinae) a rudimentary suture between the second and the third segments of the labial palp is present.

TOMKA & ELPERS (1991) regard Ameletopsidae and Acanthametropodidae as being closely related and they give three synapomorphies of these families: (1) visceral tracheae are present only in abdominal segments II-VIII; (2) larval tibiae are shorter than tarsi; (3) larval stomodaeum with a crop (characters 9 of Fig. 1 in TOMKA & ELPERS, 1991). Actually the characters (1) and (2) are not constant within the Ameletopsidae and the characters (1) and (3) are not described for the Acanthametropodidae. Moreover, these characters are found in some other mayfly families (LANDA & SOLDAN, 1985). Therefore, the relationship of Ameletopsidae and Acanthametropodidae is not proven.

Status of Dipteromimidae

Formerly the genus *Dipteromimus* (which includes the single Japanese species *D. tipuliformis* McLACHLAN, 1875) was placed in the subfamily Siphonurinae or in the family Siphonuridae s. str. For this genus we establish the new family Dipteromimidae, because all common characters of Siphonuridae and *Dipteromimus* are only symplesiomorphic and the unique apomorphic characters of Siphonuridae s. str. are absent in *Dipteromimus*: the female imago of *D. tipuliformis* does not have a sclerotized copulatory pouch and the eggs of this species lack spots formed by the tops of threads (Fig. 64). The imago and larva of *Dipteromimus* have sufficient unique characters to be distinguished from Siphonuridae s. str. and other families.

Composition and characteristics of Acanthametropodidae

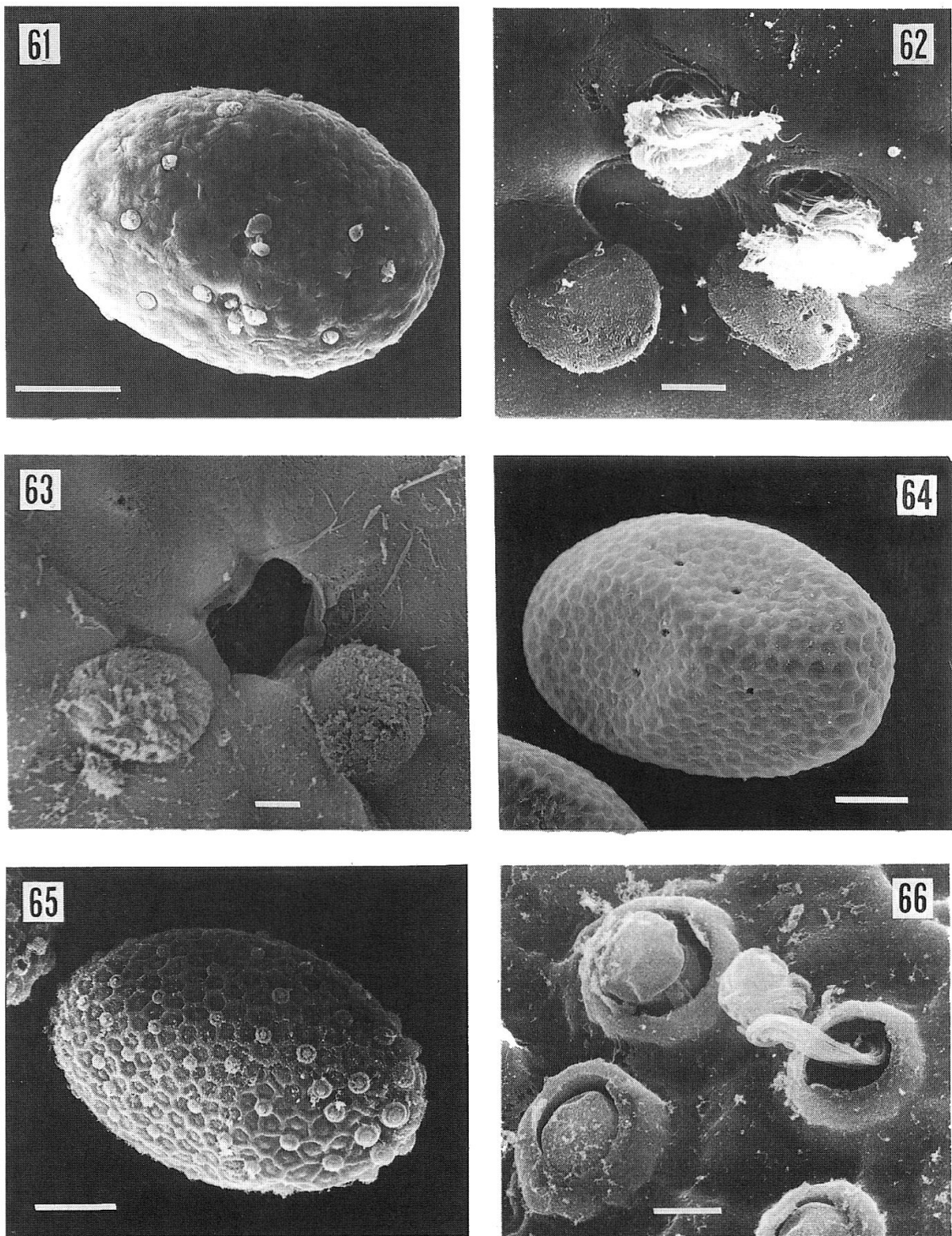
EDMUNDS & KOSS (1972) place the recent genera *Acanthametropus*, *Analetris*, *Siphuriscus*, and the Jurassic genus *Stackelbergisca* in the Acanthametropodinae.

Siphuriscus is known only as a male imago (ULMER, 1920) and a female subimago (DEMOULIN, 1955). DEMOULIN (1955) placed the genus in Isonychiidae which is more appropriate because the claws of the middle and hind legs are similar, the form of the cubital field is more similar to Isonychiidae than to Siphonuridae, and the paracercus is rudimentary. However, it is necessary to study larvae to confirm this.

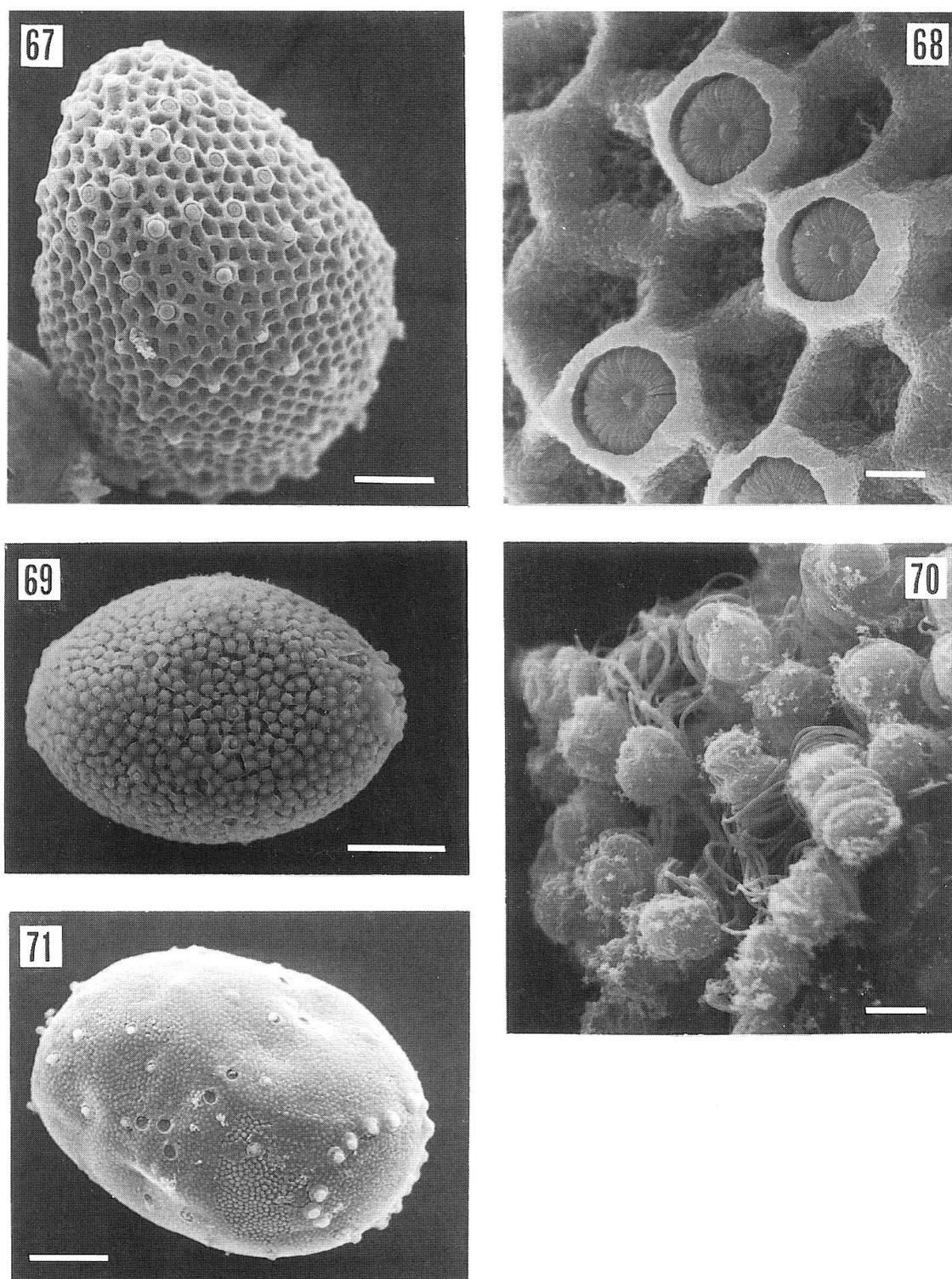
EDMUNDS & KOSS (1972) place the fossil *Stackelbergisca* in the subfamily Acanthametropodinae due to the two following characters: the legs of the larvae are directed posteriorly and the mouthparts are carnivorous. However, these two characters were not described in the original description by TSHERNOVA (1967). The legs of *Acanthametropus* and *Analetris* larvae have the same position as other Ephemeroptera. If *Stackelbergisca* larvae did have carnivorous mouthparts it would be a good character, but TSHERNOVA (1967) mentions only that "the mandibles are poorly preserved".

DEMOULIN (1974) placed *Analetris* and *Acanthametropus* in different subfamilies. However, we find enough synapomorphies to leave them together in the family Acanthametropodidae. In this we agree with EDMUNDS & KOSS (1972) who placed them in the same group, the subfamily Acanthametropodinae.

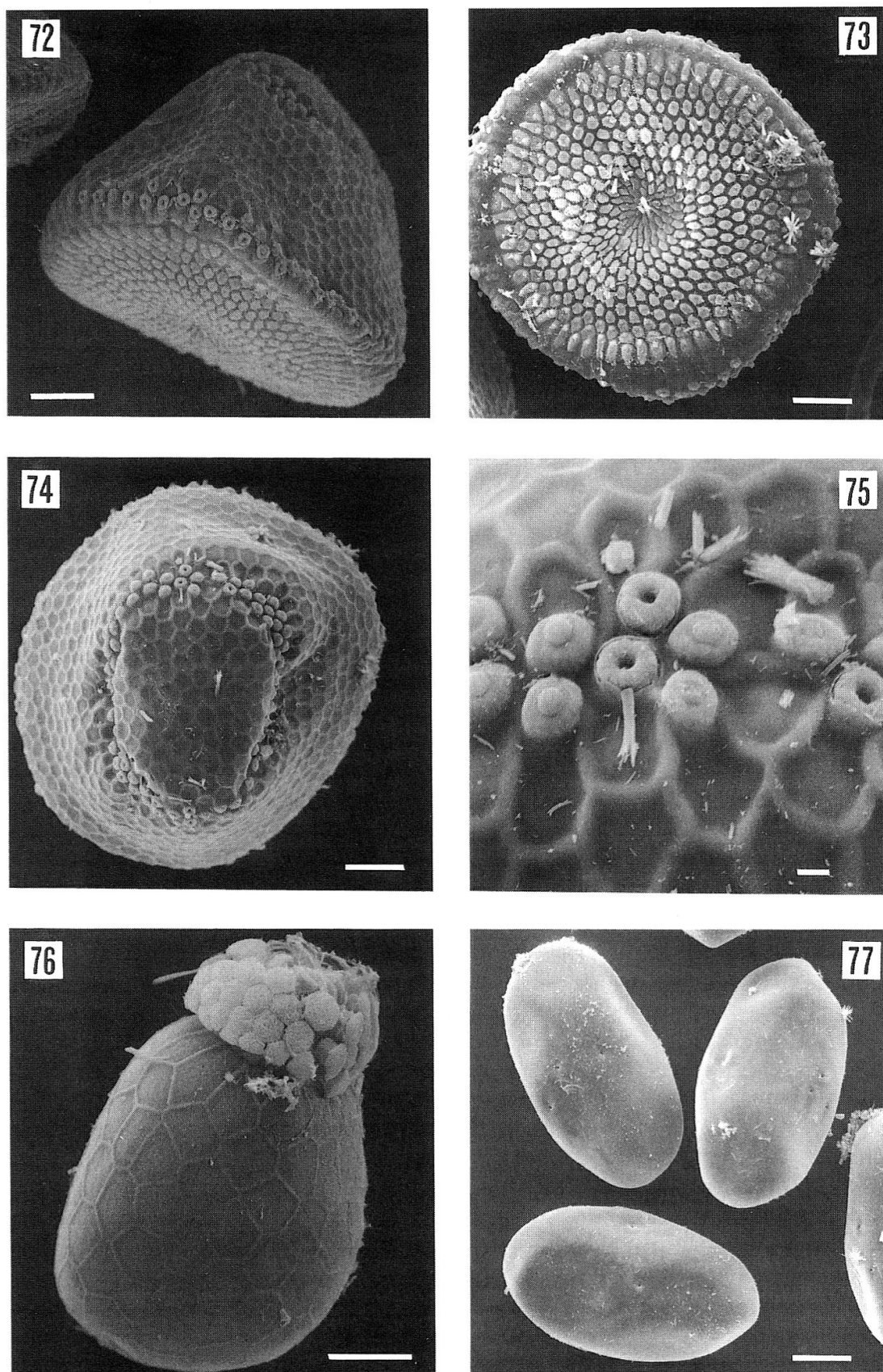
Isonychia polita BAJKOVA, 1970 (described as a single male imago from the Russian Far East), is conspecific with *Acanthametropus nikolskyi* TSHERNOVA, 1948 (known only as larvae). This synonymy was published in "Key to the insects of Far-Eastern USSR" (TSHERNOVA *et al.*, 1986) without comment. The identification of "*Isonychia*" *polita* as *Acanthametropus nikolskyi* was made by comparing the *Isonychia polita* holotype (male imago) with parts of the *Acanthametropus nikolskyi* subimago, which was well developed in the mature female larva collected from the river Never in 1948. This larva was described and figured by TSHERNOVA (1952) (Figs 54-57) (see also Figs 23-27, 34, 35, 72-75 of this paper). Both specimens have the following characters: (1) a pair of pointed projections below the bases of the antennae (Fig. 31); (2) a pair of pointed projections lateral on the pronotum (Fig. 31); (3) a pair of pointed projections on the hind margin of the pronotum; (4) unpaired pointed projection on the prosternum (Pl. 57 Figs 14-15 in TSHERNOVA *et al.*, 1986); (5) CuP of forewing relatively long (Figs 32, 34); (6) tibia greatly shortened, shorter than the first tarsal segment (Fig. 31); (7) claws of each leg dissimi-



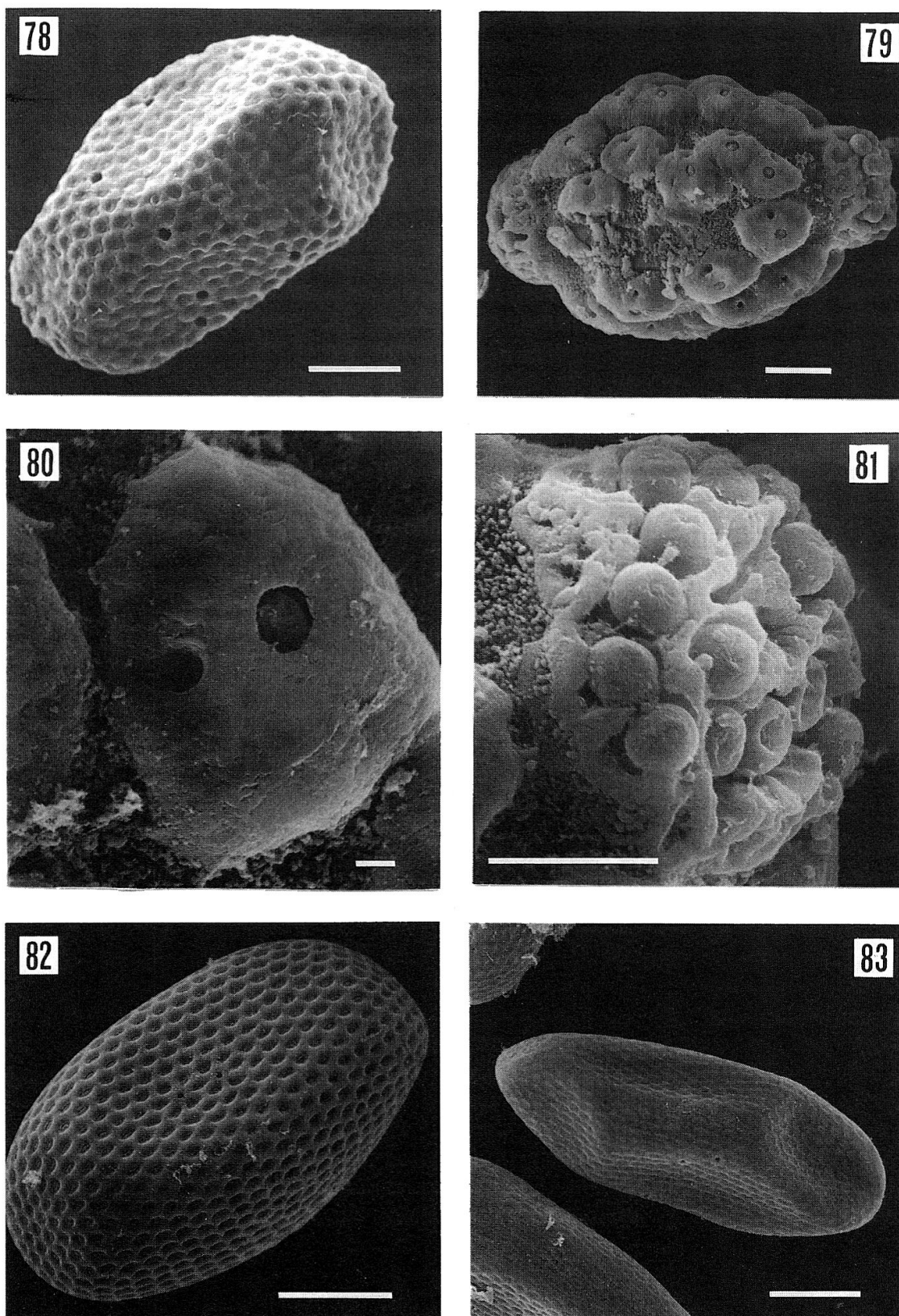
Figs 61-66. Eggs of Siphonuridae, Dipteromimidae, and Ameletidae. 61, 62 - *Siphonurus lacustris*, 63 - *Siphonisca aerodromia*, 64 - *Dipteromimus tipuliformis*, 65, 66 - *Ameletus*, undescribed species. (Scale line represents: 50 μ m in Figs 61, 64, 65; 5 μ m in Figs 62, 63, 66)



Figs 67-71. Eggs of Metretopodidae. 67, 68 - *Metretopus borealis*, 69, 70 - *Siphloplecton* sp. 1, 71 - *Siphloplecton* sp. 2.
(Scale line represents: 50 μ m in Figs 67, 69, 71; 5 μ m in Figs 68, 70)



Figs 72-77. Eggs of Acanthametropodidae, Ametropodidae, and Oniscigastridae. 72-75 - *Acanthametropus nikolskyi*, 76 - *Ametropus fragilis*, 77 - *Oniscigaster* sp. (Scale line represents: 50 μ m in Figs 72-74, 76, 77; 5 μ m in Fig. 75).



Figs 78-83. Eggs of Nesameletidae, Rallidentidae, and Ameletopsidae. 78 - *Nesameletus flavitinctus*, 79-81 - *Rallidens mcfarlanei*, 82 - *Ameletopsis perscitus*, 83 - *Chiloporter* sp. (Scale line represents: 50 mm in Figs 78, 79, 82, 83; 5 mm in Figs 80, 81)

lar; (8) paracercus as large as cerci. These characters are all absent in *Isonychia*. This combination of characters is absent in any other known mayfly, thus these two specimens are regarded as being conspecific.

Position of Oniscigastridae

MCCAFFERTY (1991) joined Oniscigastridae (his infraorder Venulata) with Furcatergalia into the suborder Rectracheata on the basis of the single following synapomorphy: presence of tracheal anastomoses in abdominal segments IV-VII. However, such a character is not sufficient to prove the monophyly of Rectracheata, because in certain abdominal segments tracheal anastomoses occur independently in different groups of Ephemeroptera. Particularly in the segments IV-VII, anastomoses are present not only in Oniscigastridae and Furcatergalia, but also in some representatives of the Ameletopsidae – in *Chiloporter*, but not in *Ameletopsis* and *Mirawara* (LANDA & SOLDAN, 1985).

Position of Rallidentidae

Although this family has some similar characters to the Setisura, most of these are not synapomorphic. (1) The presence of gills on the maxilla is not synapomorphic, because in Setisura (only in the superfamily Oligoneurioidea) gills are situated on the cardo, while in Rallidentidae the gill is situated on the stipes. (2) The presence of ventral fibrillose portion of tergalia can not be a unique synapomorphy of these groups, because in some of the Ameletopsidae (in *Chiloporter* and *Mirawara*, but not in *Ameletopsis*) such ventral fibrillose portions of the tergaliae are also present. The single probable synapomorphy between Rallidentidae and Setisura concerns the thorax: (3) in the imago and subimago the posterior arm of prealar bridge is rudimentary and does not reach the incision of scutum (Fig. 50; cf. Fig. 2); nevertheless, this synapomorphy is not sufficient to move the Rallidentidae to the Setisura. Therefore, we retain it in the paraphyletic taxon Siphonuroidea until further proof of their relationship to Setisura is given.

Position of Ameletopsidae

In KLUGE's (in press) publication the Ameletopsidae are placed in the separate infraorder Ameletopsimorpha, which, in contrast to the infraorders Bidentiseta and Tridentiseta, is characterized by the presence of five dentisetae on the larval maxilla. Subsequent examination of these five "dentisetae" in Ameletopsidae larvae has revealed that these movable appendages (which have exactly the same structure in all Ameletopsidae genera) do not originate from setae and thus cannot be dentisetae, because the new ones develop inside the old ones (Fig. 59). However, the present knowledge of the maxillary structure of the Ephemeroptera does not allow a phylogenetic interpretation.

Relationship of Ameletidae and Metretopodidae

These two families have common characters which probably are synapomorphies: (1) elongated lateroparapsidal suture* on mesonotum of the winged stages (Figs 16, 17, 22), and (2) similar structure of the egg chorion in the majority of the Ameletidae and in *Metretopus* (Figs 65-68). It can be assumed that these characters indicate a close relationship of these two families.

Relationship of Acanthametropodidae and Ametropodidae

These two families have similarities in the structure of the larvae, which demonstrates their psammophilous adaptation: the body is flattened, the legs (at least the middle and hind pairs) have shortened tibiae and elongated claws. McCafferty (1991) established the infraorder Arenata for mayflies with this type of larval structure, placing the families Acanthametropodidae, Ametropodidae, and Pseudironidae in this infraorder. Recent investigations of the maxilla (Kluge, in press) and thoracic structures (Kluge, unpublished data) show that the Pseudironidae must belong to the superfamily Heptagenioidea, and their similarity to the Acanthametropodidae and the Ametropodidae is the result of convergency. Probably the similarity of the Acanthametropodidae to the Ametropodidae is also the result of convergency, as it was assumed by McCafferty & Edmunds (1979) and Landa & Soldan (1985).

Relationships of families in Southern Hemisphere group

It is possible that the Southern Hemisphere group of families is holophyletic, because all of the examined representatives have the same progressive character: the furcasternal protuberances* of the imaginal mesothorax are separated by a median invagination* at least in their posterior portion (Figs 37, 44, 51, 54). The presence of this invagination is determined by the position of the metathoracic nerve ganglion (Figs 37, 51, 54), which is displaced from the metathorax to the furcasternum of the mesothorax between the bases of the subalar-sternal muscles (which are attached to the furcasternal protuberances and determine their form). In contrast, the structure of mesothoracic furcasternum is primitive in all examined Northern Hemisphere Siphonuroidea: the furcasternal protuberances (and bases of the subalar-furcasternal muscles) are contiguous, and the metathoracic nerve ganglion is situated in the metathorax (Fig. 31). The progressive structure of the thorax sterna in the Southern Hemisphere Siphonuroidea is not a unique apomorphy, since the same structural changes of the thorax have occurred independently in other groups of Ephemeroptera: in Baetoidea (Baetidae have the progressive structure, while Siphlaenigmatidae have the primitive one), in Setisura (Heptagenioidea have the progressive structure, while Oligoneurioidea have the primitive one), in Furcatergalia (Ephemeroidea have the primitive structure, while the others have the progressive one). Thus this character is not enough to prove the holophyly of the group with certainty.

Probably, the Siphonuroidea have a Northern Hemispherean (Laurasian) origin, and one of its representatives penetrated to Gondwana and radiated there into four families – Oniscigastridae, Nesameletidae, Ameletopsidae, and Rallidentidae. The formation of these families must have occurred before the separation of South America, Antarctica, Australia, and New Zealand. Since these families are not present on the other Gondwanian land masses India, Madagascar, and Africa, they were probably formed after the connections to these land masses had been severed. However, since the representatives of these families are generally cool-adapted, an alternative explanation is that these families were formed earlier and have become extinct in Africa, India, and Madagascar as a result of climatic change. The relationships within the families Ameletopsidae, Oniscigastridae, and Nesameletidae reflect the sequence of geologic events (Gonser, 1990): New Zealand separated first, while Australia and southern South America remained connected via an Antarctic land bridge (Smith & Hallam, 1970; Raven & Axelrod, 1972; Markl, 1974; Schönenberg, 1975; Tarling, 1981; Savage, 1987). Within all of these families the rep-

representatives of southern South America and Australia are more closely related to each other than to those of New Zealand (EDMUNDS, 1975, 1981). Similar relationships have been documented in numerous biogeographical studies on other taxonomic groups (BRUDIN, 1966; ZWICK, 1974, 1981; McLELLAN, 1975; COWLEY, 1978; PESCADOR & PETERS, 1980; TOWNS & PETERS, 1980; CAMPBELL & SUTER, 1988).

Relationship of Nesameletidae, Rallidentidae, and Ameletopsidae

The families Nesameletidae and Ameletopsidae have the same form of the lateral sclerotized pigmented area of subimaginal mesonotum (Figs 49, 57, 58) and the same form of mesothoracic furcasternal invagination* (Figs 44, 54). In Rallidentidae the structure of the subimaginal mesonotum has not been examined. The form of mesothoracic furcasternal invagination differs from that of Nesameletidae and Ameletopsidae, being more progressive (Fig. 51). In the three mentioned families the structure of the larval maxilla is highly specialized and quite dissimilar, but one common apomorphic character can be identified: the muscle which runs from the outer side of the stipes to the inner side of the galea-lacinia is strongly thickened (Fig. 59).

Relationship of Siphonuridae and Oniscigastridae

These two families have the same form of the lateral sclerotized pigmented area of the subimaginal mesonotum (Figs 4, 8, 40, 41). It is not clear if this character is synapomorphic or symplesiomorphic. If it is synapomorphic, it contradicts the proposition that the Southern Hemisphere group of families is holophyletic.

Relationship of Ameletidae, Nesameletidae, and Rallidentidae

On the basis of egg structure KOSS AND EDMUNDS (1974) proposed that Nesameletidae ("Metamonius-complex"), Ameletidae ("Ameletus-complex"), and Rallidentidae have the same origin due to the presence of "large-mesh reticulation on at least part of the chorion" in all of these groups. Besides Ameletidae and Nesameletidae (Figs 65, 78), a similar reticulation is also found in some Metretopodidae (Figs 67, 68), Acanthametropodidae (Figs 72-75), Ameletopsidae (Fig. 82, 83), and in Dipteromimidae (Fig. 64). Such reticulation is absent in some of the other representatives of Metretopodidae (Figs 69, 71). In a number of other Ephemeroptera taxa (e. g. in Baetidae) such reticulation can be present or absent in different species of the same genus, thus it is not a good indicator of phylogenetic relationships. The same groups were united into the family Rallidentidae sensu TOMKA & ELPERS, 1991, on the basis of a proposed synapomorphy – relatively narrow base of the mandibles (character 8 on Fig. 1 and Fig. 4 in TOMKA & ELPERS, 1991). Actually, these groups have specialized mandibles, but their structure is quite dissimilar in Ameletidae, Nesameletidae, and Rallidentidae. Therefore, a common origin of Ameletidae with Nesameletidae and Rallidentidae seems to be doubtful.

ACKNOWLEDGMENTS

We thank Dr. G. LAMPEL for his hospitality and Dr. I. TOMKA for constructive remarks. Drs. J. W. EARLY, G. E. EDMUNDS, K. E. GIBBS, T. FINK, S. ISHIWATA, B. C. KONDRATIEFF, W. L. PETERS, Y. TAKEMON and J. ZLOTY are thanked for the gift of diverse specimens. The scanning electron micrographs were taken in the ETH Zurich with the help of Drs. M. MÜLLER and R. HERMANN. We are grateful for the technical assistance of M. H. GACHOUD. The present study was supported by a grant from the "Fondation du Fonds de la Recherche de l'Université de Fribourg".

REFERENCES

- BAJKOVA, O. Y. 1970. New and little known species of mayflies (Ephemeroptera) from the Basin of the Amur River. *Ent. Obozr.* 49(1): 146–155 [in Russian].
- BERNER, L. 1978. A review of the mayfly family Metretopodidae. *Trans. Amer. Ent. Soc.* 104: 91–137.
- BRUDIN, L. 1966. Transantarctic relationships and their significance as evidence by chironomid midges. *K. Sven. Vetenskapsakad. Handl.* 11: 1–472.
- BURIAN, S. K. & GIBBS, K. E. 1988. A redescription of *Siphonisca aerodromia* NEEDHAM (Ephemeroptera: Siphonuridae). *Aquatic Insects* 10(4): 237–248.
- CAMPBELL, I. C. & SUTER, P. J. 1988. Three new genera, a new subgenus and a new species of Lep-tophlebiidae (Ephemeroptera) from Australia. *J. Aust. ent. Soc.* 27: 259–273.
- CARPENTER, F. M. 1979. Lower Permian insects from Oklahoma. Part 2. Orders Ephemeroptera and Palaeodictyoptera. *Psyche* 86(2-3): 261–290.
- COWLEY, D. R. 1978. Studies on the larvae of New Zealand Trichoptera. *N. Z. J. Zool.* 11: 639–750.
- DAY, W. C. 1953. A new mayfly genus from California (Ephemeroptera). *Pan. Pac. Ent.* 29(1): 19–24.
- DEMOULIN, G. 1955. Brève note sur la position systématique de *Siphuriscus chinensis* ULMER (1920) (Ephemeroptera). *Bull. Inst. Roy. Sci. Nat. Belg.* 31(80): 1–2.
- DEMOULIN, G. 1970. Remarques critiques sur des larves "Ephéméromorphes" du Permien. *Bull. Inst. Roy. Sci. Nat. Belg.* 46(3): 1–10.
- DEMOULIN, G. 1974. Remarques critiques sur les Acanthametropodidae et sur certaines formes affines (Ephemeroptera, Siphonuridae). *Bull. Inst. Roy. Sci. Nat. Belg.* 50(2): 1–5.
- EATON, A. E. 1883–1888. A revisional monograph of recent Ephemeridae or mayflies. *Trans. Linn. Soc. London (Zool.)* 3: 1–352.
- EDMUNDS, G. F., Jr. 1972. Biogeography and evolution of Ephemeroptera. *Ann. Rev. Entomol.* 17: 21–42.
- EDMUNDS, G. F., Jr. 1975. Phylogenetic Biogeography of Mayflies. *Ann. Missouri Bot. Gard.* 62: 251–263.
- EDMUNDS, G. F., Jr. 1981. Response to R. Melville: "Vicarious Plant Distribution and Paleogeography of the Pacific Region". In: NELSON, G. & D. E. ROSEN (Eds) *Vicariance Biogeography: A Critique*, pp. 287–297. Columbia University Press, New York.
- EDMUNDS, G. F., Jr. & KOSS, R. W. 1972. A review of the Acanthametropodinae with a description of a new genus. *Pan. Pac. Ent.* 48(2): 136–144.
- EDMUNDS, G. F., JR., JENSEN, S. L. & BERNER, L. 1976. *The mayflies of North and Central America*. Univ. Minnesota Press, Minneapolis, 330 pp.
- GONSER, T. 1990. *Beiträge zur Biologie südneotropischer Ephemeropteren*. [Contribution to the Biology of southern Neotropical Ephemeroptera]. Ph. D. Thesis, University of Freiburg, Germany.
- HANDELSCH, A. 1906–1908. *Die fossilen Insekten, und die Phylogenie der rezenten Formen*. Engelmann, Leipzig, 1430 pp.
- KEFFERMÜLLER, M. 1959. Nowe dane dotyczące jetek (Ephemeroptera) z rodzaju *Ametropus* ALB. i *Behningia* LEST. *Poznan. Towar. Przyjaciół Nauk, Pr. Kom. Biol.*, 19(5): 3–32.
- KLUGE, N. J. 1989. A question of the homology of the tracheal gills and paranotal processi of the mayflies larvae and wings of the insects with reference to the taxonomy and phylogeny of the order Ephemeroptera. In: CHTENIYA PAMYATI N. A. KHOLODKOVSKOGO (Eds) *Nauka*, Leningrad, 48–77 [in Russian].
- KLUGE, N. J. 1993. New data on mayflies (Ephemeroptera) from mesozoic and cenozoic resins. *Pal. J.* 27: 35–49.
- KLUGE, N. J. 1994. Pterothorax structure of Mayflies (Ephemeroptera) and its use in systematics. *Bull. Soc. Ent. France* 99 (1): 41–61.
- KLUGE, N. J. (in press). Phylogeny and higher classification of Ephemeroptera. In: CORKUM, L. & CIBOROWSKI, J. (Eds) *Current directions in research on Ephemeroptera*. Canadian Scholars' Publ., Toronto.
- KLUGE, N. J., NOVIKOVA, E. A., & BRODSKY, A. K. 1984. Movements of larvae of the Ephemeroptera during swimming, respiration and cleaning. *Zool. zhurn.* 63(9): 1345–1354 [in Russian].
- KOSS, R. W. & EDMUNDS, G. F. 1974. Ephemeroptera eggs and their contribution to phylogenetic studies of the order. *Zool. J. Linn. Soc.* 55: 267–349.
- LANDA, V. & SOLDAN, T. 1985. Phylogeny and higher classification of the order Ephemeroptera: a discussion from the comparative anatomical point of view. *Ceskoslovenska Akademie Ved, Studie CSAV* 4: 1–121.
- LEHMKUHL, 1976. Additions to the taxonomy, zoogeography and biology of *Analetris eximia* (Acanthametropodinae: Siphonuridae: Ephemeroptera). *Can. Ent.* 108: 199–207.
- MCCAFFERTY, W. P. 1991. Towards a phylogenetic classification of the Ephemeroptera (Insecta): a commentary on systematics. *Ann. Entomol. Soc. Am.* 84: 343–360.
- MCCAFFERTY, W. P. & EDMUNDS, G. F. 1979. The higher classification of the Ephemeroptera and its evolutionary basis. *Ann. Entomol. Soc. Am.* 72: 5–12.

- MCLELLAN, I. D. 1975. The Freshwater Insects. In: KUSCHEL, G. (Ed.) *Biogeography and Ecology of New Zealand*, 537-559. Dr. W. Junk Publishers, The Hague.
- MARKL, R. G. 1974. Evidence for the break-up of eastern Gondwanaland by the early Cretaceous. *Nature* 251: 196-200.
- PENNIKET, J. G. 1966. Notes on New Zealand Ephemeroptera. IV: A new Siphonurid subfamily: Ralidentinae. *Rec. Cant. Mus.* 8(2): 163-175.
- PESCADOR, M. L. & PETERS, W. L. 1980. Phylogenetic relationships and zoogeography of cool-adapted Leptophlebiidae (Ephemeroptera) in southern South America. In: FLANNAGAN, J. F. & MARSHALL, K. E. *Advances in Ephemeroptera Biology*, 43-55. Plenum Press, N.Y. and London.
- PHILLIPS, J. S. 1930. A revision of New Zealand Ephemeroptera. Part 1. *Trans. Proc. N. Z. Inst.* 61: 271-334.
- RAVEN, P. H. & AXELROD, D. I. 1972. Plate tectonics and Australia's paleobiogeography. *Science* 176: 1379-1386.
- SAVAGE, H. M. 1987. Biogeographic classification of the Neotropical Leptophlebiidae (Ephemeroptera) based upon geographical centers of ancestral origin and ecology. *Studies on Neotropical Fauna and Environment* 22(4): 199-222.
- SCHÖNENBERG, R. (Ed.) 1975. *Die Entstehung der Kontinente und Ozeane in heutiger Sicht*. Wissenschaftliche Buchgesellschaft, Darmstadt, pp. 380.
- SMITH, A. G. & HALLAM, A. 1970. The fit of the southern continents. *Nature* 225: 139-144.
- SÖDERSTRÖM, O. & NILSSON, J. 1986. Redescription of *Parameletus chelifera* BENGTSSON and *P. minor* (BENGTSSON), with keys to nymphal and adult stages of the Fennoscandinavian species of Siphonuridae (Ephemeroptera). *Ent. Scand.* 17: 107-117.
- STUDEMANN, D., LANDOLT, P. & TOMKA, I. 1988. Morphology and taxonomy of imagines and eggs of Central and Northern European Siphonuridae (Ephemeroptera). *Mitt. Schweiz. Ent. Ges.* 61: 303-328.
- STUDEMANN, D. & TOMKA, I. 1991. European Siphonuridae (Ephemeroptera): a phylogenetic system for the four genera. In: ALBA-TERCEDOR, J. & SANCHEZ-ORTEGA, A. (Eds) *Overview and strategies of Ephemeroptera and Plecoptera*, 103-114. Sandhill Crane Press, Gainesville, Florida.
- STUDEMANN, D., LANDOLT, P. & TOMKA, I. 1994. Biochemical investigations of Siphonuridae and Ameletidae (Ephemeroptera). *Arch. Hydrobiol.* 130 (1): 77-92.
- TARLING, D. H. 1981. The geologic evolution of South America with special reference to the last 200 million years. In: CICHON, R. L. & CHIARELLI, A. B. (Eds) *Evolutionary Biology of the New World Monkeys and Continental Drift*, 1-41. Plenum Press, New York.
- TILLYARD, R.J. 1933. The mayflies of the Mount Kosciusko Region. I. (Plecoptera). Introduction and family Siphonuridae. *Proc. Linn. Soc. New South Wales* 58: 1-32.
- TOMKA, I. & ELPERS, C. 1991. Problems of the phylogeny of the Ephemeroptera. In: ALBA-TERCEDOR, J. & SANCHEZ-ORTEGA, A. (Eds) *Overview and strategies of Ephemeroptera and Plecoptera*, 115-134. Sandhill Crane Press, Gainesville, Florida.
- TOWNS, D. R. & PETERS, W. L. 1980. Phylogenetic relationships of the Leptophlebiidae (Ephemeroptera) of New Zealand. In: FLANNAGAN, J. F. & MARSHALL, K. E. *Advances in Ephemeroptera Biology*, 57-69. Plenum Press, N.Y. and London.
- TSHERNOVA, O. A. 1952. Mayflies Ephemeroptera of basin of river Amur and adjoining waters and their role in nutrition of Amurian fishes. *Tr. Amur. Ichtiol. Exped. 1945-1959.* 3: 229-360 [in Russian].
- TSHERNOVA, O. A. 1965. Some fossil mayflies (Ephemeroptera, Mithodontidae) from Permian-beds of the Urals. *Ent. Obozr.* 44: 353-361 [in Russian].
- TSHERNOVA, O. A. 1967. Mayfly of the recent family in Jurassic deposits of Transbaikalia (Ephemeroptera, Siphonuridae). *Ent. Obozr.* 46 (2): 322-326 [in Russian].
- TSHERNOVA, O. A., KLUGE, N. J., SINITSHEKOVA, N. D. & BELOV V. V. 1986. Order Ephemeroptera. *Key to the insects of Far-Eastern USSR* 1: 99-142 [in Russian].
- UÉNO, M. 1931. Contribution to the knowledge of Japanese Ephemeroptera. *Ôtsu Hydrobiological Station, Kyoto*: 189-231.
- ULMER, G. 1920. Neue Ephemeropteren. *Archiv für Naturgeschichte* 85A(11): 1-80.
- ZWICK, P. 1974. Das phylogenetische System der Plecoptera. *Entomologica Germanica* 1(1): 50-57.
- ZWICK, P. 1981. Plecoptera. In: KEAST, A. (Ed.) *Ecological Biogeography of Australia*, 1171-1182. W. Junk Publishers, The Hague.

(received June 15, 1994; accepted in revised form February 28, 1995)