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Morphology and taxonomy of imagines and eggs of Central and Northern European Siphlonuridae (Ephemeroptera)

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Imagines and eggs of the Central and Northern European species of Siphlonuridae were examined with the scanning electron microscope (SEM) and the stereo microscope. Morphological comparison indicates a close relationship of *Ameletus* to *Metreletus*, and of *Siphlonurus* to *Parameletus*. A key is provided for imagines.

INTRODUCTION

The adult mayfly can be identified by its morphological structures such as wing pattern, leg parts, genital organs etc. The determination of the male is relatively simple with its genital apparatus, penis and styliger. The sclerotinised structures are stable and invariable in the animals of one species and thus well-qualified. The identification of the females is more difficult when they are taken without males. The last abdominal segments bearing the subgenital as well as the subanal plate give some helpful indications for the determination. Some authors (DEGRANGE, 1955; DEMOULIN, 1951; ELLIOTT & HUMPESCH, 1983; FIZAINE, 1931; LANDA, 1969; MALZACHER; 1981; PUTHZ, 1977 a, b; TANASIJEVIC, 1974; UJHELEYI, 1959) partially describe the adult stage of some isolated species of Siphlonuridae. SOEDERSTROEM, & NILSSON (1986) give a complete description of the two Scandinavian *Parameletus* species.

The delicate surface and the dimensions of the eggs prevented numerous investigations. BENGTSSON (1913) investigated the eggs of 28 Palaearctic species and at the same time, MORGAN (1913) published a description of the eggs of 13 species in North America. DERANGE (1960) studied 51 European Ephemeroptera species and illustrated 34 of them. He was the first to find and to describe the micropyles of the mayfly eggs. KOSS (1968, 1973) found the significance of the eggs to taxonomic and phylogenetic studies of American Ephemeroptera by comparison of the egg structures of representatives of different families or genera. Recent studies describe and compare egg structures of the species of a genus (GAINO *et al.*, 1987; KOPELKE 1980; KOPELKE & MUELLER-LIEBENAU 1981 a, b, 1982; MALZACHER, 1982).

The present work describes the morphological characters of all European species of the family Siphlonuridae, except for some endemic Iberian species. We used the scanning electron microscope (SEM) method for our investigations. We show and compare the male genital apparatus and describe the final abdominal sternites in females as well as leg parts to have further data for the taxonomy and provide a key of determination for adult males and females. Additionally we examine the eggs and demonstrate the relationship of structures for the different genera.

MATERIAL AND METHODS

Material

The representatives of the species of Siphlonuridae for our investigations were captured in localities throughout Europe.

Siphlonurus aestivalis (EATON, 1903)

- Bievjavaejjokka/Aidejavrre, Kautokeino (Finnmark, N) 24.7.1987,
- Breg/Hüfingen (Baden-Württemberg, FRG) 24.5.1987,
- Fichtenbergerrot/Mainhardt (Baden-Württemberg, FRG) 23.5.1987,

Siphlonurus alternatus (SAY, 1824)

- Vindelälven/Vindeln (Västerbotten, S) 18.7.1987,

Siphlonurus armatus EATON, 1870

- Sperbersbach/Gailenkirchen (Baden-Württemberg, FRG) 23.5.1987,

Siphlonurus croaticus ULMER, 1919

- Obrh/Pudob (Slovenia, YU) 28.5.1985,
- Zwiefalter Ach/Zwiefalten (Baden-Württemberg, FRG) 25.5.88,

Siphlonurus lacustris EATON, 1870

- Gérine/Marly (Fribourg, CH) 19.6.1984,
- Fätschbach/Argseeli (Uri, CH) 4.7.1985,
- Bregenzer Ach/Bregenz (Vorarlberg, A) 3.7.1985,

Parameletus chelifer BENGTSSON, 1908

- Bievjavaejjokka/Aidejavrre, Kautokeino (Finnmark, N) 24.7.1987,

Parameletus minor BENGTSSON, 1909

- Vindelälven/Sirapsbacken (Västerbotten, S) 27.6.1981; leg. Söderström,
- Sjodalen/Russliseter, Vaga (Oppland, N) 13.7.1987,

Ameletus inopinatus EATON, 1887

- Øvre Heimdahlvatn/Biological station (Oppland, N) 12.7.1987,
- Sjodalen /Russliseter, Vaga (Oppland, N) 13.7.1987
- Sjodalen/Mauerveien (Oppland, N) 12.7.1987,

Metreletus balanicus (ULMER, 1919)

- Sperbersbach/Gailenkirchen (Baden-Würtemberg, FRG) 23.5.1987.

Preparation for the morphological investigations

The eggs were dissected from the abdomen of frozen females in a 100 mM sodium-cacodylate/2,5% glutaraldehyde solution and transferred after 4 hours to a solution of 100 mM sodium-cacodylate/1% OsO_4. The eggs were dehydrated and mounted for the SEM investigations as described by STUDEMANN *et al.* (1987). The egg-surface observations were carried out by a Hitachi H700 SEM after coating with a 75 nm Au/Pd layer. The penes were taken from males stored in alcohol and dehydrated in the same manner as the eggs or directly air dried and mounted for the SEM-studies.

The observation of the male genitalia and the female abdominal sternites was carried out in alcohol from alcohol material or deep frozen material with a stereo microscope.

The dimensions are given for most of the structures in micrometers: Above 20 μm, the dimensions are rounded to the nearest multiple of ten, below 20 μm, the measurements are expressed to the nearest $1/10$ μm.

RESULTS

Male genital apparatus

The representatives of the Siphlonuridae, male and female, have the terminal filament reduced to a vestigial tail (= telofilum) as shown in fig. 1. The nomenclature used in the descriptions of the male genital apparatus is given in figs. 1, 2 and 3.

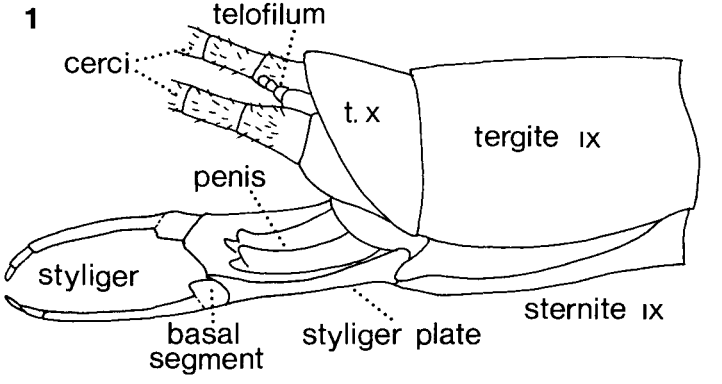


Fig. 1. General view of terminal abdominal segments of a male of Siphlonuridae after NEEDHAM *et al.* (1935).

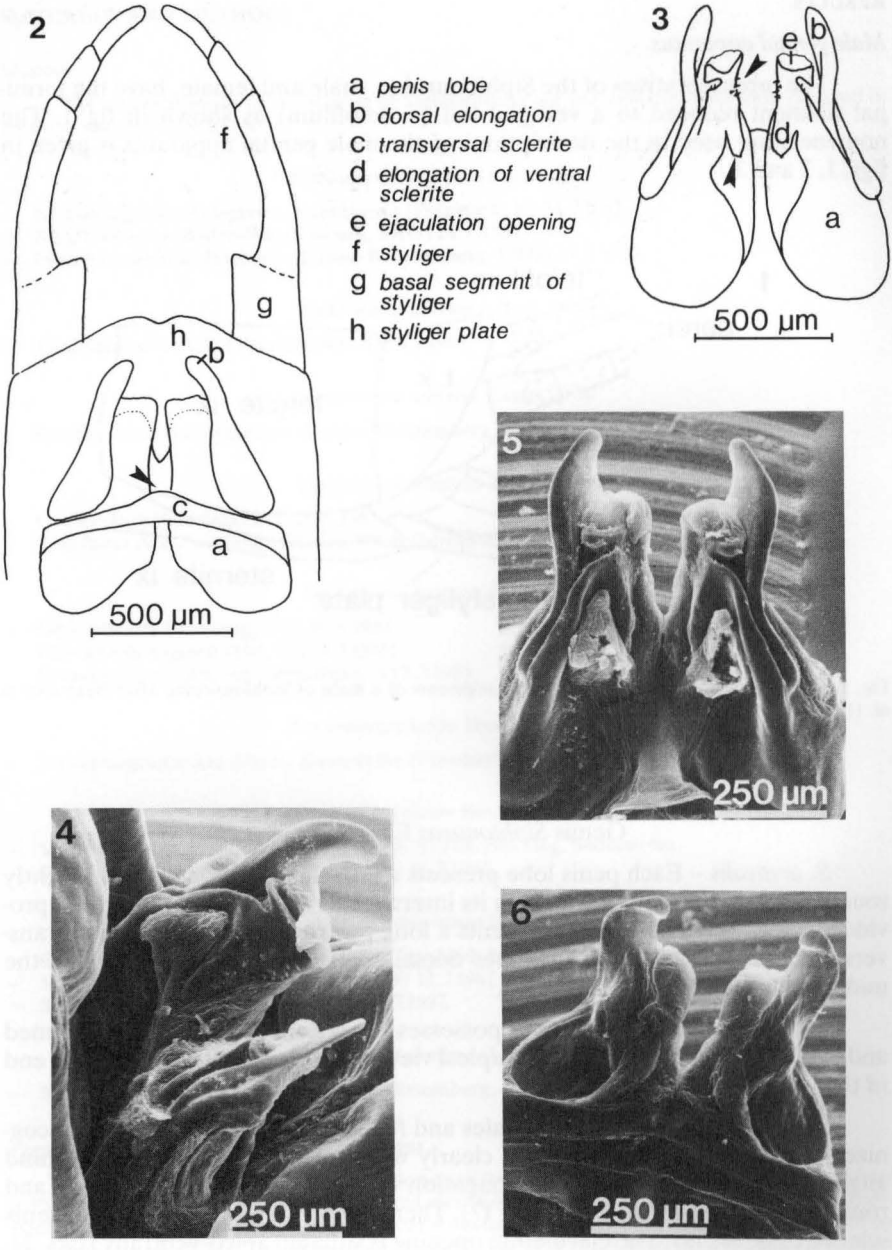
Genus *Siphlonurus* EATON, 1868

S. aestivalis – Each penis lobe presents a dorsal elongation which is slightly rounded at the apex (figs. 2–6). On its internal side, each ventral sclerite is provided with spines apically and presents a long protrusion (figs. 3–5). The transversal sclerite joining the penis lobes dorsally has a slight protuberance in the middle of its hind margin (figs. 2,6).

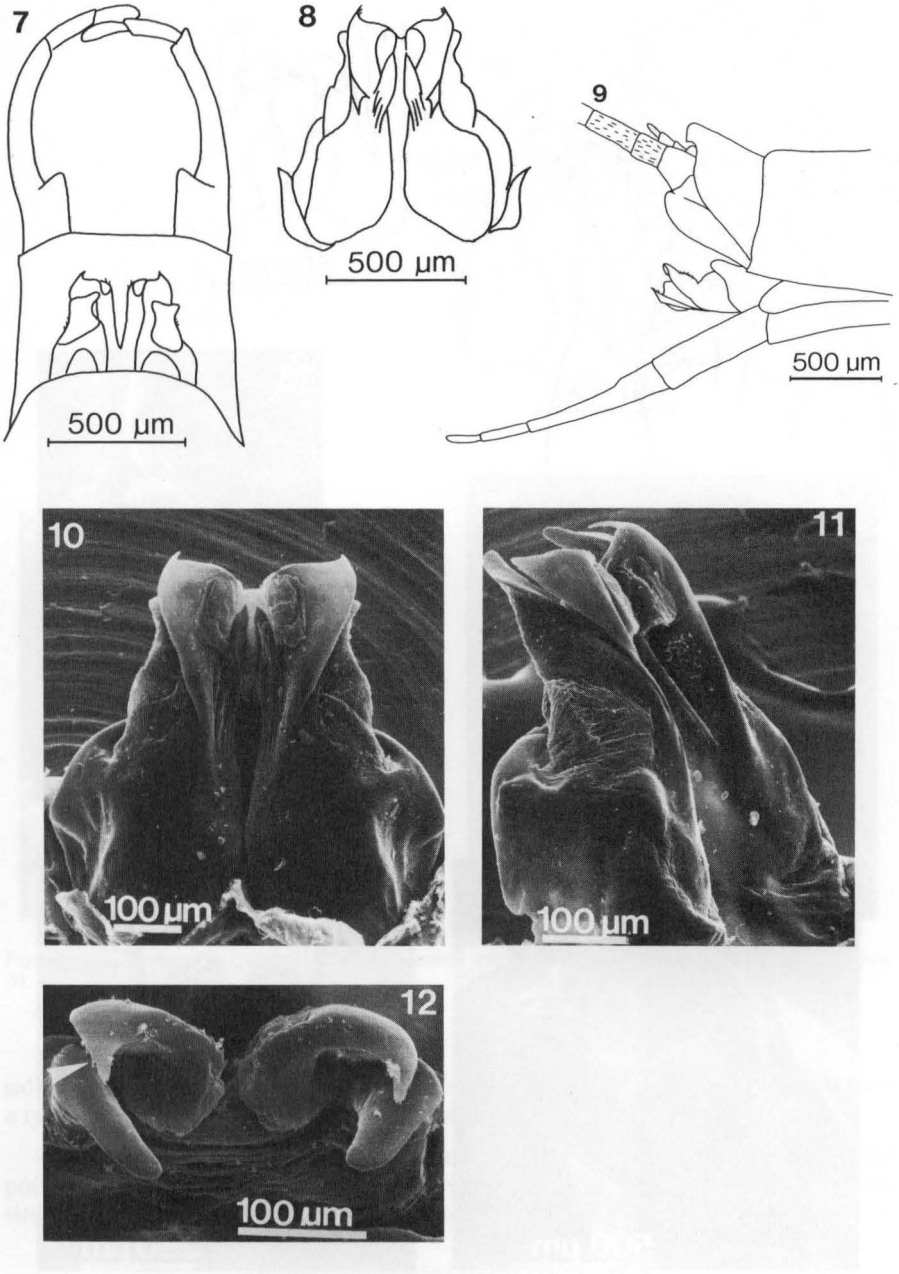
S. alternatus – Each penis lobe possesses two sclerites, but both are flattened and end in a point (figs. 7–12). The apical view shows three little spines at the end of the ventral sclerite (fig. 12).

S. armatus – The imagines (males and females) of *S. armatus* can be recognized by the ninth tergite which is clearly widened with strongly-pointed hind angles (figs. 13, 16). The dorsal elongation of the penis lobes is flattened and rounded at the apex (figs. 13, 14, 15, 17). There are no spines on the internal penis sclerite (figs. 14, 17). The ejaculation opening is situated apico-ventrally (figs. 14, 17).

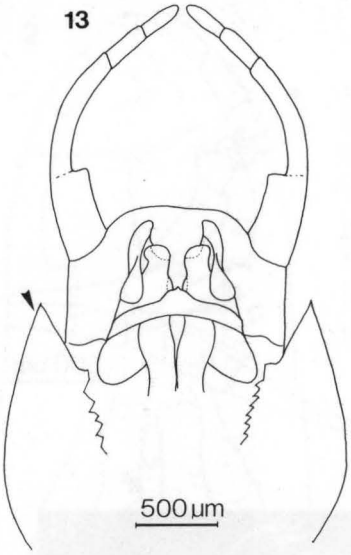
S. croaticus – The dorsal sclerite of each penis lobe is elongated and rounded at its apex (figs. 18–21). Each ventral sclerite seems to be separated into an internal sclerite, surrounding the ejaculation opening and provided marginally with strong spines, and a ventral sclerite presenting a short extension at its internal

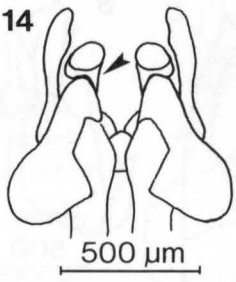


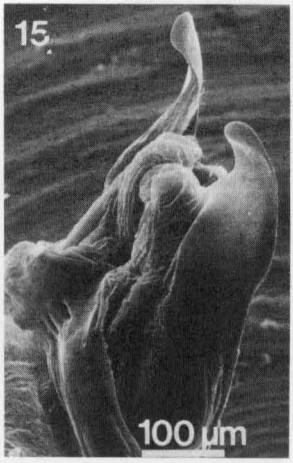
Figs. 2–6. *Siphlonurus aestivalis*. 2: male genital apparatus (penis with styliger plate and styliger), dorsal view. 3: penis, ventral view. 4: penis, latero-apical view. 5: penis, ventral view. 6: penis, apico-dorsal view.

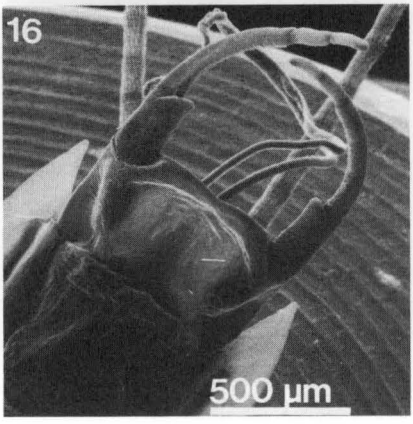


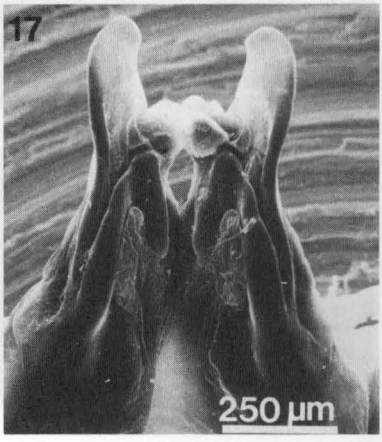
Figs. 7–12. *Siphlonurus alternatus*. 7: male genital apparatus, dorsal view. 8: penis, ventral view. 9: genital apparatus, lateral view. 10: penis, ventral view. 11: penis, latero-ventral view. 12: penis, apical view.



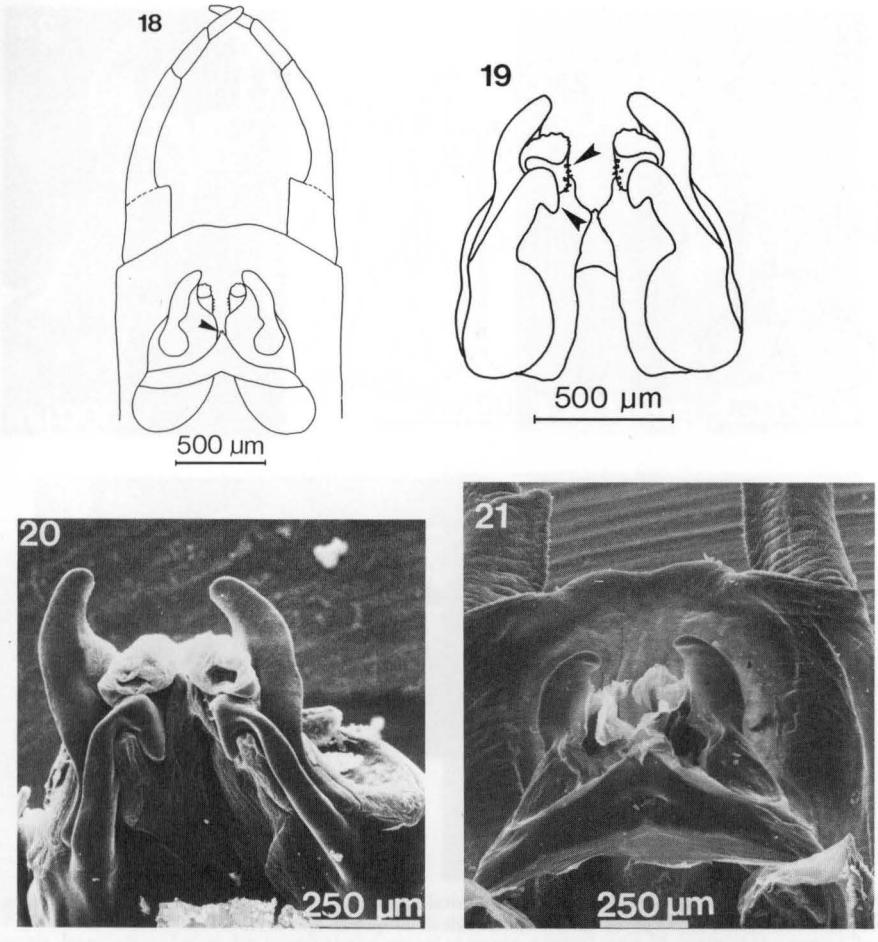








Figs. 13–17. *Siphlonurus armatus*. 13: male genital apparatus, dorsal view. 14: penis, ventral view. 15: penis, latero-dorsal view. 16: terminal abdominal segment, ventral view. 17: penis, ventral view.



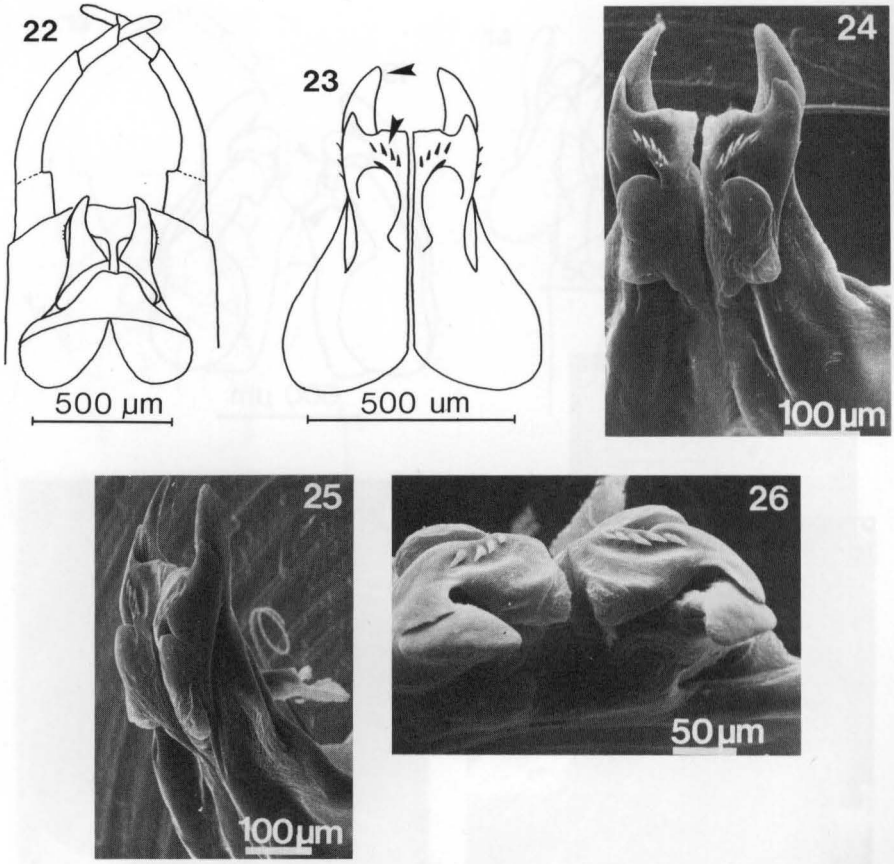
Figs. 18–21. *Siphlonurus croaticus*. 18: male genital apparatus, dorsal view. 19: penis, ventral view. 20: penis, ventral view, 21: penis, dorsal view.

side (figs. 19, 20). The transversal sclerite joining the penis lobes dorsally presents a typical median point on its hind margin (figs. 18, 21).

S. lacustris – The dorsal sclerite of the two penis lobes is elongated and pointed at the apex (figs. 22–26). Each ventral sclerite presents 3 to 5 big spines situated upon a strongly sclerotinised line (figs. 23–26).

Genus *Parameletus* BENGTSSON, 1908

P. chelifer – The styliger plate possesses a shallow indentation on each side of the curved median extension (figs. 27, 30). The penis presents two pointed latero-ventral processes which almost reach its apex, as illustrated in figs. 27, 28, 29 and 31.

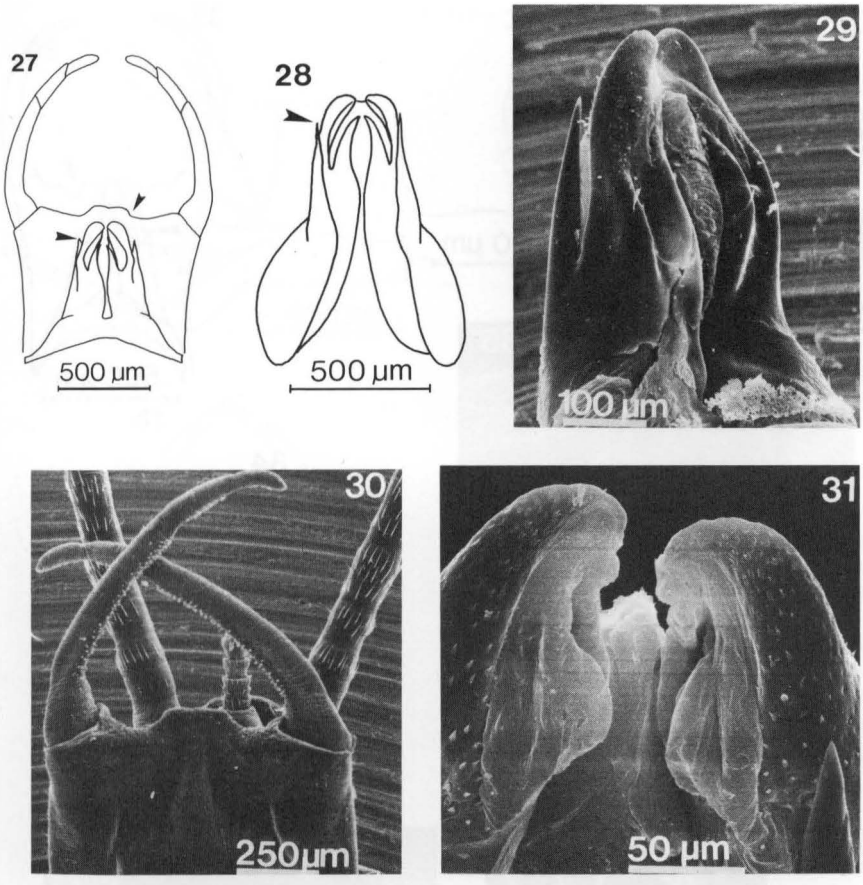


Figs. 22–26. *Siphlonurus lacustris*. 22: male genital apparatus, dorsal view. 23: penis, ventral view. 24: penis ventral view. 25: penis, latero-ventral view. 26: penis, apical view.

P. minor – The styliger plate possesses a sharp indentation on each side of the rectangular, relatively broad median extension (figs. 33, 35). The latero-ventral processes of the penis reach halfway to the hind margin, as shown in figs. 32–37.

Genus *Ameletus* Bengtsson, 1885

A. inopinatus – The profile of the abdomen shows that the styliger and the styliger plate stick out from the penis in a ventral direction (fig. 38). The styliger segments are slender and the basal segment of the styliger is swollen (figs. 39, 41, 42, 43). The median incision of the styliger plate is deep, large and limited by a spike on both sides (figs. 41–43). A membrane connects the penis to the styliger

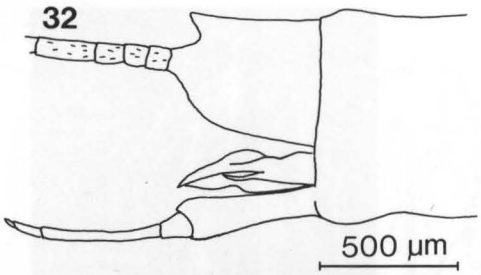


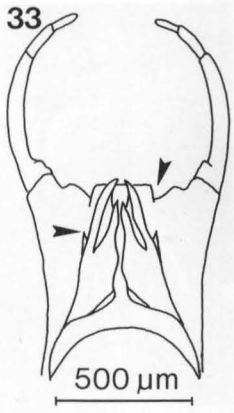
Figs. 27–31. *Parameletus chelifer*. 27: male genital apparatus, dorsal view. 28: penis, ventral view. 29: penis, latero-dorsal view. 30: terminal abdominal segment, ventral view. 31: apex of the penis lobes, ventral view.

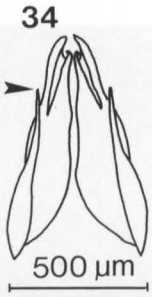
plate (fig. 38). The penis lobes are soft, with a deep median incision (figs. 39, 40, 42). The penis lobe continues well beyond the ventro-apically situated ejaculation opening (figs. 38–42, 44).

Genus *Metreletus* DEMOULIN, 1951

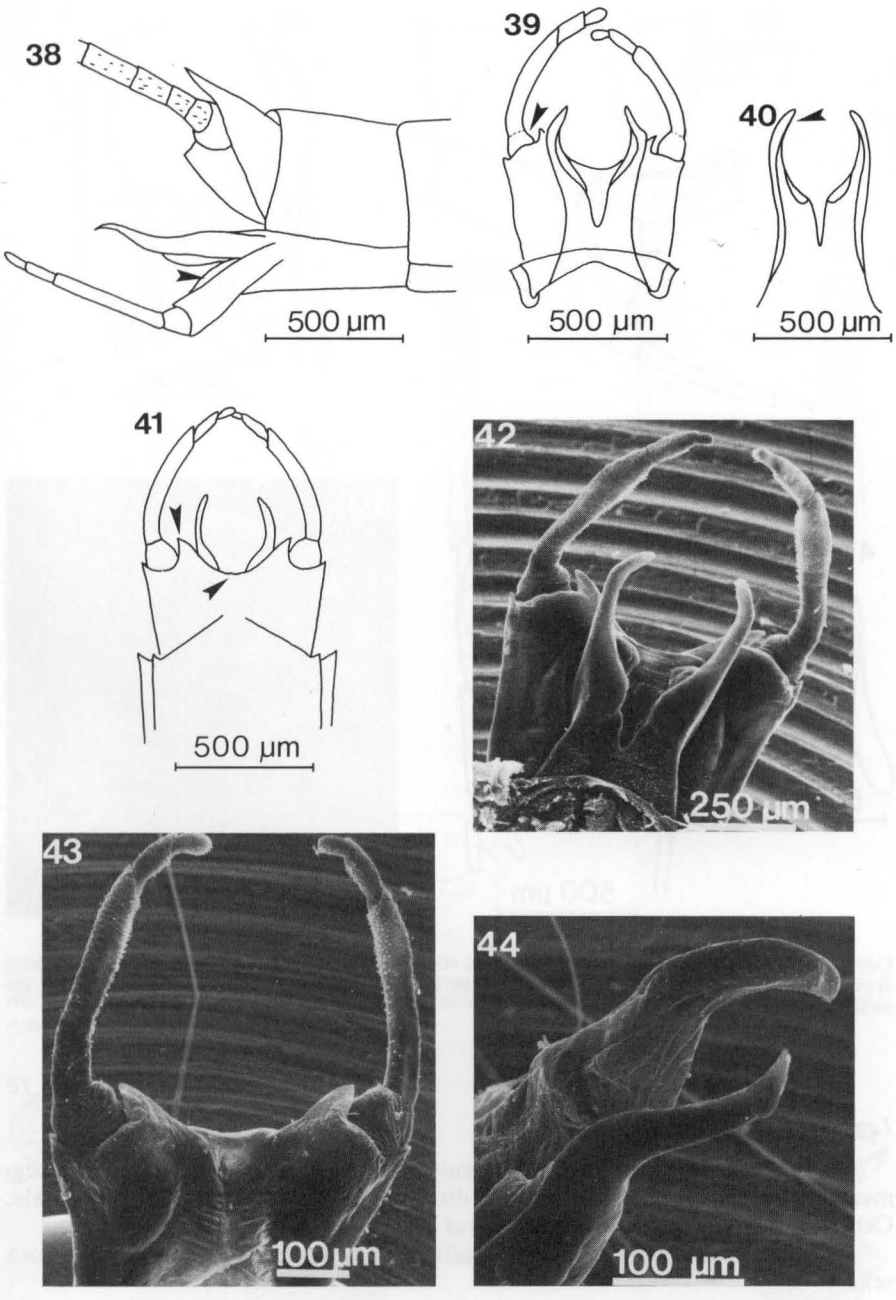
M. balcanicus – The penis is attached by a membrane to the styliger plate. The styliger and the styliger plate project away from the penis, downwards (fig. 45). The styliger segments are thick, the basal segment of the styliger is not swollen (figs. 46, 48, 49). The styliger plate has a deep and narrow median incision (figs. 48, 49). The lobes of the penis are bordered externally by a longish sclerite which goes as far as the ejaculation orifice situated apically (figs. 45–47).



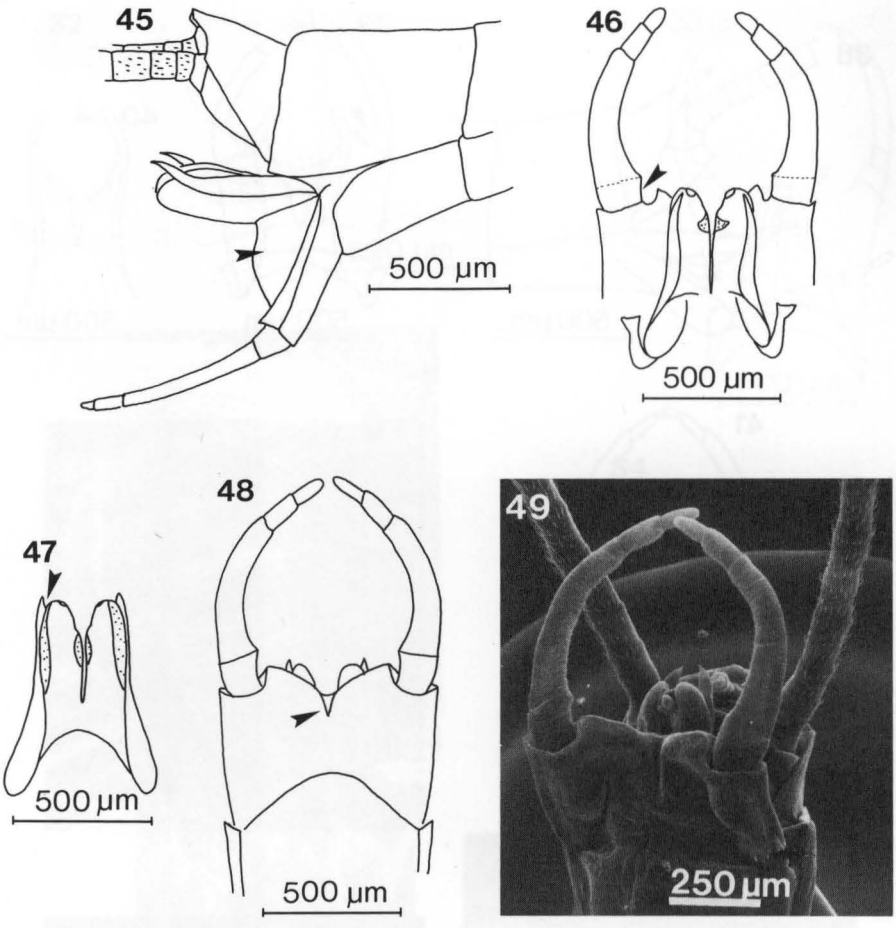




Figs. 32–37. *Parameletus minor*. 32: terminal abdominal segments, lateral view. 33: male genital apparatus, dorsal view. 34: penis, ventral view. 35: male genital apparatus, dorsal view. 36: penis, latero-dorsal view. 37: penis, apical view.



Figs. 38–44. *Ameletus inopinatus*. 38: terminal abdominal segments, lateral view. 39: male genital apparatus, dorsal view. 40: penis, ventral view. 41: terminal abdominal segments, ventral view. 42: male genital apparatus, dorsal view. 43: styliger plate and styliger, ventral view. 44: penis, latero-ventral view.



Figs. 45–49. *Metreletus balcanicus*. 45: terminal abdominal segments, lateral view. 46: male genital apparatus, dorsal view. 47: penis, ventral view. 48: male genital apparatus, ventral view. 49: male genital apparatus, apico-ventral view.

Legs

The tarsus of all species of the family Siphlonuridae is composed of five segments. However, the first segment is distinct only on the fore legs of the male. Otherwise the first segment of the tarsus and the tibia run into one another.

The following information is available for the mid and hind legs of both sexes.

Genus *Siphlonurus*

The tarsus is longer than the tibia (figs. 50 a, b) and the tarsal claws are similar, both pointed (fig. 50 d). The tarsal segments, except the distal one, bear a

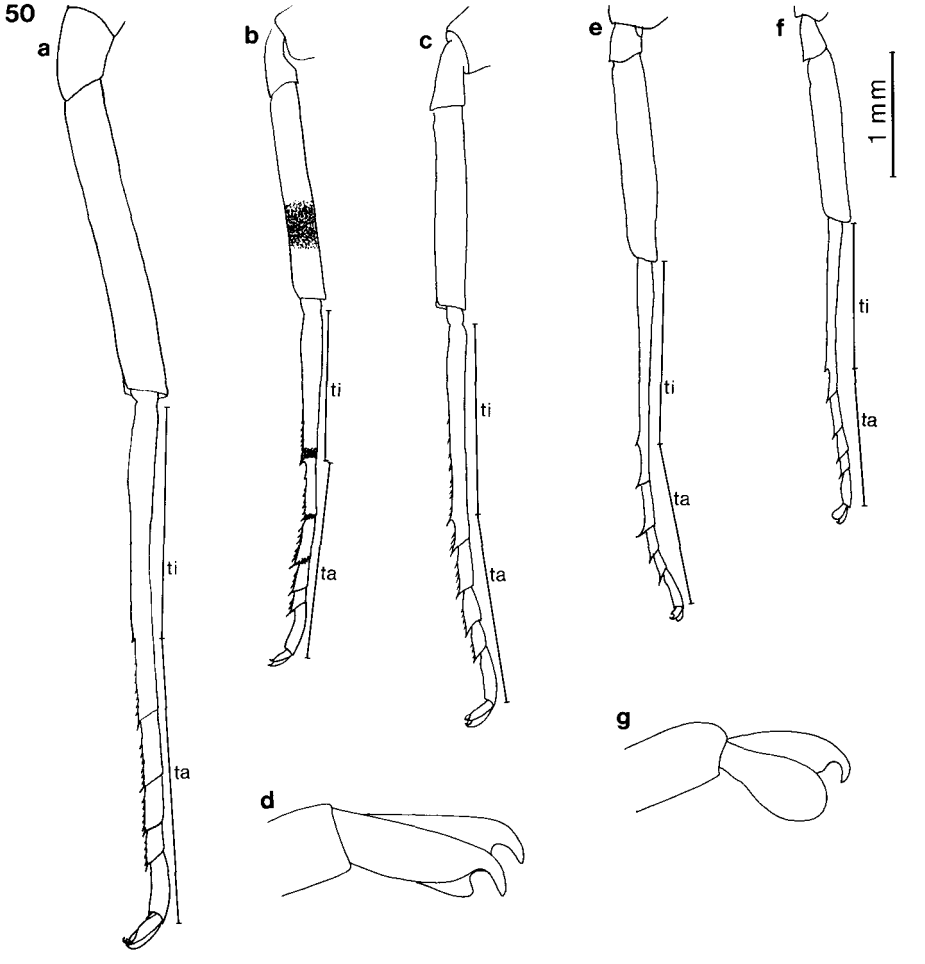


Fig. 50. Mid and hind legs of Siphlonuridae males and females. a: *S. aestivalis*. b: *S. alternatus*. c: *P. chelifer*. d: claws of *Siphlonurus* and *Parameletus* species. e: *A. inopinatus*. f: *M. balcanicus*. g: claws of *Ameletus* and *Metreletus* species.

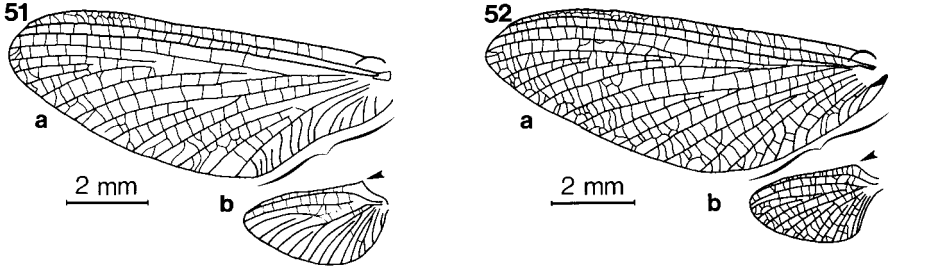


Fig. 51. *Ameletus inopinatus*. a: anterior wing. b: posterior wing.

Fig. 52. *Metreletus balcanicus*. a: anterior wing. b: posterior wing.

range of spines (figs. 50 a, b). In *S. alternatus,* the femora of all the legs of both sexes present a dark reddish brown transverse band on its outer surface (fig. 50 b).

Genus *Parameletus*

The tarsus is nearly as long as the tibia (fig. 50 c). The tarsal claws are similar, both pointed (fig. 50 d), and there are spines on the tarsal segments (except on the distal one) and on the tibia, arranged in a line (fig. 50 c).

Genera *Ameletus* and *Metreletus*

The tarsus is shorter than the tibia (figs. 50 e, f). The tarsal claws are dissimilar, one pointed, the other blunt (fig. 50 g). The tarsal segments, except the distal one, as well as the tibia possess only two little spines on their apical end (figs. 50 e, f).

Wings

The wings do not carry important taxonomic characteristics for the Siphlonuridae, except for *A. inopinatus, M. balcanicus* and *S. lusoensis.*

The wings of *S. lusoensis* are described by PUTHZ (1977 a) and reproduced in fig. 80.

A. inopinatus

The wings are translucent. Only the longitudinal veins are slightly brown. The transversal veins are colourless. The cubito-anal sector of the anterior wing has numerous intercalary veins (fig. 51 a). The costal process of the hind wing is pointed (fig. 51 b).

M. balcanicus

Anterior and posterior wings are yellowish with brown veins. The cubito-anal sector of the anterior wing possesses numerous transversal veins (fig. 52 a). The costal process of the hind wing is obtuse (fig. 52 b).

Female genital apparatus

The most important sexual characters of the females are the posterior part of the ninth sternite, called subanal plate, and the posterior part of the seventh sternite, designated as subgenital plate, which overlaps the genital opening (fig. 53). Some species possess a typical dark coloured corrugation of the cuticula on the eighth sternite.

Genus *Siphlonurus*

S. aestivalis – The swelling of the subgenital plate is deeply indented on its hind margin and presents two dark spots visible at least apically (figs. 53, 62).

S. alternatus – The subanal plate consists only of a small median pointed extension (fig. 54). The subgenital plate presents a great swelling along the hind margin of the seventh sternite (figs. 54, 63). The abdominal sternites 3 to 9 have a typical drawing pattern as shown in fig. 54.

S. armatus – The ninth tergite presents big lateral extensions. The lateral hind margin of the eighth tergite is sharp-pointed and curved on the sternite, so that two pointed angles are visible on the ventral side. The subgenital plate is slightly concave in the middle (fig. 55).

S. croaticus – The subgenital plate consists of a broad swelling, slightly indented at its hind margin, without any apical spots (figs. 56, 64).

S. lacustris – The eighth sternite presents two paired longitudinal dark corrugations. The subgenital plate consists of a median triangular hem. The subanal plate is rounded and it reaches half of the paraprocts (fig. 57).

Genus *Parameletus*

P. chelifer – The hind margin of the seventh sternite possesses a dark curved pigmentation. The eighth sternite has a dark median spot on its anterior margin. The eighth and ninth sternite never present two longitudinal corrugations. The posterior margin of the subgenital plate is blunt, evenly curved. The paraprocts are close to each other all the way to the hind margin. The subanal plate is rounded and reaches half the length of the paraprocts (fig. 58).

P. minor – The posterior margin of the seventh sternite is medially dark. The eighth sternite presents a dark curved median pigmentation at its anterior margin. The eighth and ninth sternite present longitudinal submedian corrugations. The subanal plate is short and overlays only the base of the paraprocts, which are completely separated from each other (fig. 59).

Genus *Ameletus*

A. inopinatus – The translucent subanal plate is narrow and can reach the base of the cerci. Its posterior margin can present a median indentation. The swelling of the subgenital plate does not reach the lateral margin of the sternite. Its posterior margin is slightly concave. The slightly curved corrugation on the eighth sternite is almost as long as the subgenital plate (fig. 60).

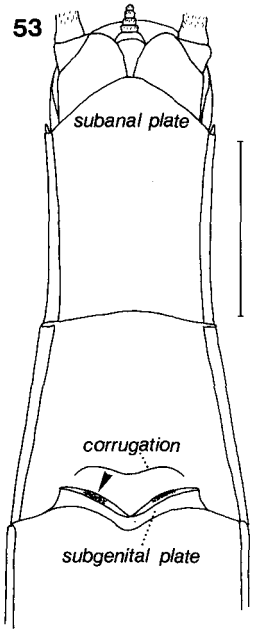
Genus *Metreletus*

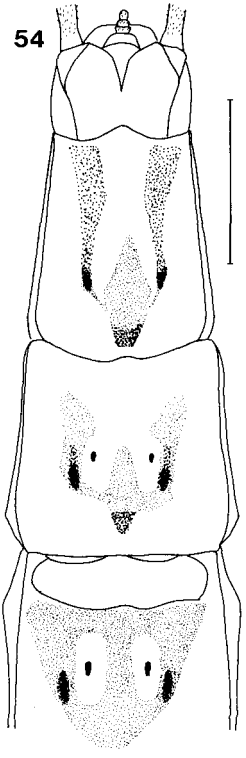
M. balcanicus – The ninth sternite looks like that of *A. inopinatus*. The u-shaped corrugation on the eighth sternite does not reach the lateral margins of the subgenital plate, which takes up the whole breadth of the sternite (fig. 61).

Morphology of the eggs

We follow the nomenclature of KOSS & EDMUNDS (1974) who designate the following different structures with their possible function: – "attachment structures" like plates, disks, threads or polar caps for the adherence of the egg on the submerged substrate; – "chorionic sculpturing" describing the constitution of the chorion; – "micropyle" with "sperm guide structures" which allow sperm to enter the egg.

The species of the family Siphlonuridae lack the polar cap. The other characters are described in the following section and resumed in Tab. 1.


53
subanal plate
corrugation
subgenital plate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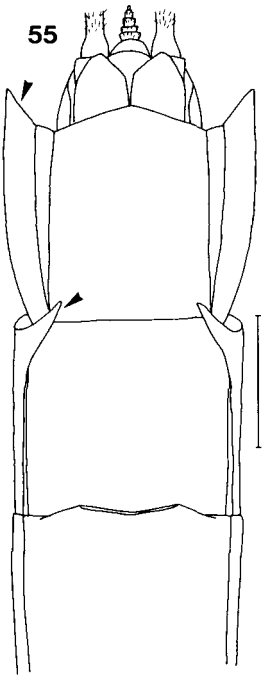
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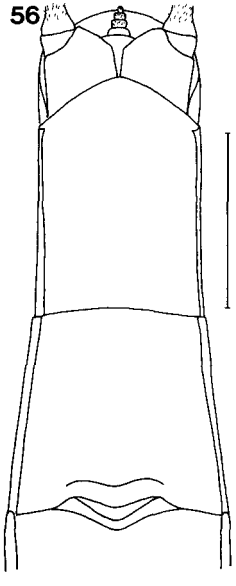
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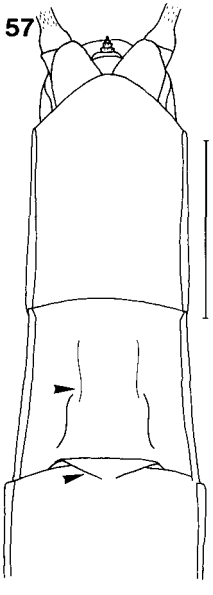
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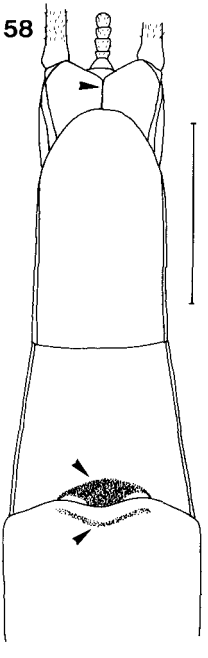
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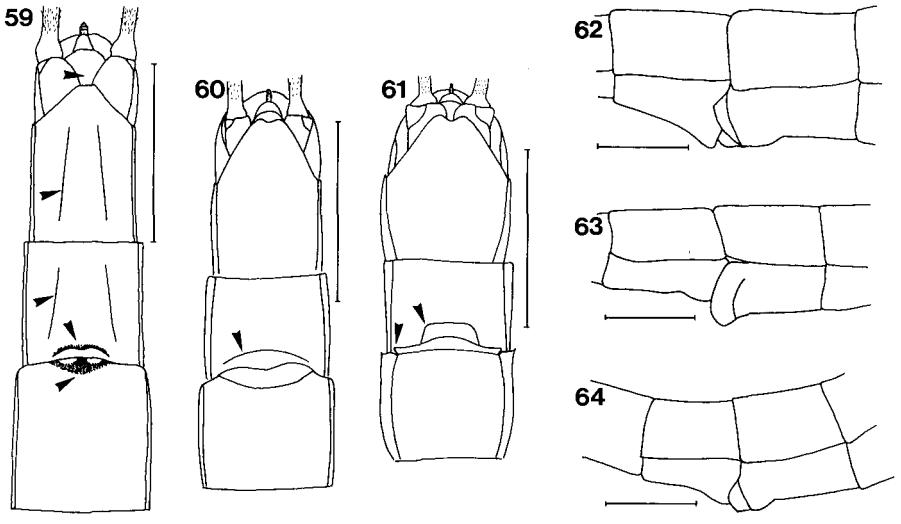


Figs. 53–61. Terminal abdominal segments of females (ventral view). 53: *S. aestivalis*. 54: *S. alternatus*. 55: *S. armatus*. 56: *S. croaticus*. 57: *S. lacustris*. 58: *P. chelifer*. 59: *P. minor*. 60: *A. inopinatus*. 61: *M. balcanicus* (scale line: 1 mm).

Figs. 62–64. Terminal abdominal segments of females (lateral view). 62: *S. aestivalis*. 63: *S. alternatus*. 64: *S. croaticus* (scale line: 1 mm).

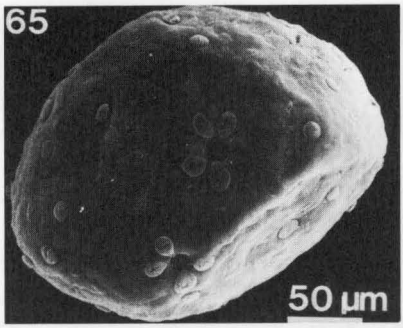
Genus *Siphlonurus*

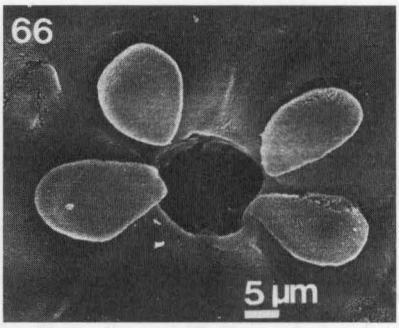
S. aestivalis – The egg is oval with a length of about 270 μm and a width of about 180 μm. The surface of the exochorion is corrugated by formations of layers under the exochorion (fig. 65). Some attachment structures (disks) are irregularly dispersed on the egg surface. The micropyles, 14.2 μm in diameter, are situated in the middle section of the eggs and surrounded by three or four pointed lobes (fig. 66).

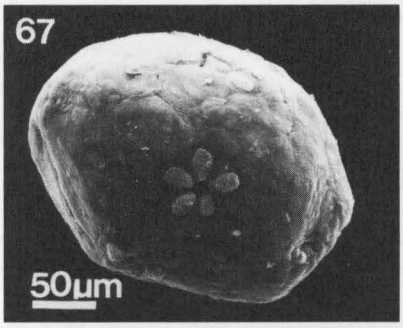
S. alternatus – The form of the egg is ovoid and has a length of 240 μm and a width of 160 μm. The egg surface is corrugated. This is produced by structures under the exochorion. The few attachment structures are dispersed irregularly all over the egg (fig. 67). The orifice of the micropyle (12 μm in diameter) is surrounded by a corona of pointed discal lobes (fig. 68).

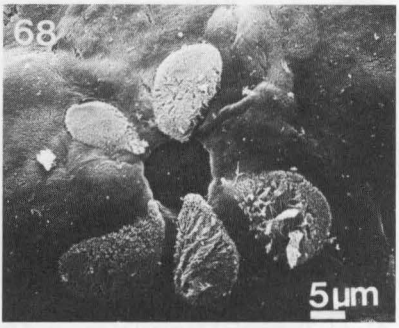
S. armatus – The general form is oval with a length of about 300 μm and a width of 230 μm. The surface is undulated and bears a lot of attachment disks dispersed over the whole egg (fig. 69). The micropyle with a diameter of 14.6 μm is bordered by pointed discoidal plates (fig. 70).

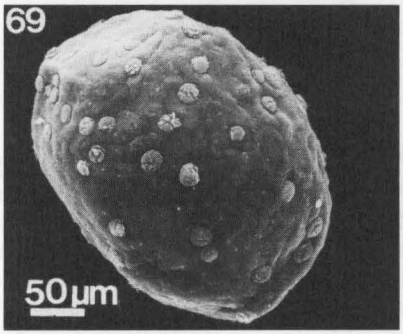
S. croaticus – The form of the egg is ovate (length 290 μm, width 230 μm). The surface of the egg is rugged and attachement disks are spread over the egg (fig. 71). The micropyle (11.3 μm in diameter) is surrounded by pointed lobes.

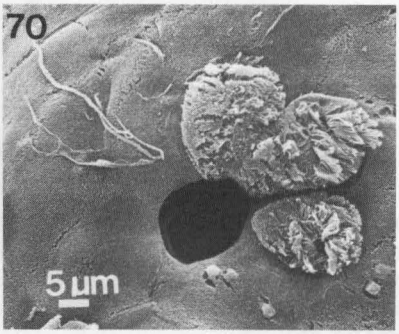

65
50 µm

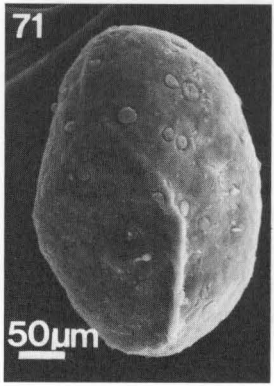

66
5 µm

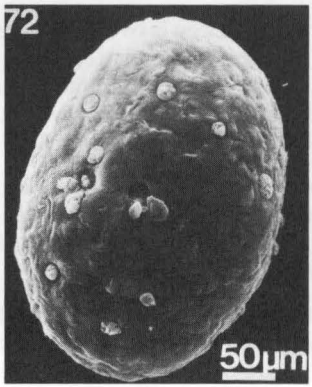

67
50µm


68
5µm

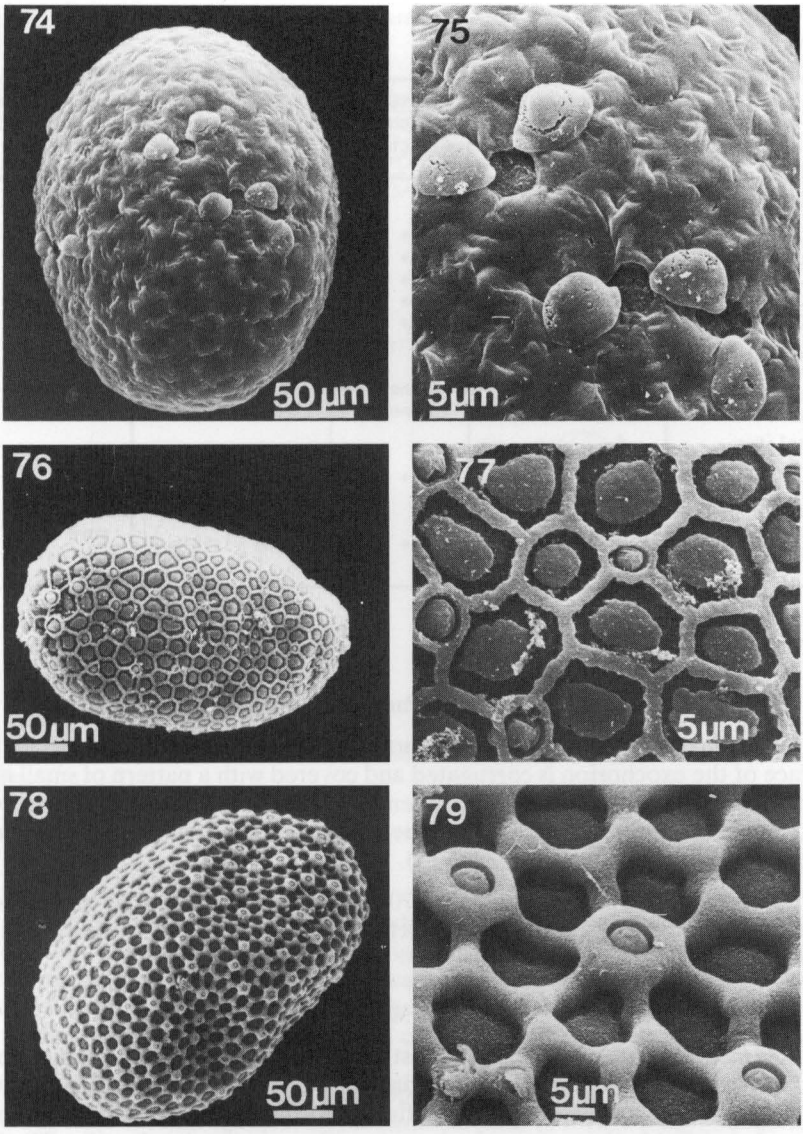

69
50µm


70
5µm


71
50µm


72
50µm


73
5 µm



Figs. 65–79. Eggs of the Siphlonuridae (general view and detail of the micropyles). 65, 66: *S. aestivalis*. 67, 68: *S. alternatus*. 69, 70: *S. armatus*. 71: *S. croaticus*. 72, 73: *S. lacustris*. 74, 75: *P. chelifer*. 76, 77: *A. inopinatus*. 78, 79: *M. balcanicus*.

S. lacustris – The egg has an ovoid form with a length of 200 µm and a width of 140 µm. The surface of the egg is corrugated and there are some disks irregularly arranged over the egg surface (fig. 72). The micropyles (10.8 µm in diameter) are situated in the middle section of the egg (fig. 73).

Tab. 1. Eggs of the Siphlonuridae. Accessory attachment structures: + = less than 10; ++ = between 10 and 20; +++ = more than 20.

	Dimensions (μm) length	width	Accessory attachment structures	Micropyle number	opening (μm)	Morphological polarity
Siphlonurus						
S. aestivalis	270	180	++	2	14,2	none
S. alternatus	240	160	+	1	12,0	none
S. armatus	300	230	+++	1	14,6	none
S. croaticus	290	230	++	1	11,3	none
S. lacustris	200	140	++	2	10,8	none
Parameletus						
P. chelifer	260	200	none	2-3	11,2	none
P. minor	220	170	none	1	10,9	none
Ameletus						
A. inopinatus	220	140	+++	no visible		more cones at one pole
Metreletus						
M. balcanicus	330	200	+++	no visible		more cones at one pole

Genus *Parameletus*

P. chelifer – The egg has an oval form (260 μm long and 200 μm wide). The surface of the exochorion is corrugated and covered with a pattern of small mesh grooves (fig. 74). There are no attachment structures visible. The few micropyles (11.2 μm in diameter) are arranged in the middle section of the egg and surrounded mostly by two pointed lobes (fig. 75).

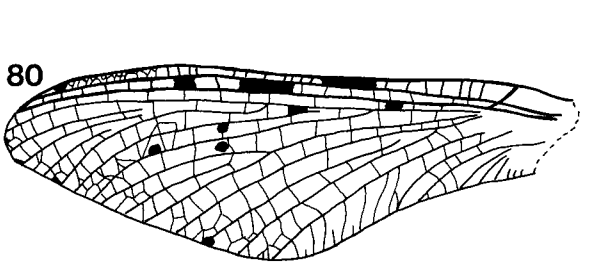
P. minor – The 220 μm long and 170 μm wide eggs are smaller than those of *P. chelifer.* We did not observe any attachment structures. The micropyle with a 10.9 μm wide hole is set in a cavity.

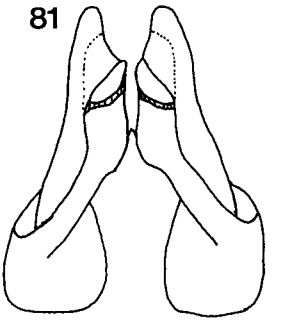
Genus *Ameletus*

A. inopinatus possesses the smallest eggs (220 μm long and 140 μm wide) of all the species of the family Siphlonuridae. The surface is composed of irregular, reticular, raised ridges all over the egg (fig. 76) forming a net-like structure. In the so produced fields there are raised areas with a similar border (fig. 77). This chorionic sculpturing is reinforced by little cones countersunk in an increasing number on the egg poles. There are no pores or micropyles visible.

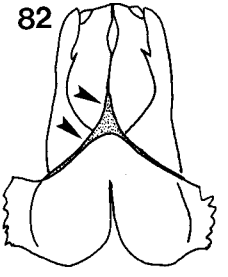
Genus *Metreletus*

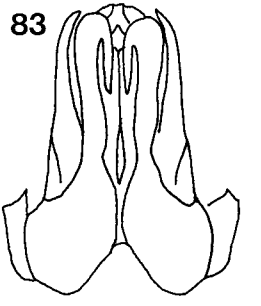
The general form of the egg of *M. balcanicus* is ovate with a length of 330 μm and a width of 200 μm (fig. 78). The chorion surface is covered with net-like ribbed structures of which the mesh diameters amount to 10 μm (fig. 79). A lot of cones countersunk are scattered in the above-mentioned net-like structures on one pole of the egg. We did not observe any distinct micropyles.





Figs. 80, 81. *Siphlonurus lusoensis* after PUTHZ (1977 a). 80: anterior wing. 81: penis, ventral view.





Figs. 82, 83. *Siphlonurus flavidus* after ALBA-TERCEDOR (1984). 82: penis, dorsal view. 83: penis, ventral view.

DISCUSSION

Our morphological studies show additional and complementary characters on the adult stages and the eggs of the Siphlonuridae. The SEM observations are specially precious for their high magnification and high depth of field. The resulting three dimensional view facilitates the interpretation of the objects observed (particularly for the egg structures) and completes the drawings most satisfactorily.

Our investigations include all European species of the Siphlonuridae except three endemic Iberian species, *Siphlonurus flavidus* (PICTET, 1865), *Siphlonurus lusoensis* PUTHZ, 1977, and *Siphlonurus hispanicus* DEMOULIN, 1958. We could not observe any specimens of *S. flavidus* nor *S. lusoensis,* but we include these two species in the key using the descriptions published by ALBA-TERCEDOR (1984) and PUTHZ (1977 a), respectively. The most important drawings are reproduced in figs. 80–83. The lack of information about the male imago of *S. hispanicus* prevents us from including this species in the key.

For the synonymisations of the *Siphlonurus* and the *Metreletus* species we refer to the publications of PUTHZ (1977 a, b).

The geographic distribution of the Siphlonuridae given in Tab. 2 is based on the data of the "Limnofauna" (PUTHZ, 1978), completed with our observations.

Tab. 2. Distribution of the Siphlonuridae after "Limnofauna" (PUTHZ, 1978) completed with our data. 1 = rivers, streams (Potamon); 2 = brooks, little rivers (Rhithron); 3 =lakes (generally stagnant water); 4 = sources (Krenon).

Species	Area	Biotope
Siphlonurus aestivalis	all Europe, except Great Britain	1
Siphlonurus alternatus	all Europe, except Iberian Peninsula	1
Siphlonurus armatus	all Europe, except Norway, Sweden	1
Siphlonurus croaticus	Alps, Balkans, Central Highlands	1
Siphlonurus flavidus	Iberian Peninsula	1
Siphlonurus lacustris	all Europe	1
Siphlonurus lusoensis	Iberian Peninsula	1
Parameletus chelifer	Fennoscandinavia	2
Parameletus minor	Fennoscandinavia	2,3
Ameletus inopinatus	Balkans, Central Highlands, Great Britain, Fennoscandinavia	2,4
Metreletus balcanicus	Balkans, Armorican Massif, Basin of Aquitaine	2

Imaginal stages

Some well-defined structures on the legs of adult mayflies are used as taxonomic characters in order to separate the genera. We chose differences in length of tibia and tarsus, the presence or absence of spines on the leg parts and the claws (fig. 50). The comparison of length of the tibia and tarsus leads to the separation of the Siphlonuridae in three groups: the genus *Siphlonurus* (tarsus longer than tibia), the genus *Parameletus* (tarsus nearly as long as tibia) and the genera *Ameletus* and *Metreletus* (tarsus shorter than tibia).

The genera *Siphlonurus* and *Parameletus* possess spines along the tibia and tarsus, except the distal segment of the tarsus (figs. 50 a, b, c), compared to the genera *Ameletus* and *Metreletus* which lack these spines (fig. 50 e, f). An analogous situation occurs for the claw structures at the end of the distal tarsal segment. *A. inopinatus* and *M. balcanicus* have dissimilar claws, one pointed the other blunt (fig. 50 g), compared to the pointed claws of *Parameletus* and *Siphlonurus* species (fig. 50 d).

The morphology of *A. inopinatus* and *M. balcanicus* is rather similar. The profiles of the abdomen in the males of both species (figs. 38, 45) look alike with their spreading styligers that are connected to the penis by a membranous, expandable cuticule bag. The volume of this bag changes with the movement of the abdomen, respectively of the styligers. Perhaps this mechanism is used for the ejaculation of the sperm in the sexual act. The penis of the other species do not show this speciality.

Males and females of *M. balcanicus* and *A. inopinatus* are distinguishable thanks to their wings. *M. balcanicus* has yellowish wings whereas *A. inopinatus* has translucent ones. The cubito-anal sector of the anterior wings possesses numerous intercalary veins in *A. inopinatus* but numerous transversal veins in *M. balcanicus* (figs. 51a, 52a). The costal process of the posterior wings is obtuse in *M. balcanicus* compared to the pointed one in *A. inopinatus* (figs. 52 b, 51 b). The females of *M. balcanicus* and *A. inopinatus* have different corrugation patterns on

the eighth sternite, u-shaped in *M. balcanicus* and slightly curved in *A. inopinatus* (figs. 60, 61).

There is no problem in separating the imagines, males and females, of the *Siphlonurus* species, except *S. aestivalis* and *S. croaticus* which are two closely related species. TANASIJEVIC (1974) compares the form of the transversal sclerite joining the penis lobe dorsally. This sclerite shows only a slight protuberance in *S. aestivalis* (fig. 2) but it is sharp-pointed in the middle in *S. croaticus* (fig. 18). The ventral sclerite of the penis lobe has a long extension in *S. aestivalis* (fig. 3) but a short one in *S. croaticus* (fig. 19). The females can be separated by the subanal plate which has two transversal dark spots in *S. aestivalis* (fig. 53) and no spots in *S. croaticus* (fig. 56).

Key to the imagines of European Siphlonuridae

The base of our key originates from those established by SOEDERSTROEM & NILSSON (1986). We enlarge their key to all European species of Siphlonuridae and complete it with additional morphological characteristics.

1 Tarsal claws dissimilar, one pointed, the other blunt (fig. 50 g). Tarsus of mid and hind leg shorter than tibia (figs. 50 e, f). No range of spines neither on tibia nor on tarsus (figs. 50 e, f) 2
– Tarsal claws similar, both pointed (fig. 50 d). Tarsus of mid and hind leg longer than or nearly as long as the tibia (fig. 50 a, b, c). A range of spines on tibia and tarsus, except the distal tarsal segment (fig. 50 a, b, c) 3

2 Wings translucent. Anterior wing with numerous intercalar veins in the cubito-anal sector (fig. 51 a). Costal process of the posterior wing pointed (fig. 51 b). *Male:* Styliger plate with large median incision, limited by a spine on both sides. Basal segment of styliger swollen (fig. 41). Penis with a deep median incision (fig. 40) and two long lateral prolongations. *Female:* Eighth sternite with a slightly curved corrugation, almost as long as the breadth of the subgenital plate (fig. 6). . . . . *Ameletus inopinatus*
– Wings yellowish with brown veins. Anterior wing with numerous transversal veins in the cubito-anal sector (fig. 52 a). Costal process of the posterior wing obtuse (fig. 52 b). *Male:* Styliger plate with narrow median incision. Basal segment of styliger not swollen (fig. 48). Lateral sclerite of penis scarcely reaching the ejaculation opening (fig. 47). *Female:* Eighth sternite with u-shaped corrugation, shorter than the breadth of the subgenital plate (fig. 61). . . . . *Metreletus balcanicus*

3 Tarsus of mid and hind leg almost as long as the tibia (fig. 50 c). 4
– Tarsus of mid and hind leg longer than the tibia (figs. 50 a, b). 5

4 After SOEDERSTROEM & NILSSON (1986): *Male:* Posterior margin of styliger plate with shallow indentation on each side of curved median extension (fig. 27). Penis with 2 pointed latero-ventral processes which almost reach its apex (fig. 28). *Female:* hind margin of sternum 7 whith dark curved pigmentation. Sternum 8 with dark median spot at anterior margin. Posterior margin of subgenital plate blunt, evenly curved. Paraprocts close to each other all the way to the hind margin (fig. 58). . . . . *Parameletus chelifer*
– *Male:* Posterior margin of styliger plate with sharp indentation on each side of a rectangular relatively broad median extension (fig. 33). Penis with two pointed latero-ventral processes that reach half a way to its apex (fig. 34).

Female: Hind margin of sternum 7 with dark median spot. Sternum 8 with dark median line at anterior margin. Paraprocts distinctly separated all the way to the hind margin (fig. 59) . . . . . *Parameletus minor*

5 Anterior wing with several little reddish spots (fig. 80) and penis as in fig. 81. Endemic species from the Iberian Peninsula (PUTHZ, 1977 a). . . . . *Siphlonurus lusoensis*

– Anterior wing without reddish spots 6

6 Transversal sclerite joining the penis lobes dorsally extremely thin with long pointed protuberance in the middle of its hind margin as in fig. 82. Endemic species from Iberian Peninsula (ALBAS-TERCEDOR, 1984) . . . . . *Siphlonurus flavidus*

– Transversal sclerite joining the penis lobes dorsally broad with parallel borders or with a broad protuberance in the middle of its hind margin. 7

7 Ninth tergite with big lateral extensions. Lateral hind margin of the eighth tergite sharp-pointed and curved on the sternite (figs. 13, 55). *Male:* Dorsal elongation of penis-lobe flattened and rounded at the apex. No spines on the internal penis sclerite (fig. 14). . . . . *Siphlonurus armatus*

– Ninth tergite without big lateral extension. 8

8 Abdominal sternites 3 to 9 with distinct drawing pattern consisting of dark-brown spots (fig. 54). Femora with dark band (fig. 50 b). *Male:* Penis lobe with flattened sclerites without elongation (figs. 7, 8). *Female:* Subanal plate consisting of only a little median pointed extension (fig. 54). . . . . *Siphlonurus alternatus*

– Sternites and femora with other or no drawing patterns 9

9 *Male:* Dorsal sclerite of the penis lobe long and pointed at the apex. Ventral sclerite with a row of 3 to 5 big spines (fig. 23). *Female:* Two paired longitudinal dark corrugations on the eighth sternite. Subgenital plate consisting of a triangular hem (fig. 57). . . . . *Siphlonurus lacustris*

– *Male:* Dorsal sclerite of the penis lobe long and rounded at the apex (figs. 2, 18). Penis with spines on the inner side of the ventral sclerite (figs. 3, 19). *Female:* No longitudinal corrugation on the eighth sternite. 10

10 *Male:* Transversal sclerite joining the penis lobes dorsally with slight protuberance in the middle (fig. 2). Ventral sclerite carrying spines with a pointed distal elongation. Sclerite length at the elongation more than twice as long as the width at the apex (fig. 3). *Female:* Subgenital plate with deep pointed median incision and with two dark transversal spots visible at least apically (fig. 53). . . . . *Siphlonurus aestivalis*

– *Male:* Transversal sclerite joining the penis lobes sharp-pointed in the middle (fig. 18). Two ventral sclerites, the internal carrying spines, the other with a short rounded distal elongation (fig. 19). *Female:* Subgenital plate with flattened apical margin and without transversal spots (fig. 56). . . . . *Siphlonurus croaticus*

Eggs

The dimensions of the eggs as shown in the table 1 agree very well with the measurements of the species published by DEGRANGE (1960) and BENGTSSON

(1913). The lengths observed in SEM-treated eggs are about 10% lower than those studied directly from alcohol material. The shrinking is due to the delicate constitution of the eggs of the Siphlonuridae. The egg chorion reveals some important morphological differences depending on the genera. The species of the genus *Siphlonurus,* consisting of *S. aestivalis, S. alternatus, S. armatus, S. croaticus* and *S. lacustris,* have very similar eggs. Their chorionic structures are characterised by attachment structures distributed all over the eggs and a corrugated exochorion caused by structures situated on layers under the exochorion (figs. 65, 67, 69, 71, 72). The micropyles are bordered with pointed lobes which may function as sperm guides (figs. 66, 68, 70, 73). The eggs of *Parameletus chelifer* and *P. minor* have a smoother surface with no attachment structures (fig. 74). The micropyles of *P. chelifer* resemble those of the *Siphlonurus* (fig. 75). The eggs of the representatives of the genera *Ameletus* and *Metreletus (A. inopinatus* and *M. balcanicus)* have net-like ridges all over the egg surface (figs. 76–79). There are no distinguishable micropyles visible, but these eggs are polarized by a higher concentration of chorionic cones at one pole of the eggs. They may play an analogous role as the attachment threads of polar caps which cause the orientation of the egg in the water flow (KOSS and EDMUNDS, 1974). The number and distribution of the attachment structures, scattered randomly on the egg in the *Siphlonurus* species or absent in the *Parameletus* species, could be related to the habitat conditions. The chorion organization of *A. inopinatus* as well as *M. balcanicus* may be related to other habitat conditions or may have arisen from an earlier genetic deviation.

The analogous morphology in the genera taken from the genital apparatus, the legs and the egg surfaces, as well as similarities between the genera indicate the narrow relationship between *Ameletus* and *Metreletus,* both distant from *Siphlonurus* and *Parameletus* which are relatively close genera. The phylogenetic relationship remains difficult to prove, but the biochemical investigations, isoenzyme electrophoresis under way in our laboratories, will clear up any uncertainty.

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RÉSUMÉ

Les adultes et les œufs des espèces de Siphlonuridae d'Europe Centrale et du Nord sont examinés au microscope électronique à balayage et à la loupe binoculaire. La comparaison de divers caractères suggère un degré de parenté élevé entre les genres *Ameletus* et *Metreletus* d'une part et entre les genres *Siphlonurus* et *Parameletus* d'autre part. L'étude comprend également une clé de détermination pour les adultes mâles et femelles.

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