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The genus *Chaetopteroides* (Trichoptera, Limnephilidae) revised by fine structure analysis of parameres

János Oláh, Halil Ibrahimi & Tibor Kovács

Abstract: The sexually dimorphic genus *Chaetopteroides* with combined chaetopterygini and stenophylacini characters was revised based on the well differentiated female external genitalia and on the diversified parameres of the phallic organ. We have reviewed why paramere diversifies so intensively. Re-diagnosis of genus was prepared and three new species are described: *C. kosovarorum* Ibrahimi et Oláh sp. n. from Kosovo, *C. tunik* Oláh sp. n. from Macedonia, and *C. veges* Oláh sp. n. from Bulgaria.

Introduction

Chaetopreyx maximus Kumanski, 1968 was described from the Vitosha Mts. (Bulgaria) as an atypical *Chaetopteryx* due to its large size, unique form of paraproct, and high tibial spur number of 134. Four spurs on the hind tibia is a stenophylacini trait. Chaetopterygini spur range is 022-133. The discovery of a second similar species, the *C. bulgaricus* Kumanski, 1969 form Pirin Mts. (Bulgaria) has elongated legs, more tibial spurs, less erected hairs on forewing as well as a characteristic genital structure. The second species was outlined as the most primitive member of the *Chaetopterygini* tribe. Both species were related close to *Stenophylacini* tribe, and particularly close to the genera of *Potamophylax* Wallengren, 1891, *Allogamus* Schmid, 1955, and *Halesus* Stephens, 1836. Kumanski (1987) has erected a new genus, *Chaetopteroides*, for the two species based on the combined stenophylacini (large size, light spotted pattern on the forewing in both sexes, hind tibia with four spurs) and chaetopterygini (erected hairs on forewing, brachyptery, robust venation in female forewing) characters. The new genus was considered the most primitive and least specialized within the *Chaetopterygini* tribe, and as a transitional one to the *Stenophylacini* tribe.

The entire genus is represented only by a few collected specimens. Kumanski (1972) in a review of the Bulgarian autumnal species has noted that it is much too questionable that *C. maximus* and *C. bulgaricus* could be discovered outside Bulgaria. *C. maximus* was recorded from Kopaonik Mountain in Serbia close to Kosovo (Marinković-Gospodnetić 1980). In the past years we have collected a few male and female *Chaetopteroides* specimens in Bulgaria, Macedonia and Kosovo, and we have found that our specimens represent 5 species as differentiated by female external genital structures as well as by the diversified parameres of males. Here we revise the genus briefly, and describe the new species based on detailed re-drawings of the female external and internal genital structure as well as by the detailed structure of the parameres. However, first we review some possible aspects of the question why parameres diversify so selectively.

Why parameres diversify?

The mere fact that we apply genitalia to distinguish closely related insect species suggests that speciation is driven inherently by reproduction. The species itself is organised or even defined by reproductive isolation. Classic explanations of intense genital divergence by lock-and-key or pleiotropy hypotheses are in the process of being discarded (EBERHARD 2010). Genitalia are more variable than legs, wings, cephalic, or thoracic structures. DARWIN (1871) observed that genera with elaborate sexual display were more species rich. Speciation rate could be measured by the number of extant species in a clade, by the net diversification rate: that is the balance of speciation and extinction. The first report that sexual selection influences speciation came from comparative evidence. Detailed comparative analysis proved that genital evolution is more than twice as divergent in polyandrous groups where females mate several times, than in monandrous groups with females mate only once (ARNQVIST 1998). This pattern is not found for other morphological traits. This comparative evidence has been revisited by meta-analysis and produced significant positive correlation between sexual selection and speciation rate (KRAAIJEVELD et al. 2011).

The effects of sexual selection on species richness differ among taxa, and the effect on speciation is most pronounced in the initial stage of divergence. Early barriers to gene flow can be identified before they become confounded with other species differences. Genomes of incipient species become temporary genetic mosaics. Ecologically important genomic regions resist gene exchange, even as gene flow continues over most of the genome (VIA 2009). Sexual selection may continuously generate new species, but their persistence depends on factors of ecological differentiation or spatial isolation. In allopatry, reproductive traits diverge rapidly, and may lead to restricted gene flow (CORDERO RIVERA et al. 2004). Sexual selection can cause population to shift on the viability landscape from a local viability peak to a new viability peak with novel ecological strategy (BONDURIANSKY 2011). Natural selection drives the divergence of mate preference by either ecological or mutation-order mechanisms (SCHLUTER 2009). Natural, ecological, sexual, and social selections are different forms of the same process with interrelations. A possible alternative idea is to consider the ecological, sexual, and social environment as stimulating and acting pressures in natural selection (OLÁH et al. 2013).

Traits that influence competition for mates are sexually selected, whereas those that directly influence offspring survival are environmentally selected. Polyandrous species of beetles, flies, butterflies, moths, and mayflies developed genital divergence about twice as great as monandrous species measured by geometric morphometrics. It has been documented that postcopulatory sexual selection can lead to rapid divergence in reproductive traits related to mating, and that cryptic female choice plays an important role in this divergence (NILSSON 2004). However, males can also gain fertilization benefits by harming their mates if damage is cumulative over successive copulations, then females should be less likely to remate with competing males (JOHNSTONE & KELLER 2000). Complicated and highly divergent morphology is unlikely arisen for the simple function of sperm transfer (HOSKEN & STOCKLEY 2004). Diversifying phallic organ, vaginal sclerite complex, or any other possible genital structures directly involved in mating process and produced by various mechanisms of sexual selection are the early products of speciation.

In allopatric populations of calopterygid damselflies (Odonata) sperm competition and/or intersex coevolution produced diversity in morphometry of aedeagus and spermathecal duct

(Cordero Rivera et al. 2004). The male cerci and female thoracic plates evolve in correlated fashion across the genus *Enallagma* (Odonata) (McPeek et al. 2009). In praying mantis (Mantodea) the shape of genital processes have been selected for efficient sperm transfer by complex mechanisms of sexual conflict, female choice, and male-male sperm competition (Holwell et al. 2010). Among water striders (Heteroptera) the genital structures are more complex and their shape more divergent than nongenital traits. Their intromittent genital traits are more complex, and have evolved more divergently than nonintromittent genital traits (Rowe & Arnqvist 2011). Tortoise beetle species (Coleoptera) have spermathecal duct and flagellum (ejaculatory duct) lengths highly correlated interspecifically. Male flagellum functions to introduce sperm or to remove sperm deposited in the spermatheca by previous mating (Rodriguez et al. 2004). Species specificity of female genitalia was demonstrated recently in dipteran Sepsidae (Puniamoorthy et al. 2010) and mecopteran Panorpidae (Ma et al. 2012) families. In caddisflies (Trichoptera) aedeagus (Oláh et al. 2012) and/or parameres (Oláh & Ito 2013, Oláh et al. 2013) have diversified, and may represent early device in reproductive isolation of the phylogenetic incipient species.

Apparently there is a diversity sequence among the insect body structures starting with the less diverse non-genital structures and ending with the most diverse parameres of the phallic organ. *Diversity sequence*: non-genital structures→non-intromittent genital structures (periphallic organs)→intromittent genital structures (aedeagus→parameres). The parameres of the phallic organ may have several functions: (1) copulatory courtship device (titillator) to ensure female acceptance of the ejaculate in the cryptic female choice; (2) harm device in the sexually antagonistic coevolution; (3) cleaning device to remove sperm in sperm competition, (4) anchor device allowing males to prolong copulation: (5) for complex mate assessment; (6) for more ejaculate; (7) for post copulatory mate guarding: (8) to deposit mating plug by either female or male accessory glands; (9) to provide living mating plug.

Diversity of parameres evolves along their various functions and interactions. Parameres diversify under the environmental pressure of mate preferences in the process of natural selection. The strength of preferences (selection) determines how quickly the preferred trait values come to match the fitness peaks defined by mate preferences. This strength determines the rate of speciation. The amount of divergence in the preferred trait value favoured by mate preferences determines the magnitude of diversification. This amount determine how easily alpha taxonomy recognises these early steps of speciation, the born of insipient species. Comparative analyses seldom differentiate clearly between the strength of selection and the amount of diversification. Therefore the diversifying effect of sexual selection is, perhaps drastically, underestimated (Rodriguez et al. 2013). The morphological diversification of genital structures, like parameres directly involved in mating, are not yet accounted reasonably in taxonomy.

Material and methods

Sakertours Eastern Europe, the Birdwatching and Hide Photography Company of the Carpathian Basin and the Danube Delta has financed the collecting trip to Macedonia and Bulgaria as well as the elaboration of the collected materials. Collection of material in Kosovo is part of a continuous investigation of aquatic insect biodiversity in Kosovo carried out by Department of Biology of the University of Prishtina, Kosovo. Adults were collected by sweep netting, manual singling, light trapping, and first of all by beating vegetation above umbrella along stream and spring area. We have applied the genital clearing, cleaning, and drawing procedures described by OLÁH (2011).

The internal vaginal sclerite complex was exposed to clear view by cutting windows into the dorsum and left pleuron with a fine scissor. The cleared and cleaned abdomen was transferred to 80% ethanol, and to glycerine for examination under microscope. The carefully cut dorsal and lateral windows on segment VIII give a clear view for the examination and drawing of internal vaginal sclerite complex in general. In the genus *Chaetopteroides* the vaginal sclerite complex incorporates several morphological informations discernible both in dorsal and lateral view. In the present species descriptions we utilise only the dorsal profile of this complex structure to differentiate between species. This dorsal profile is rather simple, but also rather stable and specific. The lateral view produces more morphological informations, but this view is extremely sensitive to the observation plane. It is almost impossible to reproduce the repeated redrawings. Various folding, curving, and bending organisations in three dimensions create very composite and complex structure composed of by the six substructures: lateral margins of the vaginal plate, the articulation sclerite, the wing-shaped vaginal stretching plate, junction sclerite, spermathecal process, bursal sclerite. This very composite structure contains more unexplored specific informations to find initial split criteria with a more detailed finer structure analysis.

Depositories: Department of Biology, Faculty of Mathematics and Natural Sciences, University of Prishtina, Prishtina, Kosovo (DBFMNSUP). Hungarian Natural History Museum, Budapest, Hungary (HNHM), Mátra Museum of the Hungarian Natural History Museum, Gyöngyös, Hungary (MM), Oláh Private Collection (OPC) under national protection of the Hungarian Natural History Museum, Budapest, Hungary.

Taxonomy

Re-diagnosis of the genus *Chaetopteroides* Kumanski, 1987

Sexually dimorphic genus having female brachyptery. Phylogenetically transitional group with combined stenophylacini (large size, light spotted forewing pattern in both sexes, hind tibia with four spurs) and chaetopterygini (erected hairs on forewing, brachyptery, robust venation in female forewing) characters.

Compared to alpine groups of *Drusus*, and some stenophylacini, chaetopterygini genera the genus *Chaetopteroides* has similar habitat and pleistocene survival strategy of glacial altitudinal shifting. Due to their limited mobility and limited habitat resources of isolated high altitude headstream area, the genus *Chaetopteroides* also evolved as incipient juvenile species complex probably in various cycles of late pleistocen. Unfortunately, this beautiful genus is also highly endangered, their habitat being rapidly disappearing on the limited distributional area (Fig. 1).

The structural organisation of the male and female genitalia is very similar among the five species. Periphallic organs of cerci, paraproct, and gonopods are almost identical (Figs 2-6). Only the cerci have differentiated in *C. kosovarorum*, *C. maximus*, *C. tunik*, and *C. veges*, producing an additional digitate setose process shifted mesad to the basement of paraproct. The cerci in *C. bulgaricus* retained its plesiomorphic intact state without subdivision. The

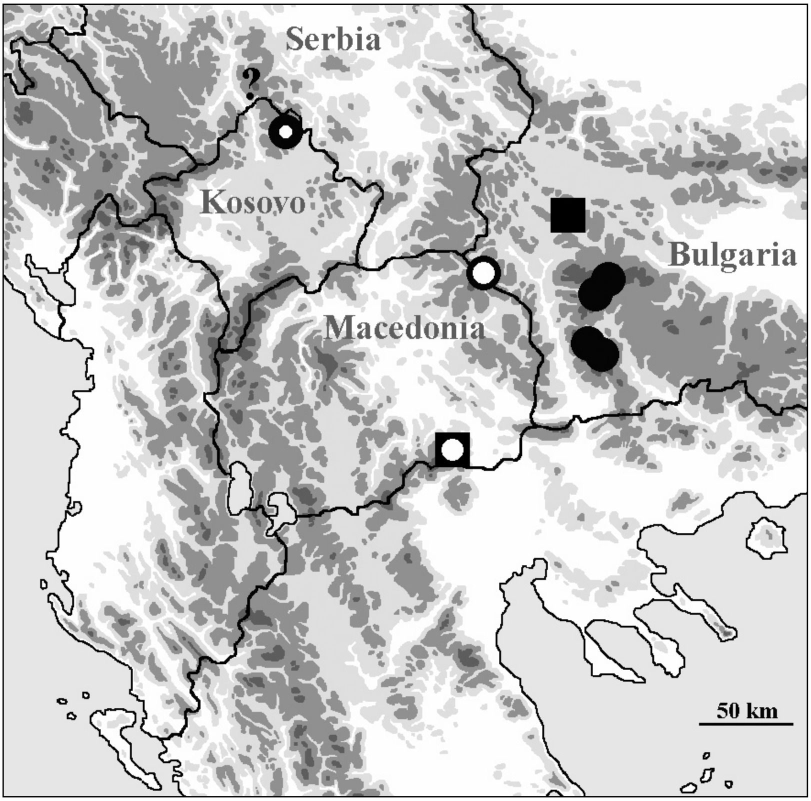


Fig. 1. Distribution of the genus *Chaetopteroides* Kumanski, 1987:
full circle = *C. bulgaricus*; full squarre = *C. maximus*; open circle = *C. veges*;
circle with central dot = *C. kosovarorum*; squarre with central dot = *C. tunik*; question mark = *Chaetopteroides* sp.
(Marinković-Gospodnetić 1980: sub nomen *C. maximus*)

lateral lobe of the subdivided cerci are differentiated at the four species, however the range of variability is unknown having only very few specimens. The cerci stalked at *C. maximus* and *C. kosovarorum*, and elongated at *C. veges* and *C. tunik*. The paraproct with their characteristic hammer-shaped head more sinuous dorsad in lateral view at *C. bulgaricus* and *C. veges*, and almost straight at *C. maximus*, *C. kosovarorum*, and *C. tunik*; longest at *C. maximus* and most short, not longer than cerci at *C. tunik*. The titillating parameres have diversified into variously denticulated apices probably in the sexual selection processes (Figs 7-11). The robust paramere and its heavily spiny apex at *C. bulgaricus* gradually changed finely slender and spineless, almost bare at *C. tunik*. The spiny harm device of sexually antagonistic coevolution evolved into a courtship device in the cryptic female choice processes of the sexual selection. The three external female genital structures well diversified and characterized at all the examined three species: “anal tube”, sternite IX, vulvar scale. The internal vaginal sclerite complex produced less diversification. Only the fused folding plica and the vaginal sclerite wings exhibit some diversity among the species, but it is difficult to visualize and to compare their highly plane-dependent complex shape.

Figs 2–11. Diagrammatic drawings of male genitalia in left lateral view (2–6), and paramere in dorsal view (7–11): 2, 7 = *C.. bulgaricus* (Kumanski, 1969); 3, 8 = *C. maximus* (Kumanski, 1968); 4, 9 = *C. veges* Oláh sp. n.; 5, 10 = *C. kosovarorum* Ibrahimi et Oláh sp. n.; 6, 11= *C. tunik* Oláh sp. n.

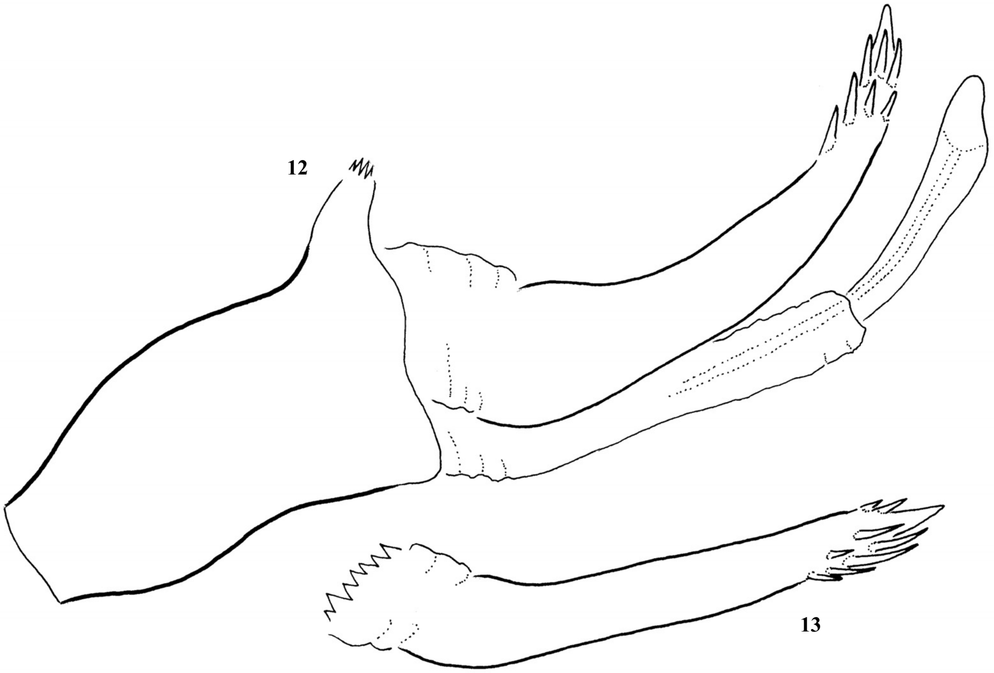
Species taxonomy and faunistics

Chaetopteroides bulgaricus (Kumanski, 1969) (Figs 12–17)
Chaetopteryx bulgaricus Kumanski, 1969 KUMANSKI (1969): 21–27.

Type materrial – „Material und Fundort: 10.X.1967, Pirin-Gebirge, Banderitza-Tal, Bach über der Berghütte „Wichren", 2♂♂, 1♀ und im Abfluss der Muratowi-Seen (gleicher Bezirk), 1♂, 2♀♀. Höhe über dem Meeresspiegel entsprechend 2100 und 2200 m. Holotypus und die Paratypen (2♂♂, 3♀♀) in Sammlung (in Alcohol) des Zoologischen Museums der Bulgarischen Akademie der Wissenschaften"

Chaetopteroides bulgaricus (Kumanski, 1969). *Chaetopteroides* gen. n. erected by KUMANSKI (1987): 15.

Records – Additional female was collected in Pirin Mts below Bezbog on 2240 m in 18.IX.1968 (KUMANSKI 1971). Later a single female in Rila Mts. at tributary of Beli Iskar ob Borowez, 2300 m, 23-24.VIII.1971 and a single male at the tributary of Beli Iskar ob Borowez 1200-1800 m, 24.VIII.1971 have been collected (KUMANSKI & MALICKY 1976). Rila Mts. Beli Iskar, 1900 m, 23.VIII.1971, leg Braasch (1♂, 1♀, OPC present from MPC). OLÁH & KOVÁCS (2012): Bulgaria, Rila Mts, Borovets, Zavrachitsa hut, Prava Maritsa, N42°10'04.9", E23°38'28.1", 2200 m, 05.10.2011, Á. Ecsedi, T. Kovács, G. Puskás (1♀, OPC). Pirin Mts, 950 m S of Demianitsa hut, left side brook of Valyavitsa stream, N41°44'02.6" E23°28'03.1", 2020 m, 07.10.2011, Á. Ecsedi, T. Kovács, G. Puskás (5♀, OPC; 1♂, 1♀, MM). Pirin Mts,

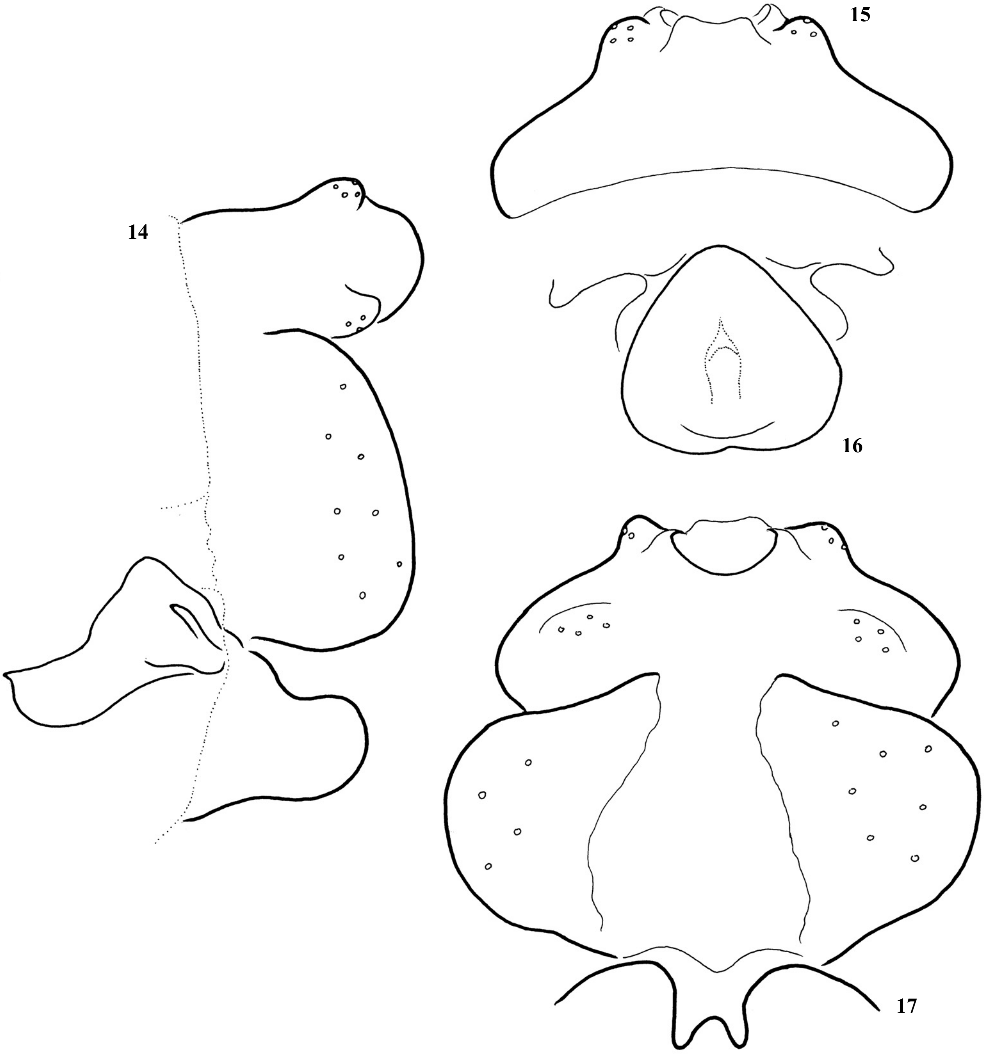


Figs 12–13. *Chaetopteroides bulgaricus* (Kumanski, 1969) male:
12 = phallic organ in lateral view; 13 = left paramere in dorsal view

1.5 km E of Begovitsa hut, Begovitsa stream, N41°40’32.6” E23°26’38.8”, 1930 m, 08.10.2011, Á. Ecsedi, T. Kovács, G. Puskás (1♂, OPC).

New records – **Bulgaria**, Blagoevgrad province, Pirin Mts, Bansko, stream in pine shrub above the Vihren hut, N41°45.293’ E23°24.933’, 1995 m, 24.10.2013, J. Kontschán, D. Murányi, T. Szederjesi (1♂, HNHM).

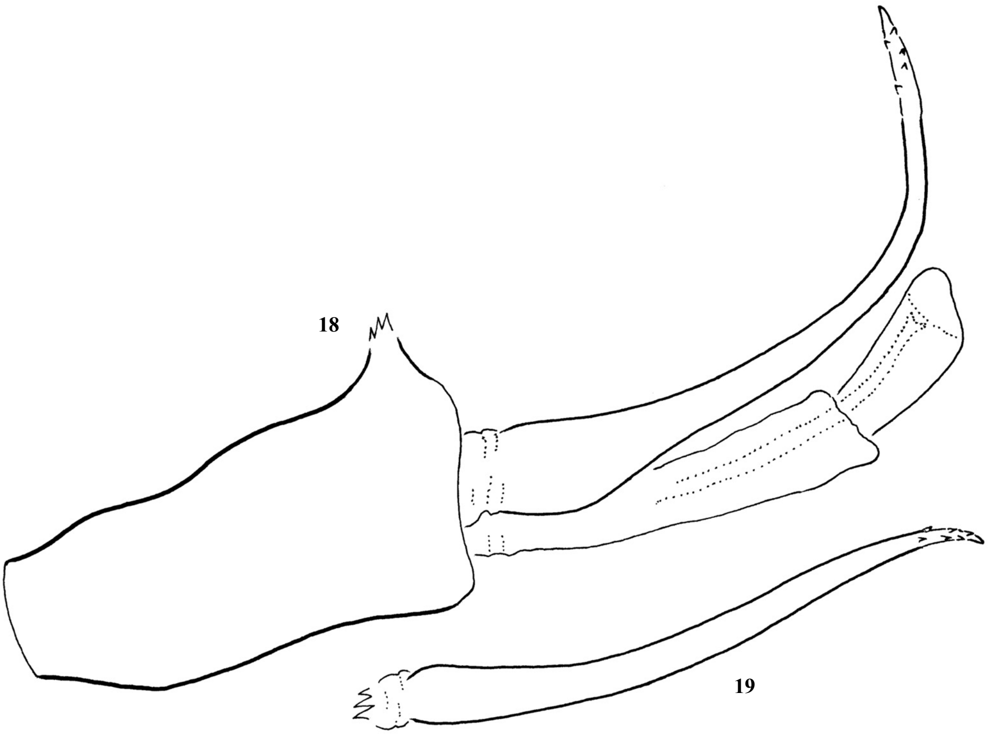
Diagnosis – Cerci simple without additional setose process of subdivion. Paramere apex multidenticulate. Anal tube with short dorsolateral setose lobe and ventrolateral lobe-like setose surface. Sternite IX high. Vulvar scale simple rounded in lateral view, median lobe short rounded.



Figs 14–17. *Chaetopteroides bulgaricus* (Kumanski, 1969) female: 14 = genitalia in lateral view; 15 = genitalia in dorsal view; 16 = vaginal sclerite complex in dorsal view; 17 = genitalia in ventral view

Chaetopteroides kosovarorum **Ibrahimi et Oláh sp. n. (Figs 18–19)**

Diagnosis – This large sized species with few light spots on male forewing and with subdivided cerci is more similar to *C. veges* sp. n., but differs by the modified parameres. Parameres became elongated thin-slender with bulbous basement, apical teeth reduced in size, almost minituarized, and their number multiplied up to 8-10.



Figs 18–19. *Chaetopteroides kosovarorum* Ibrahimi et Oláh sp. n. male: 18 = phallic organ in lateral view; 19 = left paramere in dorsal view

Type materrial – Holotype. **Kosovo**, Mitrovicë Municipality, Bajgorë area, entrance into the Kaçandoll village from Mitrovicë side, sidespring of the Kaçandoll River by the main road, N42.979°, E21.0509°, 1262 m, 29.10.2013, H. Ibrahimi, F. Asllani Ibrahimi, Irsa Ibrahimi & Idlir Ibrahimi (1♂, DBFMNSUP). Paratypes. Same as holotype (2♂, DBFMNSUP). Same place as holotype, 18.09.2012, light trap, H. Ibrahimi (2♂, DBFMNSUP); 25.10.2013, H. Ibrahimi (1♂, OPC).

Description – Male (in alcohol). Forewing 20 mm. Body and wing colour faded stramineous. Forewing narrow and long with erected setae present both on veins and membrane, pattern reduced to a few light spots. Similarly to *C. maximus* and *C. veges* cerci subdivided, it means that the usual cerci are accompanied by a short and digitate setose process shifted to mesad position near to the paraproct.

Female. Unknown.

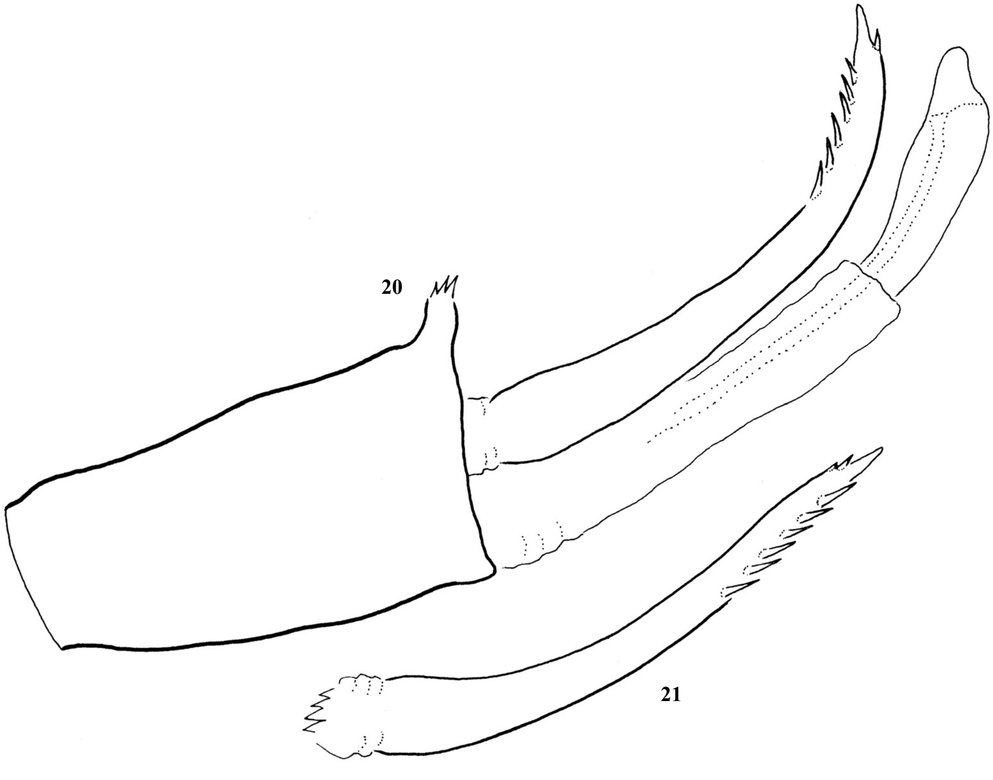
Etymology – *kosovarorum* from "kosovar", the inhabitant of Kosovo.

Chaetopteroides maximus (Kumanski, 1968) (Figs 20–25)
Chaetopteryx maximus Kumanski, 1968 Kumanski (1968): 59–61.

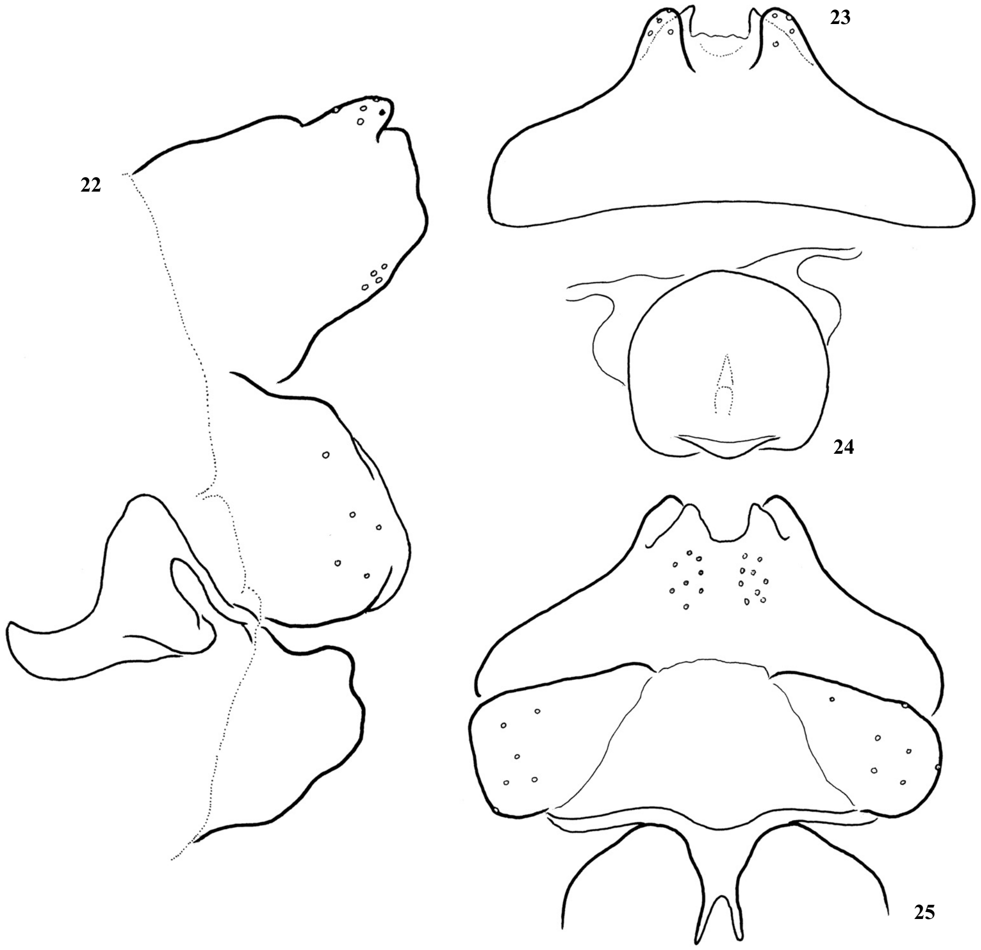
Type materrial – „Fundort: Vitosa-Gebirge, beim Bergbach, nich weit von der Berghütte „Bor", 1620 m Höhe, 1.X.1958, 7♂♂ (leg. N. Vihodcevski). Holotypus und 1 paratypus ♂ in der Kollection von F. Schmid (Ottawa); 5♂♂ Paratypen in der Inseektensammlung des Zoologischen Museums der Bulgarischen Akademie der Wissenschaften"

Chaetopteroides maximus (Kumanski, 1968). *Chaetopteroides* gen. n. erected by Kumanski (1987): 15.

Records – In Vitosha Mts Kumanski (1971) has collected 3 males in Zlatnite bridge and 1 male below Rodina in 19.10.1968. A single female was collected on Vitosha Mts on 19.10.1974, near the type locality (Kumanski 1987). Oláh & Kovács (2012): Bulgaria, Vitosha Mts, spring and brook 200 m E of Rodina hut, N42°37'09.6", E23°15'32.3", 1600 m, 03.10.2011, Á. Ecsedi, T. Kovács, G. Puskás (4♀, OPC). Vitosha Mts, Lavchemo, Boyanska Reka, N42°34'34.6" E23°16'57.7", 2050 m, 04.10.2011, Á. Ecsedi, T. Kovács, G. Puskás (1♂, 3♀, OPC; 1♂, 1♀, MM). Marinković-Gospodnetić (1980) has reported the species from Serbia: spring area of Lisinska River, Kopaonik Mts, 1♂, 2♀, 08.10.1978. Marinković-Gospodnetić's specimens have been lost: the entire collection was destroyed during the Bosnian war between



Figs 20–21. *Chaetopteroides maximus* (Kumanski, 1968) male:
20 = phallic organ in lateral view; 21 = left paramere in dorsal view



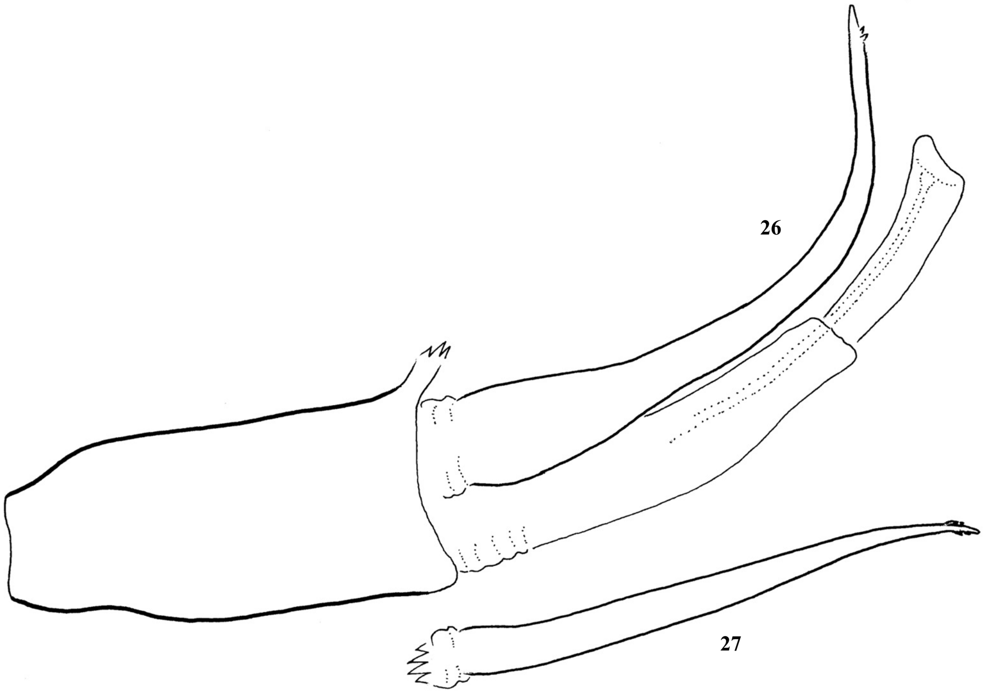
Figs 22–25. *Chaetopteroides maximus* (Kumanski, 1968) female: 22 = genitalia in lateral view; 23 = genitalia in dorsal view; 24 = vaginal sclerite complex in dorsal view; 25 = genitalia in ventral view

1992 and 1995 (personal communication by H. Malicky). New collection is required to confirm its real taxonomic position. It is probably not *C. maximus. C. maximus* is known as endemic to Vitosha Mts. Bulgaria.

Diagnosis – Cerci with additional setose process of subdivion. Paramere apex linear denticulate laterad. Anal tube with long dorsolateral setose lobe, ventral setose surface divided. Sternite IX rounded low. Vulvar scale humped rounded in lateral view; median lobe less developed triangular.

Chaetopteroides tunik **Oláh sp. n. (Figs 26–27)**

Diagnosis – This medium sized species with narrow and long forewing without any pattern and having subdivided cerci is more similar to *C. kosovarorum*, but differs by having cerci, elongated not stalked; gonopod without vertical ridge; paramere less slender, straight in dorsal



Figs 26–27. *Chaetopteroides tunik* Oláh sp. n. male:
26 = phallic organ in lateral view; 27 = left paramere in dorsal view

view, not arching mesad and the minute teeth limited to terminal position and their number are reduced to 4. This description is based on a single holotype male, female is required to confirm its position.

Type material – Holotype. **Macedonia**, Vardar region, Kožuf Mts, open brook in alpine grassland towards Ski Kožuf, N41°12.560', E22°13.170', 1670 m, 04.10.2013, T. KOVÁCS, D. MURÁNYI (1♂, OPC).

Description – Male (in alcohol). Forewing 18 mm. Body and wing colour faded stramineous. Forewing narrow and long without pattern; erected setae present both on veins and membrane. Similarly to *C. maximus* cerci subdivided, it means that the usual cerci are accompanied by a short and digitate setose process shifted to mesad position near to the paraproct. Cerci without stalk, elongated, almost as long as the paraproct. Paraproct straight and short. Paramere slender, almost setaless, only four minituarized, almost indiscernible teeth present.

Female. Unknown.

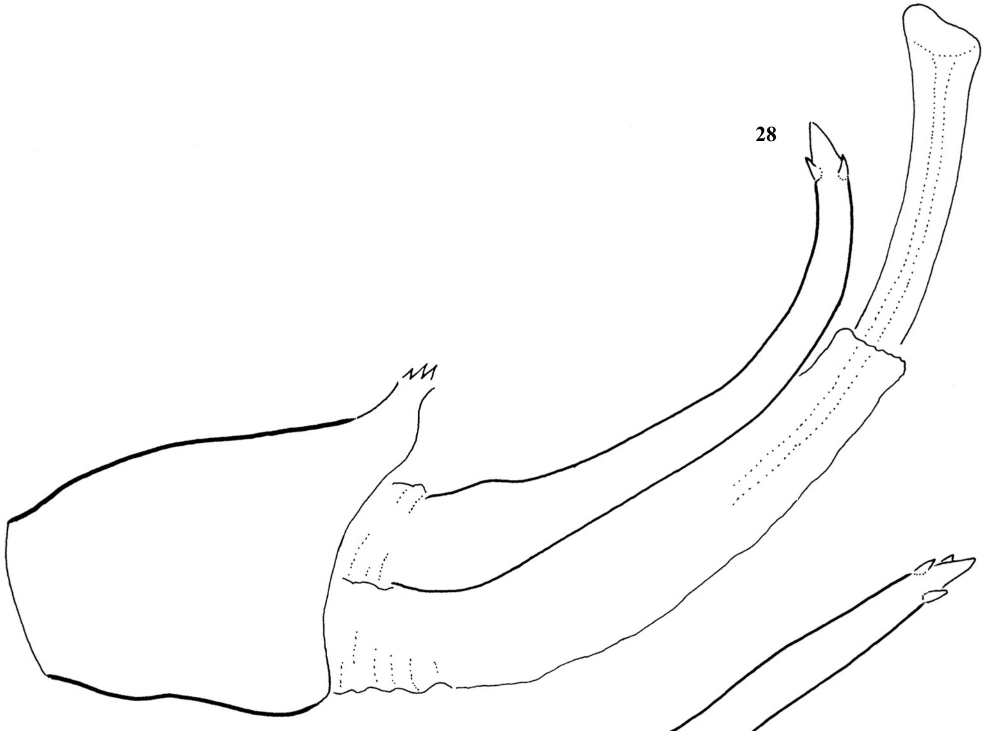
Etymology – *tunik* from "tűnik" appear and disappear in Hungarian, refers to just appearing, almost disappearing setae on the parameres.

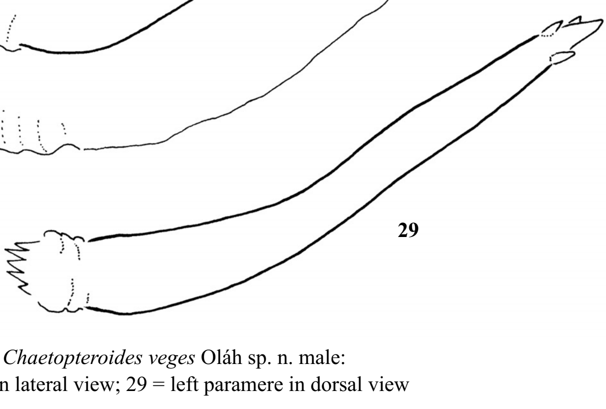
Chaetopteroides veges Oláh sp. n. (Figs 28–33)

Diagnosis – This large sized species with narrow and long light-spotted male forewing and brachypterous fused-spotted female forewing having subdivided cerci is more similar to *C. maximus*, but differs by having male with paramere setae limited to terminal position and their number are reduced to 2-3. Differs by female by having apical lateral lobes much longer than dorsolateral lobes; ventral setose surface on the anal tube fused, not divided; sternite IX higher; vulvar scale hooked in lateral view, not humped; median lobe of the vulvar scale more developed.

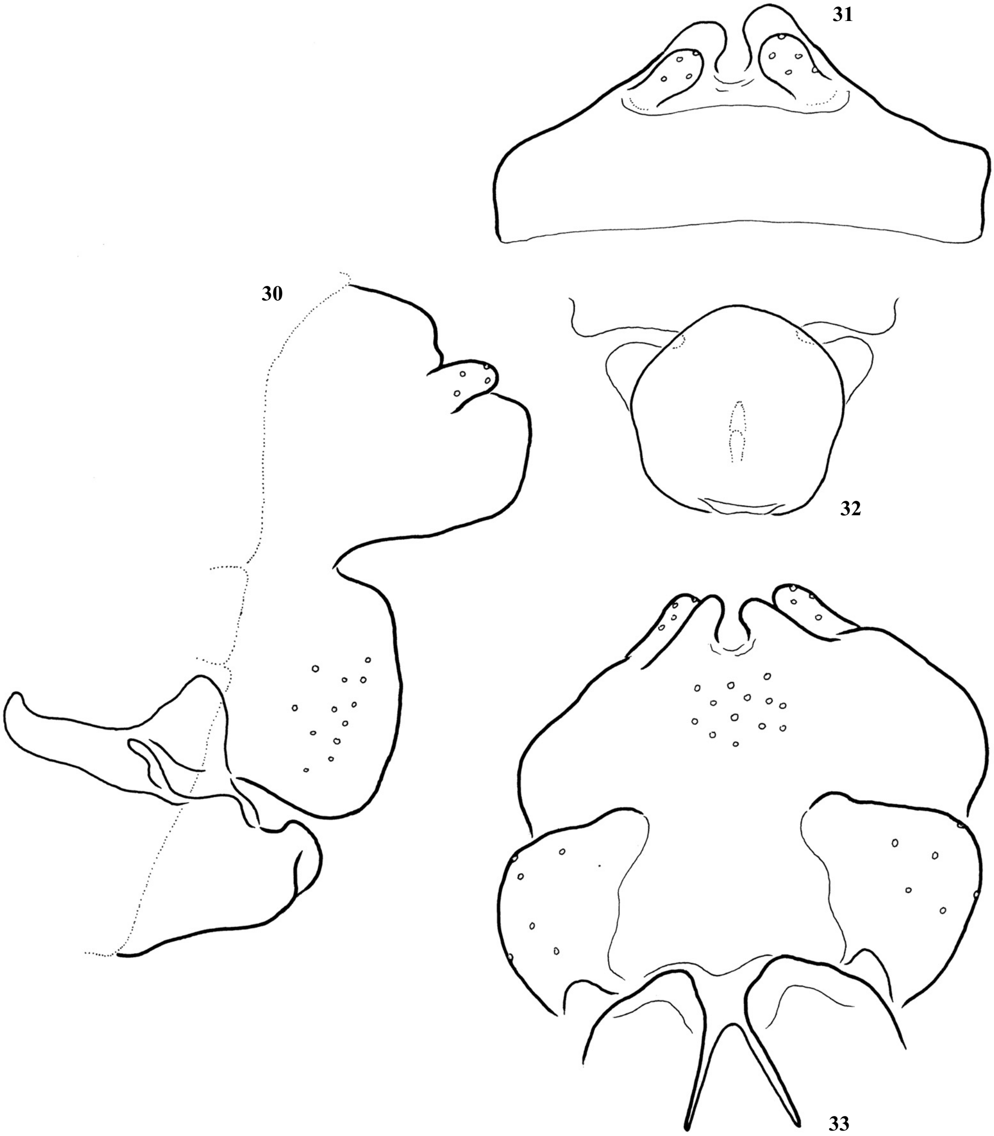
Type materrial – Holotype. **Bulgaria**, Kyustendil province, Osogovska planina, spruce forest, forest brook below Trite buki hut, N42°10.463', E22°38.066', 1520 m, 23.10.2013, J. Kontschán, D. Murányi, T. Szederjesi (1♂, HNHM). Allotype. Same as holotype (1♀, HNHM). Paratypes. Same as holotype (1♀, HNHM). Kyustendil province, Osogovska planina, beech forest and forest brook at Iglika hut, N42°13.783', E22°38.842', 1325 m, 23.10.2013, J. Kontschán, D. Murányi, T. Szederjesi (1♀, HNHM).

Description – Male (in alcohol). Forewing 20 mm. Body and wing colour faded stramineous. Forewing narrow and long with erected setae present both on veins and membrane, pattern is almost regular light-spotted. Similarly to *C. maximus* cerci subdivided, it means that the usual cerci are accompanied by a short and digitate setose process shifted to mesad position near to the paraproct.





Figs 28–29. *Chaetopteroides veges* Oláh sp. n. male:
28 = phallic organ in lateral view; 29 = left paramere in dorsal view



Figs 30–33. *Chaetopteroides veges* Oláh sp. n. female: 30 = genitalia in lateral view; 31 = genitalia in dorsal view; 32 = vaginal sclerite complex in dorsal view; 33 = genitalia in ventral view

Female (in alcohol). Forewing 14 mm. Body and wing colour stramineous. Forewing broad and abbreviated, in the light pattern the spots irregularly fused. Anal tube with long dorsolateral setose lobe, ventral setose surface undivided. Slerite IX subqudratic. Vulvar scale hooked in lateral view and the median lobe enlarged tapering triangular.

Etymology – *veges* from “véges” meaning terminal/apical in Hungarian, referring to the few setae on the parameres present and limited to the terminal/apical area.

References

Arnqvist, G. (1998): Comparative evidence for the evolution of genitalia by sexual selection. – Nature, 393: 784–786.

Bonduriansky, R. (2011): Sexual selection and conflict as engines of ecological diversification. – The American Naturalist, 178(6): 729–745.

Cordero Rivera, A., Andrés, J. A., Córdoba-Aguilar, A. & Utzeri, C. (2004): Postmating sexual selection: allopatric evolution of sperm competition mechanisms and genital morphology in calopterygid damselflies (Insecta: Odonata). – Evolution, 58(2): 349–359.

Darwin, C. (1871): The descent of man, and selection in relation to sex. – Appleton, New York, 409 pp.

Eberhard, W. G. (2010): Evolution of genitalia – theories, evidence, and new directions. – Genetica, 138(1): 5–18.

Holwell, G. I., Winnick, C., Tregenza, T. & Herberstein, M. E. (2010): Genital shape correlates with sperm transfer success in the praying mantis *Ciulfina klassi* (Insecta: Mantodea). – Behavioral Ecology and Sociobiology, 64: 617–625.

Hosken, D. J. & Stockley, P. (2004): Sexual selection and genital evolution. – Trends in Ecology and Evolution, 19(2): 87–93.

Johnstone, R. A. & Keller, L. (2000): How males can gain by harming their mates: sexual conflict, seminal toxins, and the cost of mating. – The American Naturalist, 156: 368–377.

Kraaijeveld, K., Kraaijeveld-Smit, F. J. L. & Maan, M. E. (2011): Sexual selection and speciation: the comparative evidence revisited. – Biological Reviews, 86(2): 367–377.

Kumanski, K. (1968): *Chaetopteryx maximus* n. sp. aus Bulgarien (Trichoptera, Limnephilidae). – Comptes rendus de l'Académie bulgare des Sciences, 21(1): 59–61.

Kumanski, K. (1969): *Chaetopteryx bulgaricus* – ein neue Art aus der maximus-Gruppe (Trichoptera, Limnephilidae). – Reichenbachia, 12(3): 21–27.

Kumanski, K. (1971): Beitrage zur Untersuchung der Köcherfliegen (Trichoptera) Bulgariens. – Bulletin de l'Institut de Zoologie et Musée, 33: 99–109.

Kumanski, K. (1972): Review of autumn species of caddisflies in Bulgaria (Insecta: Trichoptera). – Bulletin de l'Institut de Zoologie et Musée, 36: 197–202.

Kumanski, K. (1987): A new genus of the Chaetopterygini – tribe (Trichoptera: Limnephilidae). – Trichoptera Newsletter (Lunz, Austria), 14: 17–19.

Kumanski, K. & Malicky, H. (1976): Beitrage zur Kenntnis der bulgarischen Köcherfliegen (Trichoptera). – Bulletin Entomologique de Pologne, 46: 95–126.

Ma, N., Zhong, W., Gao, Q. & Hua, B. (2012): Female genital plate diversity and phylogenetic analysis of East Asian Panorpidae (Mecoptera). – Systematics and Biodiversity, 10(2): 159–178.

Marinković-Gospodnetić, M. (1980): Fauna Trichoptera SR Serbia. – Book of abstracts on fauna in Serbia, 1: 71–84. [in Serbian]

McPeek, M. A., Shen, L. & Farid, H. (2009): The correlated evolution of three-dimensional reproductive structures between male and female damselflies. – Evolution, 63(1): 73–83.

Nilsson, T. (2004): Polyandry and the evolution of reproductive divergence in insects. – PhD Thesis, Umea University, Umea, Sweeden, 33 pp.

Oláh, J. (2011): New species and records of Balkan Trichoptera. – Folia Historico-naturalia Musei Matraensis, 35: 111–121.

Oláh, J. & Kovács, T. (2012): New records of Chaetopterygini species (Trichoptera: Limnephilidae). – Folia Historico-naturalia Musei Matraensis, 36: 81–88.

Oláh, J., Kovács, T., Sivec, I. Szivák, I. & Urbanić, G. (2012): Seven new species in the *Chaetopteryx rugulosa* species group: applying the phylogenetic species concept and the sexual selection theory (Trichoptera, Limnephilidae). – Folia Historico-naturalia Musei Matraensis, 36: 51–79.

Oláh, J. & Ito, T. (2013): Synopsis of the *Oxyethira flavicornis* species group with new Japanese *Oxyethira* species (Trichoptera, Hydroptilidae). – Opuscula Zoologica, Budapest, 44(1): 23–46.

Oláh, J., Andersen, T., Chvojka, P., Coppa, G., Graf, W., Ibrahimi, H., Lodovici, O., Previšić, A. & Valle, M. (2013): The *Potamophylax nigricornis* group (Trichoptera, Limnephilidae): resolution of phylogenetic species by fine structure analysis. – Opuscula Zoologica, Budapest, 44(2): 167–200.

Puniamoorthy, N., Kotrba, M. & Meier, R. (2010): Unlocking the "Black box": internal female genitalia in Sepsidae (Diptera) evolve fast and are species-specific. – BioMed Central Evolutionary Biology, 10(275): 1–21.

Rodriguez, V., Windsor, D. M. & Eberhard, W. G. (2004): Tortoise beetle genitalia and demonstrations of a sexually selected advantage for flagellum length in *Chelymorpha alternans* (Chrysomelidae, Cassidini, Stolaini). – In: P. Jolivet, Santiago-Blay, J. A. & Schmitt, M. (eds): New Developments in the Biology of Chrysomelidae, pp. 739–748.

Rodriguez, R. L., Boughman, J. W., Gray, D. A., Hebets, E. A., Höbel, G. & Symes, L. B. (2013): Diversification under sexual selection: the relative roles of mate preference strength and the degree of divergence in mate preferences. – Ecology Letters, 16: 964–974.

Rowe, L. & Arnqvist, G. (2011): Sexual selection and the evolution of genital shape and complexity in water striders. – Evolution, 66(1): 40–54.

Schluter, D. (2009): Evidence for ecological speciation and its alternative. – Science, 323: 737–741.

Via, S. (2009): Natural selection in action during speciation. – Proceedings of the National Academy of Sciences of the United States of America, 106(1): 9939–9946.

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