

## Seven new species in the *Chaetopteryx rugulosa* species group: applying the phylogenetic species concept and the sexual selection theory (Trichoptera: Limnephilidae)

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**ABSTRACT:** Emerging perspectives of the phylogenetic species concepts and of the sexual selection theory were reviewed in order to apply these new findings to separate species in the obscured *Chaetopteryx rugulosa* species group. Species is no longer considered as a stage in the lineage divergence. All the separately evolving metapopulation lineages represent species, from initial separation to extinction. Species is not a taxonomic rank, but a level of biological organisation. There are newly born and there are dying species. There are no subspecies as there are no “subindividuals“ in the hierarchy of the biological organisation. Stable initial split criterion became a dominating practical guide to separate and describe species. That means that finding reliable separating morphological characters remains the central target in taxonomy and faces a challenge to taxonomist. Intense recent sexual selection processes both in the sexually antagonistic coevolution and in the cryptic female choice have produced stable diversity on the intromitten region of the edaeagus and on the female anal tube in the *C. rugulosa* species group. The male lateral subapical processes on the aedeagus and the female anal tube were applied to describe new species in this group: *C. giulienis* Oláh & Kovács sp. n., *C. idriensis* Oláh & Urbanič sp. n., *C. kamnikensis* Oláh & Urbanič sp. n., *C. papukensis* Oláh & Szivák sp. n., *C. pohorjensis* Oláh & Urbanič sp. n., *C. prealpensis* Oláh sp. n., *C. zalaensis* Oláh sp. n. Based on male and female genital characters and applying the phylogenetic species concept we have raised subspecies rank to species rank with three new combinations: *Chaetopteryx mecsekensis* Nogradi, 1986 comb. nov., *Chaetopteryx schmidi* Botosaneanu, 1957 comb. nov., *Chaetopteryx noricum* Malicky, 1976 comb. nov., and have established three new species subgroups in the *C. rugulosa* species group: *C. schmidi*, *C. rugulosa*, *C. irenae*. In the *C. rugulosa* new species subgroup we have erected two new species clusters: *C. noricum*, *C. rugulosa*.

### Introduction

The first member of this species group, the nominate species *Chaetopteryx rugulosa* Kolenati, 1848 was described from a single holotype of uncertain origin (MALICKY et al. 1986). The holotype is in good condition and is deposited in the Naturhistorischen Museum Wien. The next species, *C. clara* McLachlan, 1876 was described from two specimens with localities Krain and Görz probably from around the region of Ljubljana (MALICKY et al. 1986). The third species, *C. schmidi* Botosaneanu, 1957 was described from Romania, Southern Carpathian Mts. Cerna Valley. The fourth taxon, as a subspecies, *C. schmidi noricum* Malicky, 1976 was described from Austria. These species were revised and the *Chaetopteryx rugulosa* species group established with the description of three new species: *C. euganea* Moretti & Malicky, 1986, *C. goricensis* Malicky & Krušnik, 1986, *C. irenae* Krušnik & Malicky, 1986 and with one new subspecies: *C. schmidi mecsekensis* Nogradi, 1986 (MALICKY et al. 1986). Later the subspecies construction was modified by MALICKY (2005) into the present taxonomic state: *C. rugulosa mecsekensis*, *C. rugulosa noricum*, *C. rugulosa rugulosa*, *C. rugulosa schmidi*.

Traditional classification of several species in the group was painfully hindered by the extremely great variation of the periphallid structures inside the same populations or metapopulations.

These genital structures are the cerci, the paraproct and the gonopods which are commonly used in trichopterozoology to separate species. After a detailed examination of the fine structure of the phallic organ as well as the female anal tube in 192 populations we have detected the paramere spines pattern, the intromittent region of the aedeagus as well as the apicaodorsal profile of the female anal tube rather stable and reliable to differentiate among species. Especially the head of the aedeagus proved to be rather stable. We have detected small ranges of variation only in the populations of the two widely distributed and probably ancestral species of *C. schmidi* Botosaneanu, 1957 and *C. prealpensis* sp. n. The diversification of the inseminating and stimulating intromittent phallic organ refers to the intense ongoing processes of sexual selection. At the same time the high variability of the male periphallid structures inside populations refers to intense recent speciation processes. We have summarized briefly both the applicable species concept and the theory of sexual selection in order to apply these recent findings to separate and describe species in the obscured *Chaetopteryx rugulosa* species group.

### **Material and methods**

The adults were collected with singling, beating sheet or with sweeping net. All material is stored in 70-80% ethanol.

We have applied the methods described by OLÁH (2011).

Depositories: HNHM = Hungarian Natural History Museum, Budapest, Hungary, MM = Mátra Museum, Gyöngyös, Hungary, MPC = Hans MALICKY Private Collection, Lunz am See, Austria, OPC = János OLÁH Private Collection presently under National Protection of the Hungarian Natural History Museum, Hungary, PMS = Slovenian Museum of Natural History, Ljubljana, Slovenia as indicated in the examined material.

### **Theoretical part**

#### **Species concept**

DARWIN (1859) reformulated the old concept of species and formulated the evolutionary species concept of the lineage segment in the formula that species are “branches in the lines of descent“. However, he has compromised and retained the old taxonomic tradition that the species category is a rank in the taxonomic hierarchy. This basic conflict remained a permanent controversy and the forthcoming progress was simplified just to develop more objective ranking criteria. Placing discrete boundaries on the continuous process of diversification produced endless debate and developed over 22 species concepts (MAYDEN 1997) to overcome the limits of the old biological species concept (MAYR 1942). This widespread and dominating concept is not in accordance with the new findings that reproductive barriers are semipermeable to gene flow and species can differentiate despite ongoing interbreeding (HAUSDORF 2011). In the new unified species concept the species category is being decoupled from the hierarchy of taxonomic ranks and transferred to the hierarchy of biological organisation (DE QUEIROZ 2011). In the old concepts the species as a rank was accepted only if its lineage had reached a particular stage in the process of divergence. Lineages that had not yet reached that stage were ranked as subspecies. The conceptualization of species as population lineages is common to all species concepts. Dropping

the various species ranking criteria as well as stopping to treat the species as a taxonomic rank the species is no longer considered as a stage in the lineage divergence. All the separately evolving metapopulation lineages represent species. Species are species during their entire life span, from initial separation to extinction. Commonly spoken there are newly born and there are dying species. There are no subspecies as there are no “subindividuals“ in the hierarchy of the biological organisation. Therefore the firm and stable initial split criterion became a dominating practical guide to separate and describe species. Time is here to understand that species is not a taxonomic rank, but a level of biological organisation. The species is transferred from the hierarchy of taxonomic rank to the hierarchy of biological organisation. This phylogenetic species concept successfully unifies two roles of species serving (1) as entity of evolution theory understanding the organisation of living world and (2) describing diversity reflecting the pattern of the organised life. The new theory of sexual selection helps us to understand how to develop and apply stable initial split criterion to separate species in particular groups of living creatures.

### **Sexual selection**

How novel ecological strategies evolve in organisms that are already adapted to their ecological niche? How natural and sexual selection drive evolution? Natural selection opposes divergence from established niche-exploitation strategies and empirical studies have yielded little evidence that genetic drift plays an important role in morphological evolution. At the same time sexual selection could carry populations through fitness valleys of maladaptive intermediate phenotypes between alternative niches on the fitness landscape. This is realised by initiating reproductive isolation and resulting in ecological divergence through genetic drift or local adaptation (BONDURIANSKY 2011). In these days sexual selection is getting appreciation to understand speciation processes, especially in species complexes composed of closely related species. We understand that many of the so called “widely distributed and highly variable species“ are subject to these sophisticated studies and we will be able to unlock these “black boxes“ with fine structural studies and to demonstrate that they contain several closely related species.

Three hypotheses have been developed to explain the evolution of the extraordinary diverse male genitalia: (1) Under the lock-and-key hypothesis, selection for preinsemination reproductive isolation is predicted to favour male genitalia, that provides an exact mechanical fit to female genitalia. (2) The pleiotropy hypothesis suggests that variation in genitalic morphology is selectively neutral and that male genitalia evolve via pleiotropic effects of genes that code for both genital and general characters. (3) The sexual selection hypothesis proposes that fertilization success in postinsemination processes is nonrandom with respect to genital morphology (OLÁH & JOHANSON 2008). Sexual selection occurs if differences among male genitalia are related to sensory manipulation in mating, to the ability of removing rival sperm in sperm competition, to control fertilization in sexual conflict between male and female, and to induce post-copulatory preferential sperm utilization in cryptic female choice (ARNQVIST 1997).

Sexual selection is clearly supported by the fact that genitalia diversify much more rapidly in insect characterized by polyandrous mating systems compared with monoandry. Genital evolution is more than twice as divergent in taxa in which females mate many times in polyandry (ARNQVIST 1998). The lock-and-key hypothesis still popular among taxonomists suggests that genitalia evolve by pre-insemination hybridization avoidance. In contrast, the sexual selection hypothesis proposes that divergent evolution of genitalia is dominated by sexual selection in postinsemination processes.

Darwin developed the idea of female preference for male ornaments when distinguished direct male-male battle and female choice, but failed to recognise or appreciate that male-male competition and sexual selection continue after copulation has begun (EBERHARD 2009). Long known that selection in the insects continues after copulation by sperm competition (PARKER 1970). These male-male battles together with cryptic female choice occur within the female's body. Undoubtedly an incomplete list of 24 female controlled processes and mechanisms has been exemplified in biasing paternity if female mates with more than a single male (EBERHARD 2010a). Females are able to influence even where the sperm is stored, how it is dispensed or displaced.

Female defensive coevolution with males, the sexually antagonistic coevolution in the sexual conflict results that female genitalia coevolve and diversify together with the species specific aspect of the male genitalia. Females defend her interest against male coercion resulting in diverse female genitalia. Species specificity of female genitalia was demonstrated recently in dipteran Sepsidae (PUNIAMOORTHY et al. 2010) and mecopteran Panorpidae (MA et al. 2012) families. In contrast if cryptic female choice dominates the processes in sexual selection the male genital morphology will rapidly diversify and external female genital morphology will often not vary. When female are screening males in cryptic female choice by stimuli they coevolve rather with their sense organs (EBERHARD 2010b).

### **Sexual selection in *Chaetopteryx rugulosa* species group**

Members of the cool-adapted Chaetopterygini tribe have very long lasting copulation. Female and male spend several days in copula, at least in experimentally isolated condition when the copulating pairs are held in separate boxes (MALICKY & PAULS 2012). This long duration may function like a living copulatory plug. However it seems that coupling or fitting mechanism of the male and female genitalia in this group is not sophisticated enough to hold the copulating female and male together long in a fixed position. The intromittent structure of the phallic organ, the aedeagus is without any significant withholding sclerotic structure. Moreover the female genital chamber, the vagina is very short. The only withholding structures on the aedeagus are the subapical lateral processes and the erectile, usually trilobed endophallic membranous head. These highly inflatable apical structures are probably fitting and, when erected filling the entire internal profile of the membranous vagina. This erectile condition could hold the copula together, but not for several days. We have observed that in most of the freshly collected copula the aedeagus is almost fully withdrawn from the vagina and only the paraproct-anal tube coupling mechanism keeps the copulating female and male together. The paraproct with its more or less serrated apical curving hooks performs a grasping function anchoring into the internal sclerites inside the female anal tube. Instability of coupling is indicated by field observations. Competing males are frequently present near around the copulating pairs. It appears that species of the space-limited spring-dwelling *Chaetopteryx rugulosa* species group with high density of competing males around are especially subject to strong sexual selection. Reproductive concurrence in the space-limited environment may produce intense selection mechanisms of both the preinsemination and postinsemination male-male battles as well as the cryptic female choice within female body.

We have found stable diagnostic traits in the length and shape of the female anal tube serving as substrate for anchor, but we have found the species-specificity of male paraproct functioning as the anchor, not stable enough. Other male periphallid structures, the cerci and the gonopods

are also highly varying. This finding suggests that preinsemination mating preferences enforced by the morphological fit of male and female genital structures may change the reproductive compatibilities rapidly in speciation events. Changing compatibility will define the new species boundaries. Males vary more in their reproductive success than females (RODRIGUEZ-MUNOZ et al. 2010). Dominating female interest in polyandry may alter the condition of stabilizing selection for species mate recognition and modifies the morphological fit of male and female structures. It seems that females initiate and even direct the birth of the new species. Variability and flexibility of paraproct and other periphallallic structure are tactile male responses to this change and refers to very recent speciation with lowered rate of stabilizing selection. Compared to periphallallic structures the male paramere spine pattern is more stable. Their high diversity among species is a result of their stimulatory function on supragenital plate and in the deeper region of the upper vulvar lip. The selection of the spine pattern evolved probably in cryptic female choice. The most diverse and most stable male genital structure is the aedeagus. Having inseminating and stimulatory functions their high diversity is produced probably in various processes of the cryptic female choice. Its apical region evolved rather stable and highly species-specific in the form of the lateral subapical processes. The male lateral subapical processes and the female anal tube were applied to differentiate between the species in the obscured species complex of the *C. rugulosa* species group.

### **Mixed and/or interbreeding populations**

Without a systematic survey we have found mixed or interbreeding populations in several habitats of the following species. *Chaetopteryx kamnikensis* Oláh & Urbanič sp. n. together with *C. prealpenis* Oláh sp. n.: Slovenia: Golovec Mts, Rakovnik District; Kamnik Mts, Volovljek; Litija, Janče, stream Gostinca. *C. schmidi* Botosaneanu, 1957 together with *C. papukensis* Oláh & Szivák sp. n.: Croatia: Psunj Mts; Bosnia & Herzegovina: Kozara Mts.

## **Genital structure and copulatory function**

### **Male**

*Tergite VIII* armed with a pair of apicomeral slightly elevated spinate (microtrichial spinule-covered) protuberances, separated by bare band. Their surfaces packed with peg-like setae and may have both sensory and stimulatory functions in copulatory processes. They behave like enantiomers (optical isomers) of chirality by sensing and stimulating male and female orientation.

*Segment IX* elongated on pleural region, reduced to narrow strip dorsad and medium long ventrad.

*Segment X* structured into a membranous pouch-like double concavity divided by short mesal septum framed and enforced laterad by pairs of associated cerci and ventrad by paraprocts; this double pouched concavity spread deep anterad under tergite VIII and receives the female anal tube during copulation. Segment X concavity, cerci and paraprocts are fused and they form together a *superanal genital complex* (VSHIVKOVA 2007).

*Cerci* (superior appendages) setose, serving sensory function during coupling operation in the copulatory mechanisms; their height (low, medium, high) has diagnostic value in distinguishing species subgroups.

*Paraproct* (intermediate appendages) heavily sclerotized pair of structures located above and around the anal (proctal) opening; tripartite: composed of the apical hook formation, the connecting middle section and the variously laterad turning basal triangle frame; dorsomesal edges or surfaces on the apical hooks finely serrated; during copulation the apical hooks penetrate deep into the female anal tube and their dorsally serrated edges anchor against the internal sclerites and along its membranous margin. The pair of the enlarged basal triangles function like a fulcrum to hold the paraproct clasping movement stable.

*Gonopods* fused to segment IX with discernible suture, cumbuliform with mesal concavity, directed oblique vertical; length and shape has diagnostic value in the formation of species subgroup; gonopods have orientation and locking functions during copulation. *Apical flap of gonopods* variously developed on the free, not fused portion somehow similarly to the “apparent harpago” of the genus *Allogamus*; this lobulate portion is variously turned mesad and also variously into transversal plane giving a rather significant range of apparent variability of gonopod apex in lateral view: (blunt, single pointed, double pointed). *Apical margin of gonopods* forming various profiles in lateral view: (convex, straight, concave, undulate: double concave).

*Phallic organ* consists of the very short ring-like phallic apodeme, the medium long phallosome and endosoma (together phallobase) as well as the aedeagus and a pair of parameres.

*Aedeagus* forms a sclerotized tube with membranous head. Composed inside of the discernible ejaculatory duct, apical eversible endophallus with gonopore and armed outside with subapical processes. The lateral subapical processes are variously sclerotized and developed as a pair of gemmiform, digitiform, filiform, aliform, platform processes with various lengths directed horizontal or upward oblique. If lateral lobes are not sclerotized a pair of ventrolateral or apical supporting sclerites are developed to power the evagination rate of endophallus and the free opening of the gonopore. The membranous endophallic head of the aedeagus when everted usually have well-visible lateral and median upward projecting lobes. These lobes are visible protruded only when the endophallus is fully erected. The membranous head of the aedeagus together with the lateral processes frequently developed into elaborated lobe structures with significant lateral and dorsal extensions fitting into the internal profile of the short vagina (genital chamber) and giving a coupling and/or stimulating mechanism during copulation.

*Paramere* each composed of sclerotized shaft and various numbers of apical spines. Length and shape of *paramere shaft* has diagnostic value: (short, medium, long; rod-shaped, broad, triangular).

*Paramere spine pattern* characterized by the number, length, thickness and position of spines present on paramere tips; the pattern of these characters together is a rather stable diagnostic structure to separate species in spite of the ranges of variations in the individual characters. There are species with primary, secondary and tertiary spines. *Primary spine*: the dominating spine stout and usually single, (short, medium, long, straight or curved). *Secondary spines*: slender with various lengths from very short to almost as long as the primary lines. *Tertiary spines*: almost peg-like, stout and very short.

## **Female**

The closed *anal tube* is formed by the almost completely fused tergite IX and segment X. Its apparent upper lip is the apical dorsum of tergite IX and its apparent lower lip developed from the segment X. *Internal sclerite* inside the anal tube forms an internal second dorsal wall

inside the tube representing the vestigium of tergite X and more or less fused to the dorsum of tergite IX and forming together an important diagnostic character: the *apical pattern of the upper lip* of the anal tube. The internal sclerite (tergite X) is variously connected laterad to the lower lip of the anal tube, forming together the partially fused and vestigial segment X. Setose *ventroapical lobes* may be present on tergite IX; its presence or absence has diagnostic value in the separation of the species subgroups. Sternite IX present as a pair of lateral setose lobes connected by the setaless glabrous mesal surface, the supragenital plate. NIELSEN (1980) relates the supragenital plate or upper lip of the genital opening, (the vulva) to the ventrum of segment X taking part in the formation of the dorsal wall of the genital chamber. The lower lip of the genital opening (vulva), that is the usually trilobed vulvar scale is formed by the vestigial gonopods of segment IX (pair of lateral lobes) and by the vestigial gonopods of segment VIII (single mesal lobe). The internal parts of the vulvar scale have connections to the spermathecal sclerite forming together the vaginal sclerite complex.

### **Variability of the genital structures**

Both the male and females genital structures vary to a great extent. Especially the periphallallic structures: cerci, paraprocts, gonopods on the males and the protruding rate of the internal sclerites as well as the development of the ventrolateral processes of the tergite IX on the females. The parameres, the non-intromittent component of the phallic organ exhibit a smaller range of variation both in the shape and length of the shaft and in the number and length of the spines. Most stable is the aedeagus, the inseminating substructure that is the intromittent component of the phallic organ: especially the subapical lateral processes; the ventrolateral supporter sclerites, the shape of endophallic membranous erectile head. However the erectile head has low diagnostic value, because it is very rare to have specimens with fully erected endophallic head, and it is impossible to estimate the rate of erection of a particular aedeagus.

### **Variability of paramere spines**

Spine pattern (number, length, position) on the paramere has important diagnostic value in distinguishing species in spite of its variability. Without a systematic survey examining 192 populations we have detected higher variability in spine pattern at smaller population and/or at the distributional peripheries of the species. This finding is supported by experimental results on polyandrous seed beetle released from sexual selection. Over 18-21 generations male genital spines evolved reduced length in artificially imposed random monogamy (CAYETANO et al. 2011). This supports the sexually antagonistic or simply stimulatory role of the male genital spines. In *Chaetopteryx rugulosa* species group paramere spines seems to remain outside the vagina during copulation, and positioned on the supragenital plate or deeper along the upper vulvar lip. This position suggests that they have function to guide the aedeagus into the female genital opening and produce harm or stimulatory effect on female. Variability of spine pattern under condition of released sexual selection appears by shortening or elongating the length which is accompanied by alternate increase or decrease in spine number. Frequently both variations occur in the same population.

### **“Variability“ of genital drawings**

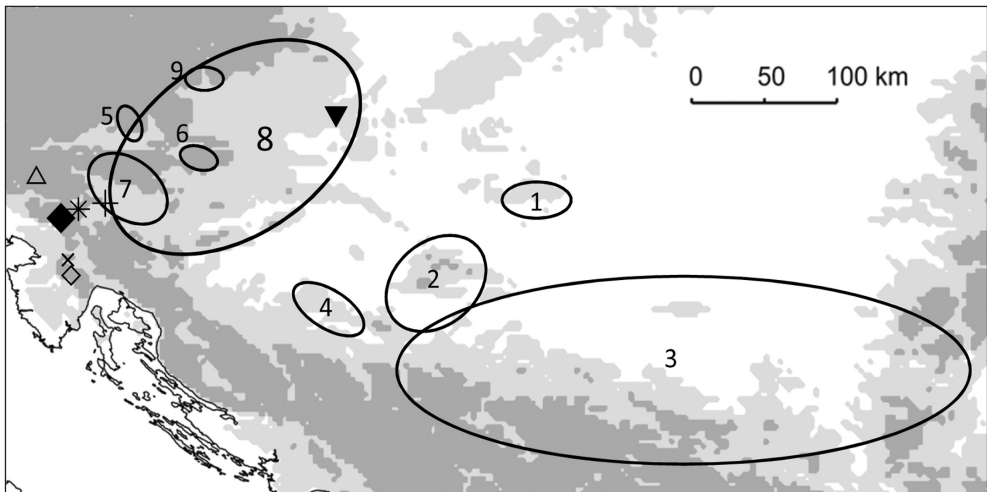
The plane or the angle of the view that is the aspect of drawing may change considerably the form and the ratio of structural elements in the final drawings as was demonstrated by

MALICKY (1988). Working with structures which are firmly fixed to segment IX and are symmetric it is possible to produce the correct lateral view by shifting the position until the corresponding structures of both sides are covering each others. It is more difficult to get the correct dorsal, ventral or caudal views even if the structure is fixed to segment IX. In these viewing aspects there are no symmetric couples to orientate our view. Those genital structures create more difficulties to produce representative and comparable drawings which are functionally moving independent. To produce comparable drawings of the paraproct is especially difficult in caudal view. The caudal outline of this very complex tripartite tree-dimensional structure is very sensitive to viewing aspects. It is impossible to find the correct caudal position, because it does not exist. Paraproct has several working position, this is the reason why drawings are so much varying in caudal view in publications.

### Systematics

#### *Chaetopteryx rugulosa* species group

Species in the *C. rugulosa* species group are characterized by pale colour, very blunt forewing with rounded apex and covered with strong and very long erect setae and with a tendency to brachyptery. Male genitalia: segment IX with bridled dorsum; segment X forming a thin-walled anterad spreading double pouch; apical hook formation of paraproct large foliform with dorsad turning serrated apex; cerci cumbuliform fused basally to the pouch of segment X; the pouche-forming segment X, the cerci and the paraproct fusing together the superanal genital complex; gonopods medium long with mesad turning apical flap; aedeagus with subapical lateral



**Fig. 51.** Distribution of *Chaetopteryx rugulosa* species group. Ellipses with numbers indicate the following species: 1 = *C. mecsekensis*, 2 = *C. papukensis* sp. n., 3 = *C. schmidi*, 4 = *Chaetopteryx* sp. n., 5 = *C. noricum*, 6 = *C. pohorjensis* sp. n., 7 = *C. kannikensis* sp. n., 8 = *C. prealpensis* sp. n., 9 = *C. rugulosa*, and symbols mark the following species: ▼ = *C. zalaensis* sp. n., ◆ = *C. goricensis*, \* = *C. idriensis* sp. n., × = *C. irinae*, △ = *C. giulienensis* sp. n., ◇ = *C. marinkovicae*

processes, and with membranous erectile as well as protrudable endophallic head comprised of variously spread lobes; simple short parameres with a few apical spines. Female genitalia: closed anal tube with upper and lower lips; tergite IX with or without setose lateral lobes; variously formed setaless supragenital plate (upper vulvar or vaginal lip) and uniform vulvar scale (lower vulvar or vaginal lip); vagina uniform and short. Based on male and female genital characters and applying the phylogenetic species concept we have raised subspecies rank to species rank with three new combinations: *Chaetopteryx mecsekensis* Nogradi, 1986 **comb. nov.**, *Chaetopteryx schmidi* Botosaneanu, 1957 **comb. nov.**, *Chaetopteryx noricum* Malicky, 1976 **comb. nov.**, and have established three new species subgroups in the *C. rugulosa* species group: *C. schmidi*, *C. rugulosa*, *C. irenae*. In the *C. rugulosa* new species subgroup we have erected two new species clusters: *C. noricum*, *C. rugulosa*. The distribution of the *C. rugulosa* species group is presented on the map (Fig. 51).

### ***Chaetopteryx schmidi* new species subgroup**

Characterized by males having medium high cerci, paramere spines short, primary spine stout. Female tergite IX without setose lateral lobes. Four species belong to this species subgroup: the widely distributed ancestral *C. schmidi* Botosaneanu, 1957, and three descendant parapatric or peripatric species: *C. mecsekensis* Nogradi, 1986, *C. papukensis* Oláh & Szivák sp. n., *Chaetopteryx* sp. n. (KUČINIĆ et al. 2013).

### ***Chaetopteryx mecsekensis* Nogradi, 1986 **comb. nov.****

*Chaetopteryx schmidi mecsekensis* Nogradi, 1986 – MALICKY et al. (1986): 8–10.

*Chaetopteryx rugulosa mecsekensis* Nogradi, 1986 – transferred by MALICKY (2005): 573.

*Material examined* – **Hungary**: Magyaregregy, Iharos-kút, 327 m, N46°13'21.90", E18°20'06.80", 06.11.2009, I. Szivák, Á. Uherkovich (2♂, OPC). Magyaregregy, Máré-forrás, N46°13'39.98", E18°19'19.39", 06.11.2009, I. Szivák, Á. Uherkovich (♂♀ in copula, OPC). Magyaregregy, Vár-völgy, Réka-forrás, N46°13'39", E18°19'19", 06.11.2011, S. Nógrádi, Á. Uherkovich (6♂, 2♀, OPC; 1♂, 1♀, MM). Mecsek Mts, Hosszúhetény, Hidasi-völgy, Csurgó, 11.11.1984, Á. Uherkovich (2♂, 2♀, OPC). Mecsek Mts, Hosszúhetény, Takanyó-völgy, 24.10.1984, Á. Uherkovich (2♂, 2♀, OPC). Mecsek Mts, Kisújbánya [Hosszúhetény], Pásztor-forrás, 436 m, N46°13'04", E18°21'27", 07.12.1983, Á. Uherkovich (7♂, 1♀, OPC); 10.12.1983, Á. Uherkovich (4♂, OPC); 26.12.1983, S. Nógrádi (4♂, 1♀, OPC); 01.01.1984, S. Nógrádi (3♂, OPC). 12.11.1986, S. Nógrádi (3♂, 1♀, OPC); 06.11.2009, I. Szivák, Á. Uherkovich (3♂, 1♀, OPC); 05.11.2010, singled, I. Szivák, J. Oláh, Á. Uherkovich (11♂, 11♀, OPC). Mecsek Mts, Mánfa, Kőlyuk, 12.11.1985, S. Nógrádi (8♂, 1♀, OPC). Mecsek Mts, Mánfa, Nagy-Mély-völgy, Cserkész-forrás, N46°08'56.73", E18°12'38.08", 14.11.2009, I. Szivák (4♂, OPC). Mecsek Mts, Pécs, Meleg-mány, 22.10.1983, S. Nógrádi (5♂, 5♀, OPC); 20.12.1983, Á. Uherkovich (1♂, 3♀, OPC); 01.01.1985, S. Nógrádi (5♂, 3♀, OPC); 28.10.1987, Á. Uherkovich (10♂, 5♀, OPC). Mecsek Mts, Pécs, Melegmányi-völgy, Anyák-kútja, N46°08'08.55", E18°13'31.46", 14.11.2009, I. Szivák (2♂, 1♀, OPC). Mecsek Mts, Pécs, Melegmányi-völgy, Mésztafa lépcső, 352 m, N46°08'12.89", E18°13'29.92", 14.11.2009, I. Szivák (3♂, OPC). Mecsek Mts, Pécs, Nagy-Mély-völgy, Kánya-forrás, 347 m, N46°08'05.16", E18°12'43.75", 14.11.2009, I. Szivák (3♂, 1♀, OPC). Mecsek Mts, Pécs, Nagy-Mély-völgy, Sziklás-forrás, N46°08'26.7", E18°12'39.96", 14.11.2009, I. Szivák (3♂, OPC). Vékény, Vár-völgy, Iharos-forrás, 28.10.1983, S. Nógrádi (3♂, 2♀, OPC); 12.11.1986, S. Nógrádi (4♂, 1♀, OPC).

*Distinguishing traits* – Male: cerci higher than at *C. schmidi* and *C. papukensis*; apical flap of gonopod less developed, resulting in gonopod apex rounded in lateral view, not with pointed or projected blunt apex like at *C. schmidi* and *C. papukensis*; dorsal hook of paraproct medium turned, less turned at *C. papukensis*, highly turned at *C. schmidi*; aedeagus with long, almost filiform lateral processes, not gemmiform of *C. schmidi* or short digitiform of *C. papukensis*; paramere shaft short rod-shaped with medium long straight primary spine, not short straight

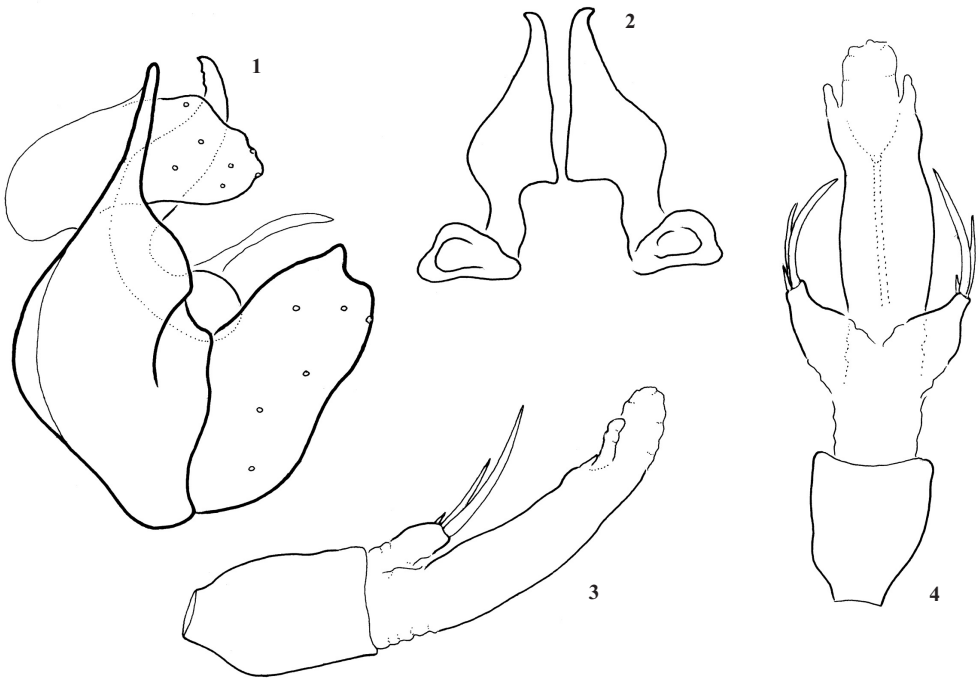
of *C. schmidi* or long curved of *C. papukensis*. Female: anal tube medium long; supragenital plate very sharp triangular in ventral view.

***Chaetopteryx papukensis* Oláh et Szivák sp. n.** (Figs 1–7)

*Diagnosis* – This new species belongs to the *C. schmidi* New Species Subgroup of the *C. rugulosa* species group. Most close to *C. mecsekensis* but differs by having cerci lower than at *C. mecsekensis*, apical flap of gonopod present, not lacking; the well developed flap producing gonopod apex with pointed or blunt projection in lateral view, not rounded like at *C. mecsekensis*; dorsal hook of paraproct less turned, medium turned at *C. mecsekensis*, highly turned at *C. schmidi*; aedeagus with medium digitiform lateral processes, not long filiform of *C. mecsekensis* or gemmiform of *C. schmidi*; paramere shaft triangular, not digitate; primary spine long curved, not short straight of *C. schmidi* or long straight of *C. mecsekensis*. Anal tube of female is long.

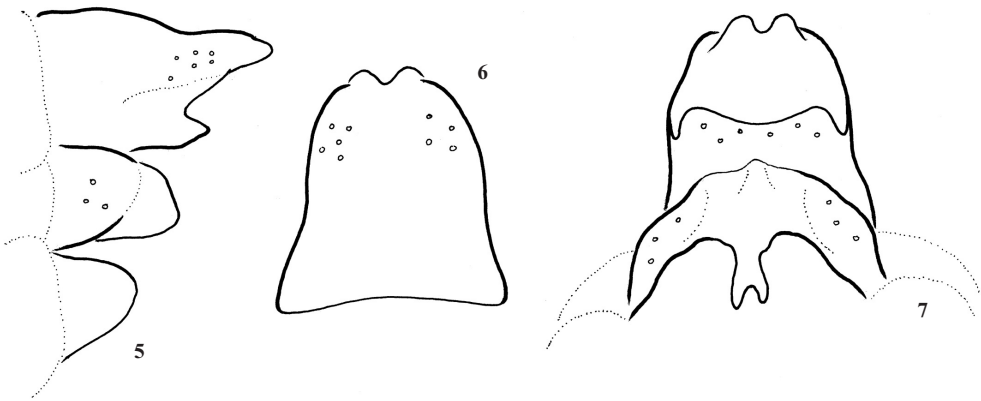
*Description* – Male and female (in alcohol). Light brown medium-sized animal with light body appendages and with yellowish-testaceous wings. Anterior wing with rounded apex and with very long erect spine-like setae present both on the membrane and on the veins; setae on the veins usually stronger. Tibial spur formula of male is 033 and that of female is 133. Forewing length of male is 9 mm, and that of allotype female is 11 mm.

Male genitalia (Figs 1–4). Posterodorsal spinate area of vestitural noncellular microtrichiae on segment VIII and its mesal light band well developed. Segment IX with short, bridle-like



**Figs 1–4.** *Chaetopteryx papukensis* Oláh & Szivák sp. n. holotype male: 1 = male genitalia without phallic organ in left lateral view; 2 = paraproct in caudal view; 3 = phallic organ in lateral view; 4 = phallic organ in dorsal view

dorsum and longer ventrum; anterior margin rounded convex with long antecosta; posterior margin concave, midlateral sclerotized angle of tergite IX pronounced. The pouch-like concavity of segment X long. Cerci medium high. Apical hook of the paraproctal complex with narrowing pointed apex and lateral angle, middle connecting section long, basal triangle exposed monolobe in lateral view. Membranous subanal lobe short. Gonopods short with apical flap developed and turning mesad resulting in a single short pointed apex in lateral view. Phallic organ composed of short rim-like phallic apodeme, short tube of phallosome, short endotheca, well-developed aedeagus and medium long triangular parameres; paramere with stout curving primary spine, 1-2 secondary spines and 0-2 tertiary spines; aedeagus supplied with a pair of digitate lateral processes directed oblique upward, the very basal part of the lateral process sclerotized and membranous after; ejaculatory duct ending with gonopore opening into a large trilobed endophallic membranous structure.



**Figs 5–7.** *Chaetopteryx papukensis* Oláh & Szivák sp. n. allotype female: 5 = female genitalia in left lateral view; 6 = anal tube in dorsal view; 7 = female genitalia in ventral view

Female genitalia (Figs 5–7). Anal tube formed by the fusion of tergite IX and X is medium long and broad, not narrowing posterad; apical margin forming rounded lateral lobes and mesal excision in dorsal view; this dorsal apical profile is created entirely by tergite X; the internal sclerites, the remnant tergite X protruding, and taking part in the formation of the apical profile. Setose ventroapical lobes of tergite IX lacking. Supragenital plate of segment X triangular in ventral view. Median lobe of the vulvar scale (lower vulvar lip) half long as the lateral lobes. Vaginal chamber medium sized reaching to the middle of sternite VIII. Vaginal sclerite pattern clearly visible.

*Type material* – Holotype. **Croatia:** Papuk Mts, Slatinski Drenovac, Jankovac, Jankovac spring, 45°31'08.1", 17°41'11.9", 510 m, 06.11.2012, T. Kovács, G. Magos (1♂, OPC). Allotype. Same as holotype (1♀, OPC). Paratypes. Same as holotype (14♂, 10♀, OPC, 5♂, 3♀, MM). Krndija Mts, 3 km N of Kutjevo, Velika rijeka, small tributary, 424 m (YL23), N45°27'55", E17°52'37", 04.11.2011, I. Szivák (1♂, OPC). Krndija Mts, 6 km N of Kutjevo, Velika rijeka, springs, 580 m, N45°28'59", E17°51'33", 04.11.2011, I. Szivák, Á. Uherkovich (4♂, 4♀, OPC); 06.11.2012, T. Kovács, G. Magos (9♂, 9♀, OPC). Krndija Mts, Kutjevo, Mala rijeka, 402 m (YL23), N45°27'48", E17°51'53", 04.11.2011, I. Szivák, Á. Uherkovich

(4♂, 1♀, OPC). Papuk Mts, forest brook below the Slatinski Drenovac – Velika road, 45°29'32.4", 17°39'10.9", 480 m, 06.11.2012, T. Kovács, G. Magos (7♂, 10♀, OPC). Papuk Mts, Jankovac, 13.10.1986, B. Horvat, I. Sivec (2♂, 2♀, PMS). Papuk Mts, Jankovac spring, cave and the surrounding beech forest, 456 m, N45°31.126', E17°41.198', 01.10.2007, L. Dányi, J. Kontschán, D. Murányi (7♂, HNHM). Papuk Mts, Slatinski Drenovac, 1.5 km S, Jankovac stream, 350 m, N45°32'01", E17°42'08", 19.10.2012, Á. Uherkovich (1♀, OPC). Papuk Mts, Slatinski Drenovac, Jankovac, Jankovački potok, 351 m (YL14), N45°31'31", E17°41'25", 04.11.2011, I. Szivák (3♂, 1♀, OPC). Papuk Mts, Slatinski Drenovac, Kovačica Potok, 541 m, N45°31'08", E17°39'54", 03.11.2012, Á. Uherkovich (1♂, OPC). Psunj Mts, Šumetlica Strmac, Creek on sandstone, 663 m, N42°22'32", E17°21'40", 23.10.2012, Á. Uherkovich (1♂, OPC). Psunj Mts, Šumetlica Strmac, small creek on crystalline rock, 722 m, N42°22'43", E17°22'04", 23.10.2012, Á. Uherkovich (2♀, OPC). Velika, Sastavi, Zagradaska rijeka, 482 m, N45°29'33", E17°39'11", 03.11.2012, Á. Uherkovich (1♂, OPC). **Bosnia & Herzegovina:** Banja Luka region, Kozara Mts, forest brook below the Vrbaška – Kozarac road, N45°02.480', E16°54.266', 560 m, 07.11.2012, T. Kovács, G. Magos (1♂, OPC). Banja Luka region, Kozara Mts, forest edge spring 1 km S of peak Lisina, N44°57.773', E16°58.342', 680 m, 07.11.2012, T. Kovács, G. Magos (5♂, 6♀, OPC).

*Etymology* – The new species is named after the Papuk Mts, where the type locality is found.

*Remarks* – Some specimens from the populations collected in Kozara and Psunj Mts have mixed characters. Few specimens have abbreviated subapical lateral lobes of aedeagus, character of *C. schmidi* and some female have abbreviated anal tube, characters of both *C. schmidi* and *C. mecsekensis*.

### ***Chaetopteryx schmidi* Botosaneanu, 1957 comb. nov.**

*Chaetopteryx schmidi* Botosaneanu, 1957 – BOTOSANEANU (1957): 190–193.

*Chaetopteryx rugulosa schmidi* Botosaneanu, 1957 – transferred by MALICKY (2005): 573.

*Material examined* – **Bosnia & Herzegovina:** Blagojevići Sivecek, Ozren Planina, 390 m, 12.10.1990, B. Horvat, I. Sivec (1♀, PMS). Čuništa, River Krivaja, 450 m, 15.10.1990, B. Horvat, I. Sivec (1♂, 1♀, PMS). Kamensko, River Krivaja, 15.10.1990, B. Horvat, I. Sivec (2♂, PMS). Kravica, Zvornik, 05.10.1986, B. Horvat, I. Sivec (1♂, PMS). Dobrovci, Gračanica, 430 m, 11.10.1990, B. Horvat, I. Sivec (4♀, PMS). Skender Vakuf, 820 m, 19.10.1990, B. Horvat, I. Sivec (2♂, PMS). **Romania:** 13 km from Baile Herculane, upper section of a small tributary to River Cerna, N44°59'10.34", E22°30'46.91", 13.11.2010, singled, Á. Ecsedi, I. Szivák (8♂, 1♀, OPC); N44°59'13.12", E22°30'49.76", 13.11.2010, singled, Á. Ecsedi, I. Szivák (4♂, OPC). 24 km from Baile Herculane, spring area of a small tributary to River Cerna, N45°02'32.14", E22°35'3.36", 13.11.2010, singled, Á. Ecsedi, I. Szivák (2♂, 2♀, OPC). 24 km from Baile Herculane, a small tributary to River Cerna, N45°02'35.05", E22°35'07.67", 13.11.2010, singled, Á. Ecsedi, I. Szivák (4♂, OPC). 30 km from Baile Herculane, a small tributary to River Cerna, N45°02'56.68", E22°37'32.09", 13.11.2010, singled, Á. Ecsedi, I. Szivák (8♂, 3♀, OPC, 3♂, 1♀, MM). **Serbia:** Đerdap Mts, Dobra, Reka Pesača, beech forest with stream, 386 m, N44°34.670', E21°59.250', 28.10.2010, L. Dányi, J. Kontschán, Zs. Ujvári, D. Murányi (2♂, 1♀, HNHM). Đerdap Mts, Donji Milanovac, Grgeci spring and its outlet in a beech forest, 500 m, N44°28', E22°02', 13.10.2006, L. Dányi, J. Kontschán, D. Murányi (1♂, 1♀, ♂♀ in copula, HNHM). Đerdap Mts, Golubinja, stream valley with young forest, N of the village, 88 m, N44°30'59.6", E22°12'41.5", 13.10.2006, L. Dányi, J. Kontschán, D. Murányi (6♂, HNHM). Miroč, Donji Milanovac, Stream Supljanka, 08.10.1984, Brancelj (1♀, PMS). Pesača, Donji Milanovac, 09.10.1986, B. Horvat, I. Sivec (1♂, PMS). Popadija, Donji Milanovac, 09.10.1986, B. Horvat, I. Sivec (1♂, PMS).

*Distinguishing traits* – Male: cerci lower than at *C. mecsekensis*, apical flap of gonopod developed, resulting in gonopod apex with pointed or blunt projection in lateral view, not

rounded like at *C. mecsekensis*; dorsal hook of paraproct very turned, medium turned at *C. mecsekensis*, less turned at *C. papukensis*; aedeagus with short gemmiform sclerotized lateral processes, not medium long digitiform of *C. papukensis* or long filiform of *C. mecsekensis*; paramere shaft rod-shaped with short straight primary spine, not long curved of *C. papukensis* or long straight of *C. mecsekensis*. Female: anal tube very short; supragenital plate blunt triangular in ventral view, not sharp triangular like at *C. mecsekensis*.

### ***Chaetopteryx* sp. n.**

*Material examined* – **Bosnia & Herzegovina:** Una-Sana Canton, Mrazovac, Svetinja Spring, N45°03.118', E16°06.324', 300 m, 07.11.2012, T. Kovács, G. Magos (14♂, 11♀, OPC; 5♂, 3♀, MM). **Croatia:** Banovina Region, Hrvatski Čuntić, 21-22.11.2009, M. Kučinić, I. Vučković (15♂, 8♀, OPC). Banovina Region, Petrinja, Kri Spring, 07.11.2009, M. Bučar, M. Kučinić (4♂, 13♀, OPC); 08.12.2009, M. Bučar, M. Kučinić (8♂, OPC). Banovina Region, Pečki Spring, 21.11.2009, M. Kučinić, I. Vučković (3♂, 2♀, OPC); 15.12.2009, M. Bučar, M. Kučinić (12♂, 7♀, OPC). Banovina Region, Slabinja Spring, Šuplji Kamen, 29.11.2009, M. Kučinić, I. Vučković (1♂, OPC).

*Remarks* – This is a new species to be described by KUČINIĆ et al. (2013).

### ***Chaetopteryx rugulosa* new species subgroup**

Characterized by males having medium low cerci, paramere spines medium or long, primary spine not stout, less enlarged. Female tergite IX with setose lateral lobes. In the *C. rugulosa* new species subgroup we have established two new species clusters: *C. noricum*, *C. rugulosa*.

### ***Chaetopteryx noricum* new species cluster**

Species belonging to this small cluster have aedeagus with subapical lateral structures which are fully membranous aliform and erectile along their entire length. These horizontal or slightly upward directed processes are accompanied below by a pair of supporting sclerites in the form of elongated ventrolateral ridges. Two species belong to this cluster: *C. noricum* Malicky, 1976, *C. pohorjensis* Oláh & Urbanič sp. n.

### ***Chaetopteryx noricum* Malicky, 1976 comb. nov.**

*Chaetopteryx schmidi noricum* Malicky, 1976 – MALICKY (1976): 98–99.

*Chaetopteryx rugulosa noricum* Malicky, 1976 – transferred by MALICKY (2005): 573.

*Material examined* – **Austria:** Carinthia, Saualpe ob Wieting, 1600 m, 28.09.1988, H. Malicky (3♀, OPC from MPC). Katschbach, STMKz, 03.11.2000, W. Graf (1♂, OPC). Saualpe, Geierkogel Klippitztörl, springs of stream Klippitzbach, 1584 m, N46°55'53.8", E14°40'49.3", 21.11.2009, A. Déry, I. Szivák (5♂, OPC). Saualpe, Hinterberg Löllinggraben, a spring in the middle reach of stream Löllingbach, 802 m, N46°54'38", E14°34'03", 21.11.2009, A. Déry, I. Szivák (4♂, OPC; 2♀, MM). Saualpe, Kliening, middle reach of stream Klieningbach, 932 m, N46°56'49.4", E14°46'24.2", 21.11.2009, A. Déry, I. Szivák (1♂, OPC).

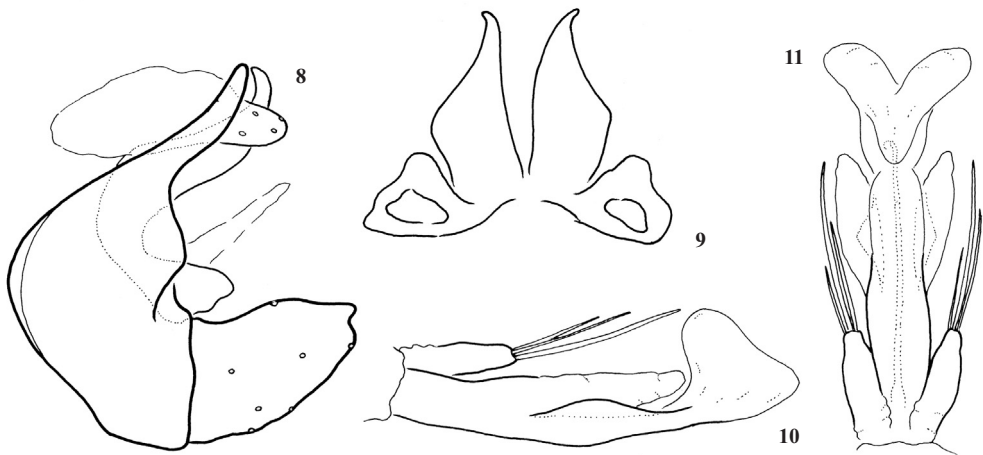
### ***Chaetopteryx pohorjensis* Oláh et Urbanič sp. n. (Figs 8–14)**

*Diagnosis* – Described and drawn, but not named by MALICKY et al. (1986). Failed to relate it clearly to any of the known taxa. This new species belongs to the *C. rugulosa* species group, *C. rugulosa* subgroup and *C. noricum* species cluster. Close to *C. noricum* sp. n. but differs by having paraproct wide and angled laterad, not narrow in caudal view; paramere shaft shorter than at *C. noricum*; number of paramere spines usually 3; position of paramere spines nested, not with a tendency to be arranged in horizontal row with laterad located primary spine and gradually mesad shortening secondary spines. There are significant differences in the genital

structures of the females: the lower lip of the anal tube is shorter than the upper lip, not equal as at the *C. noricum*; the dorsal apical profile of the anal tube characterized by deep V-shaped excision due to the highly protruded position of the internal sclerites.

*Description* – Male and female (in alcohol). Light brown medium-sized animal with light body appendages and with yellowish-testaceous wings. Anterior wing with rounded apex and with very long erect spine-like setae present both on the membrane and on the veins; setae on the veins usually stronger. Tibial spur formula of male is 033 and that of female is 133. Forewing length of male is 8 mm, and that of allotype female is 9 mm.

Male genitalia (Figs 8–11). Posterodorsal spinate area of vestitural noncellular microtrichiae on segment VIII and its mesal light band well developed. Segment IX with short, bridle-like dorsum and longer ventrum; anterior margin rounded convex with well-developed antecosta; posterior margin concave, midlateral sclerotized angle of tergite IX pronounced. The pouch-like concavity of segment X long. Cerci low. Apical hook of the paraproctal complex with narrowing pointed apex and lateral angle, middle connecting section long, basal triangle exposed monolobe in lateral view. Membranous subanal lobe narrow. Gonopods long with apical flap variously developed and turning mesad. Phallic organ composed of short rim-like phallic apodeme, short tube of phallosome, short endotheca, well-developed aedeagus and medium long parameres; primary spine of paramere is accompanied by 1-2 secondary spines; aedeagus supplied with a pair of horizontal aliform fully membranous lateral processes, pair of short erection supporter sclerites with low triangular shape; ejaculatory duct ending with gonopore opening into a large

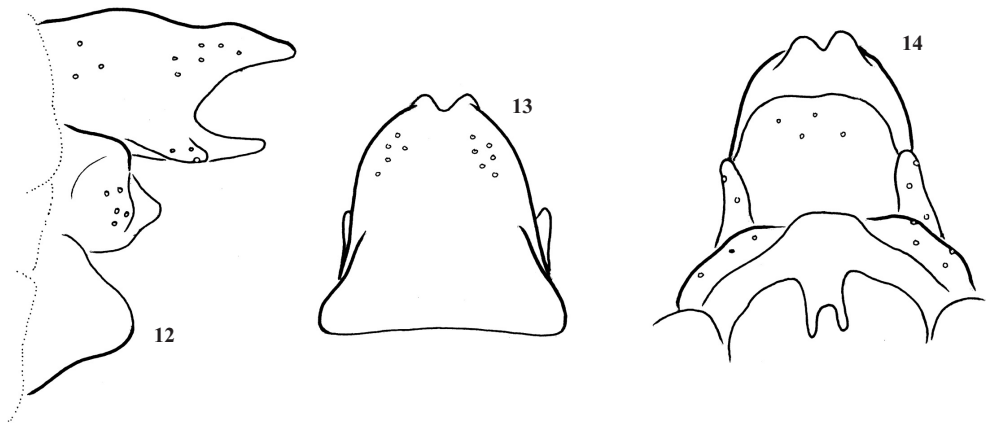


**Figs 8–11.** *Chaetopteryx pohorjensis* Oláh & Urbanič sp. n. holotype male:

8 = male genitalia without phallic organ in left lateral view; 9 = paraproct in caudal view; 10 = phallic organ in lateral view; 11 = phallic organ in dorsal view

trilobed endophallic membranous structure.

Female genitalia (Figs 12–14). Anal tube formed by the fusion of tergite IX and X is medium long, not narrowing posterad; internal sclerites protruding and forming a V-shaped excision. Setose ventroapical lobes of tergite IX present in variously developed form. Supragenital plate of segment X well-developed from triangular to blunt triangular both in lateral and ventral view.



**Figs 12–14.** *Chaetopteryx pohorjensis* Oláh & Urbanič sp. n. allotype female: 12 = female genitalia in left lateral view; 13 = anal tube in dorsal view; 14 = female genitalia in ventral view

Median lobe of the vulvar scale (lower vulvar lip) half long as the lateral lobes. Vaginal chamber medium sized reaching to the middle of sternite VIII. Vaginal sclerite pattern clearly visible.

*Type material* – Holotype. **Slovenia:** Pohorje Mts, below Pesek, spring area of river Oplotnica, 1345 m, N46°28'24.8", E15°20'55.9", 08.11.2012, T. Kovács, G. Magos, I. Sivec (1♂, OPC). Allotype. Same as holotype (1♀, OPC). Paratypes. Same as holotype (2♂, 6♀, OPC; 1♂, 1♀, MM). Same locality as holotype: 20.10.1981, I. Sivec (2♂, 2♀, OPC); 15.10.1984, B. Horvat, I. Sivec (16♂, 9♀, PMS); 27.09.2008, I. Sivec (1♂, 1♀, OPC); 10.11.2008, I. Sivec (3♂, 1♀, OPC); 28.09.2012, I. Sivec (1♂, OPC); 19.10.2012, B. Horvat, I. Sivec (18♂, 7♀, OPC); 08.11.2012, I. Sivec (3♂, 1♀, OPC). Dravograd, Ogleja puša, Vrački stream, 1170 m, N38°08'09", E15°05'24,30", 04.10.2012, I. Sivec, G. Urbanič (4♂, 1♀, OPC). Kamnik, Volovljek, N46°18'59.7", E14°42'03.1", 14.11.2010, I. Sivec (1♀, OPC). Kozji Vrh nad Dravogradom, sidestream of stream Brelejev potok, 1530 m, N46°38'26.35", E15°04'52.35", 04.10.2012, I. Sivec, G. Urbanič (3♂, OPC). Kozji Vrh nad Dravogradom, sidestream of stream Velka, 570 m, N46°37'26.0", E15°04'16.4", 04.10.2012, I. Sivec, G. Urbanič (7♂, OPC); 07.11.2012, G. Urbanič (1♀, laboratory reared, OPC). Kozji Vrh nad Dravogradom, stream Brelejev potok, 1170 m, N46°38'39.25", E15°02'52.41", 04.10.2012, I. Sivec, G. Urbanič (5♂, 1♀, OPC). Litija, Konjski graben, 16.10.1985, I. Sivec (1♀, PMS). Mislinja, Mislinjski jarek, 29.10.2010, I. Sivec (2♂, 2♀, OPC). Pohorje Mts, Pesek, 28.10.1989, B. Horvat, I. Sivec (1♂, PMS). Pohorje Mts, Pesek, N46°28'26.3" E15°20'55.9", 09.10.2010, I. Sivec (2♂, OPC).

*Etymology* – The new species is named after the Pohorje Mts, where the type locality is found.

### ***Chaetopteryx rugulosa* new species cluster**

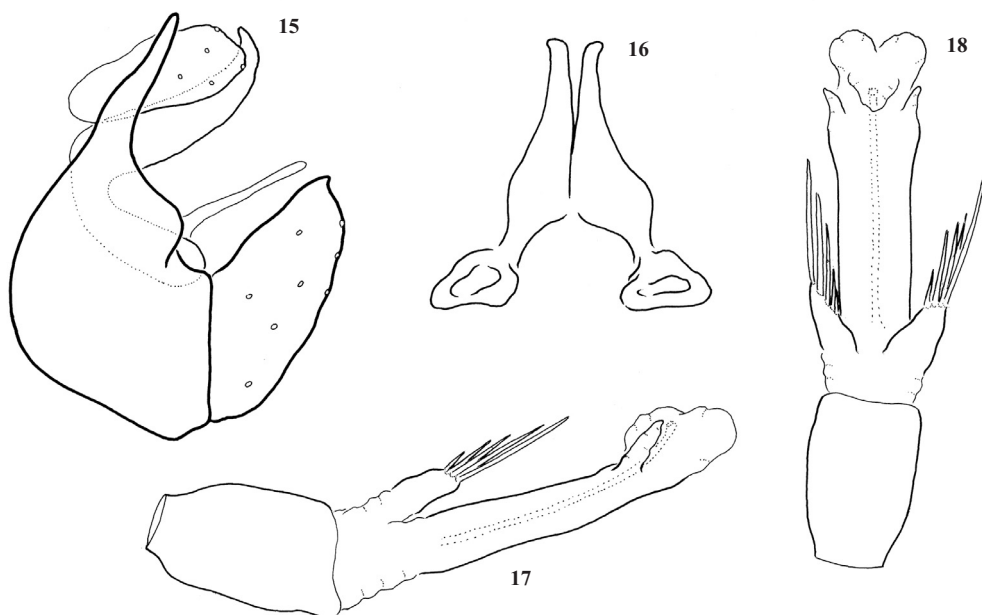
Species belonging to this cluster have aedeagus with gemmiform, digitiform or spatulate subapical lateral structures. Their basal region partially sclerotized and erectile only afterwards. The lateral processes are not accompanied below by a pair of supporting sclerites like at *C. noricum* new species cluster. Four species belong to this cluster: the widely distributed ancestral *C. prealpensis* Oláh sp. n. and three descendant parapatric or peripatric species: *C. kamnikensis* Oláh & Urbanič sp. n., *C. rugulosa* Kolenati, 1848, *C. zalaensis* Oláh sp. n.

***Chaetopteryx kamnikensis* Oláh et Urbanič sp. n.** (Figs 15–21)

*Diagnosis* – Described and drawn, but not named by MALICKY et al. (1986). Due to insufficient material failed to relate it clearly to any of the known taxa. This new species belongs to the *C. rugulosa* species group, *C. rugulosa* subgroup and *C. rugulosa* species cluster. Close to *C. prealpensis* sp. n. but differs by having subapical lateral processes on the aedeagus digitiform, not platform; 5–6 parameter spines present and gradually decreasing in length from apicad to subapicad in sagittal plane, not 2–3 spines nested. The anal tube of the female with rounded apical lobes and rounded mesal excision formed by the tergite IX, not triangular and created by the protruded segment X.

*Description* – Male and female (in alcohol). Light brown medium-sized animal with light body appendages and with yellowish-testaceous wings. Anterior wing with rounded apex and with very long erect spine-like setae present both on the membrane and on the veins; setae on the veins usually stronger. Tibial spur formula of male is 033 and that of female is 133. Forewing length of male is 9 mm, and that of allotype female is 10 mm.

Male genitalia (Figs 15–18). Posterodorsal spinate area of vestitural noncellular microtrichiae on segment VIII and its mesal light band well developed. Segment IX with short, bridle-like dorsum and longer ventrum; anterior margin rounded convex with long antecosta; posterior margin concave, midlateral sclerotized angle of tergite IX pronounced. The pouch-like concavity of segment X long. Cerci medium low. Apical hook of the paraproctal complex with narrowing pointed apex and less developed lateral angle, middle connecting section long, basal triangle exposed monolobe in lateral view. Membranous subanal lobe short. Gonopods short with apical

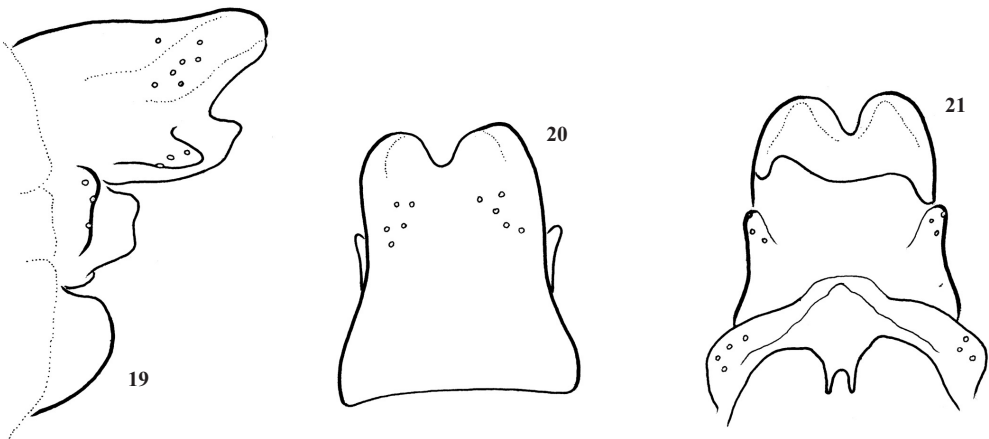


**Figs 15–18.** *Chaetopteryx kamnikensis* Oláh & Urbanič sp. n. holotype male:

15 = male genitalia without phallic organ in left lateral view; 16 = paraproct in caudal view; 17 = phallic organ in lateral view; 18 = phallic organ in dorsal view

flap developed and turning mesad resulting in a single short pointed apex in lateral view. Phallic organ composed of short rim-like phallic apodeme, short tube of phallotheca, short endotheca, well-developed aedeagus and medium long parameres; 5-6 paramere spines rather stout, arranged in a decreasing line from apicad to subapicad in vertical position; aedeagus supplied with a pair of long digitate lateral processes directed oblique upward, the very basal part of the lateral process sclerotized and membranous after; ejaculatory duct ending with gonopore opening into a large trilobed endophallic membranous structure.

Female genitalia (Figs 19–21). Anal tube formed by the fusion of tergite IX and X is medium long and broad, not narrowing posterad; apical margin forming rounded lateral lobes and mesal excision in dorsal view; this dorsal apical profile is created entirely by tergite IX, internal sclerites, the remnant tergite X not protruding and not taking part in the formation of the apical profile. Setose ventroapical lobes of tergite IX well developed. Supragenital plate of segment X triangular to blunt triangular in ventral view. Median lobe of the vulvar scale (lower vulvar lip) half long as the lateral lobes. Vaginal chamber medium sized reaching to the middle of sternite VIII. Vaginal sclerite pattern clearly visible.



**Figs 19–21.** *Chaetopteryx kannikensis* Oláh & Urbanič sp. n. allotype female: 19= female genitalia in left lateral view; 20 = anal tube in dorsal view; 21 = female genitalia in ventral view

*Type material* – Holotype. **Slovenia:** Tržič, Bistrica, Blajšnica stream, 689 m, N46°21'50.02", E14°16'55.70", 03.12.2011, A. Déry, I. Szivák (1♂, OPC). Allotype. Same as holotype (1♀, OPC). Paratypes. Same as holotype (1♂, OPC). Same locality as holotype: 13.10.2011, A. Déry, I. Szivák (1♂, OPC). Dolž, Gorjanci, stream Klampfer, 660 m, 25.10.1990 B. Horvat, I. Sivec (1♀, OPC). Golovec, brooklet near Rakovnik distinct (Ljubljana), 335 m, N46°02'27.49", E14°31'46.12", 05.12.2011., A. Déry, I. Szivák (4♂, 1♀, OPC); 08.11.2012, T. Kovács, G. Magos (1♂, 1♀, MM). Ig. Želimlje, potok Želimeljščica, 330 m, N45°53'35", E14°35'43", 27.10.1989, B. Horvat, I. Sivec (1♀, PMS). Kamniške alpe, Črna pri Kamniku, Volovljek, 1016 m, N46°24'50", E14°54'10", 26.10.2012, B. Horvat, I. Sivec (10♂, 4♀, OPC); 1028 m, N46°16'13.5", E14°41'20.8", 26.10.2012, B. Horvat, I. Sivec (11♂, 6♀, OPC). Litija, Janče, stream Gostinca, 350 m, N46°03'39.19", E14°40'48.46", 12.10.2012, G. Urbanič (2♂, 1♀, OPC). Rakovnik at Ljubljana, 20.10.1983., C. Krušnik (1♂, 1♀, MPC). Šklendrovec, Podkum,

stream Šklendrovec, 493 m, N46°04'52.6", E15°01'10.5", 25.10.2012, B. Horvat, I. Sivec (2♂, 2♀, OPC). Tržič, Brezje at Tržič, stream Blajšnica, 646 m, N46°21'46.06", E14°17'00.31", 16.11.2012, B. Horvat, I. Sivec (4♂, 5♀, OPC). Tržič, Grahovše, potok Lomščica, 860 m, N45°22'00", E14°22'03", 01.10.1990, B. Horvat, I. Sivec (1♀, PMS). Tržič, Hudi Graben, stream Hudi Graben, 683 m, N46°21'41.35", E14°15'46.64", 16.11.2012, B. Horvat, I. Sivec (1♂, 1♀, OPC).

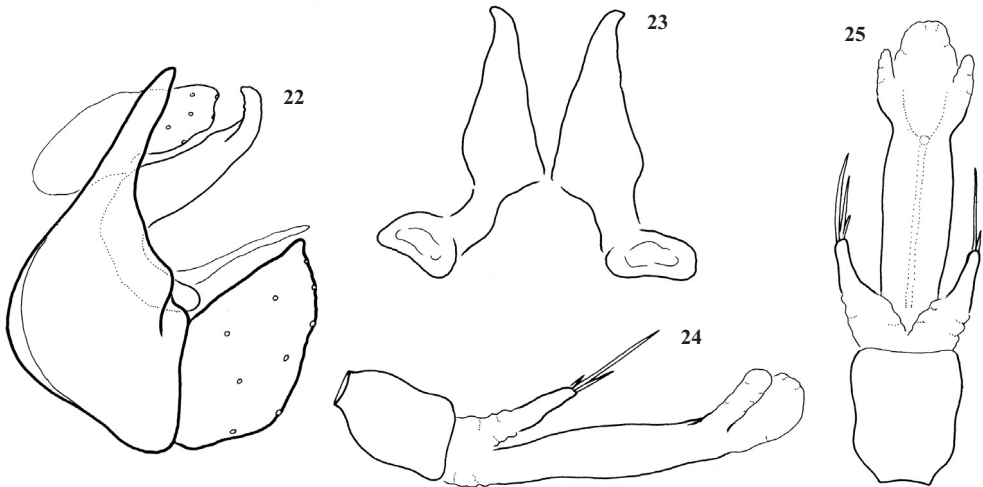
*Etymology* – The new species is named after the town Kamnik, the type locality is not far away.

***Chaetopteryx prealpensis* Oláh sp. n.** (Figs 22–29)

*Diagnosis* – Specimens of this widely distributed species collected from several populations in Austria, Bosnia & Herzegovina, Croatia, Hungary and Slovenia formerly were determined as *C. rugulosa*. However it clearly differs from the holotype of *C. rugulosa* Kolenati, 1848. This new species belongs to the *C. rugulosa* species group, *C. rugulosa* subgroup and *C. rugulosa* species cluster. Close to *C. rugulosa* Kolenati, 1848 but differs by having subapical lateral processes on the aedeagus platform and directed oblique upward, not digitiform and not horizontal. The anal tube of the female broad, not slender.

*Description* – Male and female (in alcohol). Light brown medium-sized animal with light body appendages and with yellowish-testaceous wings. Anterior wing with rounded apex and with very long erect spine-like setae present both on the membrane and on the veins; setae on the veins usually stronger. Tibial spur formula of male is 033 and that of female is 133. Forewing length of male is 8 mm, and that of allotype female is 9 mm.

Male genitalia (Figs 22–25). Posterodorsal spinate area of vestitural noncellular microtrichiae on segment VIII and its mesal light band well developed. Segment IX with short, bridle-like dorsum and longer ventrum; anterior margin rounded convex with long antecosta; posterior margin concave, midlateral sclerotized angle of tergite IX pronounced. The pouch-like concavity



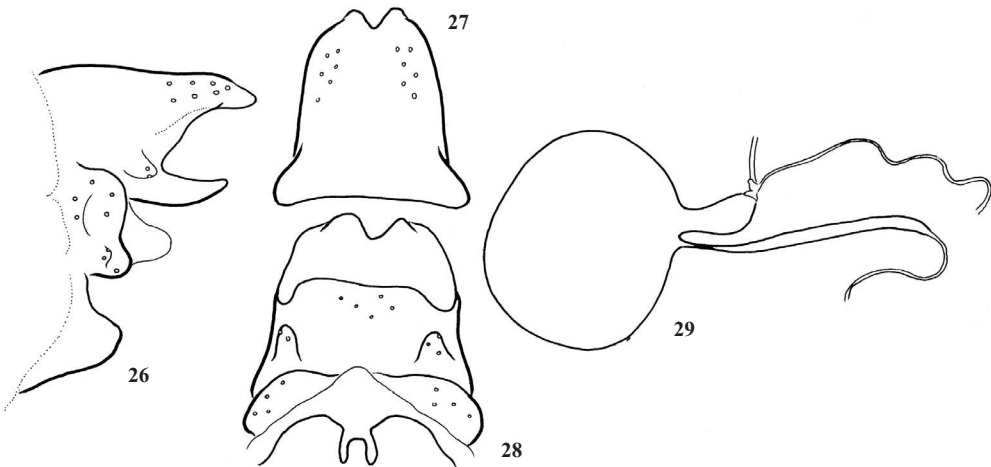
**Figs 22–25.** *Chaetopteryx prealpensis* Oláh sp. n. holotype male:

22 = male genitalia without phallic organ in left lateral view; 23 = paraproct in caudal view; 24 = phallic organ in lateral view; 25 = phallic organ in dorsal view

of segment X long. Cerci medium low. Apical hook of the paraproctal complex with narrowing pointed apex and less developed lateral angle, middle connecting section long, basal triangle exposed monolobe in lateral view. Membranous subanal lobe short. Gonopods short with apical flap developed and turning mesad resulting in a single pointed apex in lateral view. Phallic organ composed of short rim-like phallic apodeme, short tube of phallosome, short endotheca, well-developed aedeagus and medium long parameres; primary spine of paramere is accompanied by 1-2 secondary spines; aedeagus supplied with a pair of long spatulate lateral processes directed oblique upward, the very basal part of the lateral process sclerotized and membranous after; ejaculatory duct ending with gonopore opening into a large trilobed endophallic membranous structure.

Female genitalia (Figs 26–29). Anal tube formed by the fusion of tergite IX and X is medium long, not narrowing posterad; internal sclerites protruding and forming a V-shaped excision. Setose ventroapical lobes of tergite IX present in variously developed form. Supragenital plate of segment X well-developed from triangular to blunt triangular both in lateral and ventral view. Median lobe of the vulvar scale (lower vulvar lip) half long as the lateral lobes. Vaginal chamber medium sized reaching to the middle of sternite VIII. Vaginal sclerite pattern clearly visible.

*Type material* – Holotype. **Hungary**: Kőszeg Mts, Hörmann-forrás, 18.10.1986, Á. Uherkovich (1♂, OPC). Allotype. Same as holotype (1♀, OPC). Paratypes. Same as holotype (4♂, 2♀, OPC; 1♂, 1♀, MM). **Austria**: Ausserneuwald, stream, 817 m, N47°34'01.9", E16°01'10.5", 19.11.2009, A. Déry, I. Szivák (1♂, 1♀, ♂♀ in copula, OPC). Gleinalpe, GH Krautwaschl & Gleinalm Sulmhütte, 1100–1300 m, 08.10.2012, D. Stradner (1♂, 2♀, OPC). Hohegg bei Grimmenstein, spring and its outlet, 621 m, N47°36'44", E16°05'52.7", 19.11.2009, A. Déry, I. Szivák (3♀, OPC). Koralpe, Handalm, springs near Gösler Hütte (Weinebene), 1784 m, N46°50'35.89", E15°01'18.53", 21.10.2012, J. Oláh, I. Szivák (13♂, 7♀, OPC). Koralpe, St. Oswald, Wildbach, 30.09.2007, D. Stradner (4♂, 2♀, OPC). Lafnitz Quelle, 16.10.2012,



**Figs 26–29.** *Chaetopteryx prealpensis* Oláh sp. n. allotype female:

26= female genitalia in left lateral view; 27 = anal tube in dorsal view; 28 = female genitalia in ventral view; 29 = spermathecal complex

W. Graf (1 ♂, 1 ♀, OPC). Mitterneuwald, Hermann spring, 956 m, N47°32'56.3", E15°58'56.1", 19.11.2009, A. Déry, I. Szivák (2 ♂, OPC). Packalpe, spring near Knödelhütte, 1440 m, N46°59'31.20", E14°56'20.02", 20.10.2012, J. Oláh, I. Szivák (2 ♂, 3 ♀, OPC). Sommeralm, upper reach of stream Mixnitz Bach, 1327 m, N47°20'57", E15°32'56.5", 20.11.2009, A. Déry, I. Szivák (1 ♂, 1 ♀, ♂ ♀ in copula, OPC). Styria, 14 km above restaurant Krautwaschl, Gleinalm, N47°12'16", E15°08'47", 1187 m, 25.09.2011, D. Stradner (2 ♂, OPC). Styria, NW Stainz, near Marhof, N46°54', E15°13', 10.11.2006, W. Graf (1 ♀, OPC). **Croatia:** Ivanščica Mts, Potok Slugovina, 15.12.2002, K. Žganec (1 ♀, OPC). Medvednica Mts, Bliznec, pilana, stream, 09.12.2009, M. Kučinić (1 ♀, OPC). Medvednica Mts, Izvor Mrzлак, 18.11.2006, A. Popijač (3 ♂, 2 ♀, OPC). 18.11.2008, A. Popijač (1 ♂, 1 ♀, OPC). Medvednica Mts, Kraljičin Zdenac, 19.11.2009, M. Kučinić, I. Vučkavić (1 ♀, OPC). Medvednica Mts, Veliki Potok, N45°51'28.52" E15°56'08.19", 18.10.2011, A. Previšić (1 ♂, OPC). Žumberačka Mts, small stream near River Slapnica, 03.11.2012, M. Kučinić (2 ♂, 1 ♀, OPC). Žumberačka Mts, Vlašić Brdo, River Slapnica, N45°42'35.7", E15°29'40.1", 215 m, 07.11.2012, T. Kovács, G. Magos (1 ♂, 1 ♀, OPC). Žumberačka Mts, Žumberak, River Slapnica, 28.10.2009, M. Kučinić (1 ♀, OPC). **Hungary:** Kőszeg Mts, Hörmann-forrás, 694 m, N47°27'34.2", E16°27'34.2", 18.11.2009, I. Szivák (2 ♂, 1 ♀, OPC). Kőszeg Mts, Stajer-házak, 05.10.1991, Á. Uherkovich (2 ♂, OPC); 18.10.1986, Á. Uherkovich (1 ♂, 1 ♀, OPC). Velem, Borha-forrás, 04.11.1984, S. Nógrádi (1 ♂, 1 ♀, OPC). **Slovenia:** Brdo, Kranj, brooklet to the pond IX, 14.10.2003, G. Urbanič (2 ♂, PMS). Kališe, Črna pri Kamniku, 13.10.1990, I. SIVEC (1 ♂, 3 ♀, PMS). Kamniška Bistrica, 27.11.1969, B. Horvat, I. Sivec (1 ♂, 1 ♀, PMS). Kamniške alpe, Črna pri Kamniku, Volovljek, 1016 m, N46°24'50", E14°54'10", 04.10.2012, I. Sivec, G. Urbanič (3 ♂, 3 ♀, OPC). Kozje, stream Bistri graben, 01.10.1986, B. Horvat, I. Sivec (1 ♂, PMS). Ljubno, Smrekovec, potok Pod Krumpaško Planino, 1390 m, 10.09.1997, B. Horvat, I. Sivec (1 ♀, PMS). Ljubno, Smrekovec, potok Robanšek, Pod Komnom, 1200 m, N46°24'41", E14°51'02", 25.09.1997, B. Horvat, I. Sivec (1 ♂, PMS). Ljubno, Smrekovec, stream below Kugovnik, N46°25'13", E14°52'20", 1450 m, 25.09.1997, B. Horvat, I. Sivec (2 ♂, PMS). Lukovica, Trnjava, stream Drtijščica, 340 m, 12.11.1996, B. Horvat, I. Sivec (1 ♂, PMS). Moravče, Vinje, stream Drtijščica, 360 m, 12.11.1996, B. Horvat, I. Sivec (4 ♂, 1 ♀, PMS). Pečice, Brežice, stream Močnik, 15.10.1988, B. Horvat, I. Sivec (1 ♂, 1 ♀, PMS). Pohorje Mts, brooklet near Rogla, 1350 m, N46.448280°, E15.339671°, 03.12.2011, A. Déry, I. Szivák (1 ♂, 1 ♀, OPC). Pohorje Mts, brooklet near Snežinka (Rogla), 1097 m, 46.435143 N, 15.368489 E, 03.12.2011., A. Déry, I. Szivák (3 ♂, 1 ♀). Pohorje Mts, Padeški vrh, source of Gradiški graben, 1020 m, N46°25'54.1", E15°22'18.0", 08.11.2012, T. Kovács, G. Magos, I. Sivec (1 ♂, OPC). Pohorje Mts, Pesek, N46°28'26.3", E15°20'55.9", 10.11.2008, I. Sivec (1 ♀, OPC); 12.09.2009, I. Sivec (1 ♀, OPC); 09.10.2010, I. Sivec (1 ♂, OPC). Pohorje Mts, Vel. Vrh, Osankarica, 1300 m, 04.11.1984, D. Šere (1 ♂, 1 ♀, PMS). Pri koritu Ob Litijski cesti, 50 m, pod hišo Sp. Besnica 1, 25.11.1984, B. Horvat, I. Sivec (2 ♂, PMS). Smrekovec Mts, below Krumpaška planina, 1390 m, N46°24'50", E14°54'10", 26.09.2012, I. Sivec, G. Urbanič (4 ♂, OPC); 05.10.2012, B. Horvat, I. Sivec (2 ♂, 3 ♀, OPC). Smrekovec Mts, Tračka Planina, source of stream Žep, 11.09.1987, B. Horvat, I. Sivec (1 ♀, PMS). Tepe, Zagorje ob Savi, 16.10.1985, B. Horvat, I. Sivec (1 ♀, PMS). Zg. Velka, spring of the Ščavnica River, 01.10.1998, G. Urbanič (1 ♂, 1 ♀ pupae, PMS); 01.12.1998, G. Urbanič (1 ♂, PMS).

*Etymology* – The new species is named after the Prealpine region, where this widely distributed ancestral species lives.

*Variability* – Similarly to most species in *C. rugulosa* species group the non-intromittent periphallallic structures, the cerci, the paraprocts and the gonopods are highly variable. The number and length of paramere spines are less variable; the spine pattern varies especially in peripheral area with two tendencies: (1) reducing spine number down to the single primary spine that is accompanied by 1–2 very short, almost tertiary spines; (2) shortening the primary spine with increasing number of secondary spines up to 3–4. The intromittent part of the phallic organ, that is the aedeagus, and especially its head with the spatulate, platform lateral processes is rather stable even in populations of peripheral area: Žumberačka Mts in Croatia and Kőszeg Mts in Hungary.

***Chaetopteryx rugulosa* Kolenati, 1848**

*Material examined* – **Austria:** Gleinalpe, springs and springbrook 1.4 km above restaurant Krautwaschl, 1172 m, N47°12'15.31", E15°08'22.14", 22.10.2012, J. Oláh, I. Szivák (3 ♂, 6 ♀, OPC). Plenzengreith, upper reach of stream Schöcklbach, 954 m, N47°12'37.2", E15°29'00.8", 20.11.2009, A. Déry, I. Szivák (2 ♂, 1 ♀, OPC). Stiftingtal, Graz, 19.10.1998, W. Graf (1 ♂, 1 ♀, OPC); 25.09.2005, W. Graf (3 ♂, 1 ♀, 7 pupae, OPC); 10.2006, W. Graf (6 ♂, 8 ♀, OPC; 2 ♂, 1 ♀, MM).

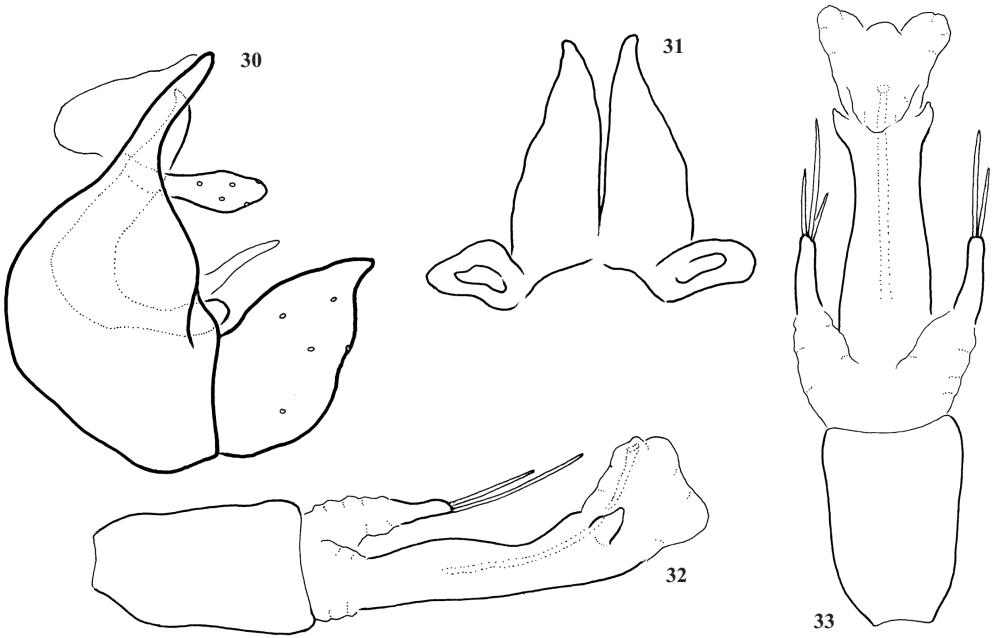
*Remarks* – Specimens from Austria, Bosnia & Herzegovina, Croatia, Hungary and Slovenia were determined as *C. rugulosa*, however we have found that specimens from only a very small area in Austria has the aedeagal structure identical with the aedeagus of the holotype, other specimens belong to four species: *C. schmidi* from Bosnia & Herzegovina, *C. kamnikensis* sp. n. from Slovenia, *C. zalaensis* sp. n. from Hungary and to the widely distributed *C. prealpensis* sp. n.

***Chaetopteryx zalaensis* Oláh sp. n. (Figs 30–36)**

*Diagnosis* – This new species belongs to the *C. rugulosa* species group, *C. rugulosa* subgroup and *C. rugulosa* species cluster. Close to *C. rugulosa* Kolenati, 1848 but differs by having subapical lateral processes on the aedeagus short and pointed gemmiform, not long digitiform; cerci stalked, not parallel-sided. The anal tube of the female very long and slender, almost tapering apicad.

*Description* – Male and female (in alcohol). Light brown medium-sized animal with light body appendages and with yellowish-testaceous wings. Anterior wing with rounded apex and with very long erect spine-like setae present both on the membrane and on the veins; setae on the veins usually stronger. Tibial spur formula of male is 033 and that of female is 133. Forewing length of male is 9 mm, and that of allotype female is 10 mm.

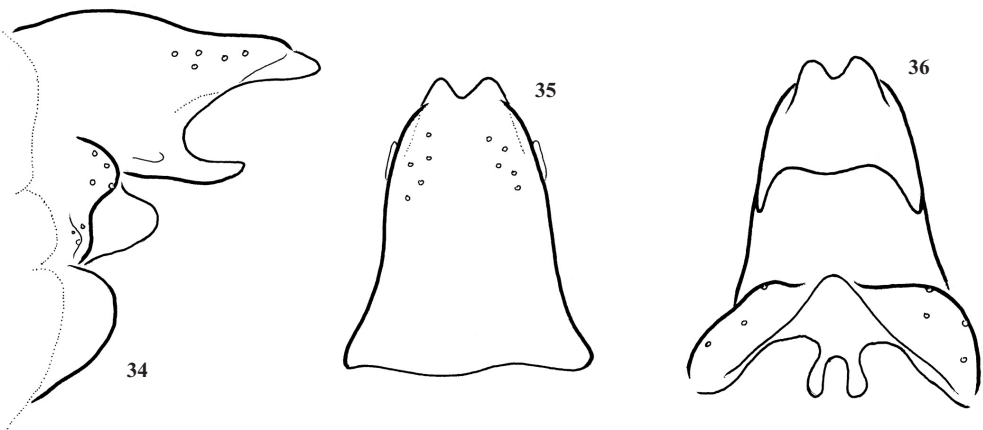
Male genitalia (Figs 30–33). Posterodorsal spinate area of vestitural noncellular microtrichiae on segment VIII and its mesal light band present. Segment IX with short, bridle-like dorsum and longer ventrum; anterior margin rounded convex with long antecosta; posterior margin concave, midlateral sclerotized angle of tergite IX pronounced. The pouch-like concavity of segment X long. Cerci very low and stalked. Apical hook of the paraproctal complex with narrowing pointed apex and less developed lateral angle, middle connecting section long, basal triangle exposed monolobe in lateral view. Membranous subanal lobe short. Gonopods short with apical flap developed and turning mesad resulting in a single short pointed apex in lateral view. Phallic organ composed of short rim-like phallic apodeme, short tube of phallosome, short endotheca, well-developed aedeagus and medium long parameres; 2-3 nested paramere spines present; aedeagus supplied with a pair of pointed short gemmiform lateral processes directed oblique upward, the very basal part of the lateral process sclerotized and membranous after; ejaculatory duct ending with gonopore opening into a large trilobed endophallic membranous structure.



**Figs 30–33.** *Chaetopteryx zalaensis* Oláh sp. n. holotype male:

30 = male genitalia without phallic organ in left lateral view; 31 = paraproct in caudal view; 32 = phallic organ in lateral view; 33 = phallic organ in dorsal view

Female genitalia (Figs 34–36). Anal tube formed by the fusion of tergite IX and X is long and narrowing posterad; apical margin forming triangular lateral lobes and mesal excision in dorsal view by the protruded internal sclerites, the vestigial tergite X. Setose ventroapical lobes of tergite IX reduced, just visible. Supragenital plate of segment X triangular in ventral



**Figs 34–36.** *Chaetopteryx zalaensis* Oláh sp. n. allotype female:

34 = female genitalia in left lateral view; 35 = anal tube in dorsal view; 36 = female genitalia in ventral view

view. Median lobe of the vulvar scale (lower vulvar lip) half long as the lateral lobes. Vaginal chamber medium sized reaching to the middle of sternite VIII. Vaginal sclerite pattern clearly visible.

*Type material* – Holotype. **Hungary:** Hegyhátszentjakab, Vadása-tó, források, N46°52'32", E16°33'03", 04.11.2010, singled, J. Oláh, Á. Uherkovich (1♂, OPC). Allotype. Same as holotype (1♀, OPC). Paratypes. Same as holotype (15♂, 11♀, OPC; 3♂, 1♀, MM). Vas Megye, Szőce, 05.11.1985, Á. Uherkovich (12♂, 7♀, OPC); 17.10.1986, Á. Uherkovich (10♀, OPC).

*Etymology* – The new species is named after the Zala region, where the type locality is found.

### ***Chaetopteryx irenae* new species subgroup**

Male genitalia is characterized by very high, broad cerci, by the presence of supplementary digital processes on the superanal complex and by the highly undulating apical margin of the gonopods; a pair of supporting sclerites present on aedeagus subventrad or apicad. Female genitalia is characterized by the very developed ventroapical processes on the tergite IX. Seven species belong to this species subgroup: *C. clara* McLachlan, 1876, *C. euganea* Moretti & Malicky, 1986, *C. giuliensis* Oláh & Kovács sp. n., *C. goricensis* Malicky & Krušnik, 1986, *C. idriensis* Oláh & Urbanič sp. n., *C. irenae* Krušnik & Malicky, 1986, *C. marinkovicae* Malicky & Krušnik, 1988.

### ***Chaetopteryx clara* McLachlan, 1876**

*Material examined* – **Slovenia:** Bormes, stream Grabnarica, 21.10.1995, B. Horvat (1♂, PMS). Ljubljana, Mostec, 1989, H. Malicky (2♂, 2♀, OPC from MPC). Ljubljana, Mostec, Pržanec stream, 293 m, N46°03'44.3", E14°28'49.3", 06.12.2009, A. Déry, I. Szivák (5♂, OPC; 2♀, MM). Medvode, Osolnik, 440 m, N46°07'24.5", E14°20'54.8", 25.11.2012, I. Sivec (1♂, OPC).

*Remarks* – Its species group position needs further studies. The supplementary digitiform processes on the superanal complex is vestigial. Paraproct spine pattern rather peculiar; characterized by the presence of primary, secondary and tertiary spines arranged in anterior shortening row in sagittal plane; primary spine slender and undulate; location and number of peg-like tertiary spines variable.

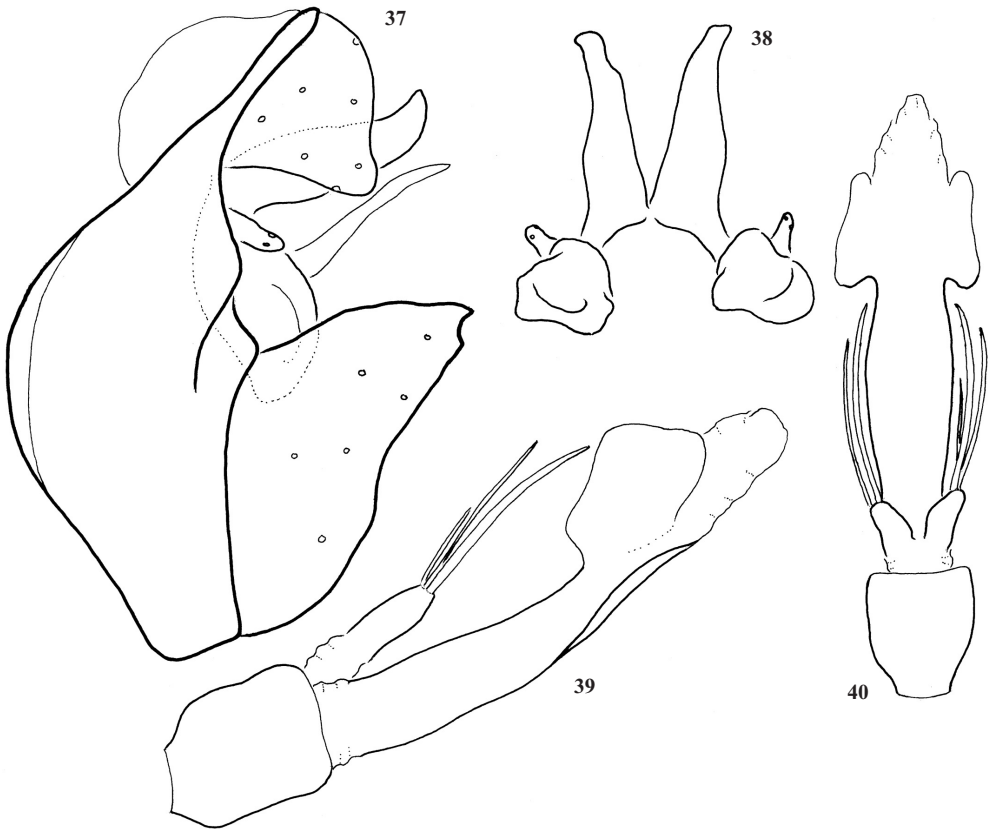
### ***Chaetopteryx euganea* Moretti & Malicky, 1986 (MALICKY et al. 1986)**

*Material examined* – **Italy:** Colli Euganei, 19.10.1987, H. Malicky (2♂, 2♀, OPC from MPC).

### ***Chaetopteryx giuliensis* Oláh et Kovács sp. n. (Figs 37–43)**

*Diagnosis* – This new species belongs to the *C. rugulosa* species group, *C. irenae* new species subgroup. Close to *C. irenae* Krušnik & Malicky, 1986 but differs by having cerci downward directed ventroapicad; paraproct more slender in apical view; supplementary processes free, not fused to the paraproctal triangle; gonopods with apical margin less undulate; lateral subapical processes platform, not digitiform; supporting sclerite broad, almost semicircular, not long and narrow. Female has apical profile of the anal tube angulate, not rounded in dorsal view.

*Description* – Male and female (in alcohol). Light brown medium-sized animal with light body appendages and with yellowish-testaceous wings. Anterior wing with rounded apex and with very long erect spine-like setae present both on the membrane and on the veins; setae on the veins usually stronger. Tibial spur formula of male is 033 and that of female is 133. Forewing length of male is 11 mm, and that of allotype female is 10 mm.



**Figs 37–40.** *Chaetopteryx giuliensis* Oláh & Kovács sp. n. holotype male:

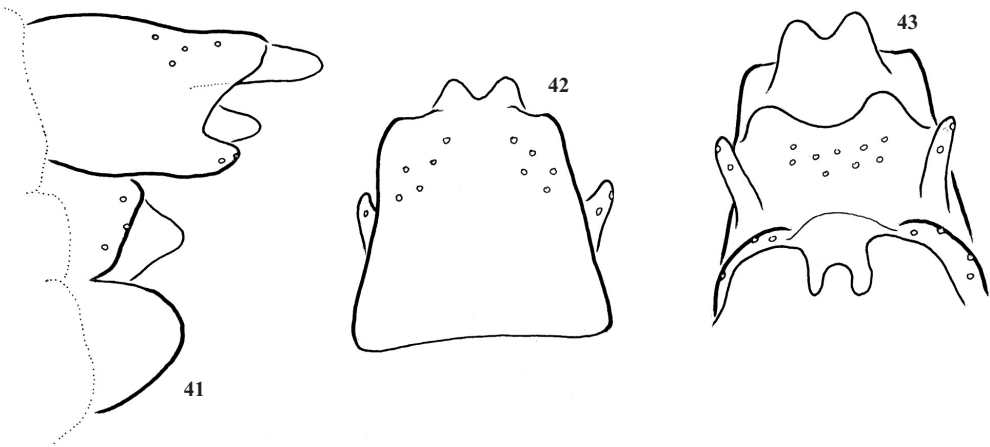
37 = male genitalia without phallic organ in left lateral view; 38 = paraproct in caudal view; 39 = phallic organ in lateral view; 40 = phallic organ in dorsal view

Male genitalia (Figs 37–40). Posterodorsal spinate area of vestitural noncellular microtrichiae on segment VIII and its mesal light band present. Segment IX with short, bridle-like dorsum and longer ventrum; anterior margin rounded convex with long antecosta; posterior margin concave, midlateral sclerotized angle of tergite IX pronounced. The pouch-like concavity of segment X short. Cerci high with downward curving ventroapical corner. Apical hook of the paraproctal complex narrow with less pointed apex and less developed lateral angle, middle connecting section long, basal triangle exposed monolobe in lateral view. Supplementary pair of setose processes of the cercal-paraproctal complex digitate. Membranous subanal lobe short. Gonopods long with apical flap developed and turning mesad resulting in a single short pointed apex in lateral view, apical margin slightly undulate. Phallic organ composed of short rim-like phallic apodeme, short tube of phallosome, short endotheca, well-developed aedeagus and medium long parameres; 2-3 nested paramere spines present, single stout primary and 2 secondary slender and shorter; aedeagus supplied with a pair of platform lateral processes directed upward; supporting sclerite in the form of broad semicircular horizontal ridge present; ejaculatory duct ending with gonopore opening into a large trilobed endophallic membranous structure.

Female genitalia (41–43). Anal tube formed by the fusion of tergite IX and X is medium long; apical margin forming rounded lateral lobes and triangular mesal excision in dorsal view shaped by the protruded internal sclerites and by the angled apicolateral corner of tergite IX. Setose ventroapical lobes of tergite IX long. Supragenital plate of segment X rounded in ventral view. Median lobe of the vulvar scale (lower vulvar lip) half long of the lateral lobes. Vaginal chamber medium sized reaching to the middle of sternite VIII. Vaginal sclerite pattern clearly visible.

*Type material* – Holotype. **Italy**: Alpi Giulie, Sella Carnizza, spring area of River Ucea, N46°20'11.4", E13°19'46.8", 1105 m, 09.11.2012, T. Kovács, G. Magos (1♂, OPC). Allotype. Same as holotype (1♀, OPC). Paratypes. Same as holotype (2♂, OPC; 1♂, MM). Alpi Giulie, between Ucea and Resia, left side brook of River Ucea, N46°18'54.2", E13°23'37.6", 725 m, 09.11.2012, T. Kovács, G. Magos (1♂, 1♀, OPC). Sorgente del T. Ucea (1050 m), Parco Naturale delle Prealpi Giulie, Com Resia prov. Udine, crenal, 09.10.1999, S. Paradisi, F. Stoch (1♂, OPC).

*Etymology* – The new species is named after the Alpi Giulie, where the type locality is found.



**Figs 41–43.** *Chaetopteryx giuliensis* Oláh & Kovács sp. n. allotype female:

41 = female genitalia in left lateral view; 42 = anal tube in dorsal view; 43 = female genitalia in ventral view

***Chaetopteryx goricensis* Malicky & Krušnik, 1986 (MALICKY et al. 1986)**

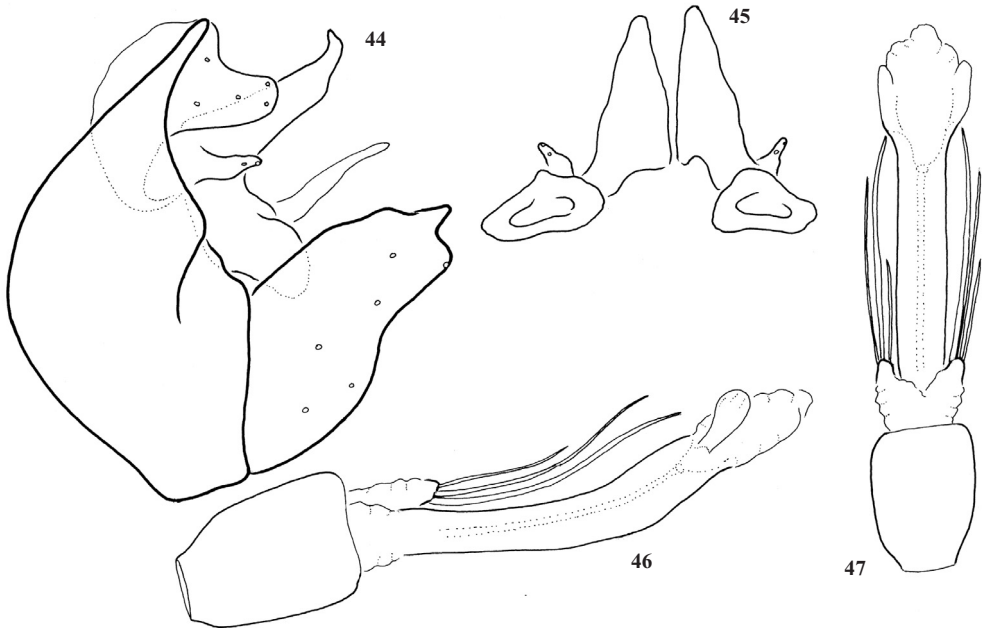
*Material examined* – **Slovenia**: Ajdovščina, Predmeja, one spring of Lokavšček stream, 695 m, N45°56'21.8", E13°52'17.8", 06.12.2009, A. Déry, I. Szivák (9♂, OPC; 1♂, MM). Ajdovščina, Predmeja, stream Lokavšček, 15.10.1992, B. Horvat, I. Sivec (1♂, PMS). Čekovnik, Blašk, spring, brooklet, 631 m, N45°59'04.6", E13°58'11.0", 05.12.2009, A. Déry, I. Szivák (4♂, OPC). Čekovnik, Hleviše, spring, brooklet, 640 m, N45°58'48.18", E13°59'9.52", 05.12.2009, A. Déry, I. Szivák (1♂, OPC). Deskle, 1986, H. Malicky (2♂, 2♀, OPC).

***Chaetopteryx idriensis* Oláh et Urbanič sp. n. (Figs 44–50)**

*Diagnosis* – This new species belongs to the *C. irenae* new species subgroup of the *C. rugulosa* species group. Close to *C. goricensis* Malicky & Krušnik, 1986 but differs by having cerci differently shaped; paraproct broader in apical view; gonopods longer; paramere spines tripled, not single; lateral subapical processes slender, not broad both in lateral and dorsal view. Female has ventrolateral setose processes differently shaped; internal sclerite of the anal tube protruding and producing lateral lobes blunt, not acute triangular; supragenital plate blunt, not pointed.

*Description* – Male and female (in alcohol). Light brown medium-sized animal with light body appendages and with yellowish-testaceous wings. Anterior wing with rounded apex and with very long erect spine-like setae present both on the membrane and on the veins; setae on the veins usually stronger. Tibial spur formula of male is 033 and that of female is 133. Forewing length of male is 9 mm, and that of allotype female is 10 mm.

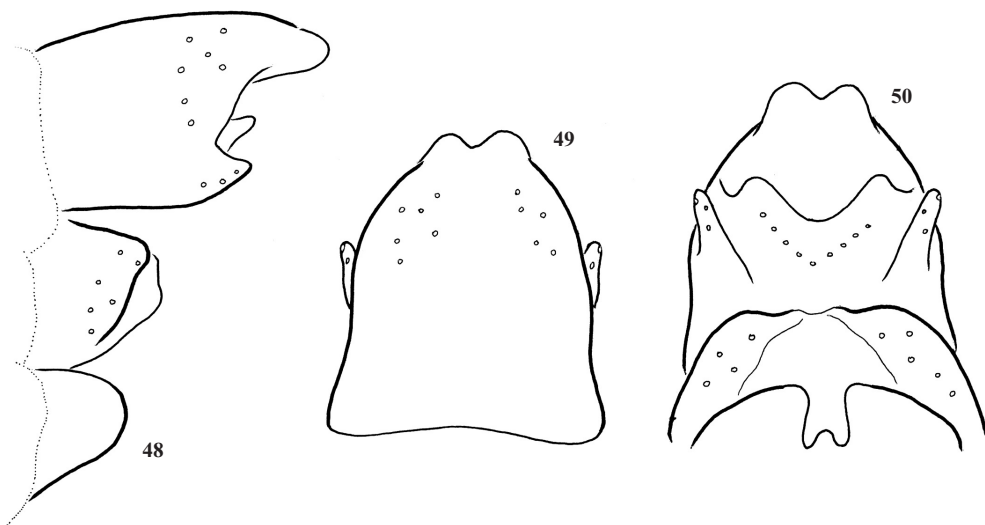
Male genitalia (Figs 44–47). Posterodorsal spinate area of vestitural noncellular microtrichiae on segment VIII and its mesal light band present. Segment IX with short, bridle-like dorsum and longer ventrum; anterior margin rounded convex with long antecosta; posterior margin concave, midlateral sclerotized angle of tergite IX pronounced. The pouch-like concavity of segment X short. Cerci high, L-shaped. Apical hook of the paraproctal complex broad with narrowing pointed apex and less developed lateral angle, middle connecting section long, basal triangle exposed monolobe in lateral view. Supplementary pair of processes on the cercal-paraproctal (superanal genital) complex digitate. Membranous subanal lobe short. Gonopods long with apical flap developed and turning mesad resulting in a single short pointed apex in lateral view, apical margin undulate with two excisions. Phallic organ composed of short rim-like phallic apodeme, short tube of phallosome, short endotheca, well-developed aedeagus and medium long parameres; 3 nested paramere spines present, stout primary and 2 secondary slender and shorter; aedeagus supplied with a pair of clavate spatulate lateral processes directed oblique upward, the very basal part of the lateral process sclerotized and membranous after; ejaculatory duct ending with gonopore opening into a large trilobed endophallic membranous structure.



**Figs 44–47.** *Chaetopteryx idriensis* Oláh & Urbanič sp. n. holotype male:

44 = male genitalia without phallic organ in left lateral view; 45 = paraproct in caudal view; 46 = phallic organ in lateral view; 47 = phallic organ in dorsal view

Female genitalia (Figs 48–50). Anal tube formed by the fusion of tergite IX and X is medium long; apical margin forming rounded lateral lobes and triangular mesal excision in dorsal view by the protruded internal sclerites that is the vestigial tergite X. Setose ventroapical lobes of tergite IX long. Supragenital plate of segment X blunt triangular in ventral view. Median lobe of the vulvar scale (lower vulvar lip) third long of the lateral lobes. Vaginal chamber medium sized reaching to the middle of sternite VIII. Vaginal sclerite pattern clearly visible.



**Figs 48–50.** *Chaetopteryx idriensis* Oláh & Urbanič sp. n. allotype female: 48 = female genitalia in left lateral view; 49 = anal tube in dorsal view; 50 = female genitalia in ventral view

*Type material* – Holotype. **Slovenia:** Idrijsko hribovje, Čekovnik, Blašk, spring, brooklet, N45°59'04.6", E13°58'11.0", 650 m, 09.11.2012, T. Kovács, G. Magos (1♂, OPC). Allotype. Same as holotype (1♀, OPC). Paratypes. Same as holotype (2♂, OPC; 1♂, MM). Same locality as holotype: 04.12.2011, A. Déry, I. Szivák (10♂, OPC); 05.12.2009, A. Déry, I. Szivák (4♂, OPC). Idrijsko hribovje, Čekovnik, Hleviše, spring, brooklet, 640 m, N45°58'48.18", E13°59'9.52", 05.12.2009, A. Déry, I. Szivák (1♂, OPC). Idrijsko hribovje, Krekovše, spring, brooklet at the Idrijca River, N45°59'01.4", E13°56'57.4", 460 m, 31.10.2003, G. Urbanič (1♀, MPC); 08.10.2002, G. Urbanič (1♂, MPC).

*Etymology* – The new species is named after town Idrija, located nearby the type locality.

### ***Chaetopteryx irenae* Krušnik & Malicky, 1986 (MALICKY et al. 1986)**

*Material examined* – **Slovenia:** Artviže stream Brusnica, 18.10.2000, G. Urbanič (1♂, reared in the laboratory, PMS). Misliče, upper reach of Sušica stream, 617 m, N45°37'14.8", E14°02'16.7", 06.12.2009, A. Déry, I. Szivák (13♂, OPC); 04.12.2011, A. Déry, I. Szivák (6♂, 2♀, OPC; 2♂, 1♀, MM).

### ***Chaetopteryx marinkovicae* Malicky & Krušnik, 1988**

*Material examined* – **Croatia:** Istria, Kompanj, 1989, H. Malicky (2♂, 2♀, OPC). Istria, Kompanj, Klobasi, N45.39111°, E14.07111°, 14.11.2009, M. Kučinić (4♂, 9♀, OPC; 1♂, 1♀, MM). **Slovenia:** Vala Zelenica, Loka, Črni kal, 17.10.1990, I. Sivec (2♂, 1♀, PMS).

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## References

- ARNQVIST, G. (1997): The evolution of animal genitalia: distinguishing between hypotheses by single species studies. – *Biological Journal of the Linnean Society*, 60: 365–379.
- 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.
- BOTOSANEANU, L. (1957): Quelques Trichopteres nouveaux de Roumanie. – *Tijdschrift voor Entomologie*, 100(2): 179–194.
- CAYETANO, L., MAKHLAKOV, A. A. BROOKS, R. C. & BONDURIANSKY, R. (2011): Evolution of male and female genitalia following release from sexual selection. – *Evolution*, 65(8): 2171–2183.
- DARWIN, C. (1859): *On the origin of species by means of natural selection, or the preservation of favoured races in the struggle for life*. – John Murray, London. 502 pp.
- EBERHARD, W. G. (2009): Postcopulatory sexual selection: Darwin's omission and its consequences. – *Proceedings of the National Academy of Sciences of the United States of America*, 106(1): 10025–10032.
- EBERHARD, W. G. (2010a): Cryptic female choice. – *Encyclopedia of Animal Behavior*, 1: 430–434.
- EBERHARD, W. G. (2010b): Evolution of genitalia – theories, evidence, and new directions. – *Genetica*, 138(1): 5–18.
- HAUSDORF, B. (2011): Progress toward a general species concept. – *Evolution*, 65(4): 923–931.
- KUČINIĆ, M., SZIVÁK, I., PAULS, S. U., BÁLINT, M., DELIĆ, A. & VUČKOVIĆ, I. (2013): *Chaetopteryx bucar* sp. n. a new species from the *Chaetopteryx rugulosa* group from Croatia (Insecta, Trichoptera) with some molecular, taxonomical and ecological notes on the group. – *Zoosymposia*: in press.
- 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.
- MALICKY, H. (1988): A comment on figuring three-dimensional structures. – *Trichoptera Newsletter*, 15: 21–24.
- MALICKY, H. (2005): Ein kommentiertes Verzeichnis der Köcherfliegen (Trichoptera) Europas und des Mittelmeergebietes. – *Linzer biologischen Beiträgen*, 37(1): 533–596.
- MALICKY, H. & PAULS, S. U. (2012): Cross-breeding of *Chaetopteryx moretii* and related species, with molecular and eidonomical results (Trichoptera, Limnephilidae). – *Annales de Limnologie*, 48: 13–19.
- MALICKY, H., KRUSNIK, C., MORETTI, G. & NÓGRÁDI, S. (1986): Ein Beitrag zur Kenntnis der *Chaetopteryx rugulosa* Kolenati, 1848, – Gruppe (Trichoptera, Limnephilidae). – *Entomofauna, Zeitschrift für Entomologie*, 7(1): 1–27.
- MAYDEN, R. L. (1997): A hierarchy of species concepts: the denouement in the saga of the species problems. – In: CLARIDGE, M. F., DAWAH, A. H. & WILSON, M. R. (eds) *Species: the units of biodiversity*. – Chapman and Hall, London. 381–424.
- MAYR, E. (1942): *Systematics and the origin of species*. – New York, Columbia University Press. 334 pp.
- NIELSEN, A. (1980): A comparative study of the genital segments and the genital chamber in female Trichoptera. – *Det Kongelige Danske Videnskabernes Selskab, Biologiske Skrifter*, 23(1): 1–200.
- OLÁH, J. (2011): New species and records of Balkan Trichoptera. – *Folia Historico-naturalia Musei Matraensis*, 35: 111–121.
- OLÁH, J. & JOHANSON, K. A. (2008): Reasoning an appendicular and functional caddisfly genital terminology. – *Braueria (Lunz am See, Austria)*, 35: 29–40.
- PARKER, G. A. (1970): Sperm competition and its evolutionary consequences in the insects. – *Biological Reviews*, 45: 525–567.

- PUNIAMOORTHY, N., KOTRBA, M. MEIER, R. (2010): Unlocking the “Black box”: internal female genitalia in Sepsidae (Diptera) evolve fast and are species-specific. – *BMC Evolutionary Biology*, 10(275): 1–21.
- DE QUEIROZ, K. (2011): Branches in the lines of descent: Charles Darwin and the evolution of the species concept. – *Biological Journal of the Linnean Society*, 103: 19–35.
- RODRIGEZ-MUNOZ, R., BRETMAN, A., SLATE, J., WALLING, C. A. & TREGENZA, T. (2010): Natural and sexual selection in a wild insect population. – *Science*, 328: 1269–1272.
- VSHIVKOVA, T. S. (2007): Phylogeny of family Limnephilidae (Insecta: Trichoptera) with emphasis on tribe Limnephilini (Subfamily Limnephilinae). – Ph.D. Thesis, Clemson University, South Carolina. 690 pp.

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