



Zootaxa 3812 (1): 001–082

www.mapress.com/zootaxa/

Copyright © 2014 Magnolia Press

Monograph

ISSN 1175-5326 (print edition)

ZOOTAXA

ISSN 1175-5334 (online edition)

<http://dx.doi.org/10.11646/zootaxa.3812.1.1>

<http://zoobank.org/urn:lsid:zoobank.org:pub:7847D731-9F66-4856-A79F-9435FED25B1D>

ZOOTAXA

3812

***Zwicknia* gen. n., a new genus for the *Capnia bifrons* species group,
with descriptions of three new species based on morphology, drumming
signals and molecular genetics, and a synopsis of the West Palaearctic and
Nearctic genera of Capniidae (Plecoptera)**

DÁVID MURÁNYI^{1,4}, MARIBET GAMBOA² & KIRILL MÁRK ORCI³

¹Department of Zoology, Hungarian Natural History Museum, Baross u. 13, H-1088 Budapest, Hungary.

E-mail: muranyi@zool.nhmus.hu

²Institute of Freshwater Ecology and Inland Fisheries (IGB), Department of Shallow lakes and Lowland rivers, Müggelseedamm 301,
12587 Berlin, Germany. E-mail: maribetg@gmail.com

³MTA-ELTE-MTM Ecology Research Group, Pázmány Péter s. 1/C, H-1117 Budapest, Hungary. E-mail: kirill@nhmus.hu

⁴Corresponding author



Magnolia Press
Auckland, New Zealand

DÁVID MURÁNYI, MARIBET GAMBOA & KIRILL MÁRK ORCI

***Zwicknia* gen. n., a new genus for the *Capnia bifrons* species group, with descriptions of three new species based on morphology, drumming signals and molecular genetics, and a synopsis of the West Palaearctic and Nearctic genera of Capniidae (Plecoptera)**

(*Zootaxa* 3812)

82 pp.; 30 cm.

6 Jun. 2014

ISBN 978-1-77557-411-8 (paperback)

ISBN 978-1-77557-412-5 (Online edition)

FIRST PUBLISHED IN 2014 BY

Magnolia Press

P.O. Box 41-383

Auckland 1346

New Zealand

e-mail: zootaxa@mapress.com

<http://www.mapress.com/zootaxa/>

© 2014 Magnolia Press

All rights reserved.

No part of this publication may be reproduced, stored, transmitted or disseminated, in any form, or by any means, without prior written permission from the publisher, to whom all requests to reproduce copyright material should be directed in writing.

This authorization does not extend to any other kind of copying, by any means, in any form, and for any purpose other than private research use.

ISSN 1175-5326 (Print edition)

ISSN 1175-5334 (Online edition)

Table of contents

Abstract	3
Introduction	4
Material and methods	4
Systematics	7
Capniidae terminalia	7
Synopsis of the West Palaearctic and Nearctic Capniidae genera	14
<i>Allocapnia</i> Claassen, 1928	14
<i>Arsapnia</i> Banks, 1897 stat. rev.	14
<i>Bolshecapnia</i> Ricker, 1965	15
<i>Capnia</i> Pictet, 1841 sensu stricto	15
<i>Capnia</i> Pictet, 1841 sensu lato	16
<i>Capnioneura</i> Ris, 1905	19
<i>Capnopsis</i> Morton, 1896	20
<i>Capnura</i> Banks, 1900	20
<i>Eucapnopsis</i> Okamoto, 1922	20
<i>Isocapnia</i> Banks, 1938	21
<i>Mesocapnia</i> Raušer, 1968	22
<i>Nemocapnia</i> Banks, 1938	22
<i>Paracapnia</i> Hanson, 1946	22
<i>Utacapnia</i> Gaufin, 1970	24
Taxonomy	24
<i>Zwicknia</i> Murányi, gen. n.	24
Morphological key to adult males of <i>Zwicknia</i>	37
<i>Zwicknia acuta</i> Murányi & Orci, sp. n.	37
<i>Zwicknia bifrons</i> (Newman, 1838) comb. n.	40
<i>Zwicknia kovacsi</i> Murányi & Gamboa, sp. n.	44
<i>Zwicknia rupprechti</i> Murányi, Orci & Gamboa, sp. n.	46
<i>Zwicknia sevanica</i> (Zhiltzova, 1964) comb. n.	49
<i>Zwicknia tuberculata</i> (Zhiltzova, 1964) comb. n.	51
<i>Zwicknia turkestanica turkestanica</i> (Kimmins, 1950) comb. n.	53
<i>Zwicknia turkestanica brevicula</i> (Berthélemy & Dia, 1982) comb. n.	55
Notes on further taxa attributed to <i>Zwicknia</i>	55
<i>Capnia dusmeti</i> Navás, 1917	55
<i>Capnia quadrangularis</i> Aubert, 1946	56
<i>Capnia bifrons</i> (Newman, 1838) drumming types sensu Rupperecht 1997	56
Discussion	57
Acknowledgements	70
References	70
Appendix 1	76
Appendix Tables 1–4	79

Abstract

Zwicknia Murányi, **gen. n.** is erected for the *Capnia bifrons* species group sensu Zhiltzova, 2001 with the description of three new species based on morphology, mating call, and the mitochondrial DNA marker cytochrome c oxidase I: *Z. acuta* Murányi & Orci, **sp. n.**, *Z. kovacsi* Murányi & Gamboa, **sp. n.** and *Z. rupprechti* Murányi, Orci & Gamboa, **sp. n.** *Zwicknia bifrons* (Newman, 1838) **comb. n.** is selected as the type species and redescribed. The other three species placed into *Zwicknia*, **gen. n.**, *Z. sevanica* (Zhiltzova, 1964) **comb. n.**, *Z. tuberculata* (Zhiltzova, 1964) **comb. n.**, and *Z. turkestanica* (Kimmins, 1950) **comb. n.** are redescribed based only on morphological characters. Comparative morphological studies and newly discovered characters of the genitalia has allowed for the first time a synopsis of the adults of the West Palaearctic and Nearctic genera of Capniidae. *Arsapnia* Banks, 1897 (type species: *A. decepta* Banks, 1897 **comb. rev.**) is removed from synonymy with *Capnia* Pictet, 1841 with new combinations, *Arsapnia arapahoe* (Nelson & Kondratieff, 1988) **comb. n.**, *A. coyote* (Nelson & Baumann, 1987) **comb. n.**, *A. pileata* (Jewett, 1966) **comb. n.**, *A. sequoia* (Nelson & Baumann, 1987) **comb. n.**, *A. teresa* (Claassen, 1924) **comb. n.**, *A. tumida* (Claassen, 1924) **comb. n.**, and *A. utahensis* (Gaufin & Jewett, 1962) **comb. n.** A new sensu stricto diagnosis of *Capnia* is proposed with comments on the taxa retained in *Capnia* sensu lato.

Key words: Capniidae, *Zwicknia* **gen. n.**, *Arsapnia*, *Capnia* s.s., new species, new combinations, synopsis, morphology, mating calls, molecular phylogeny

Introduction

The *Capnia bifrons* species group is one of the most enigmatic assemblages of species within the European Plecoptera. *Capnia bifrons* (Newman, 1838) is a common stonefly of the hilly and mountainous regions of Europe. In the monographs, morphological, and taxonomic works of the 19th and early 20th centuries (Morton 1896; Klapálek 1896, 1909; Despax 1951; Hynes 1940, 1941; Hanson 1946), the name *C. nigra* (Pictet, 1833), the type species of *Capnia* Pictet, 1841, was erroneously applied to this stonefly. Aubert (1946) clarified the identity of the real *C. nigra*, and proposed *C. quadrangularis* Aubert, 1946 as a *nomen novum* for the species known previously as *C. nigra*. However, a year later Kimmins (1947) examined the type of the previously overlooked *C. bifrons* and revised its status, designating *C. quadrangularis* as a subjective junior synonym of *C. bifrons*.

After the identification and nomenclature was clarified, *C. bifrons* was considered to be a single widespread European species exhibiting variability (Lillehammer 1974), whereas three closely related species from Transcaucasia and Middle Asia were described on the basis of the terminalia (Kimmins 1950a, Zhiltzova 1964). Later, Westermann (1993) reported distinct wing polymorphic populations of *C. bifrons* that had different life histories in geographically nearby streams in Germany. Comparative studies of mating calls recorded from most of the range of *C. bifrons* revealed that the species concept of this species included cryptic species (Rupprecht 1997). However, despite the distinct drumming signals, no other morphological distinctions were noted than differences in wing length. These cryptic taxa were not formally given specific recognition.

Intersexual communication by drumming signals plays a crucial role in the mate finding behaviour of many species of Arctoperlaria (e.g. Rupprecht 1968, 1969; Zeigler & Stewart 1977; Stewart 2001; Stewart & Sandberg 2006). Males and receptive females recognize each other as conspecific sexual partners on the basis of the species specific rhythmic pattern of drumming signals. After establishing a male-female drumming duet, a male can find the responding, stationary female by vibrotaxis. As in other groups of insects, where acoustic communication is an important component of the species specific mate recognition system (e. g. Orthoptera, Hemiptera, Neuroptera), in Plecoptera the analysis of those acoustic signals may be a relevant aspect of their taxonomic examination. Drumming signals of *C. bifrons* from the Carpathian Basin and the Balkans have not been analyzed before our study. We recorded calls of different populations from those areas during the last three years. Analyses of 13 populations indicated a patchy geographical pattern of very different calls. A morphological study of populations with different drumming signals confirmed specific distinctiveness in the epiproct and tergal characters. In this study, we describe three new species based on their morphology and mating call. In addition, we use of molecular studies, along with the morphological examination of 29 other European populations. We also give a comparative redefinition of the nominal *C. bifrons*, and preliminary morphological redescription of the three, previously named Asian species of the species group.

Morphological studies indicated that the *C. bifrons* species group was distinct from all other Capniidae genera in several genitalic characters. We therefore propose the new genus, *Zwicknia* Murányi, **gen. n.**, for the group. Due to our comparative morphological studies of 155 other Capniidae species and introduction of new distinguishing characters, a *sensu stricto* diagnosis of *Capnia*, revised status of *Arsapnia* Banks, 1897, and some other changes in Capniidae systematics are additionally proposed in a synopsis of the West Palaearctic and Nearctic genera.

Material and methods

Collecting methods, depositories, distribution and morphological studies. Adults were collected by hand or using a beating sheet. Matured larvae were collected among littoral leaf packs by hand. Specimens were preserved in both 70 and 96% ethanol in the field. Living adults for drumming signal recordings were transferred to the laboratory in plastic boxes. After recording their vibrational signals, these specimens were also stored in 70 or 96% ethanol. Terminalia of most adult specimens used for molecular studies were clipped, placed into 70% ethanol, and stored in collections. The holotypes were deposited in the Collection of Smaller Insect Orders, Department of Zoology, Hungarian Natural History Museum (HNHM). Paratypes are held in the HNHM and in the Richard W. Baumann Aquatic Insect Collection, Monte L. Bean Life Science Museum, Brigham Young University (BYUC), the collection of the former Limnologische Fluss-Station des Max-Planck-Instituts für Limnologie, presently held by Prof. Peter Zwick, Schlitz, Germany (PZC), the Gilles Vinçon Collection, Grenoble, France (GVC) and the

Mátra Museum (MM) of the HNHM, Gyöngyös, Hungary. The curators and institutions are provided with acronyms in the material examined.

Additional preserved *Zwicknia* **gen. n.** material kept in the GVC and the Wolfram Graf Collection, Wien, Austria (WGC) was studied by Dr. Gilles Vinçon (GVC) and Dr. Wolfram Graf (WGC), respectively. Material of the Wien Natural History Museum (WNHM) was studied by the first author. These data were contributed to the species descriptions as Other Material—records based on morphology only.

The comparative material of other genera studied for systematics of Capniidae deposited in the BYUC, HNHM and PZC. The list of the studied taxa is given in Appendix 1. Character states of both sexes of the Asian genera *Apteroperla* Matsumura, 1931, *Capniella* Klapálek, 1920, *Eocapnia* Kawai, 1955, *Takagripopteryx* Okamoto, 1922 and the male of *Baikaloperla* Zapekina-Dulkeit & Zhiltzova, 1973, refer to literature data extracted from the following works of Kawai (1955, 1967), Shimizu (1997), and Zhiltzova (2003).

In the material examined, specimens whose drumming signals were recorded, used for molecular studies, parts were mounted on slides, portions used for illustrations, or that were studied by SEM are indicated. Propylene glycol was used for slide preparations. SEM images were made using a Philips XL30 (BYUC) and Hitachi S-2600N (HNHM) scanning electron microscopes. Specimens for SEM study were critical point dried and sputter coated with gold-palladium.

Literature data of species distributional ranges and habitat preferences were compiled from the following works of Brinck (1949), Fochetti (2004), Fochetti & Tierno de Figueroa (2008), Hynes (1941), Illies (1978), Khoo (1964), Rupprecht (1997), Sivec (1980), Tierno de Figueroa *et al.* (2003), Westermann (1993), Zhiltzova (2003), and Zwick (1978). Terminology of adult morphology mainly follows Hanson (1946) and Nelson & Baumann (1989), whereas with larvae, terminology follows Stewart & Stark (2002). Abbreviations used for parts of the terminalia, thoracic sclerites and wing veins explained on Figs. 1–23, 35, 53–56, 63, 66–69, 71, 74–75 and 81, respectively.

Drumming studies

During this study recordings of drumming calls of 60 male specimens from 13 populations (Fig. 197) were analysed (for detailed information on the collection sites and dates see examined material used in the species descriptions). All the examined males were collected as adults. Therefore relative adult age was unknown. Since specimens were collected with an unknown timing in relation to the emergence of adults at each collecting site, our analysis is based on a quasi-random sample regarding the age of the stoneflies. Because of this sampling, we expect that the age of animals will not create a systematic bias in our analysis.

Two methods were used to record the drumming signals of captive specimens. In 2010, specimens were placed in small plastic cups, sealed with a plastic cling film membrane. Two cups (one containing a single male, the other containing a single female) were glued to each other at their bottoms to enable the transmission of vibratory signals and interactive duetting between the two adults. We recorded the airborne sounds emitted by the walls of the cups during drumming. Recordings were made with a solid-state recorder (M-Audio MicroTrack II 24/96) using its “T”-shaped accessory stereo microphone.

In 2011, specimens to be examined were placed on the diaphragm of a middle range dynamic speaker (SAL YD78, 8 Ohm), functioning as a vibration transducer. The speaker was covered with a transparent plastic sheet, allowing the examined specimen to move freely on the diaphragm but could not escape. The speaker was connected to the microphone input of a solid-state recorder with a pair of wires and a mono 1/8 TS phone jack connector. The speaker's negative lead tag was wired to the sleeve, while the speaker's positive lead tag was wired to the tip of the connector. In spite the low impedance of the speakers (compared to a microphone), the recording assembly was effective and yielded recordings with much better signal to noise ratio, and most oscillograms were made from recordings using this method.

Since females were also collected as adults of unknown reproductive status, we rarely obtained male-female duet recordings. Because of the few duet recordings available, we can present only preliminary results of male-female duets in three of the four examined species.

For a quantitative characterization of the male drumming signals only rhythmic characters were measured since the spectral properties of the signal depend on the resonant characteristics of the substrate on which the animal produces the call.

The terminology used for describing the drumming signals of the examined specimens is defined below:

Basic structural elements of the described signals: *Beat*: the smallest component of the signal controlled by the drumming animal: a short, impulse-like vibration caused by one percussive action of the abdomen of the signalling insect.

Beat group: the first order grouping of beats.

Beat repetition pattern types: *Monophasic beat repetition*: a single, continuous sequence of beats (Maketon *et al.* 1988, and as the term was used in Abbott & Stewart 1997), where beats are repeated more or less evenly with a stochastic variation in inter-beat intervals or with gradually increasing or decreasing inter-beat intervals (this term includes the monophasic and varied inter-beat interval calls of Stewart & Sandberg's terminology (Stewart & Sandberg 2006; Sandberg 2011a).

Diphasic beat repetition: beat repetition rate shows an abrupt change during the signal.

Grouped call: a call composed of several beat groups.

Call sequence: calls produced in a grouped pattern, i.e. inter call intervals are distinctively shorter between the neighbouring calls of a group than the interval between the last call of a group and the first call of the next call group.

Signal types according to the gender of signalling animal and the context of signalling: *Male call*: a functional unit of the spontaneously produced male vibro-signal which elicits one answer signal from a responding female.

Female answer: a signal produced by a female answering a male call.

Male response: a male signal produced in response to a female answer with a signal pattern different from the pattern of the male call.

Measured drumming signal characters: *Number of beats per call (NBC)*: all the recognizable beats within a male call.

Individual inter-beat intervals within a call: the time elapsed from the peak amplitude of one beat to that of the next beat in the beat sequence of a male call. Individual beat intervals were labelled as i_1 , i_2 , i_3 and so on, where numbers are serial numbers accorded to the consecutive timing of each beat starting from the beginning of a call.

Call duration (DC): the time elapse from the amplitude peak of the first beat of the male call to the amplitude peak of its last beat.

Inter-call interval within a call sequence: the time elapsed from the last beat of a call to the first beat of the next call.

Number of calls in a call sequence: the number of calls performed after each other relatively closely, apparently forming a sequence.

Mean beat interval (MBI): a derived character, which was calculated as $MBI = DC / (NBC - 1)$.

Measurements were made using the sound analysis software Adobe Audition 1.5 (www.adobe.com) in all characters except for individual inter-beat intervals, which was measured using the pulse-train analysis tool of Avisoft SASLab pro 5.2.07 (Avisoft Bioacoustics, Berlin, Germany [www.avisoft.com]). To calculate descriptive statistics presented in Tables 6–8 data points were the mean values obtained for each examined specimen using 1–10 signal measurements per specimen (mean number of examined signals per specimen was 7.73). Because of that minimum and maximum value are not integers even for count data. Statistical analysis, box plot series (Fig. 190) and a scatter plot (Fig. 191) was made using R 2.15.2 (R Core Team 2012).

DNA extraction and data analysis

Genomic DNA was extracted using DNeasy blood and tissue kits (Qiagen GmbH, Hilden, Germany). A 650 bp long region of cytochrome c oxidase subunit I gene (*coxI*) was amplified with the primers LCO-1490 and HCO-2198 (Folmer *et al.* 1994). PCR products were purified using the QIAquick PCR Purification Kit (Qiagen GmbH, Hilden, Germany) and sequenced bidirectionally using the PCR primers on an ABI 3500xL sequencer (Applied Biosystems).

Forwards and reverse reads were edited and assembled using CodonCode Aligner v 3.5 (Codon Code Corporation, Dedham, USA) and contigs were compared to the NCBI nucleotide database using blastn queries (<http://blast.ncbi.nlm.nih.gov>). All sequences were aligned using ClustalW (Thompson *et al.* 1994). Maximum parsimony (MP) and maximum likelihood (ML) methods were used to analyze the data using TnT v 1.1 (MP: Goloboff *et al.*, 2008) and PhyML v 3.0 (ML: Guindon & Gascuel, 2003).

For MP, all analyses were performed using equal weighting, unordered and non-additive characters, and a heuristic search option with 1000 replicate searches, random addition of taxa, and TBR branch swapping, with 1000 bootstrap replicates. Additionally, the consistency index (CI), retention index (RI), and rescaled consistency index (RC) were calculated with Winclada version 1.0 (Nixon, 1999) and NONA version 2.0 (Goloboff, 1999).

For the ML analyses, we used the GTR model of DNA evolution that we determined best fit our data using Modeltest v 3.7 (Posada & Crandall, 1998). We bootstrapped for 1000 replicates. *Leuctra* sp. (obtained from /ibol.org/; GenBank Accession No. FM213089, Fochetti *et al.* 2009), *Allocapnia* sp. (obtained from /ibol.org/; GenBank Accession No. AY165662, Hebert *et al.* 2003), *Allocapnia granulata* (Claassen 1924) (obtained from /ibol.org/; Embank Accession No. GU013565, Park *et al.* 2010), and new sequences of *Capnia s.l. vidua* Klapálek, 1904 were used as outgroups. Uncorrected pairwise *p*-distances among individuals were calculated in Mega 4.0 (Tamura *et al.* 2007). All newly generated DNA sequences have been deposited in GenBank (Accessions KF144838-KF144882).

Systematics

Capniidae terminalia

In addition to wing venation and thoracic sclerites (Figs. 53–57, Tables 1–2), the systematics of adult Capniidae is based mainly on the terminalia (Figs. 1–48, Tables 3–5). This study discusses the structure of the male epiproct, paraprocts, and the fusion plate. These structures are directly involved in mating. The general form and associated structures are illustrated in Figs. 1–31. These figures are shown to support new generic diagnoses that are presented. A ventral view of the male terminalia is depicted for all genera examined (Figs. 32–48). Terminology and comments are given below:

Basal sclerite (B-scl): The basal portion of the epiproct that can be divided or fused with the main and the laterobasal sclerites (Ep-scl, Lb-scl). It can be vestigial or lacking; its size is usually typical for the genera (Figs. 1–2, 5–6, 11–22, Table 3). In some genera the B-scl is developed into the *Lower limb (Ll)* of the epiproct, see below.

Laterobasal sclerite (Lb-scl): One of two lateral sclerites of the epiproct that are positioned caudally to the B-scl and laterobasally to the Ep-scl (see below). It can be divided or fused with both of those sclerites. The size is also typical for the genera (Figs. 1–6, 17–22, Table 3).

Main epiproct sclerite (Ep-scl): The main sclerite of the epiproct, sometimes called the upper limb of the epiproct (Nelson & Baumann 1987). It is open apically, usually divided in its dorsal portion, and can be divided or entire in its ventral and lateral portion; its ventral connection and lateral division are typical for the genera, as are the presence or absence of setae on its basocaudal portion (Figs. 1–22, Table 3).

Lower limb (Ll): An epiproctal sclerite is developed from the B-scl (Figs. 3–6, Table 3). It is large in *Utacapnia* Gaufin, 1970 and *Capnura* Banks, 1900, where the B-scl is completely formed into the Ll and the original sclerite is vestigial or lacking. In *Allocapnia* Claassen, 1928, a small Ll is present on the B-scl but not divided. However, the epiproctal portion previously termed Ll in this genus, is in fact the highly separated lower part of the longitudinally divided Ep-scl. A vestigial Ll also present on the vestigial B-scl fused with the Ep-scl in genus *Capnia s.s.* and in *C. s.l. vidua* Klapálek 1904 (Figs. 3–6).

Inner sclerite (I-scl): An epiproctal sclerite that is present in some genera, surrounded by the Ep-scl. It is not connected to the Ep-scl but to the membranes forming the epiproct's inner funnel that fix the Fp and lead the sperm into the apical opening of the epiproct (Figs. 1–4, 11–18, Table 3).

Eversible crest (Ec): An eversible, membranous portion of the epiproct on its dorsoapical part, connected to the Ep-scl. Its absence or presence is typical for the genera, although it is difficult to recognize in its contorted state (Figs. 1–4, 8–10, 17–18, Table 3).

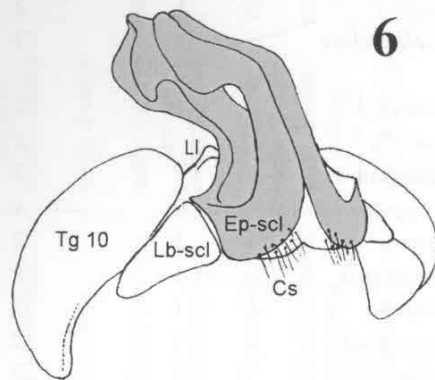
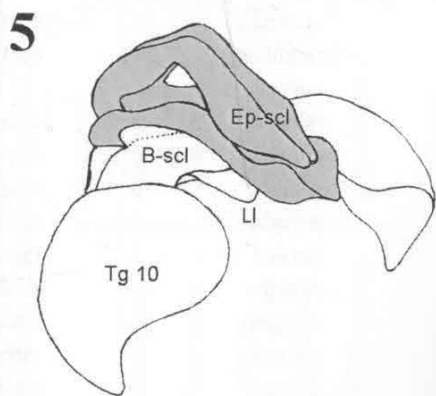
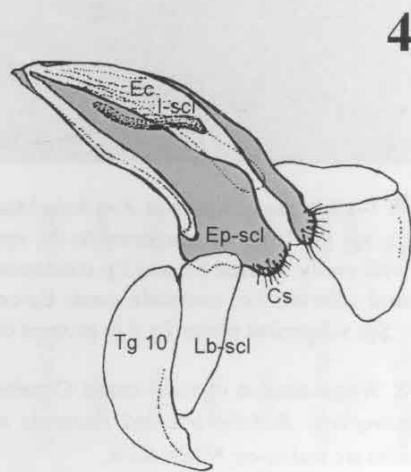
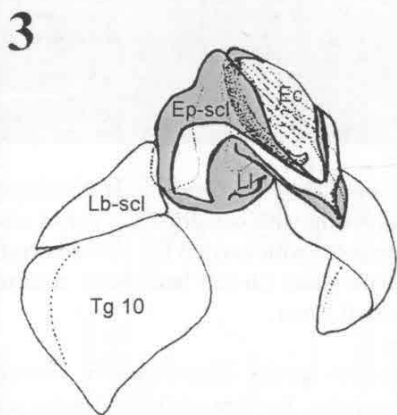
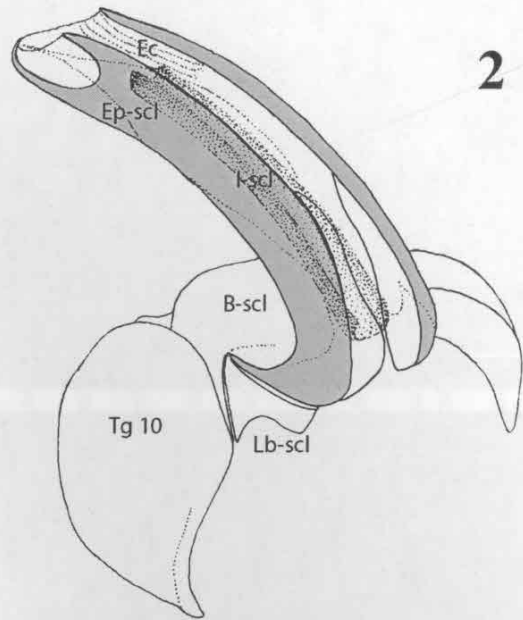
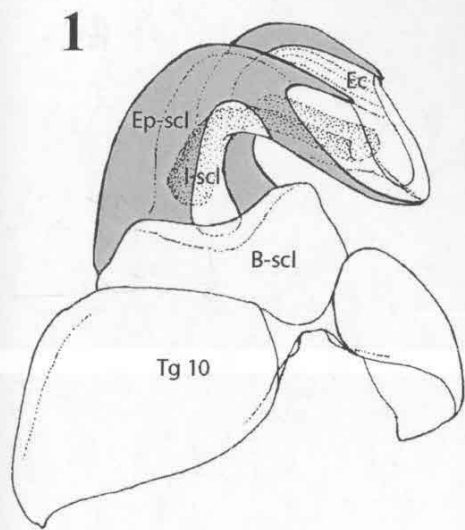
Fusion plate (Fp): As described by Klapálek (1896), this organ leads the sperm into the epiproct, and it is more or less fused with the paraprocts (Fig. 7, 9). In this study we note the relative length and width of the organ, and its division or fusion with a small basal sclerite, called the *Retractoral plate (Rp)* by Hanson (1946) (Figs. 23–31, 81, Table 4).

Paraprocts (Pp): The relative length and width of the apical part are typical for the genera, and it is usually related to the dimensions of the Fp (Figs. 32–48, 81, Table 4).

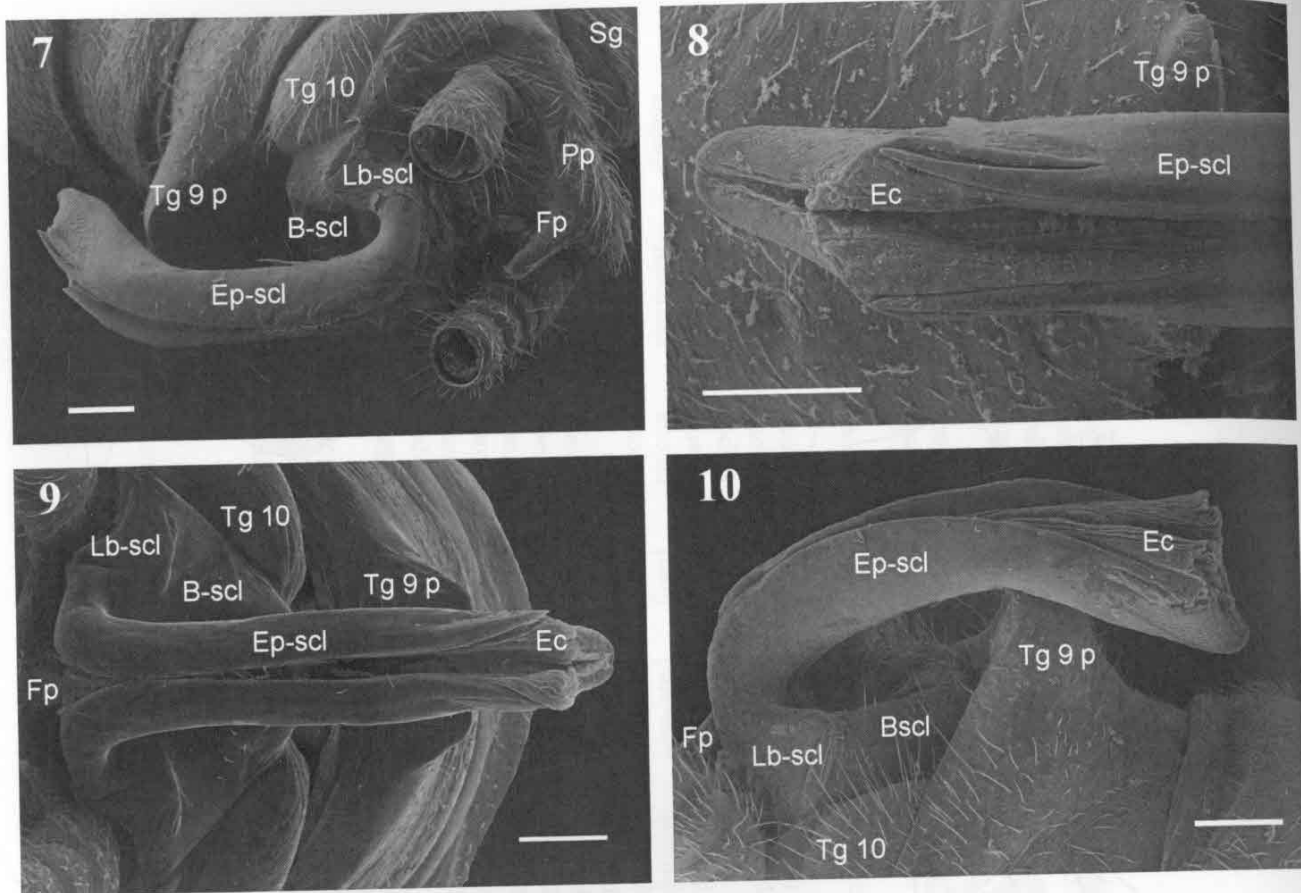
Subgenital plate (Sg): In males, its fusion or division with Sternite 9 (St 9) and through this to Tergite 9 (Tg 9) is typical for the genera. If a ventral vesicle is present, the Sg is always separated from the St 9 that is restricted to a well sclerotized arch connecting ventrobasal corners of Tg 9; the vesicle is located on this arch-like St 9, and not on the Sg (Figs. 32–48, Table 4).

TABLE 1. Ventral sclerites of valid extant Capniidae genera. — *Capniella* not included because of lacking information; in case of two character states the first one refers to the type species; for abbreviations of sclerites see Figs. 53-55.

	Pts/Bs	PFs/PBs	MPrs	MFs/St 1	MeFsp/MePfs	Bs/Kes	PPo/PFs	MBs	MeFs	MeFsa
<i>Allocapnia</i>	separated	weakly fused	elliptical	separated	separated	fused or separated	fused	oblong	triangular	distinct
<i>Apteroperla</i>	separated	separated	elliptical	separated	separated	M fused	separated	heart-shaped	triangular	distinct
<i>Arsapnia</i>	separated	fused	triangular	separated	separated	fused	fused	oblong	triangular	distinct
<i>Baikaloperla</i>	separated	fused	elliptical	separated	fused	separated	fused	oblong	triangular	reduced
<i>Bolshecapnia</i>	separated	fused	triangular	separated	separated	fused	fused	oblong	triangular	distinct
<i>Capnia</i> s.s.	separated	fused	triangular	separated	separated	fused	fused	oblong	triangular	distinct
<i>Capnioneura</i>	separated	fused	elliptical	separated	fused or separated	fused or separated	separated	oblong	transverse	distinct
<i>Capnopsis</i>	separated	weakly fused	elliptical	or fused	separated	separated	fused	oblong	triangular	distinct
<i>Capnura</i>	separated	weakly fused	triangular	separated	separated	fused	fused	oblong	triangular	distinct
<i>Eocapnia</i>	separated	separated	elliptical	separated	separated	separated	separated	heart-shaped	triangular	distinct
<i>Eucapnopsis</i>	separated	fused	triangular	separated	separated	separated	separated	oblong	transverse	distinct
<i>Isocapnia</i>	fused or separated	fused	elliptical or triangular	fused or separated	fused	fused	fused or separated	oblong	transverse	fused or distinct
<i>Mesocapnia</i>	separated	separated or weakly fused	elliptical or triangular	separated	separated	fused	separated	oblong	triangular	distinct
<i>Nemocapnia</i>	fused	fused	triangular	separated	fused	fused	separated	oblong	transverse	reduced
<i>Paracapnia</i>	separated	fused	triangular or elliptical	separated	fused or separated	fused or separated	fused	oblong	transverse or triangular	reduced or distinct
<i>Takagripopteryx</i>	separated	fused	elliptical	separated	separated	fused	fused	heart-shaped	triangular	distinct
<i>Utacapnia</i>	separated	fused	triangular	separated	separated	fused	fused	oblong	triangular	distinct
<i>Zwickia</i>	separated	fused	triangular	separated	separated	fused	fused	oblong	triangular	distinct



FIGURES 1–6. Male terminalia of West Palaearctic Capniidae—1–2: *Zwicknia bifrons* (Newman); 3–4: *Capnia s.s. nigra* (Pictet); 5–6: *Capnia s.l. vidua* Klapálek; 1, 3, 5: dorso-caudal view; 2, 4, 6: ventro-caudal view (B-scl: basal sclerite; Cs: caudal setae; Ec: eversible crest; Ep-scl: main epiproct sclerite (shaded in grey); I-scl: inner sclerite; Lb-scl: laterobasal sclerite; LI: lower limb; Tg 10: tergite 10)—not to scale.



FIGURES 7–10. Male genitalia of *Zwicknia* Murányi, **gen. n.**—7, 10: *Z. bifrons* (Newman); 8–9: *Z. rupprechti* Murányi, Orci & Gamboa, **sp. n.**; 7: Fp disconnected to the epiproct, latero-caudal view; 8: epiproct tip with contorted Ec, dorsal view; 9: epiproct with partly everted Ec and Fp connected to the Ep-scl, dorsal view; 10: epiproct with everted Ec, dorso-lateral view (B-scl: basal sclerite; Ec: eversible crest; Ep-scl: main epiproct sclerite; Fp: fusion plate; Lb-scl: laterobasal sclerite; Pp: paraproct; Sg: subgenital plate; Tg 9 p: process of tergite 9; Tg 10: tergite 10)—scales 0.1 mm.

TABLE 2. Wing venation of valid extant Capniidae genera.—refers only to macropterous species, apterous and/or micropterous genera *Apteroperla*, *Baikaloperla* and *Eocapnia* not included; Fw: forewing, Hw: hindwing, for abbreviations of veins see Fig. 56—*besides arc and m-cu; **besides h.

	Fw M/Cu1 crossveins *	Fw A veins	Hw A veins	Fw C/Sc crossveins **	Fw A1 beyond a	Fw R veins	Fw R1 before r
<i>Allocapnia</i>	1–2	2	3	1–4	straight	3–4	straight
<i>Arsapnia</i>	1	2	3	1	curved	3	curved
<i>Bolschecapnia</i>	1	2	3	1–8	straight or curved	3–6	curved
<i>Capnia</i> s.s.	1	2	3	1–2	curved	3	curved
<i>Capniella</i>	1–2	2	3	1	curved	4	curved
<i>Capnioneura</i>	1	2	4	1	straight	3	straight
<i>Capnopsis</i>	0	1	0	1	straight	3	straight
<i>Capnura</i>	1	2	3	1–3	curved	3	curved
<i>Eucapnopsis</i>	1	2	3	1–4	straight	3–4	straight
<i>Isocapnia</i>	1	2	3	1–8	straight	3–5	straight
<i>Mesocapnia</i>	1	2	3	1–3	curved	3	curved
<i>Nemocapnia</i>	1	2	3	1–2	curved	3	straight
<i>Paracapnia</i>	1	2	3	1–2	straight	3	curved
<i>Takagripopteryx</i>	0	2	3	1–2	straight	3	straight
<i>Utacapnia</i>	1	2	3	1–2	curved	3	curved
<i>Zwicknia</i>	1	2	3	2	curved	3	curved

TABLE 3. Male epiproct of valid extant Capniidae genera. — in case of two character states the first one refers to the type species; for abbreviations of parts see Figs. 1-22.

	B-scl size, /Ep-scl	Lb-scl size, /Ep-scl	Ep-scl ventral connection	Ep-scl laterally	Ep-scl caudal setae	I-scl	Ec	LI
<i>Allocapnia</i>	medium or large, fused lacking?	large, divided large?, divided?	entire	longitudinally divided entire	present	lacking	absent	present
<i>Apteroperla</i>			?		absent?	long, bifid?	present	absent
<i>Arsapnia</i>	lacking or vestigial lacking?	large, fused	entire	apically divided	present	lacking	absent	absent
<i>Baikaloperla</i>		large, divided?	?	longitudinally divided?	absent?	?	absent?	absent?
<i>Bolschecapnia</i>	large, divided	small, divided	basal & apical or apical	apically or longitudinally divided	absent	long, divided hook or tube	present	absent
<i>Capnia</i> s.s.	vestigial	large, divided	entire	longitudinally divided	present	small, curved stick	present	vestigial
<i>Capniella</i>	lacking?	large, divided?	?	longitudinally divided	present	?	absent?	present?
<i>Capnioneura</i>	lacking	large, divided	entire	entire	absent	lacking	absent	absent
<i>Capnopsis</i>	small, divided	small, fused	apical	entire	present	long, erect stick	absent	absent
<i>Capmura</i>	lacking	large, divided	entire	entire	vestigial or present	lacking	absent	present
<i>Eocapnia</i>	large?, divided?	small?, fused?	?	entire	absent?	?	absent?	absent
<i>Eucapnopsis</i>	small, divided	small, divided	full divided	entire	absent	lacking	absent	absent
<i>Isocapnia</i>	large, divided	small, divided	entire	entire	absent	lacking	absent	absent
<i>Mesocapnia</i>	small, fused or divided	small, fused	entire	entire	present	lacking	absent	absent
<i>Nemocapnia</i>	large, divided	small, divided	entire	entire	absent	lacking	absent	absent
<i>Paracapnia</i>	vestigial or large, divided	large, hardly divided	entire	entire	absent	lacking	absent	absent
<i>Takagripopteryx</i>	large, divided?	small, fused?	basal & tip?	entire?	absent?	lacking?	absent?	absent
<i>Utacapnia</i>	lacking	medium, fused	entire	entire	present	lacking	absent	present
<i>Zwicknia</i>	large, divided	small, divided	basal & tip	apically divided	absent	long, open tube	present	absent

TABLE 4. Male terminalia (besides epiproct) of valid extant Capniidae genera. — in case of two character states the first or the non-parenthesised one refers to the type species; for abbreviations of parts see Figs. 7-10, 23, 35, 81.

	Sg/Tg 9	Vesicle	Cercal segments	Pp apical part	Fp length & width	Fp/Rp	Tg processes
<i>Allocapnia</i>	fused	absent	many	long, tapering	medium, wide	divided	Tg (7-) 8
<i>Apteroperla</i>	fused	absent	many	short	short, wide	divided	Tg (6-7-) 8
<i>Arsapnia</i>	fused	absent	many	long, wide	long, narrow	divided	Tg 7
<i>Baikaloperla</i>	divided?	absent	many	long, wide	?	?	Tg 7-8
<i>Bolshecapnia</i>	divided	present	many	long, narrow	long, narrow	divided	absent or T 9
<i>Capnia</i> s.s.	fused	absent	many	narrow	long, medium	fused	Tg 7
<i>Capniella</i>	hardly separated	absent	many	long, wide	?	?	Tg 6-7 (-8)
<i>Capnioneura</i>	fused	absent	one	wide?	long, narrow	fused	absent
<i>Capnopsis</i>	fused	absent	few	needle-like	long, narrow	fused	absent
<i>Capnura</i>	divided	absent	many	short, wide	medium, wide	divided	absent
<i>Eocapnia</i>	fused	absent	many	medium, tapering	long, narrow	divided	Tg 7 (6-8)
<i>Eucapnopsis</i>	divided	present	few	long, wide?	medium, wide	fused	Tg (7) 8
<i>Isocapnia</i>	divided	present	many	medium, tapering	long, medium	fused	absent
<i>Mesocapnia</i>	fused	absent	many	long, wide	long, very narrow	divided	absent or Tg 9
<i>Nemocapnia</i>	hardly separated	absent	few	long, narrow	long, medium	divided	absent
<i>Paracapnia</i>	fused	absent	many	short, narrow	medium, wide	fused	Tg 9
<i>Takagripopteryx</i>	fused	absent	many	long, narrow	short or medium, wide	divided	absent
<i>Utacapnia</i>	fused	absent	many	medium, tapering?	short, wide	fused	Tg 8 (-9)
<i>Zwicknia</i>	divided	present	many	long, wide	long, wide	divided	absent
				short, wide	long, narrow	divided	Tg 9

TABLE 5. Female terminalia of valid extant Capniidae genera. — in case of two character states the first one refers to the type species.

	Sg to St 8 dorsal end	Sg to St 8 width	Sg shape	Sg sclerotisation	Sg keel	Inner or lateral scl
<i>Allocapnia</i>	equal or shorter	narrower	pointed or rounded	laterally different or entire	absent	absent
<i>Apteroperla</i>	equal	entire or narrowing	rounded	weak	absent	absent?
<i>Arsapnia</i>	equal	narrow	rounded	entire	absent	present
<i>Baikaloperla</i>	equal	entire	rectangular	entire	absent	absent
<i>Bolshecapnia</i>	overhanging or equal	narrower	pointed or rounded	entire	absent	present
<i>Capnia</i> s.s.	equal or shorter	entire or narrower	rounded	entire	absent	present
<i>Capniella</i>	shorter	narrower	rounded	weak	present	present?
<i>Capnioneura</i>	shorter	narrow	arrow-like	weak laterally	absent	absent
<i>Capnopsis</i>	equal	entire	rectangular	entire	absent	absent
<i>Capnura</i>	shorter or equal	narrower	incised or pointed	laterally different	absent	absent
<i>Eocapnia</i>	overhanging	entire	apically elongated	weak laterally	absent	absent?
<i>Eucapnopsis</i>	shorter	entire	stripe-like	entire	absent	present
<i>Isocapnia</i>	shorter or equal	narrower or entire	rectangular	entire or weak centrally	absent	absent
<i>Mesocapnia</i>	equal	entire	rounded or pointed	entire	absent	present
<i>Nemocapnia</i>	shorter	narrower	laterally incised	entire	absent	absent
<i>Paracapnia</i>	equal	nearly entire	rounded	entire	absent	absent
<i>Takagripopteryx</i>	shorter	entire	incised	variable	absent	absent
<i>Utacapnia</i>	slightly overhanging	narrower	pointed and incised	weak or entire	absent	present
<i>Zwicknia</i>	equal	entire	rectangular	entire	absent	present

Synopsis of the West Palaearctic and Nearctic Capniidae genera

Allocapnia Claassen, 1928

(Figs. 41, 192)

Capnella Claassen, 1924—Claassen 1924: 43. (original description, type species *Capnella granulata* Claassen, 1924).
Allocapnia Claassen, 1928—Claassen 1928: 667. (replacement name for *Capnella* Claassen, 1924 preoccupied by *Capnella* Gray, 1869; type species *Capnella granulata* Claassen, 1924); Claassen 1940: 89. (synonymy of *Capnellula* Strand, 1935 with *Allocapnia* Claassen, 1928); Ross & Ricker 1971: 7. (revision).
Capnellula Strand, 1935—Strand 1935: 304. (unnecessary replace name for *Capnella* Claassen, 1924, type species not designated).

Diagnosis. Male epiproct: B-scl medium sized to large, bearing small L1, fused with Ep-scl; Lb-scl large, divided from Ep-scl; Ep-scl laterally divided along the entire length without connecting membrane, ventrally entire, caudal setae present; I-scl and Ec absent. Male Pp: apical part long and tapering; Fp medium long and wide, divided from Rp. Male Sg: fused with St 9 and Tg 9, vesicle lacking. Female Sg: pointed or rounded, narrower than St 8; inner and lateral sclerites absent. Male tergites: Tg 8 or Tg 7–8 with process. Ventral thoracic sclerites: MPrs elliptical, MeFs triangular, MeFsp separated from MePfs. Macropterous wings: forewing A1 beyond a, and R1 before r straight; one or two crossveins between M and Cu1.

Species included. 47 valid species from the East Nearctic (DeWalt *et al.* 2014); 24 of these examined (see Appendix 1).

Remarks. On the basis of comparative morphological studies of the terminalia of the above 24 species, there is no doubt that the polytypic West Palaearctic species, *C. s.l. vidua*, can be placed into to this genus (see *Capnia* sensu lato, and Figs. 5–6, 25 of *C. s.l. vidua* possessing all the diagnostic features discussed above). However, molecular studies have indicated that the distance of $P=0.215$ between *C. s.l. vidua* and the genotype *A. granulata* is an indication that both taxa may not be congeneric (Fig. 192).

Arsapnia Banks, 1897 stat. rev.

(Fig. 40)

Arsapnia Banks, 1897—Banks 1897: 22. (original description, type species *Arsapnia decepta* Banks, 1897).
Capnia Pictet, 1841—Claassen 1924: 43. (synonymy of *Arsapnia* Banks, 1897 with *Capnia* Pictet, 1841).
Capnia decepta species group sensu Nelson & Baumann, 1989—Nelson & Baumann 1989: 310. (definition and revision).

Diagnosis. Male epiproct: B-scl lacking or vestigial; Lb-scl large, fused with Ep-scl; Ep-scl ventrally entire, laterally divided only in the apex, caudal setae present; I-scl and Ec absent. Male Pp: apical part long and wide; Fp long and narrow, divided from Rp. Male Sg: fused with St 9 and Tg 9, vesicle lacking. Female Sg: rounded and narrow; small lateral sclerites present. Male tergites: Tg 7 with process. Ventral thoracic sclerites: MPrs and MeFs triangular, MeFsp separated from MePfs. Macropterous wings: forewing A1 beyond a and R1 before r curved.

Species included. Type species: *Arsapnia decepta* Banks, 1897 **comb. rev.**; Further species: *Arsapnia arapahoe* (Nelson & Kondratieff, 1988) **comb. n.**, *Arsapnia coyote* (Nelson & Baumann, 1987) **comb. n.**, *Arsapnia pileata* (Jewett, 1966) **comb. n.**, *Arsapnia sequoia* (Nelson & Baumann, 1987) **comb. n.**, *Arsapnia teresa* (Claassen, 1924) **comb. n.**, *Arsapnia tumida* (Claassen, 1924) **comb. n.**, *Arsapnia utahensis* (Gaufin & Jewett, 1962) **comb. n.** All these West Nearctic species were examined (see Appendix 1).

Remarks. Banks (1897) erected the genus on the basis of several wing venation characters. Claassen (1924) synonymised it with *Capnia* on the basis of Pictet's (1841) drawings and description of the type species, *C. nigra*. Indeed, the venation shows much similarity between the two genera, but male terminalia, especially the epiproct differ greatly and there seems to be no reason to retain the genus *Arsapnia* in synonymy with *Capnia*. Herein, the genus is proposed only for members of the *C. decepta* group sensu Nelson & Baumann 1989, however, the *C. s.l. excavata* and *C. s.l. nana* groups sensu Nelson & Baumann 1989 may also belong to this genus. Nevertheless, we exclude *C. s.l. nelsoni* Kondratieff & Baumann, 2002, because of its different genitalic structures (see *Capnia* sensu lato).

***Bolshecapnia* Ricker, 1965**

(Figs. 17–18, 29, 33)

Capnia (*Bolshecapnia*) Ricker, 1965—Ricker 1965: 478. (misspelling in the stating of the name, used as *Bolshecapnia* elsewhere in the original description).

Capnia (*Bolshecapnia*) Ricker, 1965—Ricker 1965: 478. (original description, type species *Capnia* (*Bolshecapnia*) *gregsoni* Ricker, 1965).

Capnia Pictet, 1841—Zwick 1973: 370. (synonymy of *Capnia* (*Bolshecapnia*) Ricker, 1965 with *Capnia* Pictet, 1841).

Bolshecapnia Ricker, 1965—Ricker & Scudder 1975: 333. (first use as a generic name, without formal designation and removed from synonymy).

Diagnosis. Male epiproct: B-scl large, divided from Ep-scl; Lb-scl small, divided from Ep-scl; Ep-scl laterally divided in the apical part or the whole length with membranous connecting tissue, ventrally divided in the basal and apical or only in the apical section, caudal setae absent; I-scl long, divided hook or tube; Ec present. Male Pp: apical part long and narrow; Fp long and narrow, divided from Rp. Male Sg: divided from St 9 and Tg 9, vesicle present. Female Sg: pointed or rounded, narrower than St 8 but usually overhanging; lateral sclerites present. Male tergites: Tg 9 with process or process lacking. Ventral thoracic sclerites: MPrs and MeFs triangular, MeFsp separated from MePfs. Macropterous wings: forewing A1 beyond a straight or gently curved, R1 before r curved; crossveins between C and Sc one to eight, R veins three to six.

Species included. 7 valid species from the West Nearctic (DeWalt *et al.* 2014); 6 of these examined (see Appendix 1).

Remarks. Despite the seemingly obvious differences among the males of the species, males share similar developed epiproct structures. An exception is *B. milami* (Nebeker & Gaufin, 1967) that has much more divided Ep-scl than other members of the genus. Nevertheless, its epiproct and the entire terminalia share the other features distinctive for the genus. Lacking process on Tg 9 of the type species *B. gregsoni* (Ricker, 1965) can be regarded as a secondary loss, because of the presence of a setose hump instead of a process.

***Capnia* Pictet, 1841 sensu stricto**

(Figs. 3–4, 24, 39)

Capnia (*Capnia*) Pictet, 1841—Pictet 1841: 116. (original description, type species not designated).

Capnia Pictet, 1841—Enderlein 1909: 391. (transfer of *Capnia* (*Gripopteryx*) into Gripopterygidae Enderlein, 1909, designation of *Capnia nigra* Pictet, 1840 (sic!; = *Perla nigra* Pictet, 1833) as the type species of *Capnia*); Kimmins 1947: 261. (define the identity of *C. nigra* (Pictet, 1833)).

Capnia atra species group sensu Zhiltzova 2001—Zhiltzova 2001: 424. (definition); Zhiltzova 2003: 324. (revision, partly refers to *Capnia* Pictet, 1841 sensu lato).

Capnia nearctica species group sensu Nelson & Baumann, 1989—Nelson & Baumann 1989: 336. (definition and revision, partly refers to *Capnia* Pictet, 1841 sensu lato).

Diagnosis. Male epiproct: B-scl vestigial, fused with Ep-scl and turned into a vestigial Ll; Lb-scl large, divided from Ep-scl; Ep-scl laterally divided along entire length with connecting membrane, ventrally entire, caudal setae present; I-scl small, curved hook, Ec present. Male Pp: apical part long and wide; Fp long and medium wide, fused with Rp. Male Sg: fused with St 9 and Tg 9, vesicle lacking. Female Sg: rounded, entire or narrower than St 8; inner sclerites present. Male tergites: Tg 7 with process. Ventral thoracic sclerites: MPrs and MeFs triangular, MeFsp separated from MePfs. Macropterous wings: forewing A1 beyond a and R1 before r curved.

Species included. Type species: *Perla nigra* Pictet, 1833; Further species: *Capnia ahngeri* Koponen, 1949 (in Koponen & Brinck 1949), *C. aligera* Zapekina-Dulkeit, 1975a, *C. atra* Morton, 1896, *C. khubsugulica* Zhiltzova & Varykhanova, 1987, *C. nearctica* Banks, 1918, *C. pygmaea* (Zetterstedt, 1840), *C. zaicevi* Klapálek, 1914. 4 are Transpalaeartic, 3 from the East Palaeartic (including 1 endemic to Mongolia) and 1 is Holarctic with Transberingian connection; 5 of these examined (see Appendix 1).

Remarks. This sensu stricto diagnosis of the genus is based on the type species, *C. nigra* (Pictet, 1833). As it differs markedly from the most of the species previously placed in *Capnia*, the sensu stricto diagnosis confirms only eight species in this genus. *Capnia kurnakovi* Zhiltzova, 1978 (in Zhiltzova & Levanidova 1978) and *C. alternata* Zapekina-Dulkeit, 1975b may belong here, but no material was available for examination and illustrations and descriptions available lack exact details of the epiproct.

Capnia Pictet, 1841 sensu lato

(Figs. 11–16, 26–28, 36–38)

Capnia Pictet, 1841—Nelson & Baumann 1989: 291. (revision of the Nearctic species, partly refers to *Arsapnia* Banks, 1897 and *Capnia* Pictet, 1841 sensu stricto); Zhiltzova 2003: 318. (revision of the Palaearctic species (excluded Japan and the Himalayan ranges), partly refers to *Capnia* Pictet, 1841 sensu stricto and *Zwicknia* Murányi, gen. n.).

Species included. In addition to the species treated as *Capnia* s.s. above, 1 valid species from the West Palaearctic, 49 from the East Palaearctic, 46 from the West Nearctic and 1 is Transnearctic (DeWalt *et al.* 2014, Nelson & Baumann 1989); 47 examined (see Appendix 1).

Remarks. An adequate diagnosis cannot be given for this artificial assemblage of taxa, and the species excluded from the sensu stricto diagnosis will need to be placed in existing or newly erected genera. A revision of these species is out of the scope of the present work, and most of the East Palaearctic species were not studied; some remarks on certain groups can be made on the basis of species examined:

Capnia s.l. *cordata* species group sensu Zhiltzova 2001

This group is restricted to the high mountains of Asia with nine known species (Li & Yang 2009, Li *et al.* 2011, Zhiltzova 2003); three further species, known from only females, are attributed to this group on the basis of the female genitalia (Zhiltzova 2003). Morphologically they form a rather uniform lineage that is closer to *Zwicknia*, but distinctly differs in the males with entire Ep-scl and the lack of Ec (studied in *C. s.l. prolongata* Zhiltzova, 1969: Figs. 11–12), and females have a narrow, dark Sg.

Capnia s.l. *excavata* and *C. s.l. nana* groups sensu Nelson & Baumann 1989

As mentioned above, these West Nearctic groups of three and six species (Nelson & Baumann 1989) may belong to the genus *Arsapnia*. The morphology of their epiproct is similar, however, distinctly differ in shape.

Capnia s.l. *fialai* Nelson & Baumann, 1990

In its original description, this Californian, U.S.A. species was noted for its resemblance to *Paracapnia* Hanson, 1946 in many features. Recently, it was suggested by Kondratieff & Lee (2010) that *C. fialai* could be placed in *Paracapnia*. Despite obvious similarities, we propose to retain it in *Capnia* s.l. pending further comparative studies, because of the presence of caudal setae on the epiproctal sclerite and tergal processes on Tg 5–7. These features are lacking on other species currently placed in *Paracapnia*. Their inclusion in the generic diagnosis should further restrict the already few diagnostic features of that genus.

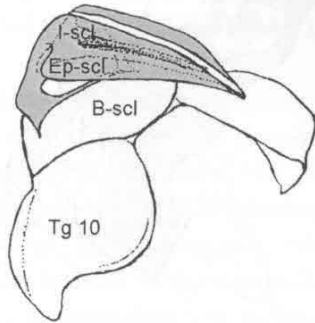
Capnia s.l. *gracilaria* and *C. s.l. vernalis* groups sensu Nelson & Baumann 1989

With respect to the structure of their terminalia, these Nearctic groups of four and three species (Nelson & Baumann 1989) probably belong to the genus *Mesocapnia* Raušer, 1968, with the exception of *C. lacustra* Jewett, 1965 (see below). The distinctive apical spine of the epiproct of *Mesocapnia* was thought to be a compact structure (Baumann *et al.* 1977, Raušer 1968, Nelson & Baumann 1989). However, SEM studies showed that it is a dorsally open structure like the epiproct apex of any other Capniidae (Lee & Baumann 2011). *Capnia* s.l. *zukeli* Hanson, 1943, a species from Idaho that was not classified in these species groups by Nelson & Baumann (1989), probably also belongs to *Mesocapnia*.

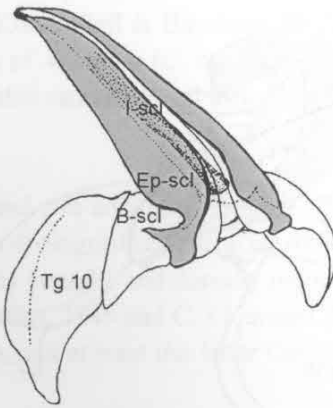
Capnia s.l. *lacustra* Jewett, 1965

This odd species, restricted to Lake Tahoe, Nevada, U.S.A. is aquatic in both the larval and adult stages, differing from all other Capniidae by having Tg 10 entire, and exceptionally reduced ventral thoracic sclerites. The male terminalia is closer to *Mesocapnia* but differ in lacking caudal setae on the epiproct. However, its designation as a separate genus would need further specimens for study. The few available specimens are nearly transparent and morphological details were difficult to ascertain using stereomicroscopes. Specimens were not examined by SEM to avoid damaging these specimens. It is worthy to note that one of the females examined, the entire abdomen and thorax to the cervical region was filled with eggs, a further uniqueness that may be related to the exceptional underwater life of this species.

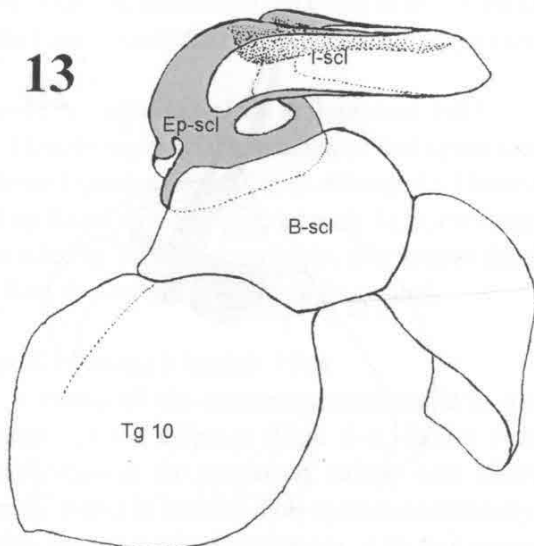
11



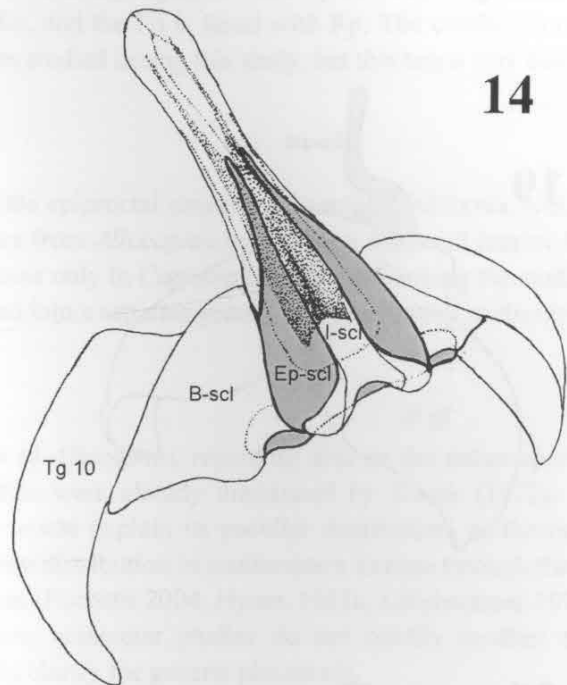
12



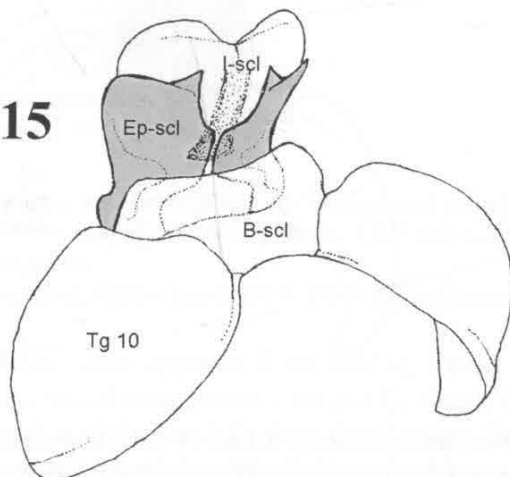
13



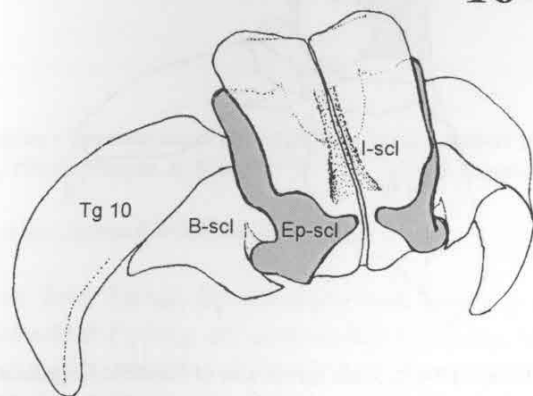
14



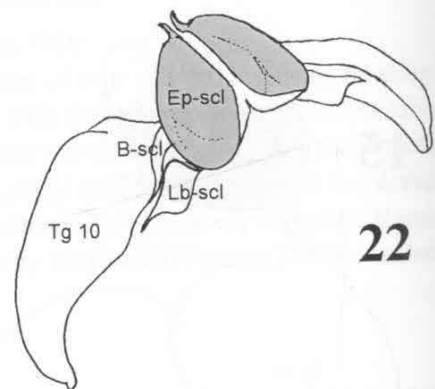
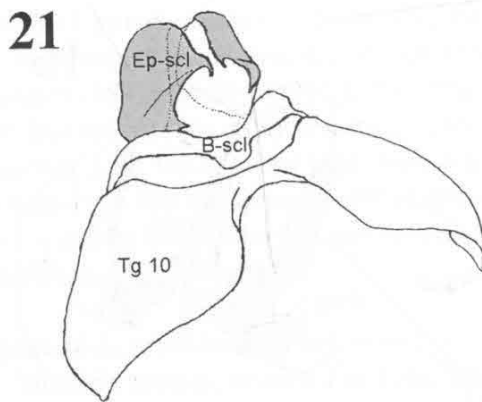
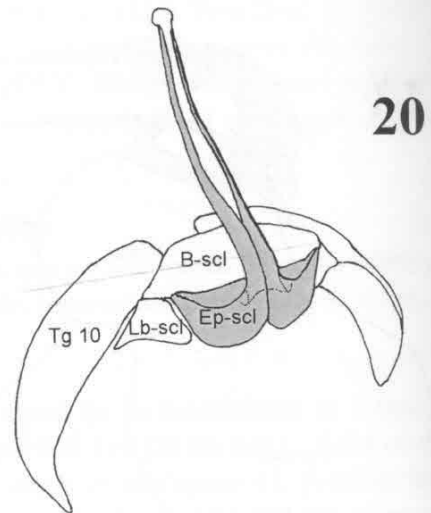
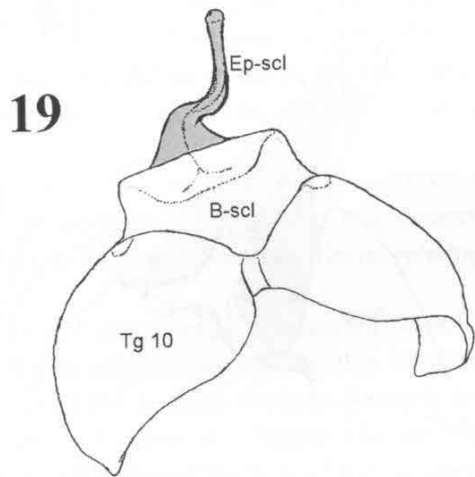
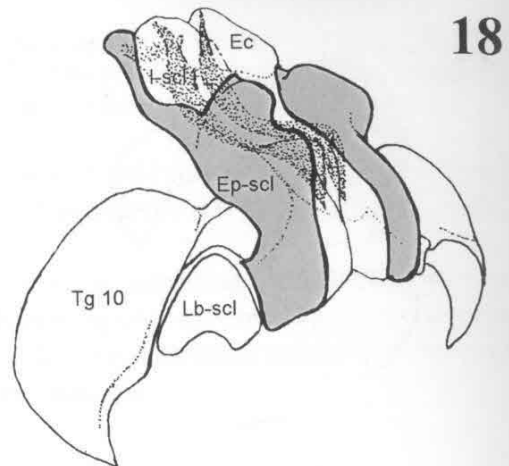
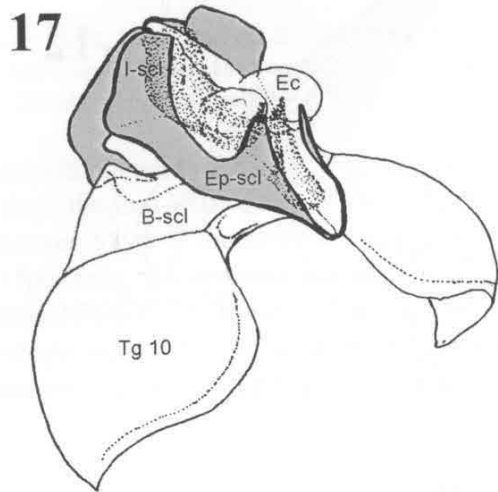
15



16



FIGURES 11–16. Male terminalia of East Palearctic *Capnia s.l.*—11–12: *C. s.l. prolongata* Zhiltzova; 13–14: *C. s.l. pedestris* Kimmins; 15–16: *C. s.l. arensi* Zhiltzova; 11, 13, 15: dorso-caudal view; 12, 14, 16: ventro-caudal view (B-scl: basal sclerite; Ep-scl: main epiproct sclerite (shaded in grey); I-scl: inner sclerite; Tg 10: tergite 10)—not to scale.



FIGURES 17–22. Male terminalia of Nearctic Capniidae—17–18: *Bolshecapnia gregsoni* (Ricker); 19–20: *Isocapnia grandis* (Banks); 21–22: *Eucapnopsis brevicauda* (Claassen); 17, 19, 21: dorso-caudal view; 18, 20, 22: ventro-caudal view (B-scl: basal sclerite; Ec: eversible crest; Ep-scl: main epiproct sclerite (shaded in grey); I-scl: inner sclerite; Lb-scl: laterobasal sclerite; Tg 10: tergite 10)—not to scale.

Capnia s.l. nelsoni Kondratieff & Baumann, 2002

The species was related to the *C. s.l. decepta* group in its original description, but the authors reluctantly placed it in the above group because of notable morphological differences (Kondratieff & Baumann 2002, Heinold *et al.* 2013). Indeed, its genital characters differ greatly from the diagnosis of *Arsapnia* (*C. s.l. nelsoni* has large B-scl, Lb-scl divided from Ep-scl and Ep-scl is longitudinally divided), but also cannot be placed in any existing groups.

Capnia s.l. pedestris species group sensu Zwick & Sivec 1980

This group was erected for nine, mainly Central Asian species and two additional species known only from females (Alouf 1992, Zhiltzova 2003, Zwick & Sivec 1980). The main distinguishing character in males is a highly developed, bicuspidate Tg 9. In addition, these taxa are characterized by laterally and dorsally reduced Ep-scl and a large B-scl (Figs. 13–16). However, the studied *C. s.l. pedestris* Kimmins, 1946 and *C. s.l. arensi* Zhiltzova, 1964 differ in many features of the terminalia (Figs 13–16, 27–28, 36, 38), and at least the latter Caucasian-Anatolian species is not monophyletic with the rest of the group.

Capnia s.l. spinulosa Claassen, 1937

This species from California, U.S.A. has both laterally and ventrally highly divided Ep-scl. The large, complex membranous parts of the epiproct lack I-scl but possess an Ec, and the Fp is fused with Rp. The combination of these genital features does not occur in any of the other species studied during this study, but this taxon may belong to the East Palaearctic genera *Takagripopteryx* or *Capniella*.

Capnia s.l. valhalla Nelson & Baumann, 1987

Despite superficial resemblance to *Capnia* sensu stricto, the epiproctal structure of another California, U.S.A. restricted species, is similar to *Allocapnia*. However, it differs from *Allocapnia* by having a long and narrow Fp, and Sg fused with St 9 but not with Tg 9; the latter feature occur only in *Capnura* Banks, 1900 among the studied taxa (see Fig. 43). Most probably, this species should be placed into a separate genus, but comparative studies with the East Palaearctic genera will be needed.

Capnia s.l. vidua Klapálek, 1904

It shares all the characters enumerated in the diagnosis of *Allocapnia*, regarding also to the rather special structure of the epiproct (Figs. 5–6, Tables 1–5); similarities were already mentioned by Zwick (1973). Its classification in the previously strictly East Nearctic genus would explain its peculiar distribution, as the only stonefly found in Iceland. This species additionally has a patchy distribution in southeastern Europe through the N British Isles and NW Scandinavia, with five named subspecies (Fochetti 2004, Hynes 1955b, Lillehammer 1972, Lillehammer *et al.* 1986, Vinçon & Sivec 2011). However, molecular studies do not readily confirm the morphological characteristics, and further studies are needed to clarify the generic placement.

***Capnioneura* Ris, 1905**

(Fig. 48)

Capnioneura Ris, 1905—Ris 1905: 94. (original description, type species *Capnioneura nemuroides* Ris, 1905); Aubert 1952: 247. (synonymy of *Napcia* Navás, 1917 with *Capnioneura* Ris, 1905); Vinçon & Sivec 2011: 118. (recent commented checklist).

Napcia Navás, 1917—Navás 1917: 398. (original description, type species *Capnia libera* (Navás, 1909)).

Diagnosis. Male epiproct: B-scl lacking; Lb-scl large, divided from Ep-scl; Ep-scl entire both ventrally and laterally, caudal setae absent; I-scl and Ec absent. Male Pp: needle-like; Fp long and narrow, fused with Rp. Male Sg: fused with St 9 and Tg 9, vesicle lacking. Female Sg: arrow-like, usually fused with St 8; lateral sclerites present or absent. Male tergites: process lacking. Cercus: unisegmented. Ventral thoracic sclerites: MPrs elliptical, MeFs transverse, MeFsp fused with or separated from MePfs; PPO separated from PFs. Macropterous wings: forewing A1 beyond a and R1 before r straight; hindwing having four A veins.

Species included. 14 valid species from the West Palaearctic (DeWalt *et al.* 2014); 6 of these examined (see Appendix 1).

***Capnopsis* Morton, 1896**

(Fig. 47)

Capnodes Rostock, 1892—Rostock 1892: 398. (original description, type species *Capnodes schilleri* Rostock, 1892).
Capnopsis Morton, 1896—Morton 1896: 61. (replace name for *Capnodes* Rostock, 1892 preoccupied by *Capnodes* Guénéé, 1852; inherited type species *Capnodes schilleri* Rostock, 1892); Zwick 1984: 2. (revision).

Diagnosis. Male epiproct: B-scl small, divided from Ep-scl; Lb-scl small, fused with Ep-scl; Ep-scl ventrally connected in the apical part, laterally entire, caudal setae absent; I-scl long, erect stick, Ec absent. Male Pp: apical part short and wide; Fp medium long and wide, divided from Rp. Male Sg: fused with St 9 and Tg 9, vesicle lacking. Female Sg: rectangular, entire; inner and lateral sclerites absent. Male tergites: process lacking. Cercus: with less than ten segments. Ventral thoracic sclerites: MPrs elliptical, MeFs triangular, MeFsp separated from MePfs. Macropterous wings: forewing without crossvein between M and Cu; single A vein beyond a and R1 before r straight; hindwing without A veins.

Species included. 1 valid species with 3 subspecies from the West Palaearctic (DeWalt *et al.* 2014); 2 of the subspecies examined (see Appendix 1).

***Capnura* Banks, 1900**

(Fig. 43)

Capnura Banks, 1900—Banks 1900: 245. (original description, type species *Capnura venosa* Banks, 1900); Nelson & Baumann 1987: 3. (stat. rev., revision).
Capnia Pictet, 1841—Hanson 1946: 229. (synonymy of *Capnura* Banks, 1900 with *Capnia* Pictet, 1841).

Diagnosis. Male epiproct: B-scl lacking, developed into small to large Ll attached to Ep-scl; Lb-scl large, divided from Ep-scl; Ep-scl entire both ventrally and laterally, caudal setae vestigial or present; I-scl and Ec absent. Male Pp: apical part medium long and tapering; Fp long and narrow, divided from Rp. Male Sg: fused with St 9 but divided from Tg 9, vesicle lacking. Female Sg: incised or pointed, lateral sides with different color than medial part; inner and lateral sclerites absent. Male tergites: Tg 7 (occasionally 6–8) with process. Ventral thoracic sclerites: MPrs and MeFs triangular, MeFsp separated from MePfs. Macropterous wings: forewing A1 beyond a and R1 before r curved.

Species included. 6 valid species from the West Nearctic and 1 from the East Nearctic (DeWalt *et al.* 2014); all 7 of these species examined (see Appendix 1).

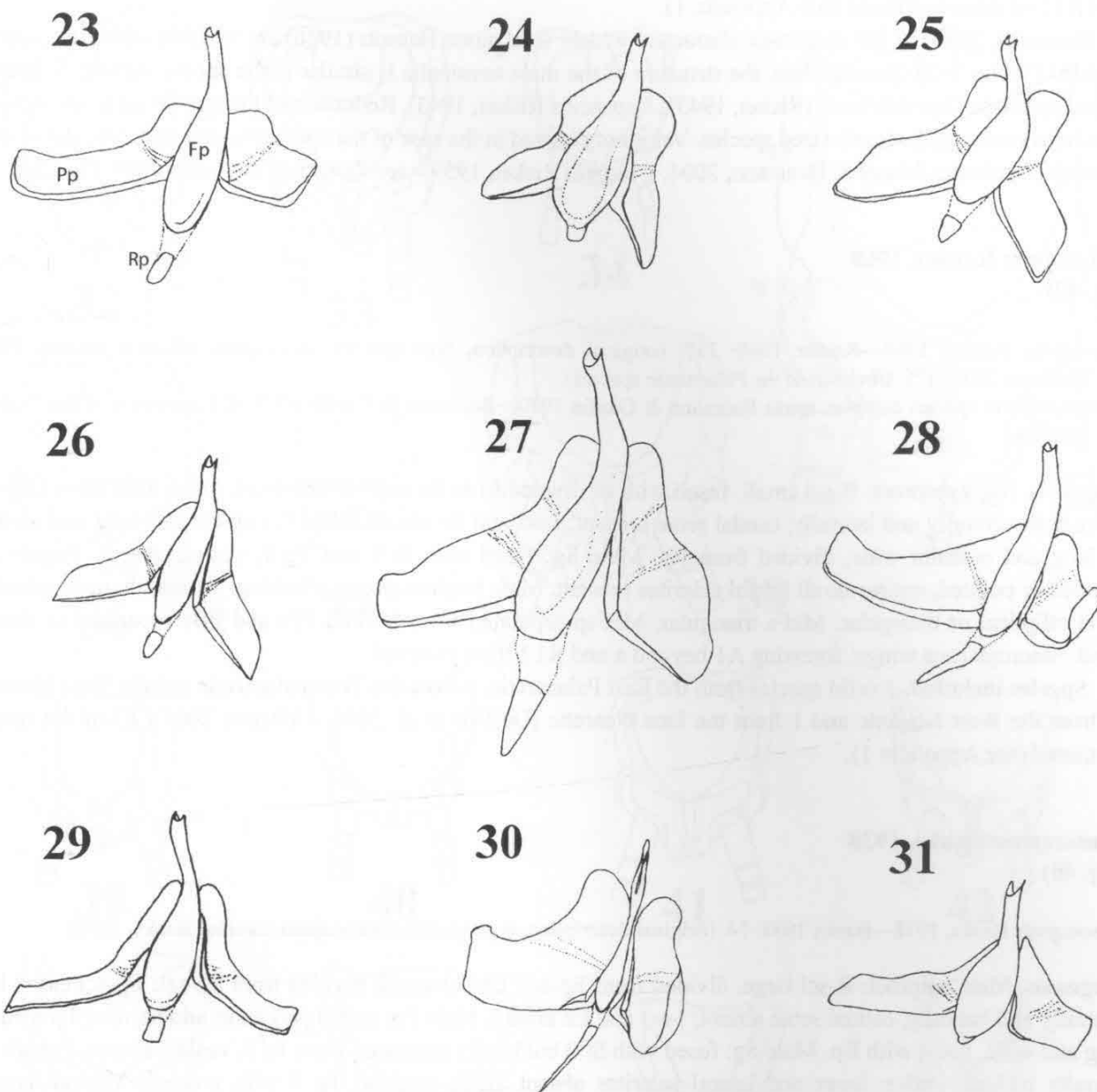
***Eucapnopsis* Okamoto, 1922**

(Figs. 21–22, 31, 34)

Eucapnopsis Okamoto, 1922—Okamoto 1922: 8. (original description, type species *Eucapnopsis stigmatica* Okamoto, 1922); Zhiltzova 2003: 391. (revision).

Diagnosis. Male epiproct: B-scl small, divided from Ep-scl; Lb-scl small, divided from Ep-scl; Ep-scl fully divided ventrally but entire laterally, caudal setae absent; I-scl and Ec absent. Male Pp: apical part medium long and tapering; Fp long and medium wide, fused with Rp. Male Sg: divided from St 9 and Tg 9, vesicle present. Female Sg: stripe-like; large lateral sclerites present. Male tergites: process lacking. Cercus: with less than ten segments. Ventral thoracic sclerites: MPrs and MeFs triangular, MeFsp separated from MePfs; PPO separated from PFs. Macropterous wings: forewing A1 beyond a and R1 before r straight.

Species included. 2 valid species from the East Palaearctic, and 1 widely distributed in the East Palaearctic and the West Nearctic (DeWalt *et al.* 2014); 2 of these species examined (see Appendix 1).



FIGURES 23–31. Male paraprocts and fusion plate of Capniidae, dorso-lateral view—23: *Zwicknia bifrons* (Newman); 24: *Capnia s.s. nigra* (Pictet); 25: *Capnia s.l. vidua* Klapálek; 26: *Capnia s.l. prolongata* Zhiltzova; 27: *Capnia s.l. pedestris* Kimmins; 28: *Capnia s.l. arensi* Zhiltzova; 29: *Bolshecapnia gregsoni* (Ricker); 30: *Isocapnia grandis* (Banks); 31: *Eucapnopsis brevicauda* (Claassen) (Fp: fusion plate; Pp: paraproct; Rp: retractoral plate)—not to scale.

Isocapnia Banks, 1938

(Figs. 19–20, 30, 35)

Isocapnia Banks, 1938—Banks 1938: 73. (original description, type species *Arsapnia grandis* Banks, 1907); Zhiltzova 2003: 398. (revision of the Palearctic species); Zenger & Baumann 2004: 66. (revision of the Nearctic species).

Diagnosis. Male epiproct: B-scl large, divided from Ep-scl; Lb-scl small, divided from Ep-scl; Ep-scl entire both ventrally and laterally, caudal setae absent; I-scl and Ec absent. Male Pp: apical part long and wide; Fp long and very narrow, divided from Rp. Male Sg: divided from St 9 and Tg 9, vesicle present. Female Sg: rectangular, entire or weak centrally; inner and lateral sclerites absent. Male tergites: process lacking or Tg 9 with process. Ventral thoracic sclerites: MPrs elliptical or triangular, MeFs transverse, MeFsp fused with MePfs; Prs/Bs, Mfs/St 1 and PPO/PFs fused with or separated from. Macropterous wings: forewing A1 beyond a and R1 before r straight; crossveins between C and Sc one to eight, R veins three to five.

Species included. 12 valid species from the West Nearctic and 7 from the East Palaearctic (DeWalt *et al.* 2014); 15 of these examined (see Appendix 1).

Remarks. Some of the diagnostic characters widely used since Hanson (1946) are variable within the species included (Tables 1–2). Nevertheless, the structure of the male terminalia is similar in the species having differently shaped epiprocts (*I. vedderensis* (Ricker, 1943), *I. spenceri* Ricker, 1943). Reduction of the number of forewing C-Sc crossveins occurs in the small-sized species. Veins not counted in the case of the species having odd, reticulated wing venation (*I. palousa* Zenger & Baumann, 2004, *I. mogila* Ricker, 1959 – see Zenger & Baumann 2004: Fig. 26).

Mesocapnia Raušer, 1968

(Fig. 42)

Mesocapnia Raušer, 1968—Raušer 1968: 337. (original description, type species *Mesocapnia silvatica* Raušer, 1968); Zhiltzova 2003: 375. (revision of the Palaearctic species).

Capnia projecta species complex sensu Baumann & Gaufin 1970—Baumann & Gaufin 1970: 435. (revision of the Nearctic species).

Diagnosis. Male epiproct: B-scl small, fused with or divided from Ep-scl; Lb-scl small, fused with Ep-scl; Ep-scl entire both ventrally and laterally, caudal setae present; I-scl and Ec absent. Male Pp: apical part long and narrow; Fp long and medium wide, divided from Rp. Male Sg: fused with St 9 and Tg 9, vesicle absent. Female Sg: rounded or pointed, entire; small lateral sclerites present. Male tergites: process lacking. Ventral thoracic sclerites: MPrs elliptical or triangular, MeFs triangular, MeFsp separated from MePfs; PFs and PBs separated or weakly fused. Macropterous wings: forewing A1 beyond a and R1 before r curved.

Species included. 3 valid species from the East Palaearctic, 1 from the Transpalaearctic and the West Nearctic, 14 from the West Nearctic and 1 from the East Nearctic (DeWalt *et al.* 2014, Zhiltzova 2003); 13 of the species examined (see Appendix 1).

Nemocapnia Banks, 1938

(Fig. 46)

Nemocapnia Banks, 1938—Banks 1938: 74. (original description, type species *Nemocapnia carolina* Banks, 1938).

Diagnosis. Male epiproct: B-scl large, divided from Ep-scl; Lb-scl small, divided from Ep-scl; Ep-scl entire both ventrally and laterally, caudal setae absent; I-scl and Ec absent. Male Pp: apical part short and narrow; Fp medium long and wide, fused with Rp. Male Sg: fused with St 9 but hardly separated from Tg 9, vesicle absent. Female Sg: laterally incised, entire; inner and lateral sclerites absent. Male tergites: Tg 9 with process. Ventral thoracic sclerites: MPrs triangular, MeFs transverse, MeFsp fused with MePfs; Prs and Bs fused; PPO and PFs separated; MeFsa reduced. Macropterous wings: forewing A1 beyond a curved, R1 before r straight.

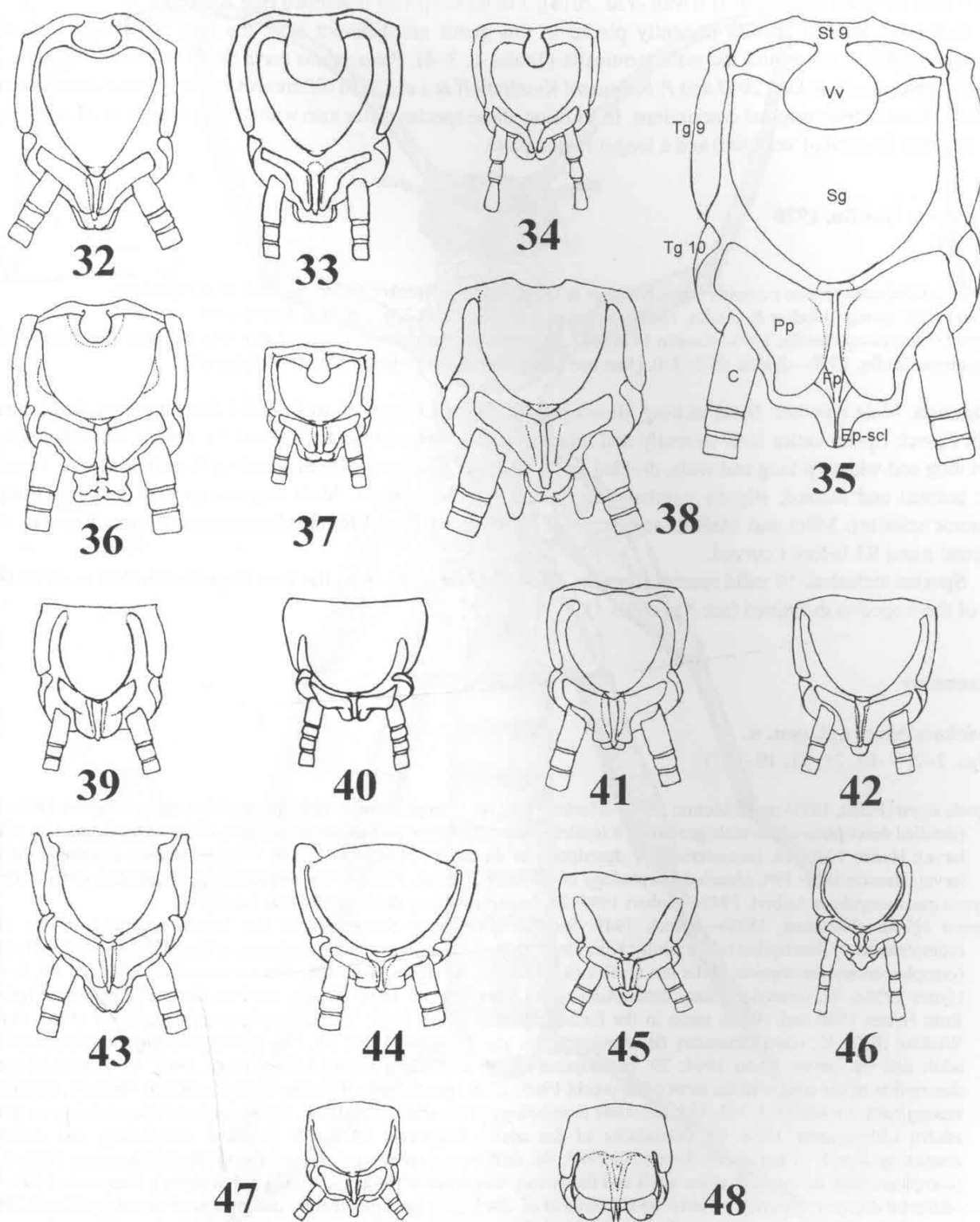
Species included. 1 valid species from the East Nearctic and 1 from the East Palaearctic (DeWalt *et al.* 2014); one was examined (see Appendix 1).

Paracapnia Hanson, 1946

(Fig. 45)

Paracapnia Hanson, 1946—Hanson 1946: 225. (original description, type species *Paracapnia curvata* Hanson, 1946 = *Chloroperla opis* Newman, 1839); Zhiltzova 2003: 385. (revision of the Palaearctic species); Stark & Baumann 2004: 97. (revision of the Nearctic species).

Diagnosis. Male epiproct: B-scl vestigial or large, divided from Ep-scl; Lb-scl large, hardly divided from Ep-scl; Ep-scl entire both ventrally and laterally, caudal setae absent; I-scl absent, Ec present. Male Pp: apical part long and narrow; Fp short or medium long and wide, divided from Rp. Male Sg: fused with St 9 and Tg 9, vesicle absent. Female Sg: rounded, entire; inner and lateral sclerites absent. Male tergites: process lacking. Ventral thoracic sclerites: MPrs triangular or elliptical, MeFs transverse or triangular, MeFsp fused with or separated from MePfs; MeFsa reduced or distinct. Macropterous wings: forewing A1 beyond a straight, R1 before r curved.



FIGURES 32–48. Male terminalia of Capniidae, ventral view—32: *Zwicknia bifrons* (Newman); 33: *Bolshecapnia gregsoni* (Ricker); 34: *Eucapnopsis stigmatica transversa* Aubert; 35: *Isocapnia grandis* (Banks); 36: *Capnia s.l. arensi* Zhiltzova; 37: *C. s.l. prolongata*; 38: *C. s.l. pedestris* Kimmins; 39: *C. s.s. nigra* (Pictet); 40: *Arsapnia decepta* Banks; 41: *Allocaupnia granulata* (Claassen); 42: *Mesocapnia silvatica* Raušer; 43: *Capnura venosa* Banks; 44: *Utacapnia lemoniana* (Nebeker & Gaufin); 45: *Paracapnia opis* (Newman); 46: *Nemocapnia carolina* Banks; 47: *Capnopsis schilleri schilleri* (Rostock); 48: *Capnioneura nemuroides* Ris (C: cercus; Ep-scl: main epiproct sclerite; Fp: fusion plate; Pp: paraproct; Sg: subgenital plate; St 9: sternite 9; Tg 9: tergite 9; Tg 10: tergite 10; Vv: ventral vesicle)—scale 1 mm.

Species included. 1 valid species from the East Nearctic, 1 from the Transnearctic, 5 from the West Nearctic and 4 from the East Palearctic (DeWalt *et al.* 2014); 7 of these species examined (see Appendix 1).

Remarks. Several species presently placed in this genus are different from the type species, in both the thoracic ventral sclerites and the male terminalia (Tables 1, 3–4). *Paracapnia boris* Stark & Baumann, 2004, *P. humbolta* Baumann & Lee, 2007 and *P. baumannii* Kondratieff & Lee, 2010 differences of the ventral sclerites were already noted in their original descriptions. In addition, these species differ also with having a large basal sclerite of the epiproct (instead of vestigial) and a longer fusion plate.

Utacapnia Gaufin, 1970

(Fig. 44)

Capnia columbiana species complex sensu Nebeker & Gaufin 1965—Nebeker & Gaufin 1965: 469. (revision).

Capnia (Utacapnia) Nebeker & Gaufin, 1967—Nebeker & Gaufin 1967: 236. (original description).

Capnia (Utacapnia) Gaufin, 1970—Gaufin 1970: 197. (type species designation: *Capnia lemoniana* Nebeker & Gaufin, 1965).

Utacapnia Gaufin, 1970—Zwick 1973: 390. (first use as a generic name, without former designation).

Diagnosis. Male epiproct: B-scl lacking, developed into large L1 attached to Ep-scl; Lb-scl medium sized, fused with Ep-scl; Ep-scl entire both ventrally and laterally, caudal setae present; I-scl and Ec absent. Male Pp: apical part long and wide; Fp long and wide, divided from Rp. Male Sg: fused with St 9 and Tg 9, vesicle absent. Female Sg: pointed and incised, slightly overhanging, lateral sclerites present. Male tergites: process lacking. Ventral thoracic sclerites: MPrs and MeFs triangular, MeFsp separated from MePfs. Macropterous wings: forewing A1 beyond a and R1 before r curved.

Species included. 10 valid species from the West Nearctic and 1 from the East Nearctic (DeWalt *et al.* 2014); 10 of these species examined (see Appendix 1).

Taxonomy

Zwicknia Murányi, gen. n.

(Figs. 1–2, 7–10, 23, 32, 49–197)

Capnia nigra (Pictet, 1833) sensu Morton 1896—Morton 1896: 60. (complementary description of the adult); Klapálek 1896: 19. (detailed description of the male genitalia); Klapálek 1909: 55, 88 (complementary description of the adult, description of the larva); Hynes 1940: 18. (complementary description of the adult); Hynes 1941: 498. (complementary description of the larva); Hanson 1946: 194. (detailed morphology of the adult); Despax 1951: 154. (complementary description of the adult).

Capnia quadrangularis Aubert, 1946—Aubert 1946: 24. (complementary description of the larva).

Capnia bifrons (Newman, 1838)—Brinck 1949: 96. (complementary description of the adult); Kimmins 1950a: 188. (complementary description of the larva); Brinck 1952: 56, 111. (complementary description of the adult and the larva); Hynes 1955a: 92. (complementary description of the larva); Hynes 1958: 37, 67. (revised complementary descriptions from Hynes 1940 and 1955a; same in the further editions); Illies 1955: 78. (complementary description of the adult); Winkler 1957: 43. (complementary description of the adult); Aubert 1959: 73, 125. (complementary description of the adult and the larva); Khoo 1964: 29. (description of the aestivating larva); Lillehammer 1965: 49. (complementary description of the adult and the larva); Rupperecht 1965: 1258. (groundplan of mating call); Rupperecht 1968: 43. (details of mating call); Zwick 1973: 163, 183. (terminal morphology of the male); Kis 1974: 119. (complementary description of the adult); Lillehammer 1974: 92. (variability of the adult); Rupperecht 1976: 38. (terminal morphology and different drumming signals of the male); Rupperecht 1982: 96. (different drumming signals of the male); Lillehammer 1988: 136. (complementary description of the adult and the larva); Westermann 1993: 137. (wing polymorphy); Rupperecht 1997: 94. (different drumming signals); Tierno de Figueroa *et al.* 2003: 242. (complementary description of the adult); Zwick 2004: 320. (further larval characters); Fochetti & Tierno de Figueroa 2008: 227. (complementary description of the adult).

Capnia bifrons species group sensu Zhiltzova 2001—Zhiltzova 2001: 424. (definition); Zhiltzova 2003: 345. (revision).

Diagnosis. Male epiproct: B-scl large, divided from Ep-scl; Lb-scl small, divided from Ep-scl; Ep-scl ventrally fused at base and tip, laterally divided in the apex, caudal setae absent; I-scl long, open tube, Ec present. Male Pp: apical part short and wide; Fp long and narrow, divided from Rp. Male Sg: divided from St 9 and Tg 9, vesicle present. Female Sg: rectangular, entire, small lateral sclerites present. Male tergites: Tg 9 with process. Ventral thoracic sclerites: MPrs and MeFs triangular, MeFsp separated from MePfs. Macropterous wings: forewing A1 beyond a and R1 before r curved.

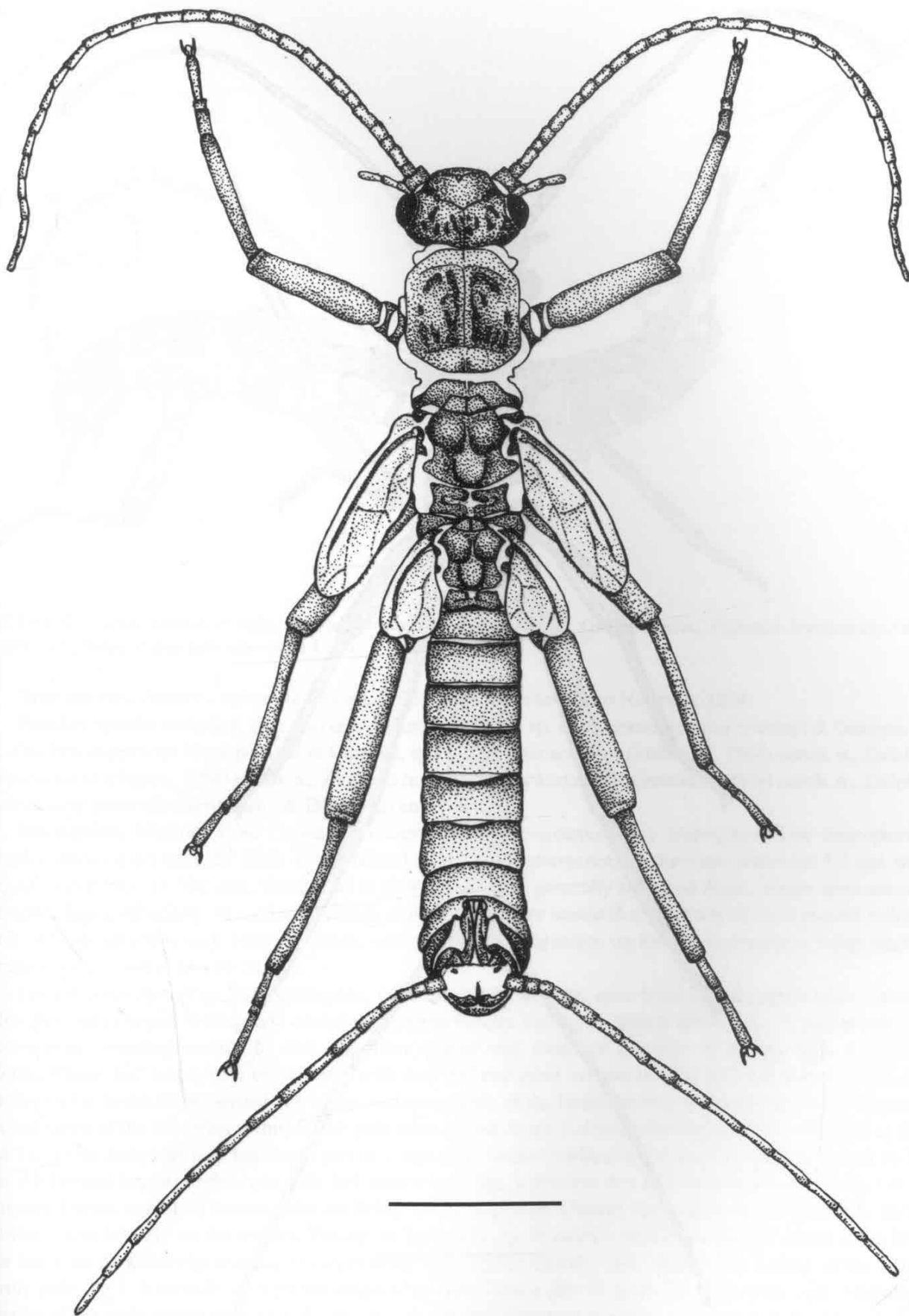


FIGURE 49. Dorsal habitus of male holotype *Zwicknia kovacsi* Murányi & Gamboa, **sp. n.**; Romania, Maramureş County, Rodna Mts., Borşa-Staţiunea Borşa—scale 1 mm.

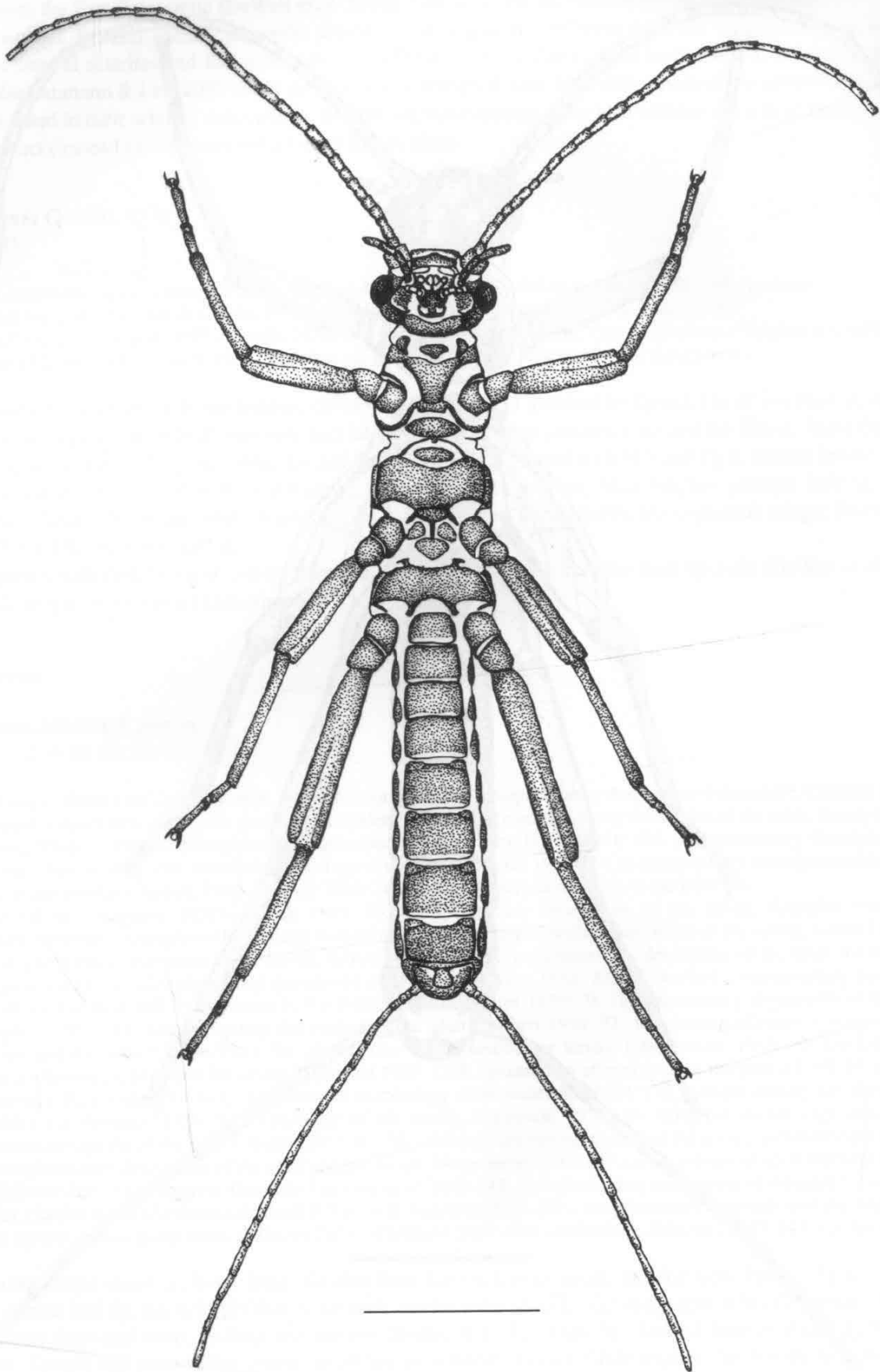


FIGURE 50. Ventral habitus of male holotype *Zwicknia kovacsi* Murányi & Gamboa, sp. n.; Romania, Maramureş County, Rodna Mts., Borşa-Staţiunea Borşa—scale 1 mm.

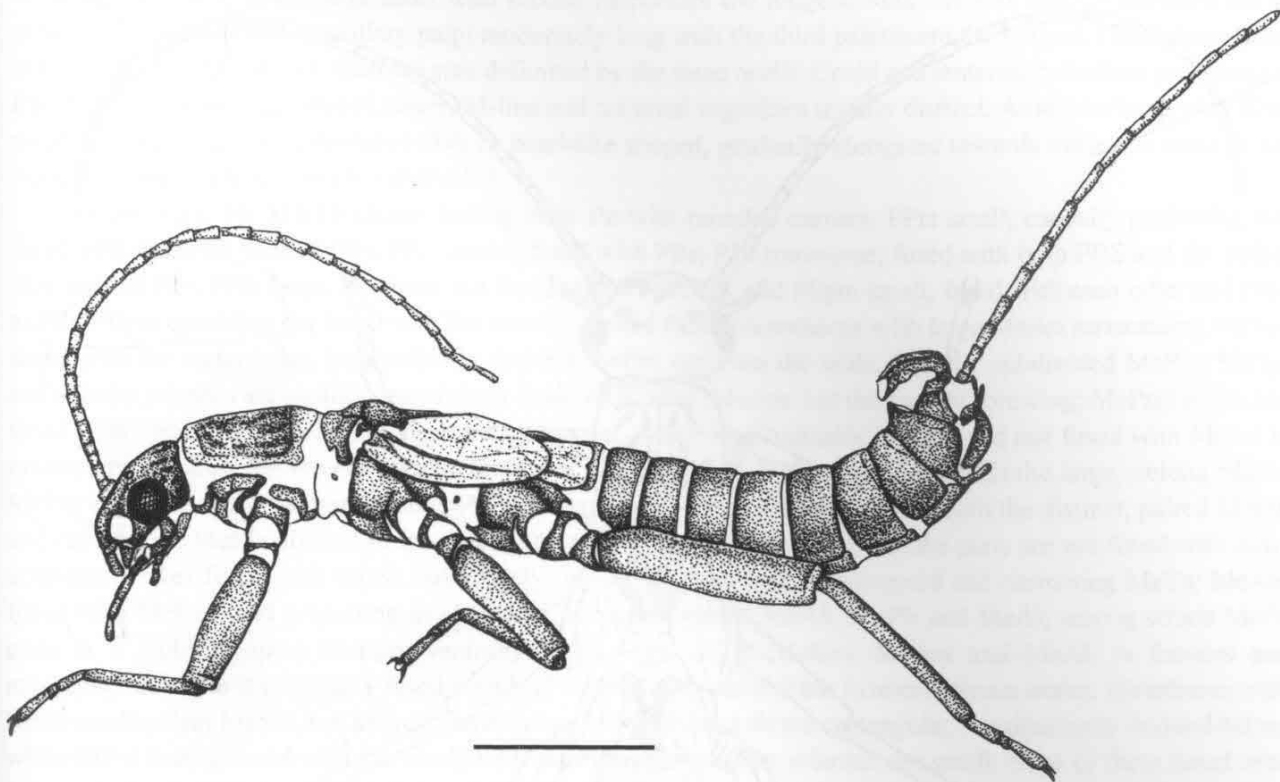


FIGURE 51. Lateral habitus of male holotype *Zwicknia kovacsi* Murányi & Gamboa, **sp. n.**; Romania, Maramureş County, Rodna Mts., Borşa-Staţiunea Borşa—scale 1 mm.

Type species. *Zwicknia bifrons* (Newman, 1838) = *Chloroperla bifrons* Newman, 1838.

Further species included. *Zwicknia acuta* Murányi & Orci, **sp. n.**, *Zwicknia kovacsi* Murányi & Gamboa, **sp. n.**, *Zwicknia rupprechtii* Murányi, Orci & Gamboa, **sp. n.**, *Zwicknia sevanica* (Zhiltzova, 1964) **comb. n.**, *Zwicknia tuberculata* (Zhiltzova, 1964) **comb. n.**, *Zwicknia turkestanica turkestanica* (Kimmins, 1950a) **comb. n.**, *Zwicknia turkestanica brevicula* (Berthélemy & Dia, 1982) **comb. n.**

Description. Medium sized Capniidae, males usually micropterous, also brachypterous or macropterous, females always macropterous. Body length related to season of emergence, smallest late males are 4.5 mm while largest early males are 10.0 mm; females up to 12.0 mm. Pilosity generally short and dense, longer setae occur on the appendages, especially on cerci and femora; male epiproct bare beside B-scl, pilosity of Tg 9 process reduced. Fully sclerotized adults dark brown to black, with even darker rugosities on head and pronotum; wings hyaline, venation dark brown (Figs. 49–51).

Teneral coloration (Fig. 52): Mouthparts, palpi and antennae pale, eyes black. Head capsule pale, tentorial callosities and enlarged M-line dark; occipital rugosities usually lacking on teneral specimens. Pronotum pale with brown areas extending around the dark rugosities, central line, front and posterior delimiting folds of pronotal sclerite. Meso- and metanotum of the male with dark Scl and inner corners of Pra, Sct with paired lateral dark patches and a darker stripe beyond Scl. Meso- and metanotum of the female mostly pale with dark inner corners of Pra and limits of the Scl. Wings whitish with pale veins in both sexes. Laterally the thorax is pale with parts of Epm and Tn or Etn dark; legs pale but dorsal part of coxae dark. Ventral surface of the thorax is pale with dark Fs and Fsp. Abdominal tergites of the male with dark brown antecosta, transverse row of four spots present on Tg 1–9. Tg 1 mostly brown, extent of brown color declining on the segments towards the terminalia but gradually darken anteriorly and laterally on the tergites. Process of Tg 9 pale, Tg 10 entirely pale but with two lateral spots. B-scl pale but with dark anterior margin, Lb-scl entirely pale, Ep-scl entirely dark. Abdominal tergites of the female mostly pale, Tg 1–9 laterally with paired longitudinal patch and a pair of spots; Tg 10 entirely pale. Abdominal sternites of the male mostly pale, St 3–8 with anterior sclerites forming a medially interrupted, dark transverse line; Sg with a paired anterolateral spot, vesicle pale. Pp pale with brown tip, cerci pale. Ventral surface of the female abdomen entirely pale.

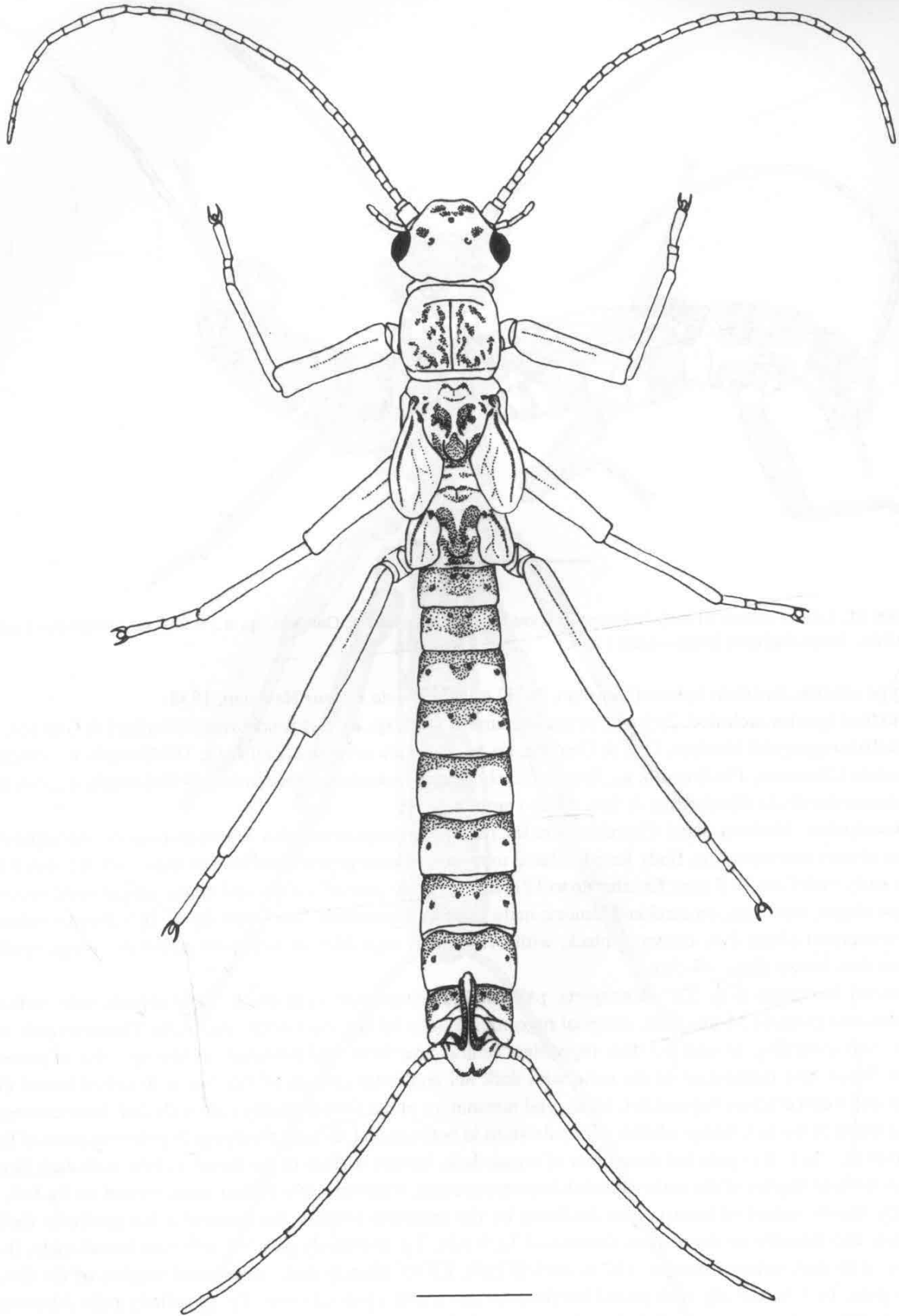


FIGURE 52. Dorsal pattern of teneral male *Zwicknia bifrons* (Newman, 1838); Hungary, Pest County, Pilis Mts., Szentendre—scale 1 mm.

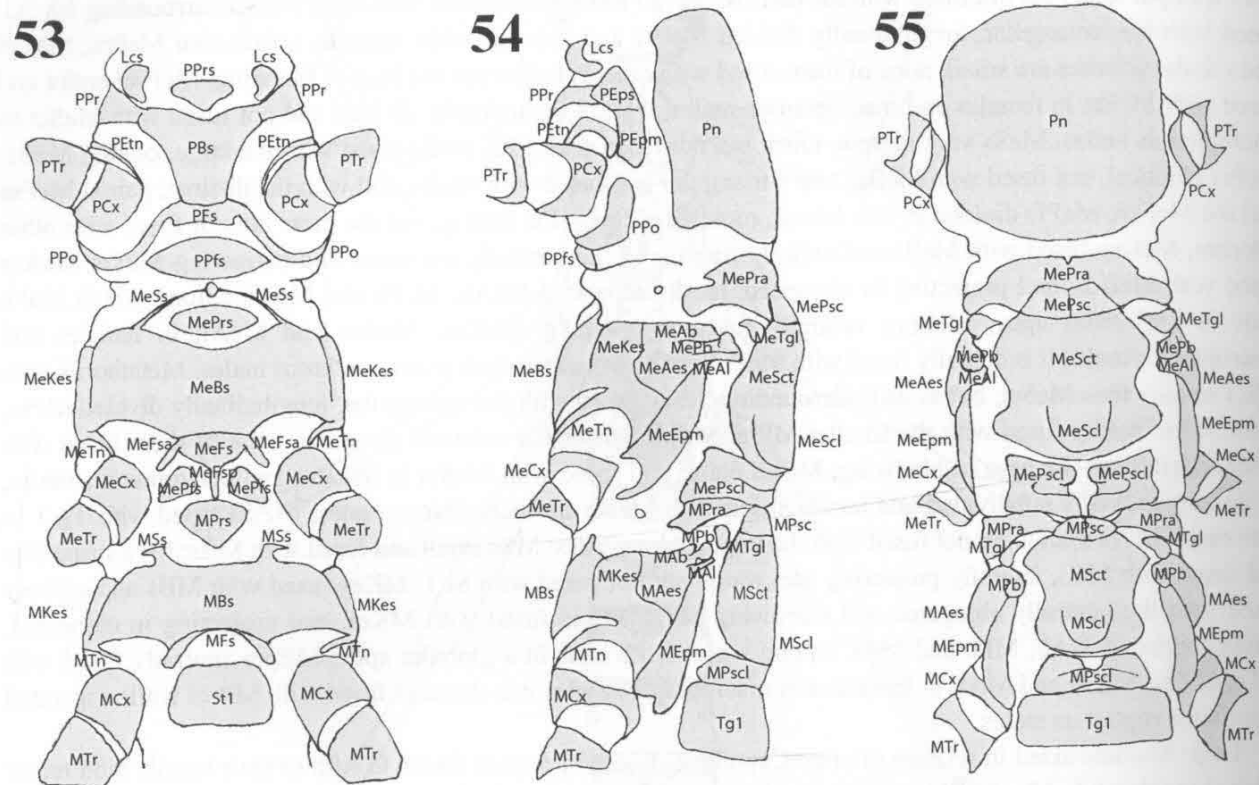
Head: Submentum and mentum small, general Capniidae shaped; glossae apically rounded, paraglossae weakly subdivided, labial palpi short with second palpomere the longest. Maxillae and other mouthparts are of general Capniidae shape, maxillary palpi moderately long with the third palpomere the longest. Head shape usual of Capniidae, eyes smaller than the area delimited by the three ocelli. Ocelli and tentorial callosities prominent in fully sclerotized adults, ecdysial suture, M-line and occipital rugosities usually distinct. Antennae long, with 30 or more antennomeres. Antennomeres club or pearl-like shaped, gradually elongated towards the apex; some of the basal 4–6 antennomeres usually subdivided.

Thorax (Figs. 53–55): Prothorax having large Pn with rounded corners. PPrs small, caudally projecting, not fused with the heart-shaped PBs; PPr narrow, fused with PBs; PFs transverse, fused with both PBS and the stripe-like, curved PPO; PPfs large, elliptical, not fused with PFs. PEps and PEpm small, fused with each other and Peps to PPr, PEpm touch but not fused with the narrow, curved PETn. Mesothorax with large MeSct surrounding MeScl, fused with the rectangular, longitudinally divided MePsc and then the wide, laterally subdivided MePra; MeTgl and subalar sclerites are small, none of them fused with other sclerites but the base of forewing; MePsc entire and fused with MeSct in females and macropterous males, while longitudinally divided and not fused with MeSct in micropterous males. MeSs very narrow, touch but not fused with PPfs while fused with the large, oblong MeBs; MePrs elliptical, not fused with MeBs; MeFs triangular and fused with MeBs, and with the distinct, paired MeFsa and the MeFsp; MePfs divided in two lateral, rounded parts by the MeFsp, but the parts are not fused with other sclerites. MeKes fused with MeBs and entirely fused with the ventrally elongated and narrowing MeTn; MeAes fused with MeKes, and projecting in elongated, hardly separated MeAb, MePb and MeAl, among which MePb ends in a globular apex; MeEpm ventrally fused with MeTn, MeKes, MeAes and MeAl, in females and macropterous males it is dorsally fused with MePsc while separated from in micropterous males. Metathorax with MSct smaller than MeSct, but as well surrounding MScl, fused with the rectangular, longitudinally divided MPsc, while MPsc hardly fused with the smaller MPra; MTgl and subalar sclerites are small, none of them fused with other sclerites but the base of hindwing; MPsc entire and fused with MeSct in females and macropterous males, while longitudinally subdivided and hardly fused with MeSct in micropterous males; MPsc fused with Tg 1 in both cases. MPrs triangular, not fused with the large, oblong MBs; MSs small and fused with MBs; MFs stripe-like and fused with MBs, laterally projecting backwards but not fused with St 1. MKes fused with MBs and entirely fused with the ventrally elongated and narrowing MTn; MAes fused with MKes, and projecting in elongated, hardly separated MAb, MPb and MAI, among which MPb ends in a globular apex; MEpm ventrally fused with MTn, MKes, MAes and MAI, in females and macropterous males it is dorsally fused with MPsc while separated from in micropterous males.

Legs: Medium sized in relation of other Capniidae. Width of femora fourth to fifth of their length, hind femur reach about the end of Tg 5. Tibiae as long as the femora but less than half the width. Tarsi as wide as tibiae, length of tarsi about half of the corresponding tibia; second tarsomere much shorter than the others, basitarsus shorter than metatarsus on foreleg while as long as on hind leg. Claws symmetrical, smooth and gradually curved, arolium relatively small.

Wings: Macropterous wings about as long as the body, covering more than half of the cerci; wing venation show little variability (Figs. 56–57). Forewing: C simple, narrowing gradually from R4+5 towards Cu1; Sc parallel to C, there are two crossveins between C and Sc besides h, Sc curves abruptly beyond the last crossvein and join R around r; h is closest to arc than to wing base; R1 is distinctly curved between its branching with Rs and r, gives one leaning crossvein towards C shortly after r or at least before halfway to C; R2+3 and R4+5 branching at r or with a short crossvein between r and r-m; M branch out to M1+2 and M3+4 with r-m before r; there is only one crossvein between M and Cu1 besides arc and m-cu, this crossvein continues in cu between Cu1 and Cu2; Cu2 ends before half of the wing length, very narrow or interrupted before arc; usually a thin cu-a presents between Cu2 and A1 around a; A1 ends around the R end of arc, distinctly curved and usually thickened beyond a; A2 reaches only as far as h is positioned. Hindwing: C, Sc and their crossveins similar to the forewing; R1 is straight, not branching with R, but starts separately from arc, gives one leaning crossvein towards C shortly after r or at least before halfway to C; R2+3 and R4+5 branching with a crossvein between r and r-m; M branch out to M1+2 and M3+4 after r-m and m-cu; M thin before branching and there is no crossvein between M and Cu1 between arc and m-cu, but sometimes there is one between M3+4 and Cu1, and cu always present; Cu2 parallel to A1 in its posterior two thirds and ends beyond the position of r, but very narrow or interrupted before arc; usually a thin cu-a present between Cu2 and A1 around a; anal field large, the fold of the wing extending between the parallel Cu2 and A1; A1

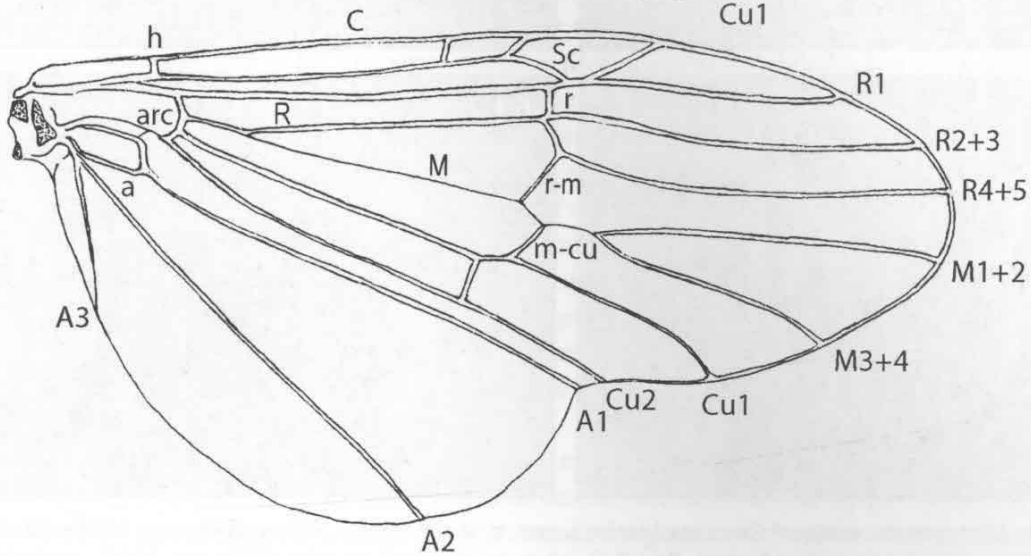
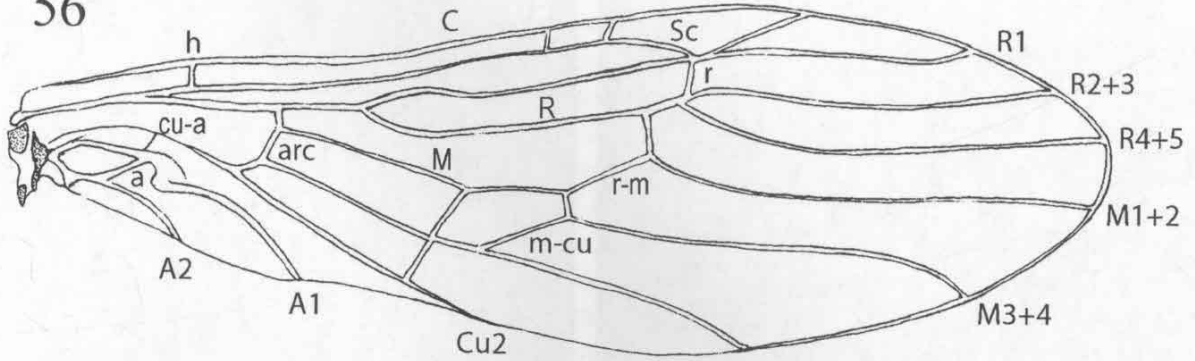
straight beyond a, runs close to Cu2; A2 straight, ends around the position of cu, the nearly longitudinally directed a sometimes not reach A2 but terminates backcurved to the wing base; A3 as long as the distance of arc and wing base, extending perpendicular to the longitudinal veins. In case of micropterous or brachypterous males, the wing length is usually constant in some species but may vary intraspecifically (Figs. 58–61). On these winglets, R is the thickest vein and the wing is folded with about 60° around this vein; arc is distinct on the forewing and sets as far as on the macropterous wings, but usually obscured on the hindwing; single M and Cu run to the wing tip, sometimes also with a few crossveins on the forewing; anal veins of the forewing similar in length to the macropterous ones, usually a normal a and the curve of A1 also conspicuous; anal field of the hindwing proportional enlarged but the veins are vestigial.



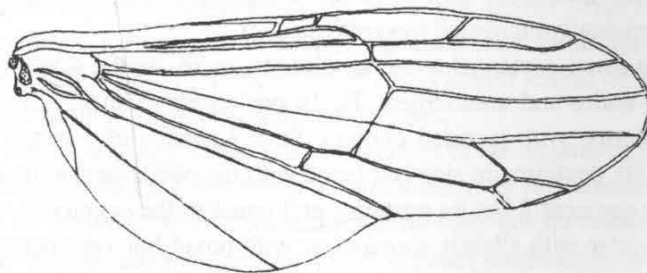
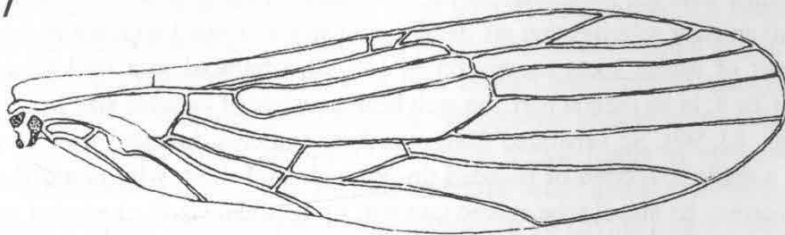
FIGURES 53–55. Thoracic sclerites of male *Zwicknia kovacsi* Murányi & Gamboa, *sp. n.*—53: ventral view; 54: lateral view; 55: dorsal view (P: prothoracic; Me: mesothoracic; M: metathoracic—Ab: anterior basalare; Aes: anepisternum; Al: alifer; Bs: basisternum; Cx: coxa; Epm: epimeron; Eps: episternum; Etn: eutrochantin; Fs: furcasternum; Fsa: furcasternal arm; Fsp: furcasternal pit; Kes: katepisternum; Lcs: lateral cervical sclerite; Pb: posterior basalare; Pfs: postfurcasternum; Pn: pronotum; Po: postcoxal bridge; Pr: precoxal bridge; Pra: prealar bridge; Prs: presternum; Psc: prescutum; Pscl: postscutellum; Sct: scutum; Scl: scutellum; Ss: spinasternum; St1: Sternite 1; Tgl: Tergite 1; Tgl: tegula; Tn: trochantin; Tr: trochanter—wings and subalar sclerites omitted—not to scale.

Male abdomen: Tg 1–8 entire and unmodified with sinuous antecosta that is entire on Tg 2–9, entire or medially interrupted on Tg 1; transverse row of four spots present on Tg 1–9. Tg 9 with a raised posteromedial process of different shape characteristic to species; its sclerotization not thicker than the remainder of the tergite, and its caudal face is membranous with specific shape of lateral sclerotization (Figs. 148–164). Tg 10 subdivided with the entire antecosta forming a thick, rectangular U-shaped process in the medial 1/5 of the segment's width (Fig. 1). Epiproct consists of a large, anteriorly rounded and raised B-scl that is indented medio-apically and divided from both the Ep-scl and the two Lb-scl (Fig. 1); paired Lb-scl small and triangular with sinuous dorsal margin, divided from both the Ep-scl and the B-scl (Fig. 2). Ep-scl long and curved, caudal setae lacking but spines of specific shape and distribution present on the apex; basally wide but abruptly tapering in the basal third; apical two thirds of the sclerite with the same width or medially swollen; dorsally divided in its full length, ventrally connected at the base and the tip, while laterally divided in the apex – concrete shape is characteristic for the species (Figs. 106–119, 127–147); LI lacking; I-scl is a long, dorsally open tube that is curved like the Ep-scl (Figs. 1–2); Ec present in the apical third, between the upper corns of the laterally divided part of Ep-scl (Figs. 1–2, 8–10).

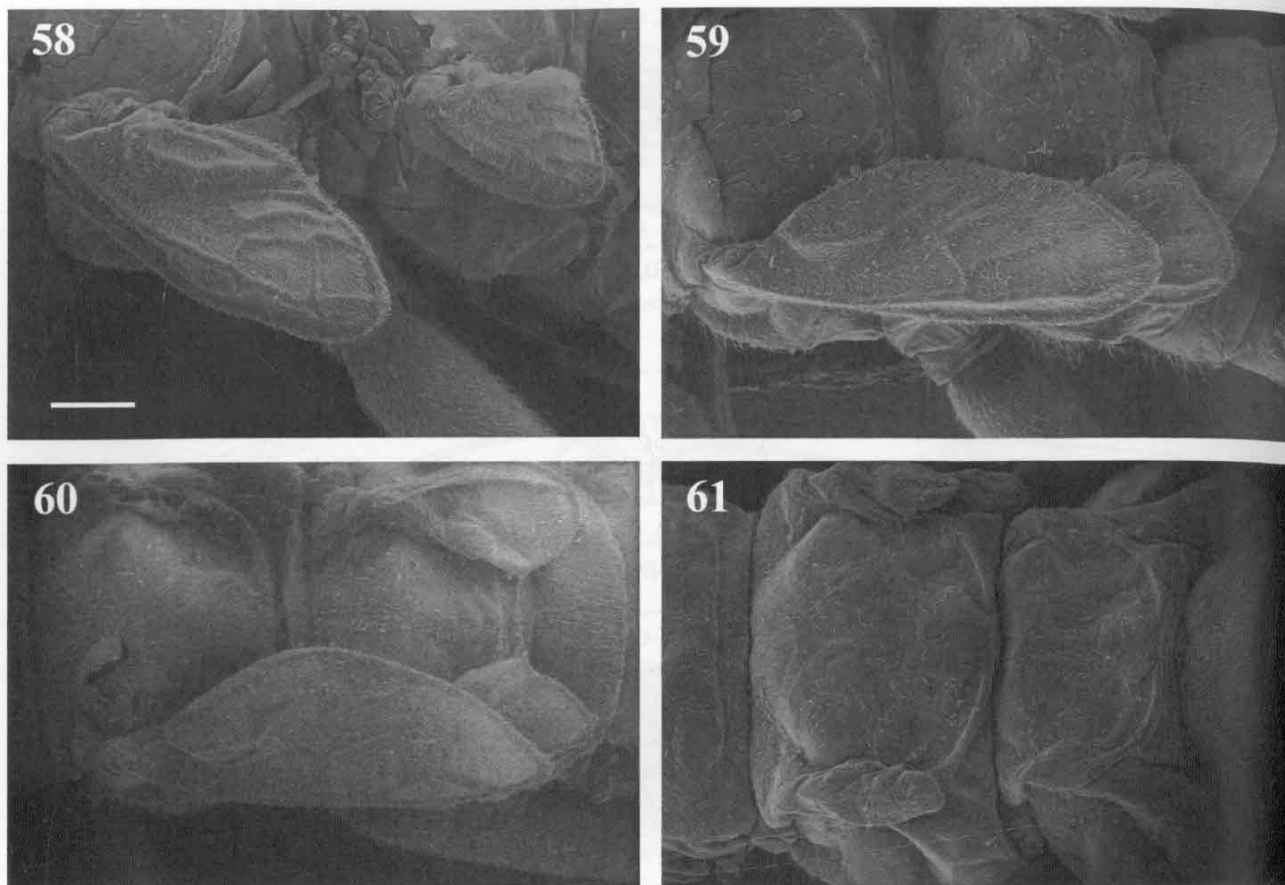
56



57



FIGURES 56–57. Macropterous wings of *Zwicknia* Murányi, **gen. n.**—56: Female *Z. bifrons* (Newman, 1838); 57: male *Z. tuberculata* (Zhiltzova, 1964) (A: anal vein; a: anal crossvein; arc: arcus; C: costa; Cu: cubital vein; cu-a: cubitoanal crossvein; h: humeral crossvein; M: medial vein; m-cu: mediocubital crossvein; R: radial vein; r: radial crossvein; r-m: radiomedial crossvein; Sc: subcosta)—scale 1 mm.



FIGURES 58–61. Micropterous wings of *Zwicknia* Murányi, **gen. n.** males—58: *Z. bifrons* (Newman, 1838); 59: *Z. acuta* Murányi & Orci, **sp. n.**; 60: *Z. rupprechtii* Murányi, Orci & Gamboa, **sp. n.**; 61: *Z. sevanica* (Zhiltzova, 1964)—scale 0.2 mm.

St 1 entire and unmodified but smaller than the additional sterna, with rounded corners. St 2–8 consist of a large, rectangular posterior and two small anterior sclerites that are declining in size and fused with the posterior sclerite towards the apical segments; a pair of lateral spots present on St 1–8. St 9 reduced to a well sclerotized arch connecting the ventro-basal part of Tg 9; in its medial part, the arch bear a vesicle of variable size from one third of segment's width to vestigial (Figs. 83, 99). Sg separated from all other segments, rounded with a more or less triangular shape, apical part with a distinct, incised or rounded tip. Pp wide and short, with rounded apex that is also short and wide. Fp long and narrow, its apical tube curved upward; Rp medium sized, elongated and rounded, divided from Fp (Fig. 23). Cerci longer than the abdomen, with 15 or more segments; segments cylindrical, the basal ones slightly club shaped or pearl-like, gradually elongated towards the apex.

Female abdomen: Tg 1–8 divided into two small, rectangular lateral sclerites; small, hardly sclerotized median plates may also present on Tg 2–6. Tg 9–10 entire and unmodified, Tg 10 posteriorly rounded. St 1 entire and unmodified but smaller than the additional sterna, with rounded corners. St 2–7 consist of a large, rectangular posterior and two small anterior sclerites that are declining in size and fused with the posterior sclerite towards the apical segments. Sg large, covers most of the segment 8 but its posterior end equal to the segment's end, or only very slightly overhanging; the plate is rectangular with slightly rounded or with broad but very narrow indented posterior margin; sclerotization entire without keel, two small antero-lateral nook usually present (Figs. 62, 64–65). Color of the plate is entirely brown, sometimes a bit paler medially; two small lateral sclerites fused with posterio-lateral edges of the Sg. Vaginal complex with broad genital opening, membranous genital cavity reach back to segment 7 where it branching into the oviducts; inner sclerites lacking (Fig. 63). St 9 entire, rectangular; Pp large, having short, rounded tips; epiproct simple, membranous. Cerci as long as or shorter than the abdomen, with 15 or more segments; segments cylindrical, the basal segments slightly clubbed, gradually elongated towards the apex.

Mature larva: Body relatively stout, body length 5.5–12.5 mm. General color pale yellowish brown with very faint pattern; head, dorsal thoracal sclerites besides wing pads, and abdominal terga usually darker. General coloration apparent below cuticle on pharates, together with dark wing pads. Setation long, but inconspicuous.

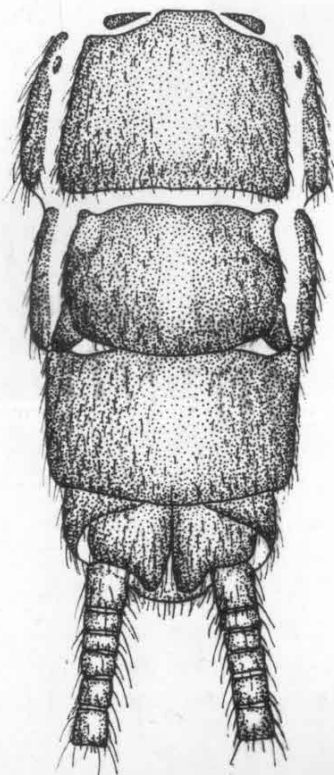
Head shape typical of Capniidae, eyes smaller than the area delimited by the three ocelli (Fig. 66). Ocelli and ecdysial suture are prominent, tentorial callosities less pronounced, M-line and occipital rugosities are hard to observe. Mentum small, typical of the Capniidae; glossae long and apically rounded, paraglossae weakly subdivided, labial palpi short with second palpomere the longest. Maxillae and other mouthparts are of general Capniidae shape and structure, maxillary palpi moderately long with the third palpomere the longest (Fig. 67). Antennae long, with 50 or more antennomeres. Antennomeres cylindrical, the first ten beyond pedicel very short, then gradually elongated towards the apex where antennomeres are about $3\times$ longer than wide. Pn elongated trapezoidal with rounded corners, smooth; rear edge of meso- and metathorax between wing pads rounded, the paired sclerites widely separated from wing pads. Shape of wing pads are typical of Capniidae in macropterous specimens, the mesothoracic pair reach the anterior end of Tg 1, metathoracic pair reach the anterior end of Tg 3; micropterous wing pads always still distinct and separated from the paired sclerites. Lateral thoracic sclerites similar to adults but Epm yet reduced and Aes dorsally not yet divided into Ab, Pb and Al. Ventral thoracic sclerites mostly obscure but Etn, Tn and Fs distinct. PFs longer than of the adult, more elliptical than transverse; MeFs triangular, anterior width half of the intercoxal distance, MeFsa indistinct while MeFsp distinct (forming a Y-ridge with the MeFs); MFs laterally indented (Figs. 68–69). Legs typical of Capniidae, width of femora $\frac{1}{3}$ of their length, hind femur reach about the midline of Tg 5. Tibiae as long as the femora but $\sim\frac{1}{2}$ as wide. Tarsi as wide as tibiae, length of tarsi $<\frac{1}{2}$ of the corresponding tibia; basitarsus slightly longer than the second tarsomere on the foreleg, about $2\times$ longer on hind leg but $<\frac{1}{2}$ half of the length of metatarsus. Claws symmetrical, smooth and with a basal swelling, regularly curved, arolium vestigial. Abdomen relatively stout, segments 1–9 divided by pleura, integument light and matt. Tg 10 rounded in females, projecting in males; length of the latter equal or shorter than length of Tg 8 and 9, tip blunt, or only slightly raised upwards (Figs. 74–75). Pp wide and short, tip blunt. Cerci usually longer than the abdomen, with 30 or more segments; segments cylindrical, the basal ones short but gradually elongated towards the apex where segments are very slender; the width of segments 11–13 is half to third of their length (Figs. 76–77).

Setation: Head with not so dense, moderately long and thick setae and hairs; eye bear small elongated setae between the ocelli; mouthparts with scarce setation besides the sensilla and apical spines but labrum with a pronounced apical tuft of setae rows (Figs. 66–67). Antennal segments with apical whorl of short setae and hairs; campaniform sensillae occur on their distal $\frac{1}{2}$. Dorsal surface of thorax with similar setation like the head, Pr lacks marginal row or longer marginal setae; setae placed in lines on wing pads. Ventral surface of thorax with scarce, thin and short hairs and setae (Figs. 68–69). Legs with dense setation. All femora bear long, acute setae and thin hairs, and armed with a row of long, erect setae on both dorsal and ventral edges; length of these setae are less than the half of the femur's width (Figs. 72–73). A bald median line is conspicuous on the dorsal surface of all femora. Tibiae and tarsi covered with long hair-like setae, strong setae present only on the ventral edges of the tibiae; tibiae lack apical spines or the spines are vestigial, scarce dorsal fringe of swimming hairs usually present. Tergal segments with moderately dense, uniform long and blunt setae; apical row lacking, length of the setae are fourth to fifth of segment's length (Fig. 70). Projection of male Tg 10 having a bare medial line and bare at the apex (Figs. 74–75). Ventral surface of abdomen with fewer but similar setae like tergites; setae dense on the Pp (Fig. 71). Cercal segments with apical row of acute, long setae, short setae and thin hairs; campaniform sensillae occur on the whole surface (Figs. 76–77). Longest setae are $\frac{1}{2}$ to full length of the segment on segments 11–13, as long as or slightly longer than the segment on the apical ones.

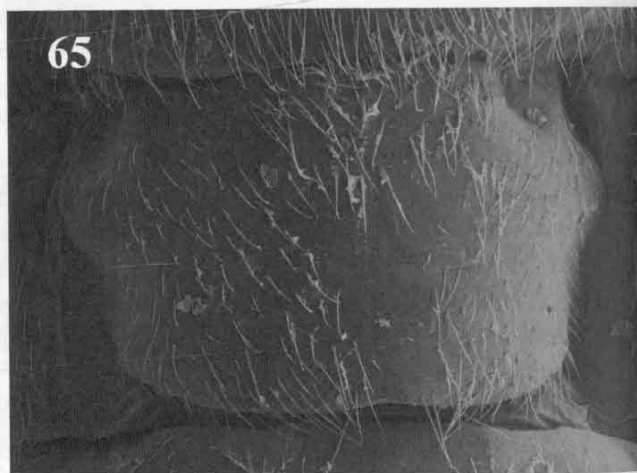
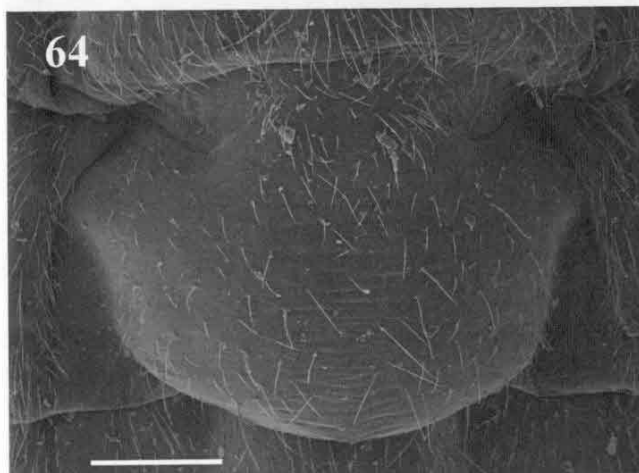
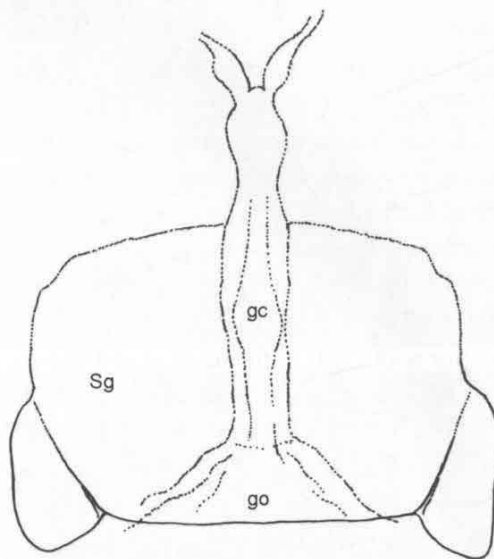
Drumming: A comprehensive characterization of the drumming signals used in the genus cannot be given until the drumming signals of *Z. sevanica*, *Z. tuberculata*, *Z. turkestanica turkestanica*, *Z. turkestanica brevicula* are unknown. The presently known male drumming calls are monophasic beat-groups with gradually decreasing or increasing inter-beat intervals. Solitary males produce single calls sporadically or 1–4 calls in a sequence. The beat repetition patterns (Figs. 169–184) of male calls are species-specific. Male female drumming signal exchanges are male call—female answer or male call—female answer—male response duets (Figs. 185–189).

Genetics: Sequencing *coxI* of 64 *Zwicknia* specimens yielded 29 distinct haplotypes with 123 informative characters. Same topology was found with both MP (L = 441, CI = 83, and IR = 93) and ML (ln L = -2470.19612; Fig. 192) approaches. Overall divergence among new haplotypes was 6.5 %. Our phylogeny reflected the spatial arrangement of haplotype clusters in the landscape with each newly defined species forming a monophyletic haplotype clade. In GenBank data analyzed under *coxI*, the closest related clade was *Allocapnia* sp. with 89% sequence similarities, and was used as an outgroup.

62



63

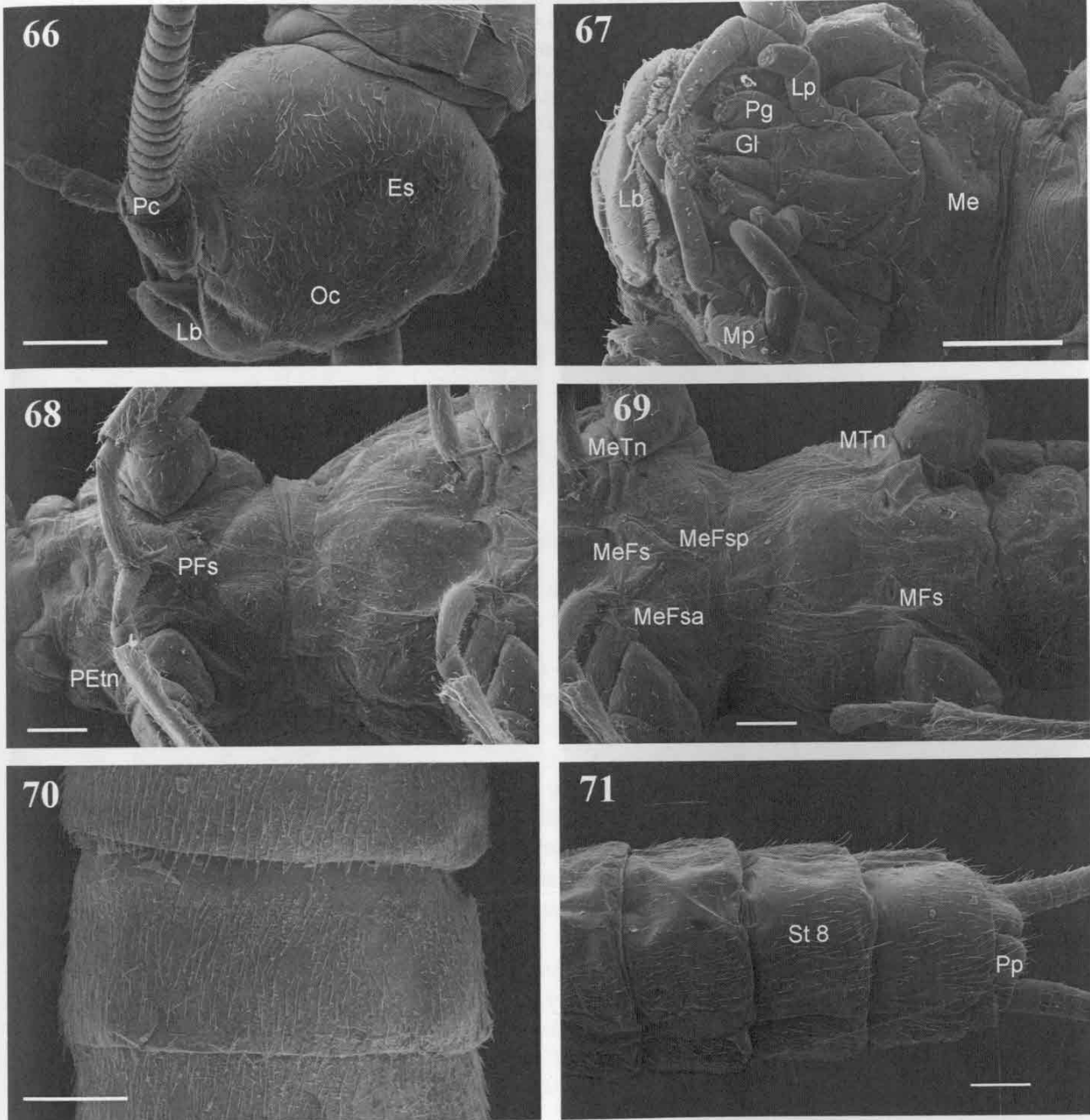


FIGURES 62–65. Female genitalia of *Zwicknia* Murányi, *gen. n.*—62–63: *Z. bifrons* (Newman, 1838); 64: *Z. acuta* Murányi & Orci, *sp. n.*; 65: *Z. rupprechti* Murányi, Orci & Gamboa, *sp. n.*; 62: terminalia, ventral view; 63: inner genital organs, dorsal view; 64–65: subgenital plates, ventral view (gc: genital cavity; go: genital opening; Sg: subgenital plate)—scales 0.2 mm.

Affinities. In the West Palaearctic, the genus is distinguishable from other Capniidae in features discussed in the diagnosis of the male and female terminalia. Males of *Zwicknia* are apparently more closely related to the West Nearctic *Bolshecapnia*, but differ with having long, undivided tube-like I-scl instead of divided, and the apical part of the Pp short and wide instead of long and narrow. Females of *Bolshecapnia* have narrower Sg that is usually pointed and overhanging St 8, instead of entire, rectangular Sg with length equal to St 8. *Zwicknia* is also closely related to the montane Asian *Capnia s.l. cordata* species group, but the males differ by their lateroapically divided Ep-scl instead of entire, presence of Ec instead of its absence, and the apical part of the Pp short and wide instead of long and narrow. Females of the *C. s.l. cordata* species group have narrow, dark Sg instead of entire and similar in color to sterna. Larvae are difficult to separate from other Capniidae and an adequate diagnosis cannot be given here. Since no specific characters useful for separation were found, larvae of the species included are not described, only a general description is given. However, matured male larvae usually can be identified on the basis of the epiproct transparent through larval skin. Drumming signals are known only in a small proportion of species in

Capniidae. Therefore it would be too early to make a detailed examination of the affinities of *Zwicknia* species regarding their drumming signals. Mitochondrial DNA showed that *Zwicknia* species have a range of 19%–22% of overall divergence with respect of *Capnia s.l. vidua* and a decrease of glutamine of 68% in nucleotide composition, compared with others species of Capniidae.

63



FIGURES 66–71. Larva of *Zwicknia* Murányi, **gen. n.**—66: *Z. bifrons* (Newman, 1838); 67–69, 71: *Z. acuta* Murányi & Orci, **sp. n.**; 70: *Z. ruppreehtii* Murányi, Orci & Gamboa, **sp. n.**: 66: head, dorso-lateral view; 67: mouthparts, ventral view; 68: pro- and mesothorax, ventral view; 69: meso- and metathorax, ventral view; 70: Tergite 5, dorsal view; 71: female terminalia, ventral view (Es: ecdysial suture; Etn: eutrochantin; Gl: glossa; Lb: labrum; Lp: labial palp; Me: mentum; MeFs: mesothoracic furcasternum; MeFsa: mesothoracic furcasternal arm; MeFsp: mesothoracic furcasternal pit; MeTn: mesothoracic trochantin; MFs: metathoracic furcasternum; Mp: maxillary palp; MTn: metathoracic trochantin; Oc: frontal ocellus; Pc: pedicell; PFs: prothoracic furcasternum; Pg: paraglossa; Pp: paraproct; St 8: Sternite 8)—scales 0.2 mm.

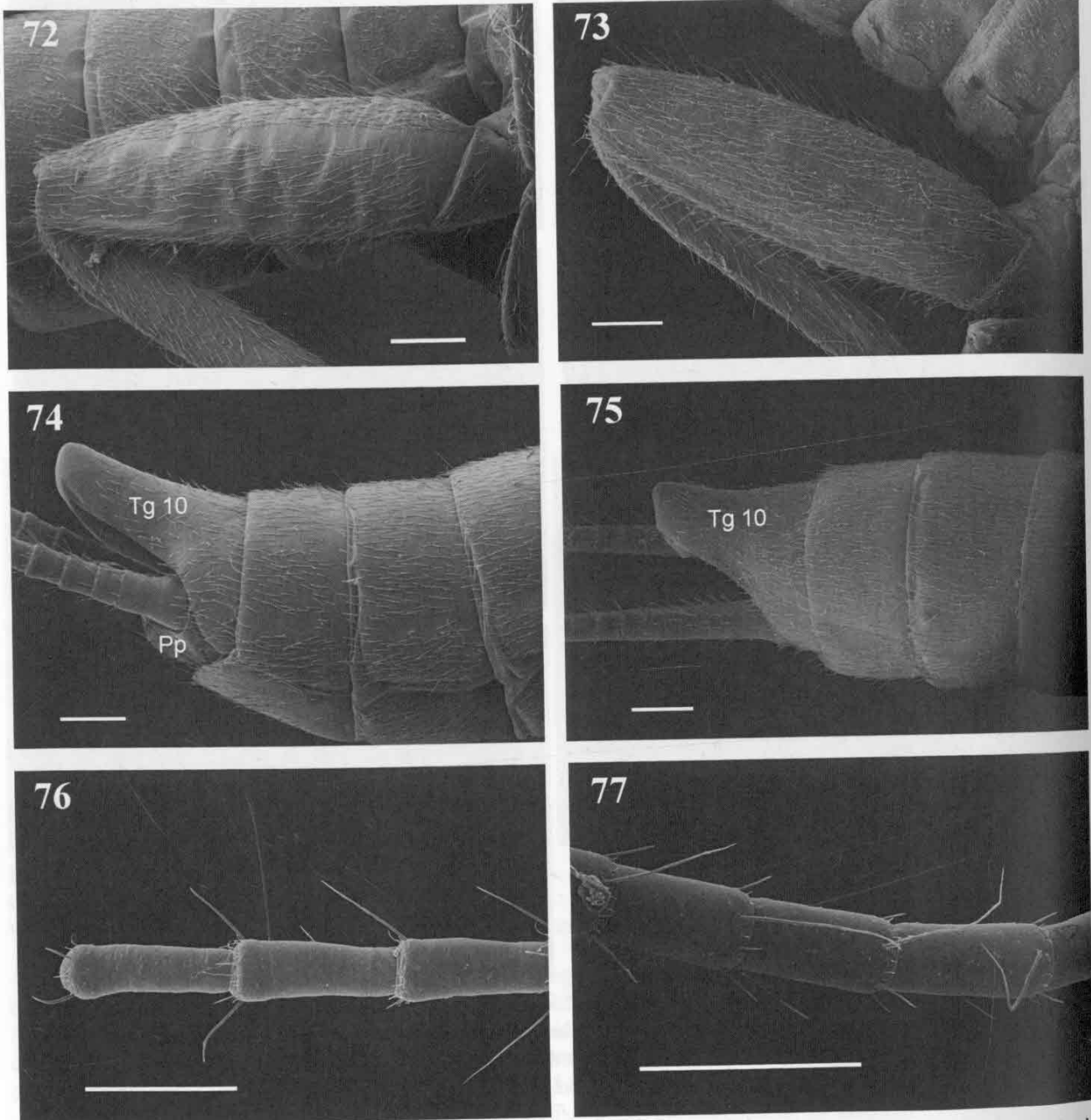
Distribution and ecology. The genus has a Palearctic distribution. While common in most parts of Europe, it is absent from North Africa, the Mediterranean Isles, and the Far North (Iceland, northern Scandinavia). It is reported from the Levant only from Lebanon, but widespread in the northern part of Anatolia, the Caucasus, and

Murányi &
Orci, 2012
p. 22
2 mm.

discussed in
the West
biogeographi-
cal part
of Europe
is usually
found
to be closely
related
to other
species
of the
genus
divided
into
several
species
instead of
one
species
similar in
morphology
to be given
as a
new
species,
as the
description
of the
species in

Transcaucasia. At least two species enter the East Palaearctic as far as Middle Asia (Fig 196). Adults occur from the second half of January to June. The peak of emergence is in March in most areas. European species inhabit usually slow, medium-sized forest streams of hilly and submontane regions, but they were reported also from small temporary brooks and even high montane streams. Asian species were found generally in later periods and higher elevations up to 2,400 m.

Etymology. The genus is dedicated to Prof. Peter Zwick, Schlitz, Germany, in recognition of his major contributions and establishing leadership in many fields of study of the Plecoptera. The name composed with the ending “nia” corresponding to *Capnia*; gender feminine.



FIGURES 72–77. Larva of *Zwicknia* Murányi, **gen. n.**—72, 74, 76: *Z. bifrons* (Newman, 1838); 73, 75: *Z. rupprechtii* Murányi, Orci & Gamboa, **sp. n.**; 77: *Z. acuta* Murányi & Orci, **sp. n.**; 72–73: hind femur, lateral view; 74–75: male terminalia, lateral view; 76–77: 11–13 cercal segments, lateral view (Pp: paraproct; Tg 10: tergite 10)—scales 0.2 mm.

Morphological key to adult males of *Zwickenia*

- 1 Ep-scl medially swollen (Figs. 110, 142–143). Process of Tg 9 very wide and distinctly bicornuated (Fig. 160) *Z. kovacsi*
- Ep-scl not swollen medially. Process of Tg 9 narrower and without distinct corns 2
- 2 Tip of Ep-scl upcurved in lateral view (Figs. 106–107, 132, 134, 136, 138–141). Ep-scl wide and blunt in dorsal view (Figs. 114–115, 117). Spines present only on the membranous part of the epiproct apex (Figs. 106–107) 3
- Tip of Ep-scl straight or slightly curved down in lateral view. Ep-scl narrow and more or less pointed in dorsal view. Spines present also on the apical part of Ep-scl 4
- 3 Process of Tg 9 low and caudally projecting (Figs. 92, 157–159) *Z. rupprechtii*
- Process of Tg 9 high and perpendicularly elevated (Figs. 84, 148–151) *Z. bifrons*
- 4 Tip of Ep-scl acute in lateral view (Figs. 108–109, 127–131). Process of Tg 9 very high, rectangular and with indenting sides caudally (Figs. 152–156) *Z. acuta*
- Tip of Ep-scl blunt in lateral view. Process of Tg 9 lower, rounded and sides not indenting caudally 5
- 5 Tip of Ep-scl straight in lateral view (Figs. 111, 144–145). Process of Tg 9 slightly wider than the epiproct (Fig. 94) *Z. sevanica*
- Tip of Ep-scl slightly downcurved in lateral view. Process of Tg 9 obviously wider than the epiproct 6
- 6 Process of Tg 9 perpendicularly elevated (Fig. 102). Ep-scl comparatively more slender (Fig. 102, 104–105, 147) *Z. turkestanica*
- Process of Tg 9 slightly folded backwards (Fig. 100). Ep-scl comparatively more robust (Figs. 98, 100–101, 146) *Z. tuberculata*

Zwickenia acuta Murányi & Orci, sp. n.

(Figs. 59, 64, 67–69, 71, 77, 78–81, 108–109, 119, 121, 127–130, 148–151, 166, 174–178, 186–187, 190–193, 196–197).

Capnia nigra (Pictet, 1833)—figures in Klapálek 1896 and Despax 1951 (enumerated under the general synonymies) possibly referring to *Z. acuta*.

Capnia bifrons (Newman, 1838)—figures in Winkler 1957 (enumerated under the general synonymies) possibly referring to *Z. acuta*.

Diagnosis. Male epiproct: Ep-scl narrow and pointed in dorsal view, tip straight, long and acute in lateral view; ventral membranous section ends far before the base in lateral view, apical spines stout, distributed also on the apex of Ep-scl. Process of male Tg 9: high, perpendicularly elevated, 2× wider than Ep-scl, rectangular and with indenting sides caudally. Males produce sequences of (2)-3-4-(6) drumming calls (Figs. 166, 174–178). Calls are monophasic beat series in which beats are produced with gradually increasing inter-beat intervals (Fig 190, red box plots). Inter beat intervals vary between 70–130 ms. Call duration varies between 350–750 ms and calls contain 4–10 beats. Inter call intervals increase during call sequence and vary between 350–3250 ms. All these parameters refer to signals produced at ambient air temperature between 15–21 °C. Male female drumming duet is a long sequence of male call—female answer alternations, where female answers may overlap the terminal part of male calls (Figs 186–187).

Type material. Holotype male: SLOVAKIA: Banskobystrický Region, Krupinská Planina, Pôtor, Stará Rieka Stream, N 48°13.731' E 19°24.946', 200 m a.s.l., 16.03.2010, leg. D. Murányi, K. Orci (HNHM: PLP3882; drumming recorded as 2010/No.1). Paratypes: same locality and date: 1f (HNHM: PLP3883; drumming recorded as 2010/No.1, pair of the holotype), 1m (HNHM: PLP3884; drumming recorded as 2010/No.2), 1m (HNHM: PLP3885; drumming recorded as 2010/No.3), 1m (HNHM: PLP3886; drumming recorded as 2010/No.4, Fig. 175), 1m (HNHM: PLP3887; drumming recorded as 2010/No.5), 1m (HNHM: PLP3888; drumming recorded as 2010/No.6), 15m, 1f larva (HNHM: PLP3372), 4m (BYUC); 24.03.2006, leg. L. Dányi, J. Kotschán, D. Murányi: 6m 2f, 1f larva (HNHM: PLP1832; two male, two male terminalia, one female and the larva prepared for SEM, specimens used for drawings and photos Figs. 59, 64, 67–69, 71, 77, 78–81, 108–109, 119, 121, 127, 148), 2m (GVC), 2m (PZC); 23.03.2009, leg. N. Hordós, D. Murányi, J. Papp, Zs. Ujvári: 2m 2f, 1f larva (HNHM: PLP3044); 23.03.2011, leg. K. Orci: 1m (HNHM: PLP3811; used for molecular studies as 300985, drumming recorded as 2011/No.1), 1m (HNHM: PLP3812; used for molecular studies as 300982, drumming recorded as 2011/No.2), 1m (HNHM: PLP3813; drumming recorded as 2011/No.3), 1m (HNHM: PLP3814; used for molecular studies as 300992, drumming recorded as 2011/No.4), 1m (HNHM: PLP3815; used for molecular studies as 301003, drumming recorded as 2011/No.5), 1m (HNHM: PLP3816; drumming recorded as 2011/No.6), 1m (HNHM: PLP3808; used for molecular studies as 300983, drumming recorded as 2011/No.7), 1m (HNHM:

PLP3881; used for molecular studies as 300981, drumming recorded as 2011/No.8), 1m (HNHM: PLP3817); HUNGARY: Borsod-Abaúj-Zemplén County, Zemplén Mts., Kishuta, Kemence Stream, N 48°27.298' E 21°28.707', 175 m, 08.03.2011, leg. T. Kovács, D. Murányi, K. M. Orci, G. Puskás: 3m (HNHM: PLH1242; one male used for drawings Figs. 128, 149), 1m (HNHM: PLH1258; used for molecular studies as 300989, drumming recorded as 2011/No.1), 2m (HNHM: PLH1300; used for molecular studies as 30100 and 30101, drumming not recorded), 1m (only bioacoustic study, specimen escaped; drumming recorded as 2011/No.4, Fig. 174); SERBIA: Syrmia District, Fruska Gora, Vrdnik, stream NW of the village, N 45°08.583' E 19°46.299', 275 m, 15.03.2011, leg. T. Kovács, G. Magos, D. Murányi: 1m (HNHM: PLP3818; used for drawings Figs. 129, 150, for molecular studies as 300996, drumming recorded as 2011/No.1, Fig. 176), 1m (HNHM: PLP3889; used for molecular studies as 300962); Braničevo District, Homoljske Planina, Krepoljin, stream N of the village, N 44°16.582' E 21°36.553', 290 m, 16.03.2011, leg. T. Kovács, G. Magos, D. Murányi: 1m (HNHM: PLP3820; used for molecular studies as 300965, drumming recorded as 2011/No.1, Fig. 177), 1m (HNHM: PLP3821; used for molecular studies as 300951); Zlatibor District, Zlatibor Mts., Crni Rzav Stream along the road No.21, N 43°39.731' E 19°42.575', 1010 m, 17.03.2011, leg. T. Kovács, G. Magos, D. Murányi: 1m (HNHM: PLP3582; used for drawings Figs. 130, 151), 1m (HNHM: PLP3819; used for molecular studies as 300994, drumming recorded as 2011/No.1), 1f (HNHM: PLP3890; used for molecular studies as 300952), 1m (only bioacoustic study, specimen escaped; drumming recorded as 2011/No.3, Fig. 178).

Other material—Records based on morphology: AUSTRIA: Lower Austria State, Purgstal, Bahnhof, im Flug, 18.03.1971, leg. Ressler: 1m (PZC); only as 'Austria', 1861, leg. Rogh.: 2m (WNHM); GERMANY: Schleswig-Holstein State, Busdorf, Kr. Schleswig, 15.01.1951, leg. H. Dittmar: 2m (PZC); Saxony-Anhalt State, Harz, Nagelbach, 15.03.2005, Lutz Tappenbeck: 3m 1f (PZC); HUNGARY: Nógrád County, Cserhát Mts., Nógrádszakál, Ipoly River at the gorge of Párizs Stream, 03.04.2005, leg. T. Kovács: 1m (MM); Borsod-Abaúj-Zemplén County, Zemplén Mts., Kishuta, Komlóska Stream, 220 m, 14.03.2004, leg. D. Murányi, Zs. Sívári: 1m (HNHM); Borsod-Abaúj-Zemplén County, Zemplén Mts., Kishuta, Kemence Stream, 175 m, 14.03.2004, leg. D. Murányi, Zs. Sívári: 1f larva (HNHM); SLOVAKIA: Banskobistrický Region, Javorie Mts., Horný Tisovník, Kostolné, Tisovník Stream, 470 m, 24.03.2006, leg. L. Dányi, J. Kotschán, D. Murányi: 8m 1f (HNHM); further 20 males present in the WNHM, collected during second half of the 19th century, but without any reliable labels (some are possibly from Mainz or Bergen, collected by F. Brauer in 1865).

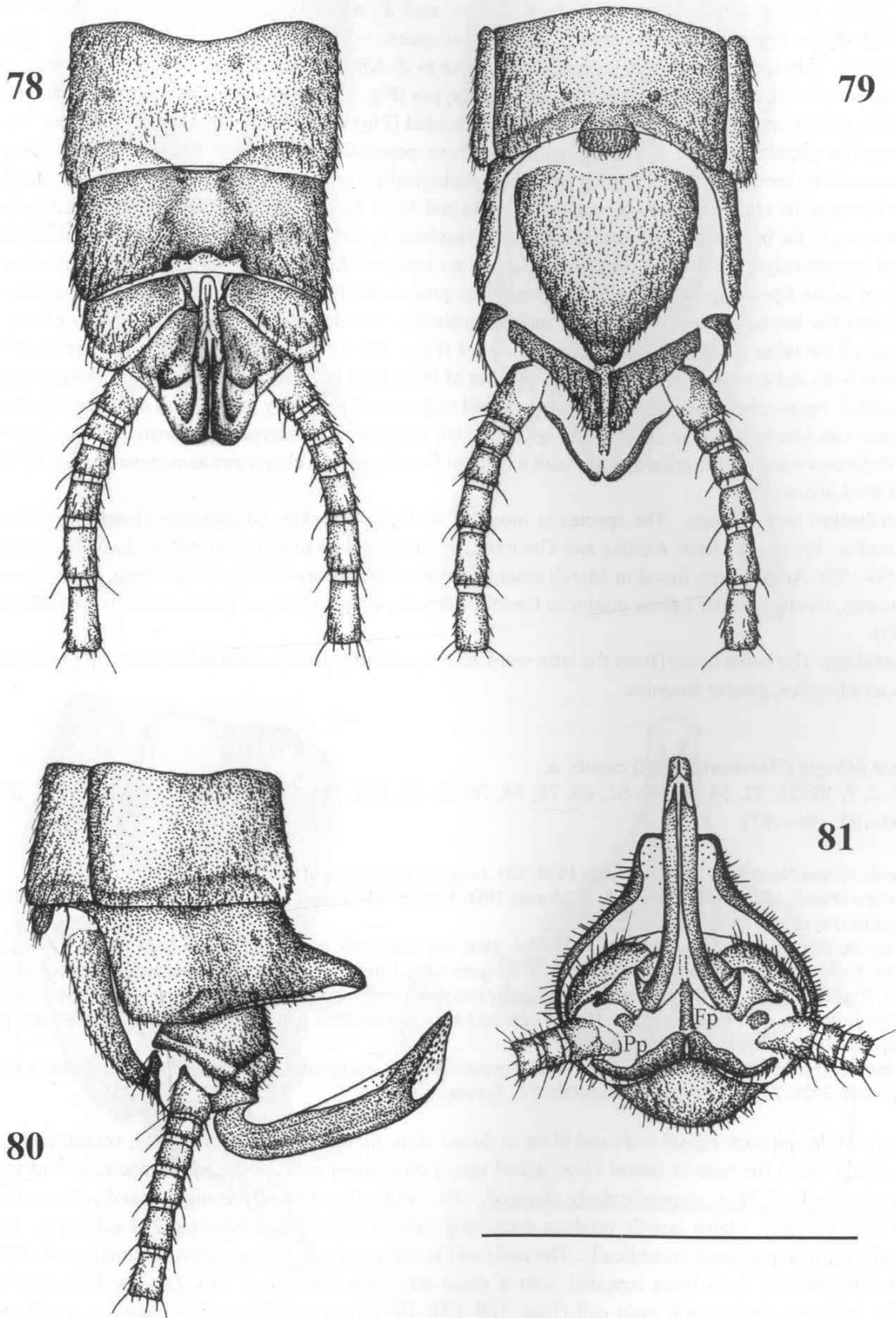
Description. Head, thorax, appendages and basal segments of the abdomen generotypic. Males micropterous, females macropterous. Body length: holotype 7.5 mm, male paratypes 6.5–8.0, female paratypes 8.0–10.5 mm; forewing length: holotype 1.6 mm, male paratypes 1.3–1.7 mm, female paratypes 8.5–11.0 mm.

Male terminalia (Figs. 78–81, 121): Process of Tg 9 high, perpendicularly elevated, apex 2× wider than the medial section of Ep-scl; rectangular in shape, apex bearing two small hump-like tips; sides indented in caudal view, forming the membranous portion narrowest medially (Figs. 148–151). Tg 10, B-scl and Lb-scl generotypic. Ep-scl narrow and pointed in dorsal view, medially not swollen, its medial width ½ to ⅓ of basal width; tip straight and acute in lateral view, divided section long. Ventral membranous part between the division of Ep-scl ends far before the base in lateral view; apical spines stout, distributed not only on the membranous part but extend to the Ep-scl (Figs. 108–109, 119, 127–130). I-scl generotypic, Ec long and rarely everted on the non in-copula specimens. St 9 slightly projecting medially, vesicle medium sized to large, Fig. 79 illustrates the smallest of the range. Sg rounded with pronounced triangular shape, tip usually incised. Pp, Fp, Rp and cerci generotypic.

Female subgenital plate (Fig. 64): Less rectangular than usual, posterior margin rounded and sometimes slightly overhanging the segment. Antero-lateral recess usually distinct, the plate is entirely brown; lateral sclerites relatively large.

Drumming: Males produce (2)-3-4-(6) drumming calls in a sequence (Fig. 166). Calls in a sequence are similar to each other. However, the first call is generally shorter and of lower amplitude than the following ones. Calls are monophasic signals consisting of one beat group with inter beat intervals increasing gradually toward the end of beat group (Fig 190: red box plots, Appendix Table 1). The amplitude envelope of calls are of the following main types: a full length crescendo (e.g. see the second call in Fig. 175), an initial crescendo+nearly constant main part (see 4th call in Fig. 176) or a crescendo first half+decreasing second half pattern (e.g. 4th call in Fig. 177). Calls follow each other with increasing inter-call intervals. See Figs. 174–178 for the oscillographic pattern of the male drumming calls of this species. Descriptive statistics of five drumming characters are presented in Table 6. See Fig. 190 for a box plot series showing the variation of inter-beat intervals within a call in relation to the other three *Zwicknia* species, where drumming signals are characterized in this study. Appendix Table 1 contains the

measurement data of inter-beat intervals of this species. The male female drumming duet is a long sequence of male call—female answer, where the female answers sometimes overlaps the terminal part of male calls (Figs. 186–187).



FIGURES 78–81. Male terminalia of *Zwicknia acuta* Murányi & Orci, sp. n.; paratype, Slovakia, Banskobystrický Region, Krupinská Planina, Pôtor—78: dorsal view; 79: ventral view; 80: lateral view; 81: caudal view (Fp: fusion plate; Pp: paraprot) —scale 1 mm.

Genetics: Three different haplotypes were found corresponding well to the geographical distribution (Hungary, Serbia, and Slovakia). The Slovakia haplotypes clustered at the same node as the northern Hungarian population, resulting in 0.4% nucleotide divergence and two diagnostic characters. We found that the specimens from Maljen Mts. of Serbia included individuals of both *Z. bifrons* and *Z. acuta* (Fig. 192). However, despite that the morphology and mating calls correspond to *Z. bifrons* in all cases.

Affinities. This species is morphologically very close to *Z. bifrons*. One of the Serbian populations (Maljen Mts.) may be hybrids, as they share mitochondrial haplotypes (Fig. 192). Individuals have drumming signals and morphology similar to *Z. bifrons* and illustrations are provided (Figs. 143, 156, 173). However, nearby Slovakian and Hungarian populations not sympatric with *Z. bifrons* populations and other Serbian populations exhibit differences in both morphology and mating calls. Morphologically, the males differ by having narrow and pointed Ep-scl with an acute and straight apex, instead of wide and blunt Ep-scl and upcurved tip; ventral membranous section terminate far before the base instead of nearly reaching it, and Tg 9 process with indented sides caudally instead of consistently narrow sides. Males of *Z. acuta* are easily distinguishable from other *Zwicknia* species on the basis of acute Ep-scl tip and very high, rectangular process of Tg 9. Females are difficult to separate with certainty and the larvae are morphologically indistinguishable. The drumming signals of *Z. acuta* clearly differ from those of the other three *Zwicknia* species analysed (Figs. 165–184). Male drumming calls are shorter (Fig. 191, Tables 6–8) and contain generally a fewer number of beats than in *Z. bifrons*, but are much longer than in *Z. kovacsi* and *Z. rupperti*. The number of calls in a call sequence is generally higher, and calls are repeated with shorter inter call intervals than in *Z. bifrons* (Figs. 165–166, Tables 6–7). Molecular diagnostics of this species also yielded differences among the other species with a node of four diagnostic characters as compared to *Z. bifrons* and 1–5% of total divergence.

Distribution and ecology. The species is found in southern Slovakia, northeastern Hungary, northern and central Serbia. Specimens from Austria and Germany are attributed to this species on the basis of morphology (Figs. 196–197). Adults were found in March emerging from slow or moderately fast flowing, large to medium-sized streams, mostly in alder (*Alnus glutinosa* Gaertn.) forests, but also in open grasslands between 200–1,000m (Fig. 193).

Etymology. The name *acuta* (from the latin word *acutus*, meaning acute) refers to the acute tip of the epiproct. Used as an adjective, gender feminine.

***Zwicknia bifrons* (Newman, 1838) comb. n.**

(Figs. 1–2, 7, 10, 23, 32, 56, 58, 62–63, 66, 72, 74, 76, 82–85, 106, 114, 120, 139–143, 152–156, 165, 169–173, 185, 190–192, 196–197).

Chloroperla bifrons Newman, 1838—Newman 1838: 401. (original description of the adult)

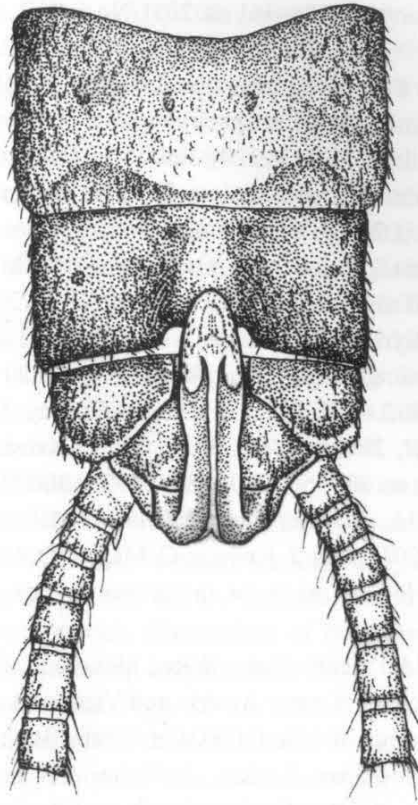
Capnia nigra (Pictet, 1833)—figures in at least Morton 1896, Hynes 1940, Hynes 1941 and Hanson 1946 (enumerated under the general synonymies) refers to *Z. bifrons*.

Capnia bifrons (Newman, 1838)—Kimmins 1947: 261. (stat. rev and comb. n.);—figures in at least Brinck 1949, Kimmins 1950a, Kimmins 1950b, Brinck 1952, Hynes 1955a, Hynes 1958, Illies 1955, Khoo 1964, Lillehammer 1965, Lillehammer 1974, Rupperecht 1976 and Lillehammer 1988 (enumerated under the general synonymies) refers to *Z. bifrons*;—drumming signals in Rupperecht 1965, Rupperecht 1968, Rupperecht 1976 (enumerated under the general synonymies) and partly in Rupperecht 1982 (Fig. 2b) refers to *Z. bifrons*.

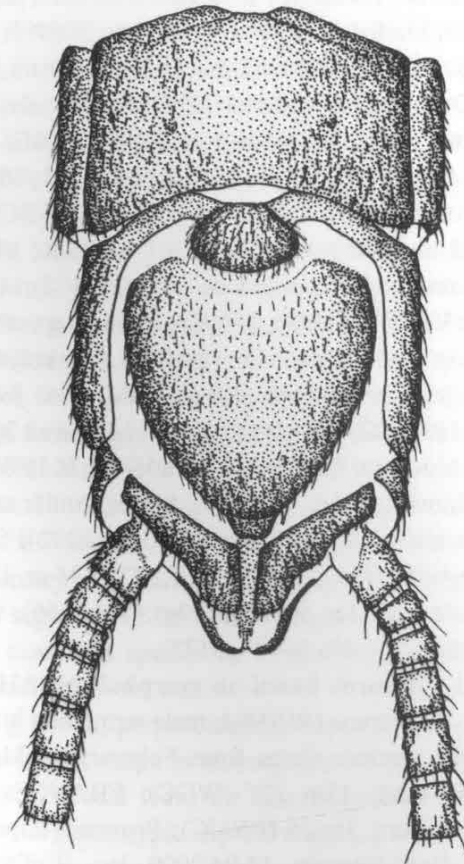
Capnia bifrons (Newman, 1838) Capnor race sensu Rupperecht 1997—Rupperecht 1997: 94. (drumming signals); Enting & Rupperecht 2001: 71 (clarification as the nominal *C. bifrons*).

Diagnosis. Male epiproct: Ep-scl wide and blunt in dorsal view, tip upcurved in lateral view; ventral membranous section nearly reach the base in lateral view, apical spines distributed only on the membranous part of the apex. Process of male Tg 9: high, perpendicularly elevated, <1½× wider than Ep-scl, rectangular, and with continuously narrow sides caudally. Males usually produce drumming calls in sequences containing 2–3 calls (Fig. 165), but single calls are also produced sporadically. The male call is a monophasic beat-group with duration of 1400–2400 ms and composed of 7–16 beats repeated with a mean inter-beat interval of 140–230 ms. Inter-beat interval gradually increases during each male call (Figs. 169–173, 190). Inter-call interval increases as a call sequence proceeds, but its mean value is between 1400–6300 ms. All of these drumming character values refer to signals produced at ambient air temperature between 15–21°C. The male-female drumming duet is a long sequence of male call—female answer alternation (Fig. 185).

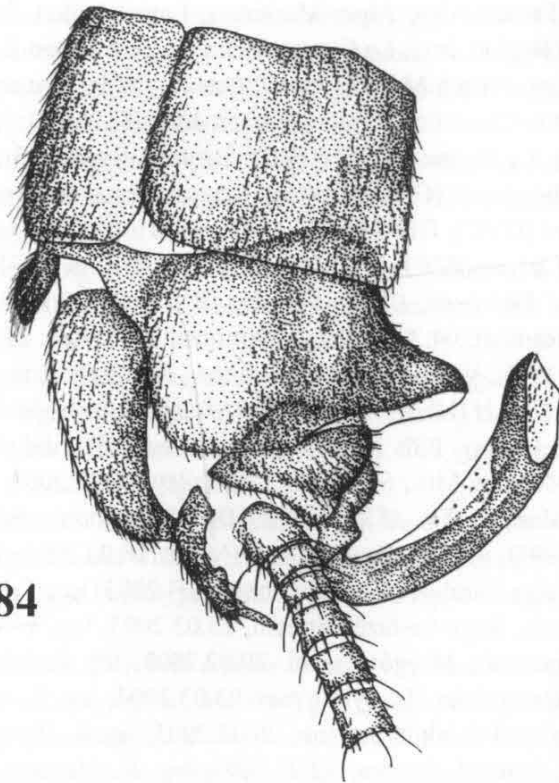
82



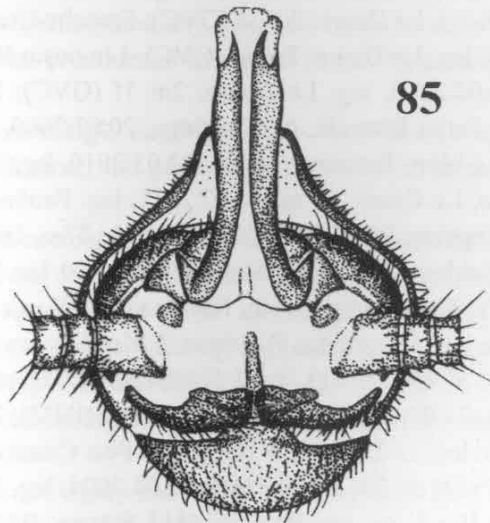
83



84



85



FIGURES 82–85. Male terminalia of *Zwicknia bifrons* (Newman, 1838); Hungary, Pest County, Pilis Mts., Szentendre—82: dorsal view; 83: ventral view; 84: lateral view; 85: caudal view—scale 1 mm.

Material examined. HUNGARY: Veszprém County, Bakony Mts., Bakonybél, Gerence Stream at Borostyán Spring, N 47°14.596' E 17°43.835', 275 m, 24.02.2011, leg. D. Murányi, K. M. Orci: 1m (HNHM; used for drawings Figs. 142, 155, for molecular studies as 300995, drumming recorded as 2011/No.1, Fig. 170); Pest County, Pilis Mts., Szentendre, Dömörkapu, Bükkös Stream, N 47°41.751' E 18°59.904', 260 m, 23.02.2010, leg. D. Murányi, K. M. Orci: 7m 4f, 1m larva (HNHM; one male, three male terminalia, one female and the male larva prepared for SEM, two female and parts of a male terminalia prepared on slides, specimens used for drawings and photos Figs. 1–2, 7, 10, 23, 32, 56, 58, 62–63, 66, 72, 74, 76, 82–85, 106, 114, 120), 6m 7f (HNHM; drummings recorded as 2010/No.1–3, 6–9), 4m (BYUC), 1m 1f (GVC; drummings recorded as 2010/No.4), 1m 1f (PZC; drummings recorded as 2010/No.5); 26.02.2011, leg. K. M. Orci: 2m (HNHM; used for molecular studies as 300991, 300978, drummings recorded as 2011/No.1–2); 14.03.2011, leg. K. M. Orci: 3m (HNHM; used for molecular studies as 300979, 300986, 300984, drummings recorded as 2011/No.3–4, Fig. 169); 27.03.2011, leg. K. M. Orci: 1m (HNHM); Pest County, Börzsöny Mts., Szokolya-Királyrét, Szén Stream, N 47°53.672' E 18°58.706', 255 m, 05.03.2011, leg. D. Murányi: 4m (HNHM; used for drawings Figs. 139, 152, for molecular studies as 300990, 300977, 301002, 300980, drummings recorded as 2011/No.1–2, 4, Fig. 171); Heves County, Mátra Mts., Gyöngyössolymos, Monostor Stream, N 47°49.918' E 19°55.801', 260 m, 07.03.2011, leg. T. Kovács: 12m 2f (HNHM; used for drawings Figs. 140, 153, for molecular studies as 300950, 300972, 300976, 300953, 300954, 300975, drummings recorded as 2011/No.1–5, Fig. 172); SERBIA: Zlatibor District, Maljen Mts., Brajkovići, stream N of the village, N 44°02.244' E 19°54.827', 445 m, 17.03.2011, leg. T. Kovács, G. Magos, D. Murányi: 2m 1f (HNHM; one male used for drawings Figs. 143, 156), 9m (HNHM; used for molecular studies as 300994, drummings recorded as 2011/No.1–7 Fig. 173).

Other material—Records based on morphology: AUSTRIA: Vienna State, Wien, Maubach, 03.03.1953, leg. E. Pomeisl: 1m 1f, 3 larvae (WNHM; male terminalia in microvial); Lower Austria and Vienna States, Vienna Woods, many brooks, various dates from February to March, leg. W. Graf (WGC); Styria State, Lanzegg, 16.03.2004, leg. W. Graf: 15m 22f (WGC); FRANCE: Rhône-Alpes Region, Ardèche, Rivere de Celle, 20.03.1950, leg. J. Aubert: 3m 3f (BYUC); Provence-Alpes-Côte d'Azur Region, Southern French Alps, Var, Artuby, La Martre, Pont Romain, 13.04.2009, leg. Brulin: 1m (GVC); Provence-Alpes-Côte d'Azur Region, Southern French Alps, Alpes-de-Haute-Provence, Esteron, Soleihas, 1100 m, 21.02.2009, leg. Le Doare: 7m 9f (GVC); Provence-Alpes-Côte d'Azur Region, Southern French Alps, Alpes-Maritimes, Lane, Andon, 1145 m, 13.04.2009, leg. Le Doare: 2m 1f (GVC); Franche-Comté Region, Jura, La Clauge, Belmont, Jura Forest Reserve, 10.04.2009, leg. Le Doare: 2m 1f (GVC); Limousin Region, French Massif Central, Creuse, Tarde, Champagnat, 440 m, 03.03.2010, leg. Le Doare: 2m 1f (GVC); Poitou-Charentes Region, French Massif Central, Vienne, Moulisme, Petite Blourde, N147 bridge, 20.02.2009, leg. Le Doare: 3m 4f (GVC); Brittany Region, Bretagne, Finistère, Le Men, Tremorel, 105 m, 21.03.2010, leg. Brulin: 5m 1f (GVC); Brittany Region, Bretagne, Morbihan, Pont Drimo, Le Cours, 65 m, 12.02.2011, leg. Brulin: 1m (GVC); GERMANY: Schleswig-Holstein State, Plön, stream at Engelau, 26.02.1966, leg. P. Zwick: 33m, 1m 2f larvae (PZC); 03.1966, leg. P. Zwick: 13m 2f, 3f larvae (BYUC); Schleswig-Holstein State, Dallsek, 30 km E of Hennburg, 01.03.1966, leg. P. Zwick: 18m (BYUC); HUNGARY: Vas County, Őrség, Kercaszomor, Kerca Stream, 16.04.2002, leg. A. Ambrus, T. Kovács: 2f (MM); 11.03.2003, leg. A. Ambrus, P. Juhász, T. Kovács: 1m 1f (MM); Veszprém County, Bakony Mts., Döbrönte, Bittva Stream, 230 m, 30.03.2006, leg. J. Kontschán, D. Murányi: 2m 1f (HNHM); Veszprém County, Bakony Mts., Zirc-Szarvaskút, 21.04.1988, leg. S. Tóth: 3m (HNHM); Pest County, Pilis Mts., Pilisszentkereszt, Szurdok Stream, 25.03.2006, leg. L. Dányi: 2m (HNHM); Pest County, Börzsöny Mts., Szokolya, Les Valley, 08.02.2003, leg. L. Papp, Zs. P.-Bajza: 3m 4f (HNHM); 08.04.2004, leg. D. Murányi: 1m, 4f larvae (HNHM); Pest County, Börzsöny Mts., Szokolya-Királyrét, Bagoly-bükki Stream, 25.03.2003, leg. T. Kovács: 1m (MM); 18.03.2004, leg. A. Ambrus: 3m 7f (MM); Pest County, Börzsöny Mts., Szokolya-Királyrét, Szén Stream, 25.03.2003, leg. T. Kovács: 1m (MM); Pest County, Börzsöny Mts., Szokolya-Királyrét, Nagy-vasfazék Stream, 25.03.2003, leg. T. Kovács: 1m (MM); Pest County, Börzsöny Mts., Kismaros, Káposztás, Morgó Stream, 20.02.2003, leg. P. Juhász, T. Kovács: 3m (MM); Nógrád County, Cserhát Mts., Cserhátszentiván, Zsunyi Stream, 03.03.2004, leg. K. Harnos: 3m (HNHM); Nógrád County, Cserhát Mts., Ecseg, Zsunyi and Cserkúti Streams, 26.02.2003, leg. K. Harnos: 9m 11f (HNHM); Nógrád County, Cserhát Mts., Felsőtold, Szurdok Stream, 12.03.2003, leg. K. Harnos: 8m 6f (HNHM); Nógrád County, Cserhát Mts., Garáb, Garábi Stream, 04.03.2003, leg. K. Harnos: 16m 5f, 1m 4f larvae (HNHM); Nógrád County, Mátra Mts., Bátorterenyé, Lengyendi Stream at the forester house, 14.02.2004, leg. K. Harnos: 1m (HNHM); Heves County, Mátra Mts., Mátraszentimre, Csörgő Stream, 13.03.2004, leg. K. Harnos:

2m, 1 f larva (HNHM); Heves County, Mátra Mts., Mátrafüred, Bene Stream, 20.02.2004, leg. D. Murányi: 1m (HNHM); Heves County, Mátra Mts., Gyöngyössolymos, Cserkő-bánya, Monostor Stream, N 47°49.918' E 19°55.801', 260 m, 16.03.2001, leg. T. Kovács: 3m 1f (MM); 25.03.2001, leg. T. Kovács: 3f (MM); 19.04.2001, leg. T. Kovács: 8f (MM); 14.03.2002, leg. T. Kovács: 3f, 3f exuviae (MM); 19.04.2002, leg. T. Kovács: 1f (MM); 22.02.2003, leg. T. Kovács: 1m 3f (MM); Heves County, Mátra Mts., Gyöngyössolymos, Cserkő-bánya, Nagy Stream, 25.03.2001, leg. T. Kovács: 1m 1f (MM); 14.03.2002, leg. T. Kovács: 7m (MM); 08.03.2003, leg. D. & T. Kovács: 2m (MM); 31.03.2004, leg. T. Kovács: 1m (MM); 13.03.2005, leg. T. Kovács: 2m (MM); Heves County, Mátra Mts., Domoszló, Tarjánka Stream, 16.03.2002, leg. D. Murányi: 3m (HNHM); Heves County, Bükk Mts., Nagyvisnyó, Nagy-völgyi Stream, 22.01.2003, leg. D. Murányi: 2m (HNHM; one male used for drawings Figs. 141, 154); Borsod-Abaúj-Zemplén County, Zemplén Mts., Vágáshuta, Hercegekúti Stream, 170 m, 14.03.2004, leg. D. Murányi, Zs. Sóvári: 3m 1f, 1m larva (HNHM); Borsod-Abaúj-Zemplén County, Zemplén Mts., Erdőhorváti, Tolcsva Stream at the third bridge, 170 m, 15.03.2003, leg. D. Murányi, Zs. Sóvári: 4m, 2m larvae, 1m exuviae (HNHM); ITALY: Lazio Region, Falscione Brooklet, 450m, 06.03.1989, leg. ?: 3m 2f (BYUC); NORWAY: Akershus County, Hürdal, Fallbekken, 13.04.1969, leg. Smedstad: 1m 1f (BYUC); ROMANIA: Cluj County, Cluj-Napoca, Gorbo valley, 14.03.1964, leg. B. Kis: 36m 26f (HNHM); SLOVAKIA: Banskobystrický Region, Krupinská Planina, Čebovce, Čebovský Stream, 180 m, 24.03.2006, leg. L. Dányi, J. Kontschán, D. Murányi: 1m, 3f larva (HNHM); SWEDEN: Gotland County, SK Rövarkulan, 25.03.1949, leg. P. Brinck: 2m 2f (BYUC); UNITED KINGDOM: Scotland, Carlisle, early 20th century?, leg. K.J. Morton?: 1m (WNHM).

Description. Head, thorax, appendages and basal segments of the abdomen generotypic. Males micropterous, females macropterous. Dimensions of the presently examined specimens: body length: males 7.0–9.0, females 8.0–10.5 mm; forewing length: males 0.8–1.3 mm, females 8.0–9.5 mm.

Male terminalia (Figs. 82–85, 120): Process of Tg 9 high, perpendicularly elevated, its apex is less than one and a half times wider than the medial section of Ep-scl; its shape is rectangular, the apex smooth or bears two hardly visible hump-like tips; sides constantly narrow in caudal view, the membranous portion narrowest in the apical portion (Figs. 152–156). Tg 10, B-scl and Lb-scl generotypic. Ep-scl wide and blunt in dorsal view, not swollen medially, medial width the $\frac{2}{3}$ of basal width; tip upcurved in lateral view, divided section short. Ventral membranous part between the divisions of Ep-scl nearly reaches the base in lateral view; apical spines short, distributed only on the membranous part (Figs. 106, 114, 139–143). I-scl generotypic, Ec short and often partly or fully everted on the non in-copula specimens. St 9 slightly projecting medially, vesicle large to medium sized, Fig. 83 shows the largest size of the range. Sg rounded with not so pronounced triangular shape, tip usually rounded. Pp, Fp, Rp and cerci generotypic.

Female subgenital plate (Fig. 62): Rectangular, posterior margin slightly rounded and usually equal to the segment's posterior margin. Antero-lateral recess usually distinct; the plate is entirely brown; lateral sclerites relatively large.

Drumming: Males produce repeated sequences of 2–3 drumming calls (Fig. 165), but sporadically single calls can also be observed. Calls are monophasic: inter-beat intervals increase gradually during the beat sequence of a call (Figs. 169–173, 190, Appendix Table 2). Calls in a sequence are rather similar to each other. The peak amplitude of beats generally shows a crescendo-decrescendo pattern during each call. See Figs. 169–173 for the oscillographic pattern of the male drumming calls of this species and also Table 7 for descriptive statistics of the examined five sonometric parameters. The male female drumming duet a long sequence of male call—female answer interchange (Fig. 185).

Genetics: Three different haplotypes were found, two from Hungary and one from Serbia (Fig. 192), with 0.5% of divergence, and with seven diagnostic characters separating them. *Zwicknia bifrons* specimens from Maljen Mts. of Serbia share haplotypes with *Z. acuta*. Despite this, morphology and mating calls correspond to *Z. bifrons* in all cases.

Affinities. *Zwicknia bifrons* is closely related to *Z. acuta*, and this affinity is discussed above. The epiproct is similar to *Z. rupprechtii*, but the Tg 9 process is high and perpendicularly elevated in contrast to being low and caudally projecting in *Z. rupprechtii*. In addition to *Z. acuta* and *Z. rupprechtii*, males of *Z. bifrons* are easily distinguishable from other *Zwicknia* on the basis of upcurved Ep-scl tip and high, rectangular process of Tg 9. Females are difficult to distinguish, and the larvae are morphologically indistinguishable. The drumming signals of *Z. bifrons* are clearly different from those of the other three *Zwicknia* species where drumming was examined. This species produce the longest calls and drums with the slowest beat repetition rate among the investigated species.

These two rhythmic characters clearly separate the calls of this species from the calls of the other three species which drum faster and produce shorter male calls (see Figs 190, 191). Regarding the number of calls in a sequence, the male drumming signals of *Z. bifrons* are intermediate and overlap with *Z. acuta* and *Z. rupperti* (and *Z. kovacsi*). *Z. bifrons* differs genetically from the other species with 10 diagnostic characters and with > 2% nucleotide divergence.

Distribution and ecology. This species was originally described from Scotland. Drumming data has confirmed the occurrence of this species throughout the British Isles, Scandinavia, and southwards into the Alps (Fig. 196). We have confirmed *Z. bifrons* in northern and Central Hungary. Specimens of this species have also been identified from Austria, France, Germany, and Romania on the basis of morphology (Fig. 196–197). Adults were collected in January to May from the vicinity of slow to moderately fast flowing, medium-sized streams, usually in alder (*Alnus glutinosa*), but also in beech (*Fagus sylvatica*) forests between 150 and 600 m.

Remarks. The species was described on the basis of one or more females. A single female type apparently existed (Morton 1896). Despite that females of *Zwicknia* are difficult to specifically distinguish, its identity with the above material studied is supported by the homogeneity of British populations, both in drumming signals (Ruppert 1997) and morphology based on the previously published figures (see under synonymies).

TABLE 6. Descriptive statistics for the examined rhythmic characters of the male drumming calls of *Zwicknia acuta* Murányi & Orci, sp. n., and also for the ambient air temperature during the sound recordings.—"n" is the number of male specimens examined. In each character data points where mean values obtained for each examined male on the basis of 1–10 signal measurements per specimen. Number of examined specimens per population: Hungary: Zemplén Mts—4; Slovakia: Krupinská Planina—10; Serbia: Fruska Gora—4, Homoljske Planina—1, Zlatibor Mts—4.

	n	mean	SD	min	max
Call duration (ms)	23	546.8	102.07	378.8	727
Number of beats per call	23	6.577	1.469	4.6	10
Mean beat interval (ms)	23	100.6	12.44	81.6	128
Inter-call interval within a call sequence (ms)	23	888	548.2	379	3216
Number of calls in a call sequence	23	3.238	1.037	2	6
Air temperature (°C)	23	18.7	1.46	15.1	20.8

***Zwicknia kovacsi* Murányi & Gamboa, sp. n.**

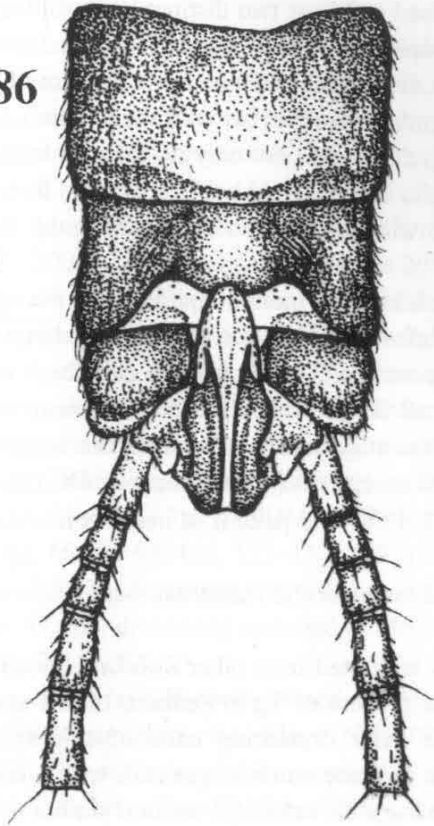
(Figs. 49–51, 53–55, 86–89, 110, 116, 123, 131–132, 160, 168, 183–184, 190–192, 194, 196–197).

Diagnosis. Male epiproct: Ep-scl medially swollen, wide and blunt in dorsal view, tip straight in lateral view; ventral membranous section terminates far before the base in lateral view, apical spines thin and long, distributed also on the apex of Ep-scl. Process of male Tg 9: wide, perpendicularly elevated, 2 × wider than the swollen part of the Ep-scl, bearing two distinct apical horns. Males produce short (150–160 ms), monophasic, percussive calls. A call is composed of 6–7 beats that follow each other with nearly constant inter-beat intervals (27–34 ms at 17–18 °C ambient air temperature). Calls are produced sporadically.

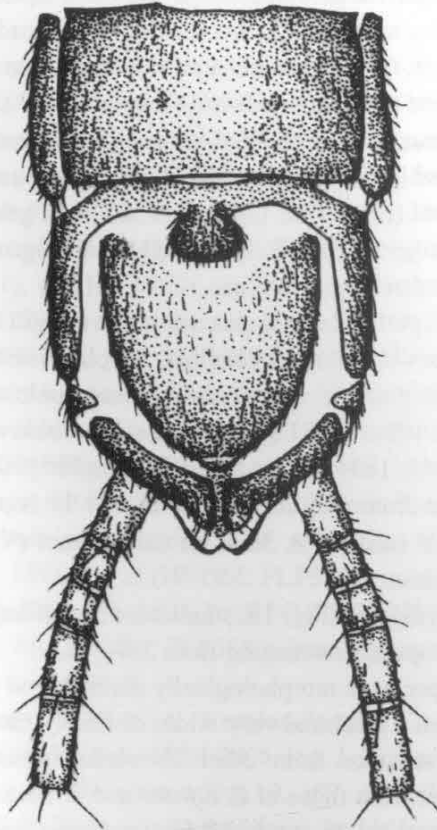
Type material. Holotype male: ROMANIA: Maramureş County, Rodna Mts., Borşa-Staţiunea Borşa, Cimpioies Stream above the village, N 47°36.323' E 24°46.828', 930 m a.s.l., 02.04.2011, leg. T. Kovács, D. Murányi (HNHM: PLP3809; used for drawings Figs. 49–51, 53–55). Paratypes: same locality and date: 1m (BYUC; used for drawings Figs. 86–89, 123, 131–132, 160, for molecular studies as 300988, drumming recorded as 2011/No.2), 1m (HNHM: PLP3807; terminalia prepared for SEM to Figs. 110, 116, used for molecular studies as 300987, drumming recorded as 2011/No.1, Figs. 183–184), 1f (MM).

Description. Head, thorax, appendages and basal segments of the abdomen generotypic. Males micropterous, females macropterous. Body length: holotype 5.5 mm, male paratypes 5.5, female paratype 8.0 mm; forewing length: holotype 1.2 mm, male paratypes 1.2–1.4 mm, female paratype 7.0 mm.

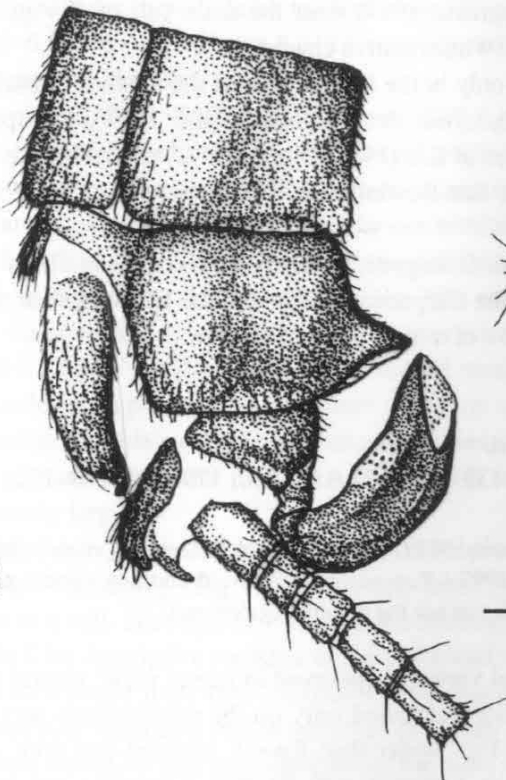
86



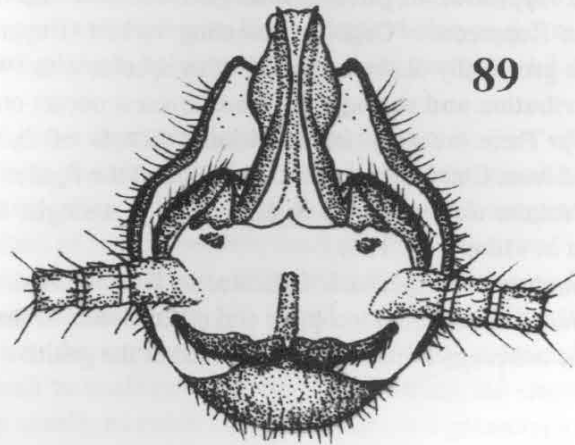
87



88



89



FIGURES 86–89. Male terminalia of *Zwicknia kovacsi* Murányi & Gamboa, sp. n.; paratype, Romania, Maramureş County, Rodna Mts., Borşa-Staţiunea Borşa—86: dorsal view; 87: ventral view; 88: lateral view; 89: caudal view—scale 1 mm.

Male terminalia (Figs. 86–89, 123): Process of Tg 9 high and wide, its apex $1\frac{1}{2}\times$ wider, membranous section in dorsal view $2\times$ wider than the medial swollen section of Ep-scl; apex perpendicularly elevated but the base slightly fold backwards; its sides are slightly sinuous, the apex broadly incised and bear two distinct horns; sides slightly indenting in caudal view, the membranous portion narrowest in the apical part (Fig. 160). Tg 10, B-scl and Lb-scl generotypic. Ep-scl wide and blunt in dorsal view, medially swollen, its medial width is nearly the same like basal width; tip straight in lateral view, divided section short. Ventral membranous part between the division of Ep-scl ends far before the base in lateral view; apical spines thin and long, distributed not only on the membranous part but extend to the Ep-scl (Figs. 110, 116, 131–132). I-scl generotypic, Ec short and contorted in the three known specimens. St 9 not projecting medially, vesicle small. Sg rounded with not so pronounced triangular shape, tip rounded. Pp, Fp, Rp and cerci generotypic.

Female subgenital plate: Rectangular, posterior margin rounded, slightly incised and equal to the segment's posterior margin. Antero-lateral recess distinct, the plate is entirely brown; lateral sclerites relatively large.

Drumming: Males produce single, short monophasic calls sporadically. Within each call, beat repetition frequency is nearly constant (see Fig 190, Appendix Table 4). A call is composed of beats with nearly constant amplitude. See Figs. 168, 183–184 for the oscillographic pattern of the male drumming calls of this species. Mean values of the examined drumming call parameters for the two studied specimens (male 1, male 2): DC (ms): 157.4, 154; NBC: 6.3, 6; MBI (ms): 29.8, 30.8; air temperature ($^{\circ}\text{C}$): 17.7, 17.4. The pattern of male-female drumming duet is presently unknown.

Genetics: The phylogeny (Fig. 192) indicates a well-supported node for the Romanian population separated from other *Zwicknia* populations ranging from 2%–3%.

Affinities. This species is morphologically distinct, and readily separated from other *Zwicknia* known species on the basis of swollen Ep-scl and very wide, distinctly bicornuate process of Tg 9. Females of this species are difficult to reliably separate from other *Zwicknia* species. The male drumming calls of this species are conspicuously different from those of *Z. bifrons* and *Z. acuta* which produce much longer calls with much slower beat repetition rate. Short call duration and fast beat repetition make the male calls of *Z. kovacsi* similar to the calls of *Z. rupprechtii*. Despite the small sample of drumming calls available from *Z. kovacsi* our results suggest that this species produces longer calls composed of more beats, repeated more evenly and with longer inter-beat intervals, than in *Z. rupprechtii*. Regarding its longer mean beat interval the male call of *Z. kovacsi* apparently is less closely similar to Rupprecht's "Capbif" drumming variant (Rupprecht 1997) than the male call of *Z. rupprechtii*. This species is genetically distinct from the other species with 19 informative characters.

Distribution and ecology. *Zwicknia kovacsi* occurs only in the Rodna Mts. of the Eastern Carpathians (Figs. 196–197). There are only four additional records of *Zwicknia* from Romania (Kis 1974), the specimens we examined from Cluj-Napoca are *Z. bifrons*, and the figures of Kis (1974: Fig. 64 A–C) probably also refer to this species. Adults were collected in early April at a single, fast flowing and medium-sized mountain stream at an elevation of 930 m (Fig. 194).

Etymology. The species is dedicated to Tibor Kovács, Gyöngyös, Hungary, in recognition of his contribution to our knowledge on the Plecoptera and other insects of the Carpathian Basin and the Balkans; furthermore, he is one of the collectors of the type series. Used as the genitive of a noun of male gender.

Zwicknia rupprechtii Murányi, Orci & Gamboa, sp. n.

(Figs. 8–9, 60, 65, 70, 73, 75, 90–93, 107, 115, 117, 122, 133–138, 157–159, 167, 179–182, 188–192, 195–197)

Capnia bifrons (Newman, 1838)—drumming signals in Rupprecht 1982 (Fig. 2c) probably refers to *Z. rupprechtii*.

Capnia bifrons (Newman, 1838) Capbif race sensu Rupprecht 1997—Rupprecht 1997: 94. (drumming signals, probably refers to *Z. rupprechtii*); Enting & Rupprecht 2001: 71 (clarification as not the nominal *C. bifrons*).

Diagnosis. Male epiproct: Ep-scl wide and blunt in dorsal view, tip upcurved in lateral view; ventral membranous section nearly reach the base in lateral view, apical spines distributed only on the membranous part of the apex. Process of male Tg 9: very low, caudally projecting, $<1\frac{1}{2}\times$ wider than Ep-scl, rounded and with continuously narrow sides caudally. Male drumming calls are short beat groups with 60–80 ms duration and including 4–6 percussive beats produced with a mean inter beat interval of 17–23 ms. Inter-beat intervals gradually decrease, while the amplitude of beats noticeably increase during a call. Sometimes two calls follow each other with an inter-

call interval of 1.5–5.5 seconds, but generally single calls are produced sporadically. The male-female drumming duet consists of a single male call—female answer or male call—female answer—male response signal exchanges as in Figs. 188–189.

Type material. Holotype male: HUNGARY: Baranya County, Mecsek Mts., Komló-Zobákpuszta, Völgységi Stream, N 46°11.642'E 18°19.071', 305 m a.s.l., 09.03.2010, leg. D. Murányi, K. M. Orci (HNHM: PLH1277; drumming recorded as duett 2010/No.6). Paratypes: same locality and date: 6m, 2m 2f larvae (HNHM: PLH1184; three male terminalias, one female and one male larva prepared for SEM, specimens used for drawings and photos Figs. 8, 70, 73, 75, 115, 135–136, 158), 1m 1f (HNHM: PLH1274; drumming recorded as 2010/No.8), 1f (HNHM: PLH1275; drumming recorded as 2010/No.2, male escaped), 1m 1f (HNHM: PLH1276; used for molecular studies as 300970, 300971, drummings recorded as 2010/No.1), 1f (HNHM: PLH1278; drumming recorded as duett 2010/No.6, pair of the holotype), 1m 1f (HNHM: PLH1279; drumming recorded as 2010/No.5), 1m 1f (HNHM: PLH1280; drumming recorded as 2010/No.7, Figs. 179–180), 3m (BYUC), 1m 1f (HNHM: PLH1297; used for molecular studies as 300948, 300949, drummings recorded as 2010/No.3), 1m 1f (HNHM: PLH1298; used for molecular studies as 300963, 300964, drummings recorded as 2010/No.4), 1f (HNHM: PLH1299; used for molecular studies as 300967, drumming recorded as 2010/No.9); CROATIA: Krapina-Zagorje County, Ivanščica Mts., Stari Golubovec, Reka Stream below the village, N 46°10.54' E 16°02.99', 345 m, 06.04.2010, leg. L. Czigány, D. Murányi: 7m (HNHM: PLP3401; one male prepared for SEM, specimens used for drawings and photos Figs. 60, 90–93, 122, 133–134, 137–138, 157, 159), 1m 1f (HNHM: PLP3878; used for molecular studies as 300973, 300974, drummings recorded as 2010/No.2, Figs. 181–182), 1m (HNHM: PLP3879; used for molecular studies as 300968, drumming recorded as 2010/No.1), 1m (HNHM: PLP3880; drumming recorded as 2010/No.3), 2m (GVC), 2m (PZC).

Other material—Records based on morphology: CROATIA: Krapina-Zagorje County, Ivanščica Mts., Lobar, Reka Stream above the village, N 46°09' E 16°05', 330 m, 01.04.2006, leg. J. Kontschán, D. Murányi: 5m 1f (HNHM; one male terminalia prepared for SEM, used for photos Figs. 9, 107, 117); HUNGARY: Baranya County, Mecsek Mts., Komló, Hidas Valley, 360 m, 28.02.2004, leg. D. Murányi: 3m, 1f larva (HNHM); Baranya County, Mecsek Mts., Pécs, Éger Valley, 250 m, 29.02.2004, leg. D. Murányi: 1m 2f, 5m 6f larvae, 2m exuviae (HNHM; one female prepared for SEM Fig. 65).

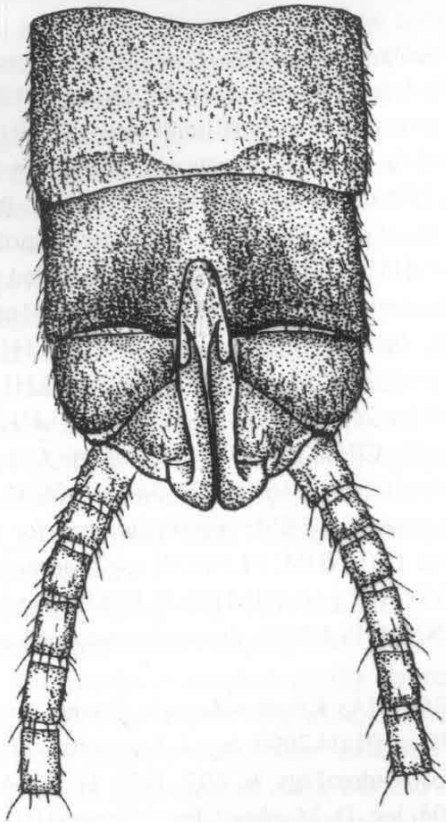
Description. Head, thorax, appendages and basal segments of the abdomen generotypic. Occipital rugosities present on teneral specimens. Males micropterous, females macropterous. Body length: holotype 6.5 mm, male paratypes 6.0–6.5, female paratypes 8.0–8.5 mm; forewing length: holotype 1.6 mm, male paratypes 1.3–2.0 mm, female paratypes 8.0–8.5 mm.

Male terminalia (Figs. 90–93, 122): Process of Tg 9 very low, caudally projecting, its apex is $1\frac{1}{2} \times$ wider than the medial section of Ep-scl; its shape is flattened elliptical, the apex smooth, rounded; sides continuously narrow in caudal view, the membranous portion narrowest apically (Figs. 157–159). Tg 10, B-scl and Lb-scl generotypic. Ep-scl wide and blunt in dorsal view, medially not swollen, its medial width $\frac{2}{3}$ basal width; tip upcurved in lateral view, divided section short. Ventral membranous part between the division of Ep-scl nearly reach the base in lateral view; apical spines short, distributed only on the membranous part (Figs. 107, 115, 117, 133–138). I-scl generotypic, Ec short and often partly or fully everted on the non in-copula specimens, even on tenerals (Figs. 133–138). St 9 slightly projecting medially, vesicle small to medium-sized, Fig. 91 illustrates the smallest size range. Sg rounded with pronounced triangular shape, tip usually rounded. Pp, Fp, Rp and cerci generotypic.

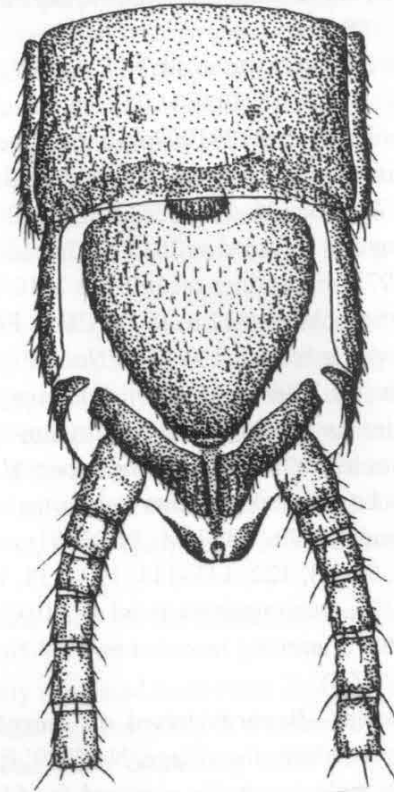
Female subgenital plate (Fig. 65): Rectangular, posterior margin slightly rounded, usually slightly incised and equal to the segment's posterior margin. Antero-lateral recess usually distinct, the plate is entirely brown; lateral sclerites relatively large.

Drumming: Males produce generally single, monophasic calls in a sporadic pattern. Within each call inter-beat intervals decrease gradually (Fig 190, Appendix Table 3). Peak amplitude of beats generally increases along the beat sequence of a call. See Figs. 179–182 for the oscillographic pattern of the male drumming calls of this species, and also Table 8 for descriptive statistics of the examined three sonometric parameters. The male-female drumming duet consists of a single male call—female answer signal exchanges, but also male call—female answer—male response intersexual signalling can be observed (Fig. 189.) Female answer signals are monophasic beat sequences of a similar beat repetition rate as observable in the male call, but are longer and contain more beats than the male signals. For a more detailed quantitative analysis of the male-female duet pattern, recordings from more females will be necessary.

90



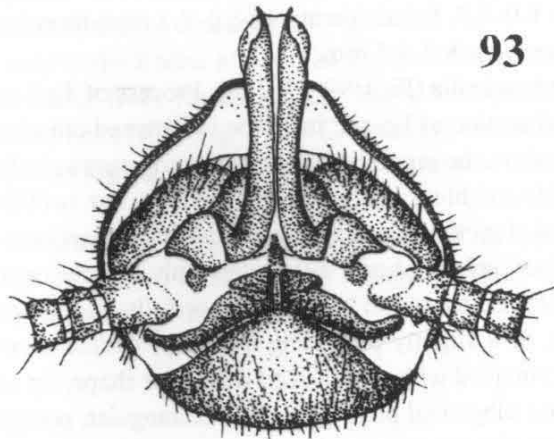
91



92



93



FIGURES 90–93. Male terminalia of *Zwicknia rupprechtii* Murányi, Orci & Gamboa, *sp. n.*; paratype, Croatia, Krapina-Zagorje County, Ivanščica Mts., Stari Golubovec—90: dorsal view; 91: ventral view; 92: lateral view; 93: caudal view—scale 1 mm.

TABLE 7. Descriptive statistics for the examined rhythmic characters of the male drumming calls of *Zwicknia bifrons* (Newman, 1838), and also for the ambient air temperature during the sound recordings.—"n" is the number of male specimens examined. In each character data points where mean values obtained for each examined male on the basis of 1-10 signal measurements per specimen. Number of examined specimens per population: Hungary: Pilis Mts—7, Bakony Mts—2, Börzsöny Mts—4, Mátra Mts—5; Serbia: Maljen Mts—7.

	n	mean	SD	min	max
Call duration (ms)	25	1811	264.7	1443	2389
Number of beats per call	25	11.26	1.684	7.33	15.5
Mean beat interval (ms)	25	178.1	19.2	147.6	229
Inter-call interval within a call sequence (ms)	21	3061	1411.1	1447	6295
Number of calls in a call sequence	24	1.992	0.575	1	3
Air temperature (°C)	25	18.5	1.407	15.8	20.8

Genetics: Two different haplotypes from southwestern Hungary and northern Croatia clustered on the same node with 1% divergence with 5 informative characters separating them. All individuals collected in Hungary and Croatia clustered together.

Affinities. The relationship of *Z. rupprechtii* to *Z. bifrons* is discussed above. In addition, *Z. rupprechtii* males are easily distinguishable from other *Zwicknia* on the basis of upcurved Ep-scl tip and low, caudally projecting process of Tg 9. Females cannot be distinguished from other species of the genus as are larvae morphologically indistinguishable. The male drumming calls of *Z. rupprechtii* are of short duration and have a fast beat repetition, differing from those of *Z. bifrons* and *Z. acuta*, but similar to the calls of *Z. kovacsi*. Distinctive characters of the male calls of *Z. rupprechtii* that differ from those of *Z. kovacsi* are shorter call durations, inter-beat intervals exhibiting a gradual decrease, and the beat peak amplitude with a characteristic increase during the beat call sequence. The calls of *Z. kovacsi* exhibit less of a change in those signal parameters during a call. With their short mean inter-beat intervals the calls of *Z. rupprechtii* are closer to Rupprecht's "Capbif" call variant than the slightly slower calls of *Z. kovacsi*, which stand a little farther from "Capbif". However, regarding the number of beats per call, it is *Z. kovacsi* that is closer to "Capbif" (compare our results to the "Capbif" drumming data in Rupprecht 1997). Male call differences are minor and to examine their significance in female mate choice will require additional studies including play-back experiments. However, the male terminalia of *Z. rupprechtii* is similar to populations producing "Capbif" type signals and *Z. kovacsi* exhibits clear distinctive features from them. *Zwicknia rupprechtii* differs from other species of the genus by 8% genetic divergence with 17 informative characters.

Distribution and ecology. *Zwicknia rupprechtii* occurs in southwestern Hungary and northern Croatia (Figs. 196–197). Populations from the southern Alps have similar drumming signals (Rupprecht 1997), but are not considered to be this species because of the close similarities of the drumming calls with those of *Z. kovacsi*. Adults of *Z. rupprechtii* are active from March to early April and are associated with slow or moderately fast, medium-sized streams flowing through alder (*Alnus glutinosa*) forests between 250 and 350 m (Fig. 195).

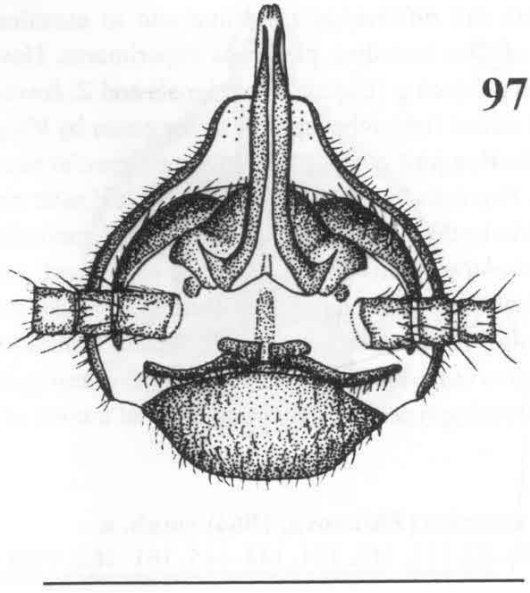
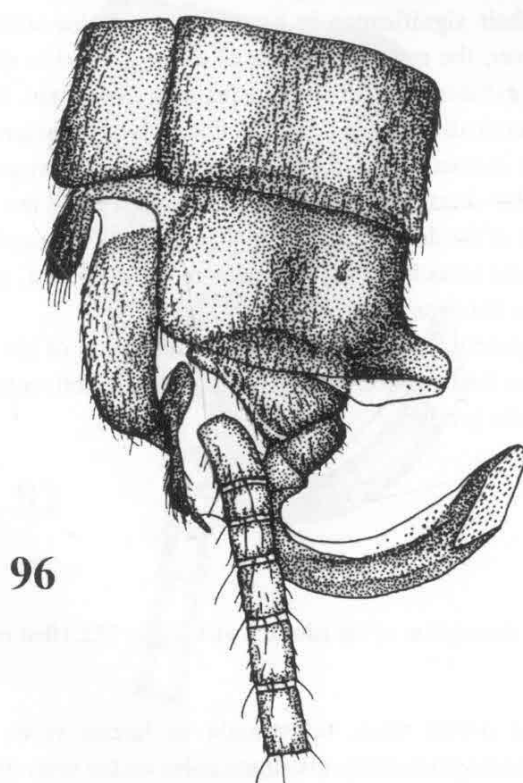
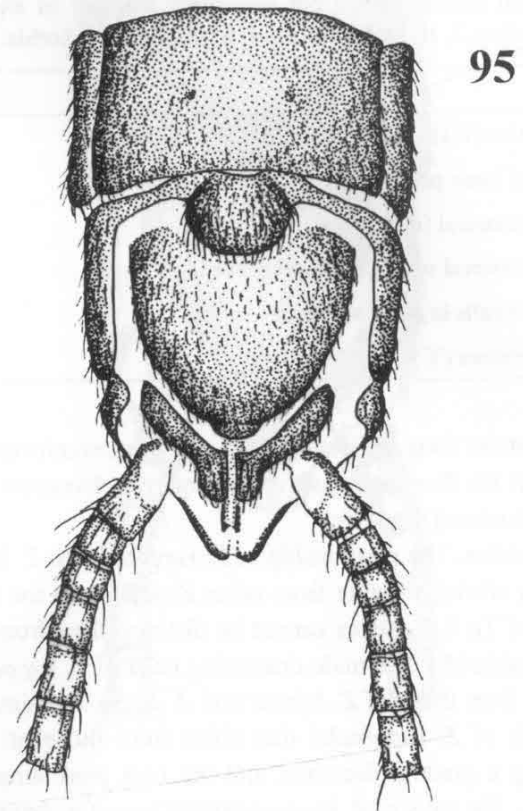
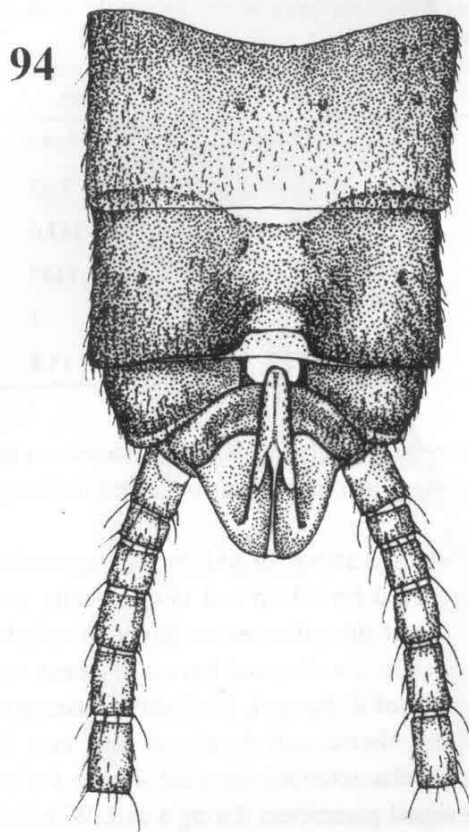
Etymology. The species is dedicated to Dr. Rainer Rupprecht, Mainz, Germany, in recognition of his primary contribution to our knowledge on Plecoptera drumming calls; furthermore, he recognized the distinctiveness of the present drumming type. Used as the genitive of a noun of male gender.

***Zwicknia sevanica* (Zhiltzova, 1964) comb. n.**

(Figs. 61, 94–97, 111, 118, 124, 144–145, 161–162, 196)

Capnia sevanica Zhiltzova, 1964—Zhiltzova 1964: 356. (original description of the adult); Zwick 1971: 252. (first record for Turkey).

Diagnosis. Male epiproct: Ep-scl narrow and pointed in dorsal view, tip straight in lateral view; ventral membranous section nearly reach the base in lateral view, apical spines short, distributed also on the apex of Ep-scl. Process of male Tg 9: high, perpendicularly elevated, 2× wider than Ep-scl, rounded and with continuous narrow sides caudally.



FIGURES 94–97. Male terminalia of *Zwicknia sevanica* (Zhiltzova, 1964); Turkey, Ankara Province, Akyarma Pass—94:

dorsal view; 95: ventral view; 96: lateral view; 97: caudal view—scale 1 mm.

Material examined. TURKEY: Ankara Province, Akyarma Pass, 1300–1400 m, 30.03.1977, leg. R. Kinzelbach, det. P. Zwick: 27m 3f, 3m 19f larvae (PZC; used for drawings Figs. 94–97, 124, 144–145, 161–162; one entire male and one male terminalia prepared for SEM to Figs. 111, 118), 3m 2f, 2f larvae (BYUC).

Description. Head, thorax, appendages and basal segments of the abdomen generotypic. Males micropterous, females macropterous. Dimensions of the presently examined specimens: body length: males 5.0–6.0, females 7.5–9.0 mm; forewing length: males 0.5 mm, females 8.0–9.5 mm.

Male terminalia (Figs. 94–97, 124): Process of Tg 9 high, perpendicularly elevated, its apex is slightly wider than the medial section of Ep-scl; its shape is rounded, the apex smooth; sides constantly narrow in caudal view, the membranous portion narrowest in the apical part (Figs. 161–162). Tg 10, B-scl and Lb-scl generotypic. Ep-scl narrow and pointed in dorsal view, medially not swollen, its medial width is the half or the third of basal width; tip straight in lateral view, divided section moderately long. Ventral membranous part between the division of Ep-scl nearly reach the base in lateral view; apical spines short, distributed not only on the membranous part but extend to the Ep-scl (Figs. 111, 118, 144–145). I-scl generotypic, Ec long and contorted on the available specimens. St 9 not projecting medially, vesicle large but can be vestigial. Sg rounded with not so pronounced triangular shape, tip rounded. Pp, Fp, Rp and cerci generotypic.

Female subgenital plate: Rectangular, posterior margin rounded and slightly incised, equal to the segment's posterior margin. Antero-lateral recess indistinct, plate entirely brown; lateral sclerites relatively small (see Zhiltzova 1964, Fig. 19, repeated as Fig. 577 in Zhiltzova 2003).

Affinities. This species is closely related to *Z. tuberculata* and *Z. turkestanica*, but the males differ with having a straight Ep-scl tip instead of slightly downcurved tip. From other species of the genus, males are easily distinguishable by high, but rounded Tg 9 process. As with most other females of the genus, separation is difficult with any certainty and the larvae are morphologically indistinguishable.

Distribution and ecology. The species was described from Armenia, later reported from the Central Pontic Mts. of northern Anatolia (Fig. 196). Adults are active from March to May at high mountain streams, between 1,500 and 2,200 m.

***Zwicknia tuberculata* (Zhiltzova, 1964) comb. n.**

(Figs. 57, 98–101, 112, 125, 146, 163, 196)

Capnia tuberculata Zhiltzova, 1964—Zhiltzova 1964: 359. (description of the adult); Zwick 1975: 391. (first record for Turkey).

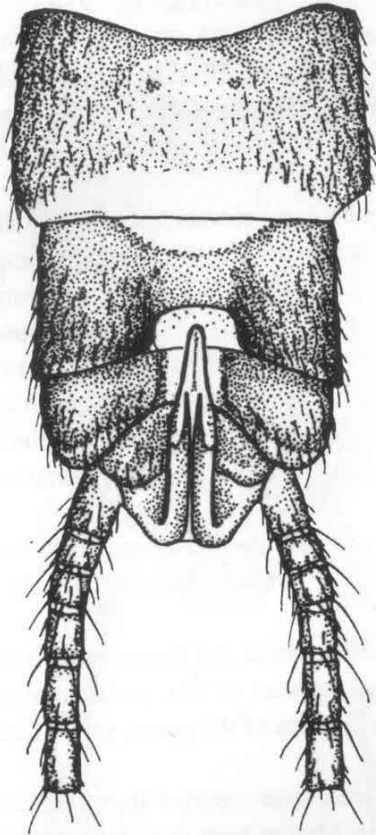
Diagnosis. Male epiproct: Ep-scl narrow and pointed in dorsal view, long, tip slightly downcurved in lateral view, membranous part long; ventral membranous section reach the base in lateral view, apical spines long, a few spines distributed also on the apex of Ep-scl. Process of male Tg 9: high, slightly folded backwards, <2× wider than Ep-scl, rounded and with constantly narrow sides caudally. Female Sg: vaginal complex dark, transparent through the Sg.

Material examined. KAZAKHSTAN: Jambyl Province, Karatau Mts., Bajaldyrtal, 22–28.04.1970, leg. F. Klima, det. P. Zwick: 2m 5f (PZC; used for drawings Figs. 57, 98–101, 125, 146, 163; one male terminalia prepared for SEM Fig. 112).

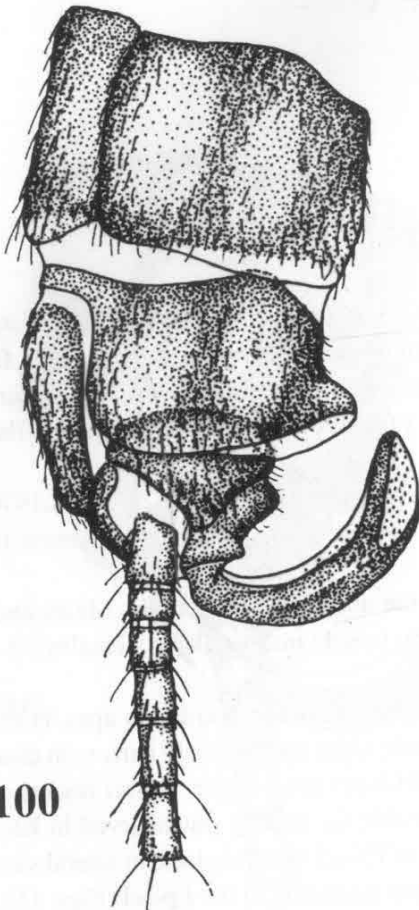
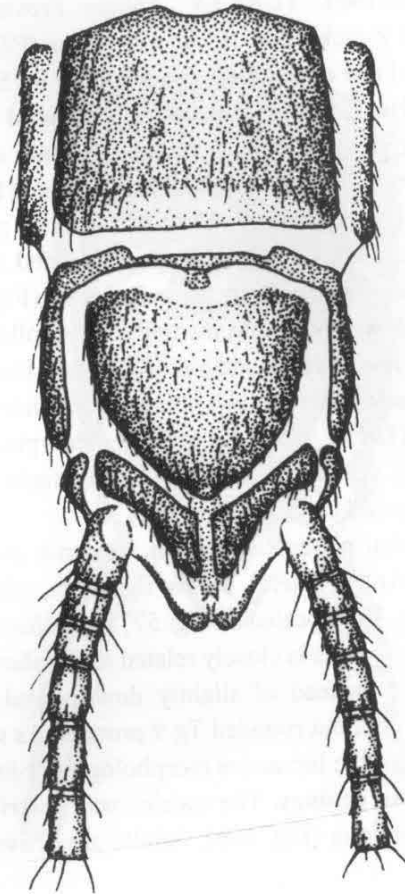
Description. Head, thorax, appendages and basal segments of the abdomen generotypic. Males and females macropterous. Dimensions of the presently examined specimens: body length: males 6.0–6.5, females 7.5–9.0 mm; forewing length: males 5.5–6.0 mm, females 7.0–8.5 mm.

Male terminalia (Figs. 98–101, 125): Process of Tg 9 high, slightly fold backwards, its apex is about 1½× wider than the medial section of Ep-scl; rounded in shape, apex smooth; sides continuously narrow in caudal view, membranous portion narrowest apically (Fig. 163). Tg 10, B-scl and Lb-scl generotypic. Ep-scl narrow and acute in dorsal view, medially not swollen, width medially <½ of basal width; tip slightly downcurved in lateral view, divided section long. Ventral membranous part between the division of Ep-scl reaching base in lateral view; apical spines long, distributed not only on the membranous portion but spines extending to the Ep-scl (Figs. 112, 146). I-scl generotypic, Ec long and contorted on the available specimens. St 9 not projecting medially, vesicle vestigial. Sg wide and rounded with not so pronounced triangular shape, tip rounded. Pp, Fp, Rp and cerci generotypic.

98

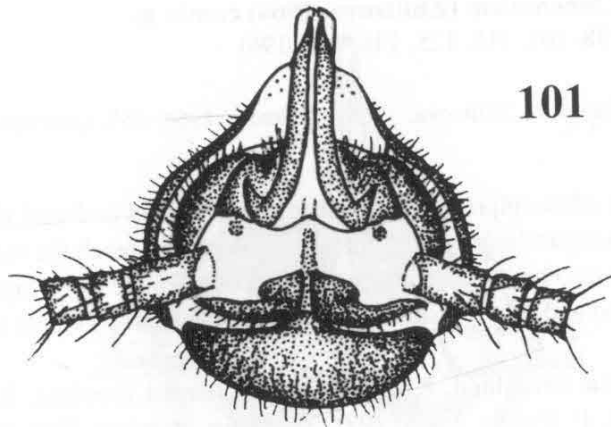


99



100

101



FIGURES 98–101. Male terminalia of *Zwicknia tuberculata* (Zhiltzova, 1964); Kazakhstan, Jambyl Province, Karatau Mts., Bajaldyrtal—98: dorsal view; 99: ventral view; 100: lateral view; 101: caudal view—scale 1 mm.

Female subgenital plate: Rectangular, posterior margin nearly linear and sometimes slightly incised, equal to the segment's posterior margin. Antero-lateral recess indistinct, the plate brown with darker longitudinal median lines caused by transparency of the unusually dark vaginal complex; lateral sclerites small (see Zhiltzova 1964: Fig. 28, repeated as Fig. 581 in Zhiltzova 2003).

Affinities. The relationship of *Z. tuberculata* with *Z. sevanica* is discussed above. The species is apparently nearer to *Z. turkestanica*, but the males differ by having a more robust Ep-scl and Tg 9 process that is slightly fold backwards instead of perpendicularly elevated. In addition to the above species, males of *Z. tuberculata* are easily distinguishable from other *Zwicknia* by the high, but rounded process of Tg 9. Unlike other *Zwicknia* species, the females are also distinct with their dark vaginal complex, transparent through the Sg. The larva is unknown.

Distribution and ecology. The species was described from Armenia, known also from the Russian part of the Caucasus, Georgia and the Pontic Mts. of northern Anatolia, and herein reported from Kazakhstan (Fig. 196). Adults are active from April to August but mostly in May near brooks to small rivers of mountainous areas between 1,000 and 2,000m.

Remarks. The two males and five females listed above are morphologically agree with the original description of *Z. tuberculata*, especially in regard to the distinctive female, despite that this material is geographically far outside the known range of this species. However, drumming calls of the Asian *Zwicknia* species are unknown and no fresh material is available for molecular studies. Their identification is presently based only on morphological characters and was not confirmed with drumming and molecular studies.

***Zwicknia turkestanica turkestanica* (Kimmins, 1950) comb. n.**

(Figs. 102–105, 113, 126, 147, 164, 196)

Capnia nigra (Pictet, 1833)—Morton 1896: 60. (Fig. 3 on Plate 2 refers to the holotype of *Z. turkestanica*).

Capnia turkestanica Kimmins, 1950—Kimmins 1950a: 187. (original description of the adult); Zhiltzova 1969: 603. (complementary description and comparison with *Z. tuberculata*); Zhiltzova 2003: 349. (complementary description).

Diagnosis. Male epiproct: Ep-scl narrow and acute in dorsal view, short, tip slightly downcurved in lateral view, membranous portion long; ventral membranous section reaching base in lateral view, apical spines long, distributed also on the apex of Ep-scl. Process of male Tg 9: high, perpendicularly elevated, <2× wider than Ep-scl, rounded and with continuously narrow sides caudally.

Material examined. KAZAKHSTAN: East Kazakhstan Province, Tarbagatai Mts., River Ayagos 270km SW of Öskemen (Ust-Kamenogorsk), 05.04.2003, leg., det. V. I. Devyatkov: 6m 6f (PZC; used for drawings Figs. 102–105, 126, 147, 164; one male terminalia prepared for SEM to Fig. 113).

Description. Head, thorax, appendages and basal segments of the abdomen generotypic. Males micropterous or macropterous, females macropterous. Dimensions of the presently examined specimens: body length: males 5.5–6.5, females 6.0–7.5 mm; forewing length: males 1.0–6.0 mm, females 6.5–7.5 mm.

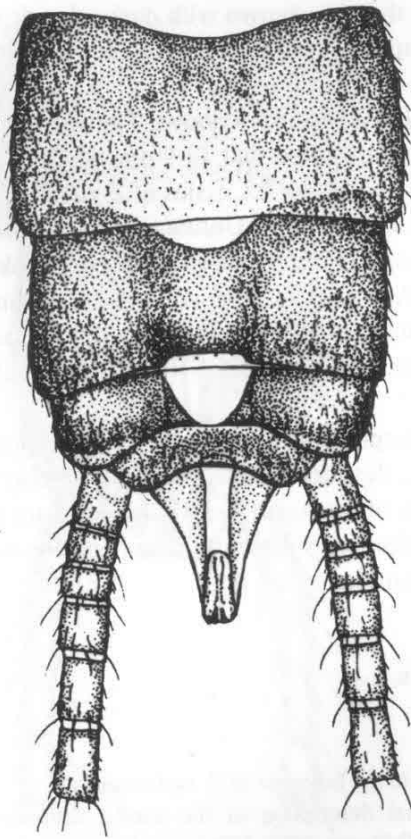
Male terminalia (Figs. 102–105, 126): Process of Tg 9 high, perpendicularly elevated, apex is <2× wider than the medial section of Ep-scl; its shape is rounded, the apex smooth; sides continuously narrow in caudal view, the membranous portion narrowest apically (Fig. 164). Tg 10, B-scl and Lb-scl generotypic. Ep-scl narrow and acute in dorsal view, short, medially not swollen, its medial width is ~½ of basal width; tip slightly downcurved in lateral view, divided section long. Ventral membranous portion between the division of Ep-scl reaching base in lateral view; apical spines moderately long, extending to the Ep-scl (Figs. 113, 147). I-scl generotypic, Ec long and contorted on the available specimens. St 9 not projecting medially, vesicle vestigial. Sg wide and rounded not as pronounced triangular shape, tip rounded. Pp, Fp, Rp and cerci generotypic.

Female subgenital plate: Rectangular, posterior margin rounded, equal to the segment's posterior margin. Antero-lateral recess distinct, the plate brown, sometimes with paler lateral areas; lateral sclerites small (see Zhiltzova 2003: Fig. 585).

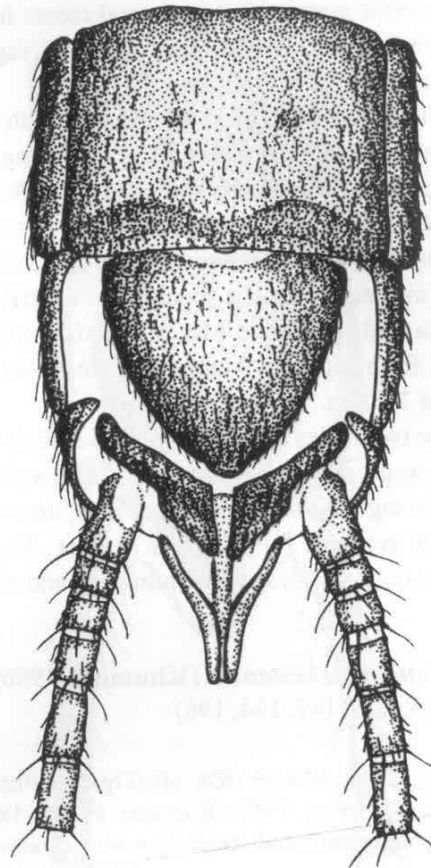
Affinities. The relationship of *Z. turkestanica* with closely related *Z. tuberculata* and *Z. sevanica* is discussed above. Males are easily distinguishable from all other *Zwicknia* species by high, but rounded process of Tg 9. Females are difficult to distinguish from other species of the genus. The larva is unknown.

Distribution and ecology. The species was described from a single male from 'Turkestan' without exact locality. It is known from Tajikistan, Kyrgyzstan and Kazakhstan (Fig. 196). Adults apparently are active from March to April associated with mountain streams as high as 2,400 m.

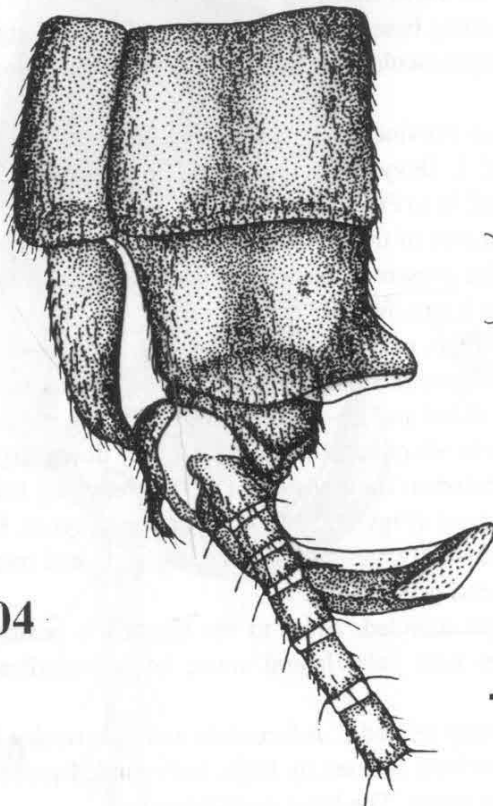
102



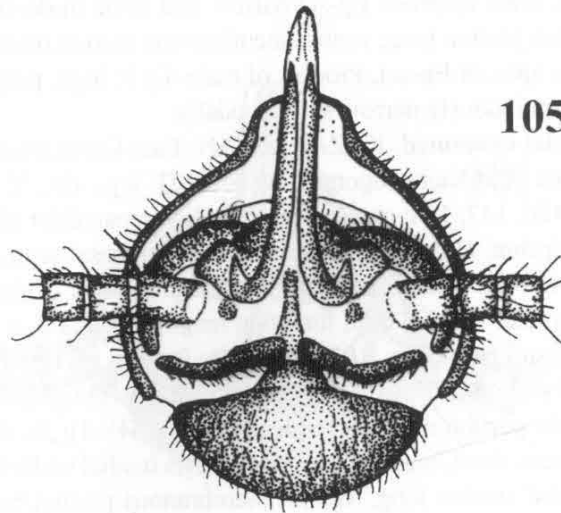
103



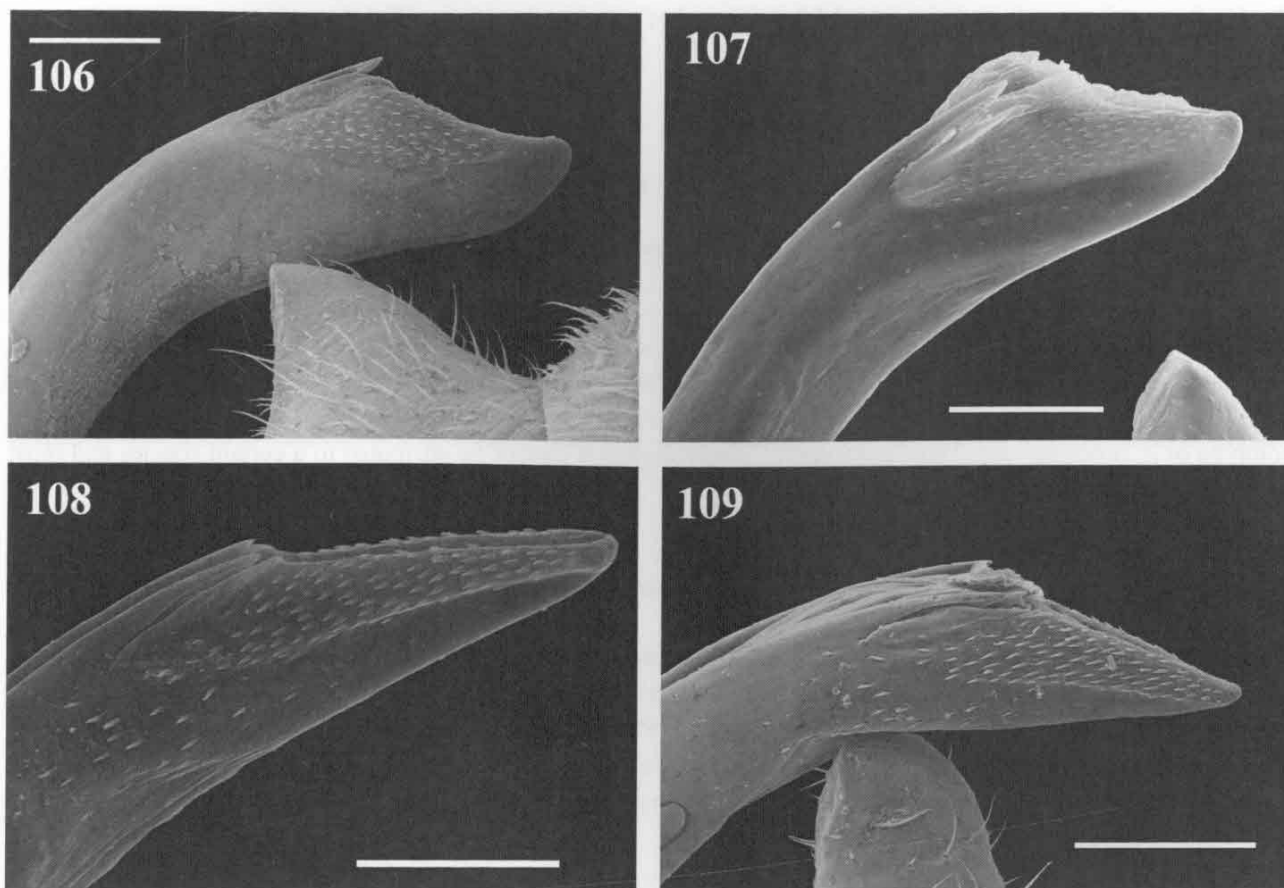
104



105



FIGURES 102–105. Male terminalia of *Zwicknia turkestanica turkestanica* (Kimmins, 1950); Kazakhstan, East Kazakhstan Province, Tarbagatai Mts., Ayagos—102: dorsal view; 103: ventral view; 104: lateral view; 105: caudal view—scale 1 mm.



FIGURES 106–109. Lateral view of male epiproct of *Zwicknia* Murányi, **gen. n.**—106: *Z. bifrons* (Newman, 1838); 107: *Z. rupprechti* Murányi, Orci & Gamboa, **sp. n.**; 108–109: *Z. acuta* Murányi & Orci, **sp. n.**—scale 0.1 mm.

***Zwicknia turkestanica brevicula* (Berthélemy & Dia, 1982) comb. n.**

(Fig. 196)

Capnia turkestanica brevicula Berthélemy & Dia, 1982—Berthélemy & Dia 1982: 210. (original description of the adult and the larva).

This subspecies was described from Lebanon, tentatively considered as a subspecies of *Z. turkestanica*. Berthélemy & Dia (1982) indicated that this form was related to *Z. tuberculata*. Microptery of specimens was used as the distinguishing character separating from the nominate *Z. t. turkestanica*. However, the studied Kazakh specimens of the nominate form included both micropterous and macropterous individuals, similar to Asian *Zwicknia*, drumming and molecular studies of topotype series would be needed to clarify the status of this taxon.

Notes on further taxa attributed to *Zwicknia*

***Capnia dusmeti* Navás, 1917**

Capnia dusmeti Navás, 1917—Navás 1917: 396. (original description of the adult).

Capnia bifrons (Newman, 1838)—Aubert 1952: 247. (synonymy of *Capnia dusmeti* Navás, 1917 with *Capnia bifrons* (Newman, 1838)).

This species was described on the basis of a female from Spain. The type specimen is lost, however, it was synonymized with *Z. bifrons* on the basis of the original description (Aubert 1952). As the drumming signals of

several Iberian populations differ from that of *Z. bifrons* (Rupprecht 1997), their conspecificity cannot be confirmed. *Capnia dusmeti* is regarded as a nomen dubium instead of a junior synonym of *Z. bifrons*.

Capnia quadrangularis Aubert, 1946

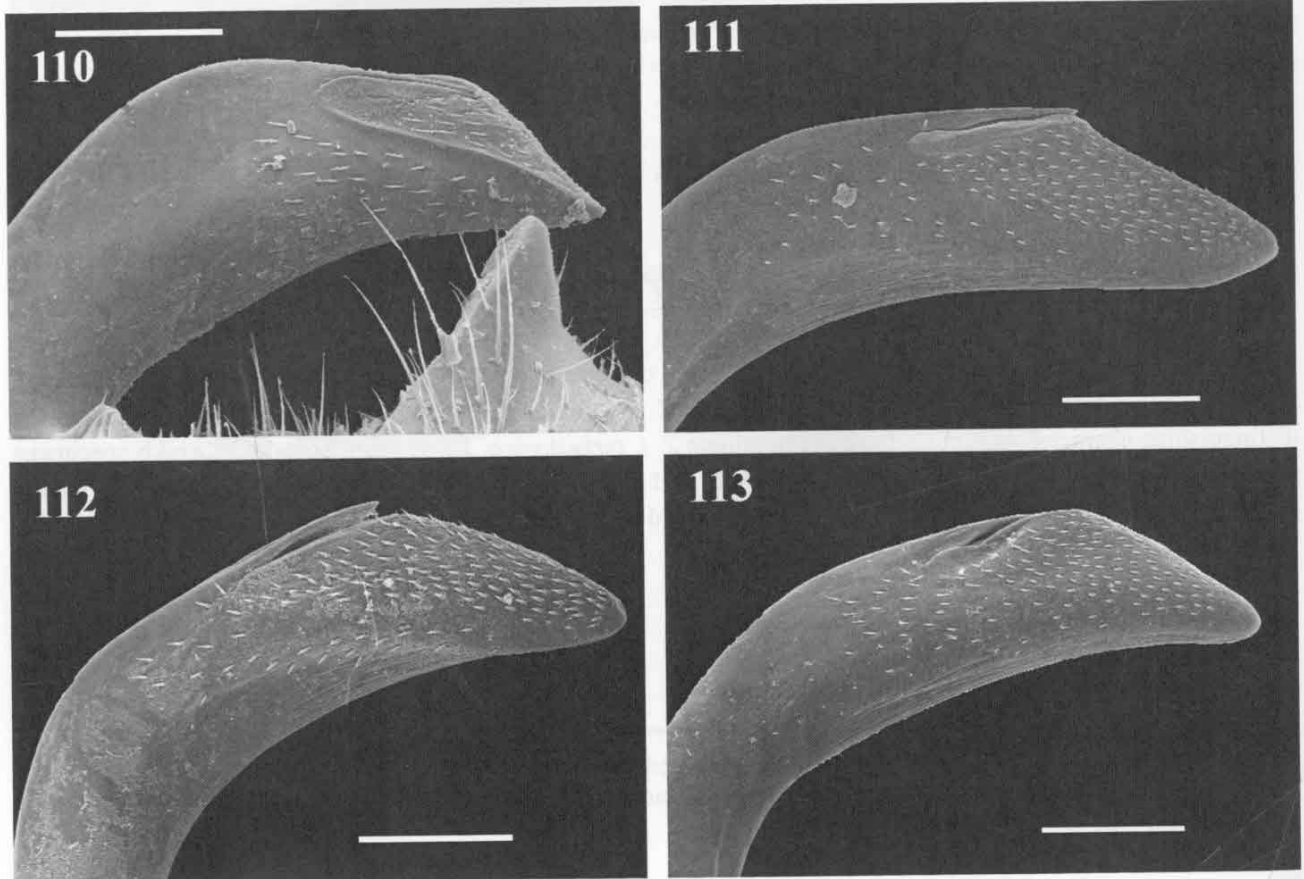
Capnia quadrangularis Aubert, 1946—Aubert 1946: 22. (nomen novum for *Capnia nigra* sensu Morton 1896, and complementary description of the larva).

Capnia bifrons (Newman, 1838)—Kimmins 1947: 261. (synonymy of *Capnia quadrangularis* Aubert, 1946 with *Capnia bifrons* (Newman, 1838).

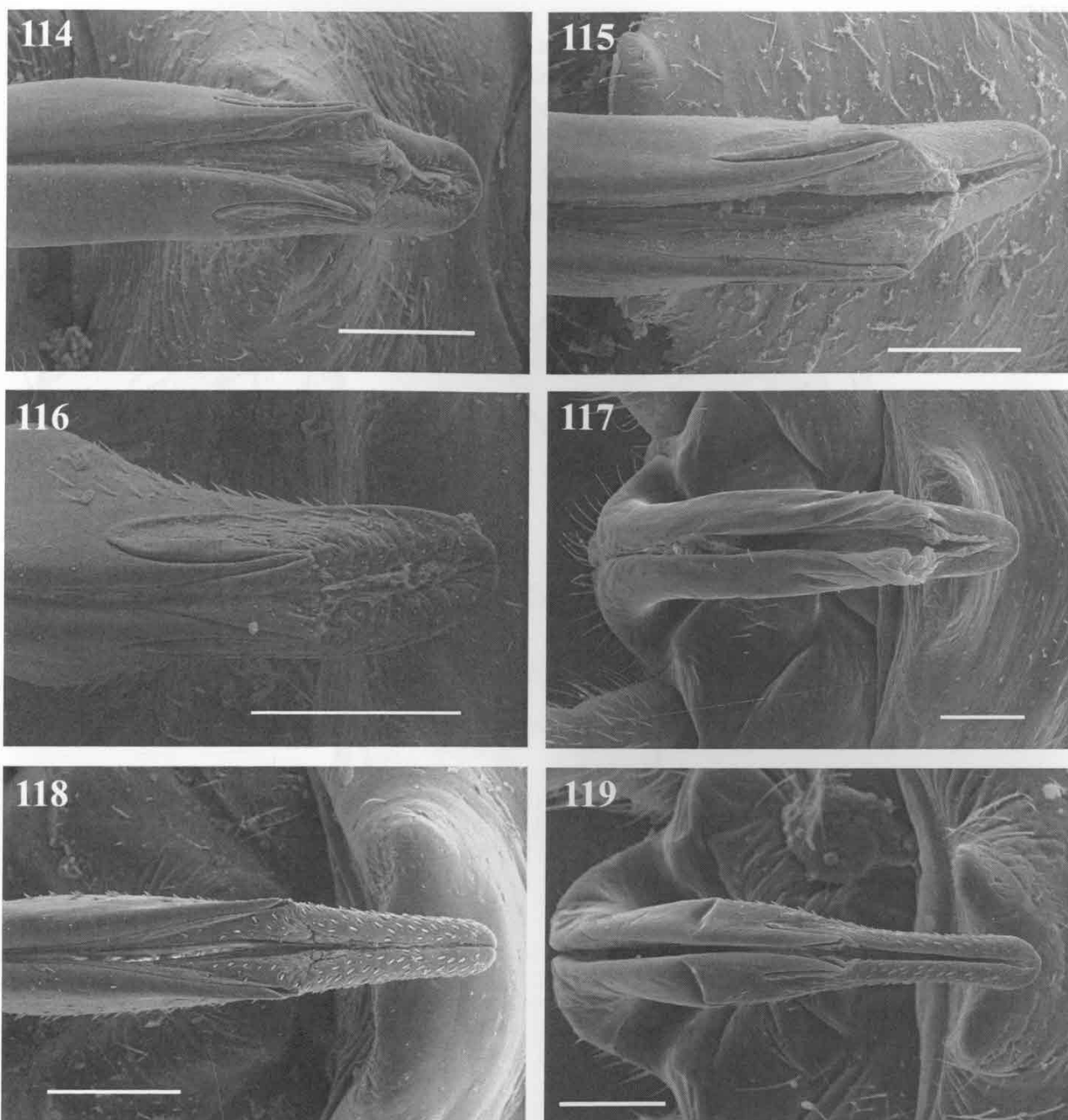
This name was given as a nomen novum for *C. nigra* sensu Morton 1896. Unfortunately, a type was not designated. Morton (1896) referred to British, Austrian, Czech, and Turkestan specimens without further specification. He provided an illustration of a Scottish (obviously *Z. bifrons*) and of a Turkestan specimen (the later holotype of *Z. turkestanica*). Thus, the name *C. quadrangularis* cannot be attributed to a certain species and must be regarded as a nomen dubium.

Capnia bifrons (Newman, 1838) drumming types sensu Rupprecht 1997

In addition to drumming signals of the real *Z. bifrons* (under the name Capnor) and the type of *Z. rupprechti* and *Z. kovacsi* (under the name Capbif), Rupprecht (1997) described further four mating call types from Western Europe that are undoubtedly refer to undescribed species. In the PZC material we find morphologically distinct specimens from the Jura Mts., Dr. Gilles Vinçon informed us about another distinct form found in the French Massif Central. These are possibly referred to by Rupprecht's drumming types. Further comparative studies will be needed to establish the identity of these forms.



FIGURES 110–113. Lateral view of male epiproct of *Zwicknia* Murányi, gen. n.—110: *Z. kovacsi* Murányi & Gamboa, sp. n.; 111: *Z. sevanica* (Zhiltzova, 1964); 112: *Z. tuberculata* (Zhiltzova, 1964); 113: *Z. turkestanica turkestanica* (Kimmins, 1950)—scale 0.1 mm.



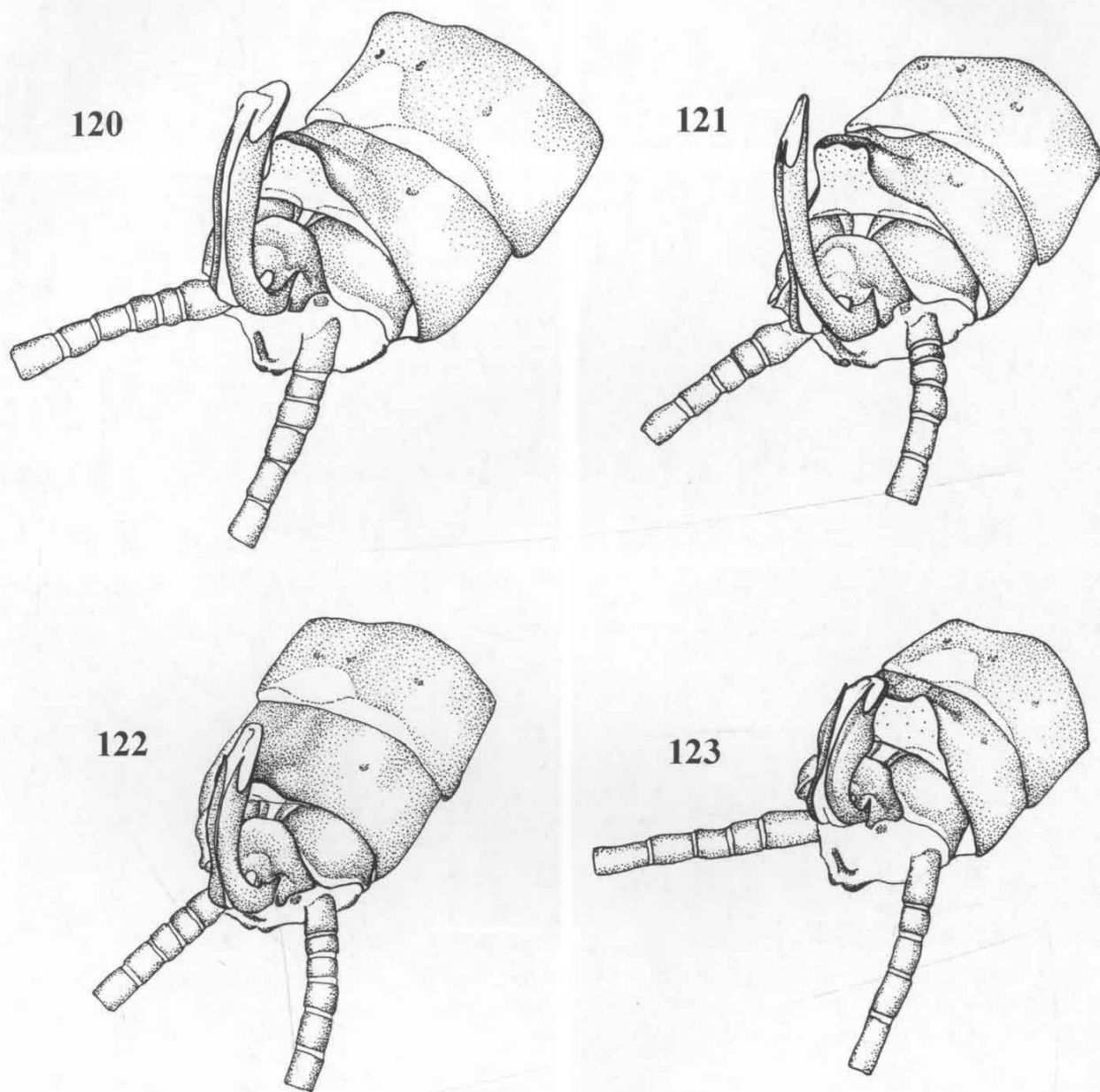
FIGURES 114–119. Dorsal view of male epiproct of *Zwicknia* Murányi, **gen. n.**—114: *Z. bifrons* (Newman, 1838); 115, 117: *Z. rupprechtii* Murányi, Orci & Gamboa, **sp. n.**; 116: *Z. kovacsi* Murányi & Gamboa, **sp. n.**; 118: *Z. sevanica* (Zhiltzova, 1964); 119: *Z. acuta* Murányi & Orci, **sp. n.**—scale 0.1 mm.

Discussion

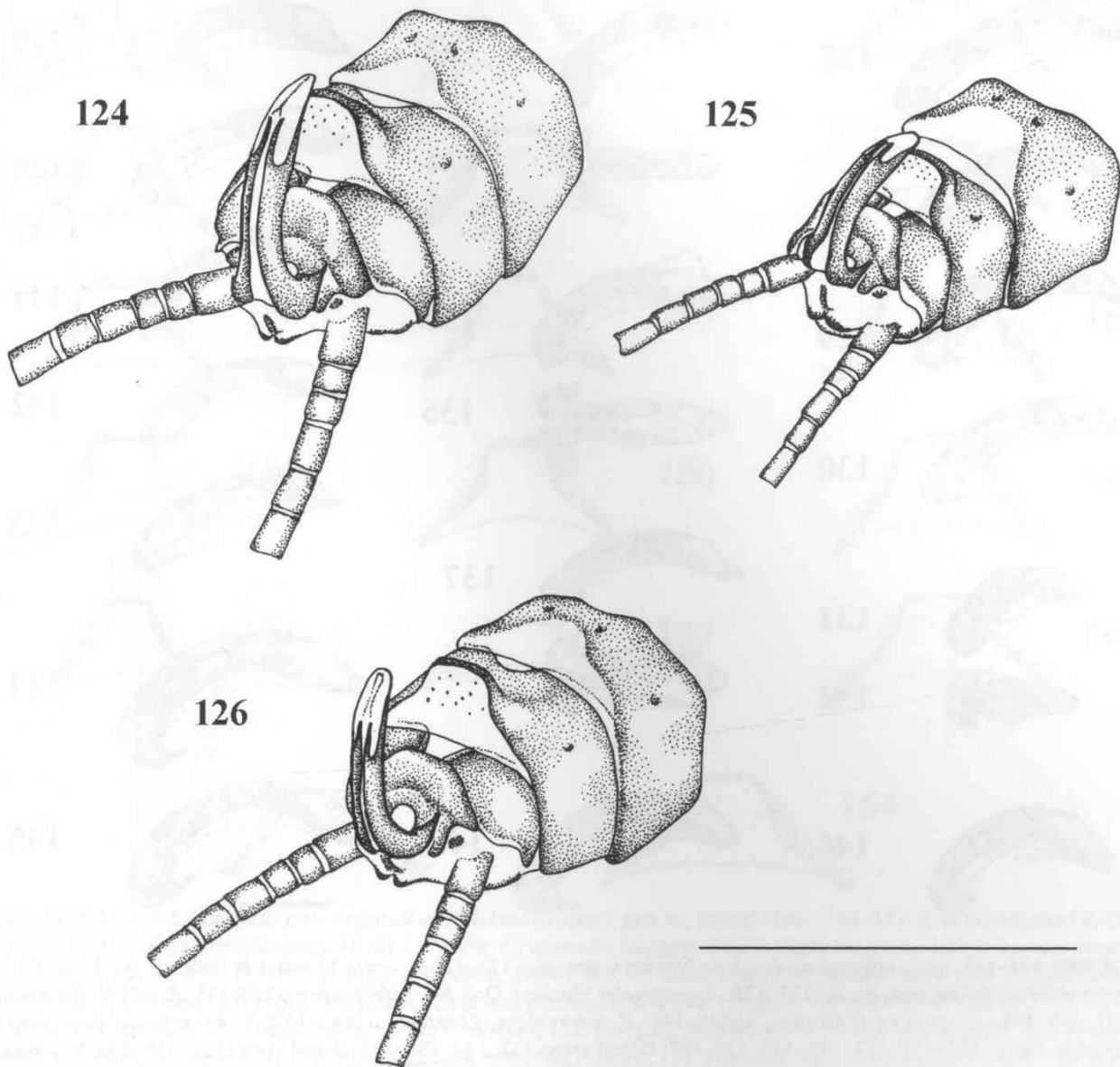
Morphotaxonomy and systematics. The genus *Zwicknia* is proposed for the *C. bifrons* species group because of distinct differences in male genitalia from *C. nigra*, type species of the genus *Capnia*. These characters include the presence of B-scl, lack of LI, Lb-scl small, Ep-scl only partially divided and lacking caudal setae, I-scl elongated, Rp separated from Fp, presence of a ventral vesicle, Tg 9 bearing a process, process absent on Tg 7. The new genus forms a clade that is diagnostic in both male and female terminalia, ventral thoracic sclerites, and wing venation from other named Capniidae genera. *Zwicknia* is considered most closely related to the West Nearctic *Bolshecapnia*. Among the general diagnostic characters, the long, open tube-like I-scl is considered a

synapomorphy. The genus has a West Palaearctic distribution but extending into the East Palaearctic as far as Middle Asia.

Examination of the Carpathian Basin and northern Balkan populations revealed that the taxa previously considered as *Z. bifrons* were cryptic species with different drumming signals that corresponded to morphological differences. The analyses of drumming signals and morphology were supplemented with molecular information. Using this evidence, we recognize four species, the nominal *Z. bifrons* and three new species, *Z. acuta*, *Z. kovacsi*, and *Z. rupprehti*.

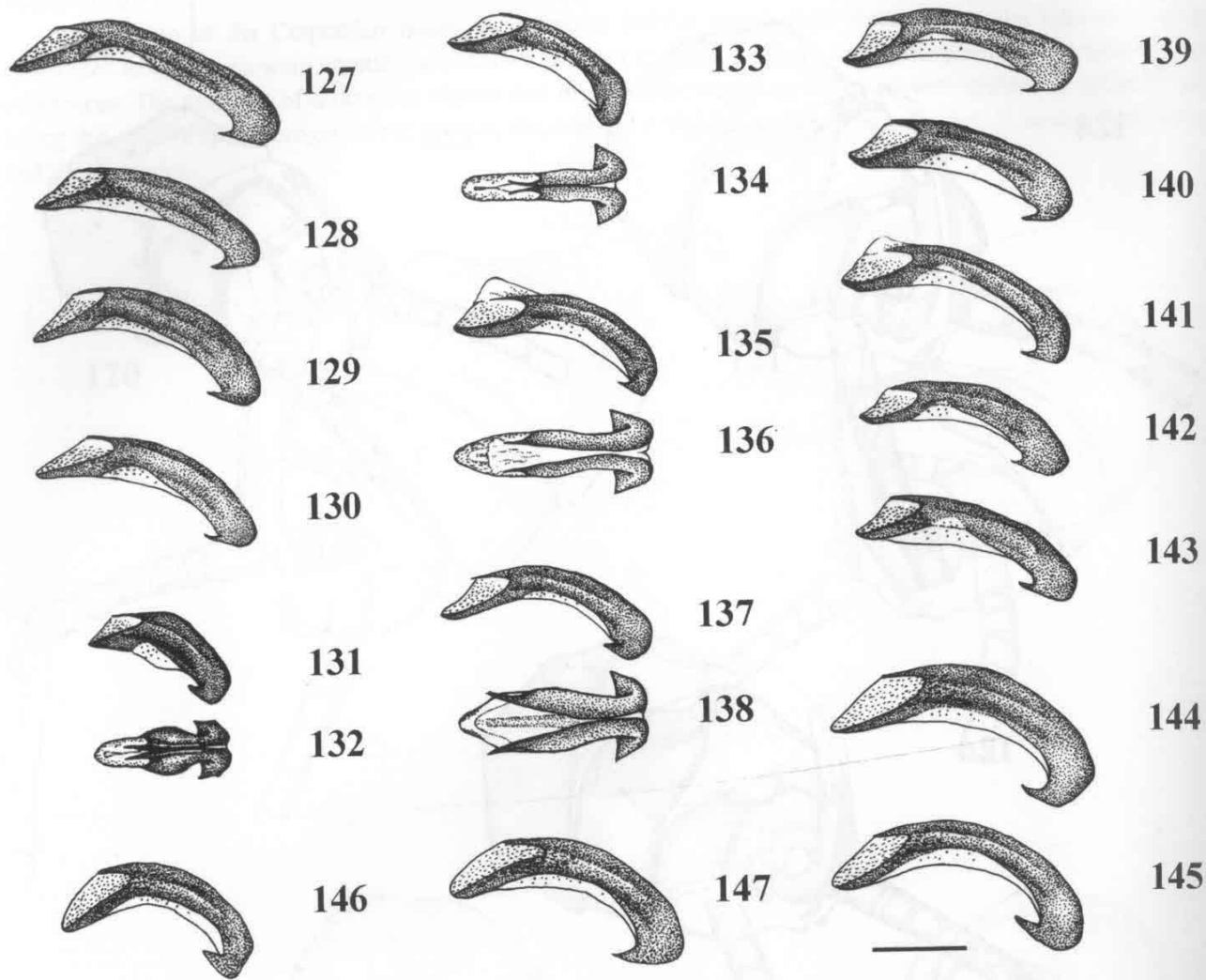


FIGURES 120–123. Male terminalia of *Zwicknia* Murányi, **gen. n.**, dorso-caudal view—120: *Z. bifrons* (Newman, 1838); 121: *Z. acuta* Murányi & Orci, **sp. n.**; 122: *Z. rupprehti* Murányi, Orci & Gamboa, **sp. n.**; 123: *Z. kovacsi* Murányi & Gamboa, **sp. n.**—scale 1 mm.

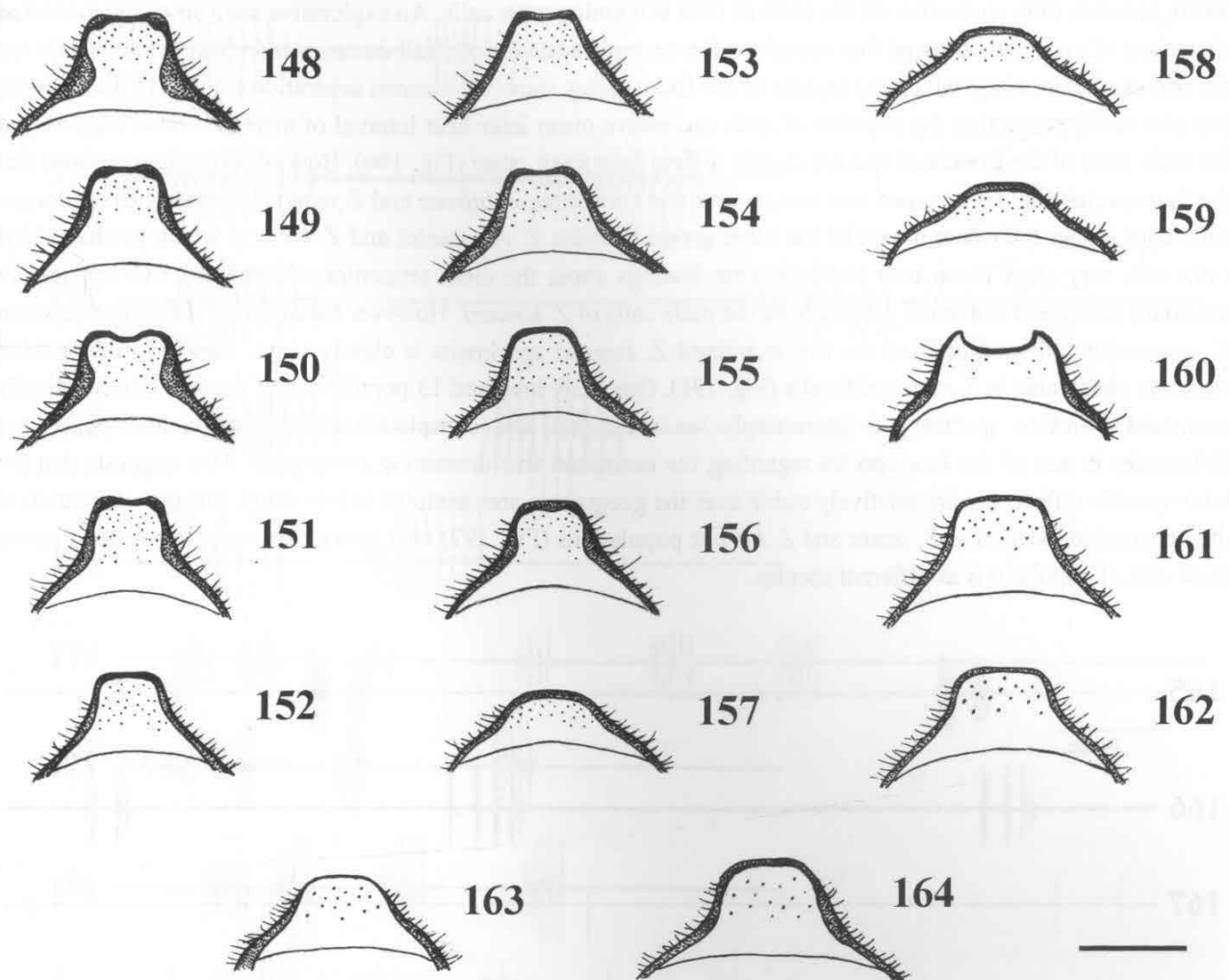


FIGURES 124–126. Male terminalia of *Zwicknia* Murányi, **gen. n.**, dorso-caudal view—124: *Z. sevanica* (Zhiltzova, 1964); 125: *Z. tuberculata* (Zhiltzova, 1964); 126: *Z. turkestanica turkestanica* (Kimmins, 1950)—scale 1 mm.

An identification key based on morphology is provided for the seven recognized *Zwicknia* species. Additional studies may discover other undescribed and further clarify poorly-known species, for example *Z. tuberculata*. The three named *Zwicknia* species from Anatolia, the Caucasus, Transcaucasia, the Levant, and Middle Asia are described only on the basis of morphological characters. Future studies must include mating calls and molecular analyses, but living materials seem hardly accessible in the near future. Additional new morphological forms from West Europe were discovered during the morphological study of comparative materials. Their description will be completed during further study regarding also drumming signals and molecular methods.



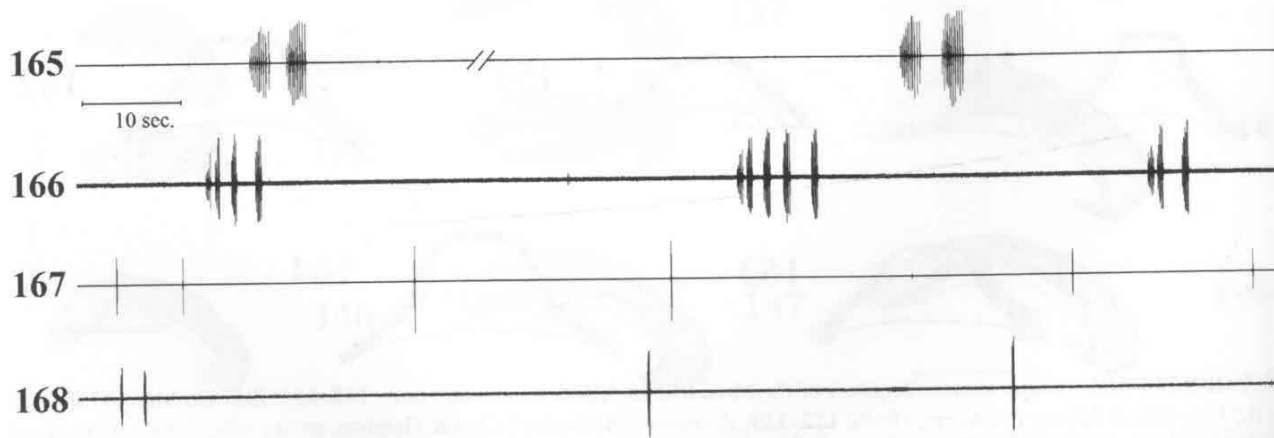
FIGURES 127–147. Male epiproct of *Zwicknia* Murányi, **gen. n.**—127–130 *Z. acuta* Murányi & Orci, **sp. n.**; 131–132: *Z. kovacsi* Murányi & Gamboa, **sp. n.**; 133–138: *Z. rupprechtii* Murányi, Orci & Gamboa, **sp. n.**; 139–143: *Z. bifrons* (Newman, 1838); 144–145: *Z. sevanica* (Zhiltzova, 1964); 146: *Z. tuberculata* (Zhiltzova, 1964); 147: *Z. turkestanica turkestanica* (Kimmins, 1950); 127–131, 133, 135, 137, 139–147: lateral view; 132, 134, 136, 138: dorsal view (127: Slovakia, Krupinská Planina, Pôtor; 128: Hungary, Zemplén Mts., Kishuta; 129: Serbia, Fruska Gora, Vrdnik; 130: Serbia, Zlatibor Mts., Crni Rzav; 131–132: Romania, Rodna Mts., Borşa–Staţiunea Borşa; 133–134, 137–138: Croatia, Ivanščica Mts., Stari Golubovec; 135–136: Hungary, Mecsek Mts., Komló-Zobákpusztá; 139: Hungary, Börzsöny Mts., Szokolya-Királyrét; 140: Hungary, Mátra Mts., Gyöngyössolymos; 141: Hungary, Bükk Mts., Nagyvisnyó; 142: Hungary, Bakony Mts., Bakonybél; 143: Serbia, Maljen Mts., Brajkovići; 144–145: Turkey, Akyarma Pass; 146: Kazakhstan, Karatau Mts., Bajaldyrtal; 147: Kazakhstan, Tarbagatai Mts., Ayagos)—scale 0.2 mm.



FIGURES 148–164. Humps of male Tergite 9 of *Zwicknia* Murányi, **gen. n.**, caudal view—148–151: *Z. acuta* Murányi & Orci, **sp. n.**; 152–156: *Z. bifrons* (Newman, 1838); 157–159: *Z. rupprechtii* Murányi, Orci & Gamboa, **sp. n.**; 160: *Z. kovacsi* Murányi & Gamboa, **sp. n.**; 161–162: *Z. sevanica* (Zhiltzova, 1964); 163: *Z. tuberculata* (Zhiltzova, 1964); 164: *Z. turkestanica turkestanica* (Kimmins, 1950) (148: Slovakia, Krupinská Planina, Pôtor; 149: Hungary, Zemplén Mts., Kishuta; 150: Serbia, Fruska Gora, Vrdnik; 151: Serbia, Zlatibor Mts., Crni Rzav; 152: Hungary, Börzsöny Mts., Szokolya-Királyrét; 153: Hungary, Mátra Mts., Gyöngyössolymos; 154: Hungary, Bükk Mts., Nagyvisnyó; 155: Hungary, Bakony Mts., Bakonybél; 156: Serbia, Maljen Mts., Brajkovići; 157, 159: Croatia, Ivanščica Mts., Stari Golubovec; 158: Hungary, Mecsek Mts., Komló-Zobákpuszt; 160: Romania, Rodna Mts., Borșa-Stațiunea Borșa; 161–162: Turkey, Akyarma Pass; 163: Kazakhstan, Karatau Mts., Bajaldyrta; 164: Kazakhstan, Tarbagatai Mts., Ayagos)—scale 0.2 mm.

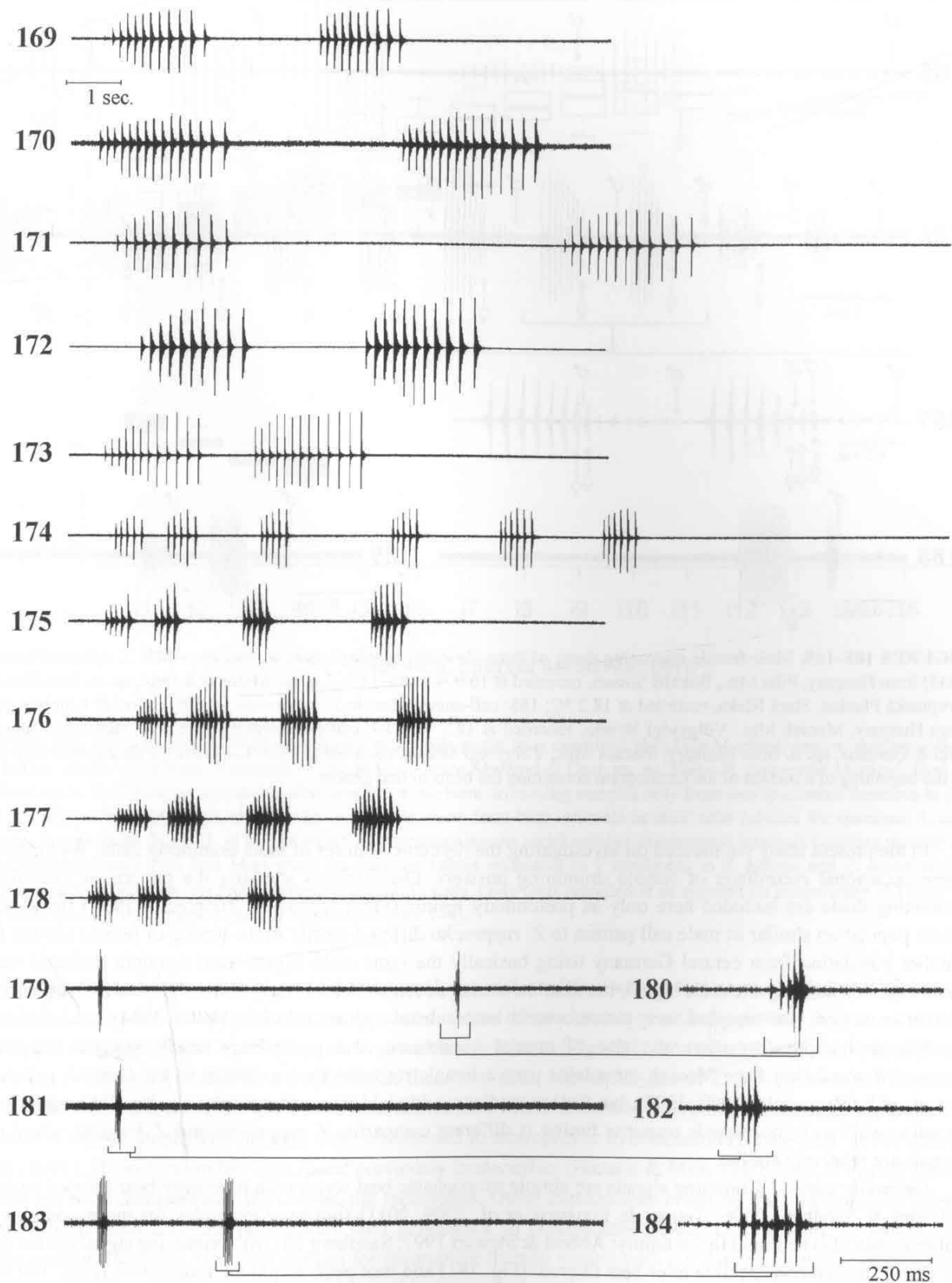
To support the establishment of the new genus *Zwicknia*, we examined >150 Capniidae species representing 14 extant Holarctic genera. New characters of the genitalia were introduced to support preliminary changes in the Capniidae systematics. A new sensu stricto diagnosis is proposed for the genus *Capnia* based on the type species. We restrict this formerly large all inclusive genus to only eight confirmed species. In this treatment, *Capnia* now is a morphologically uniform group of North Holarctic species with a single widespread Eurasian species, *C. nigra* that extends its range into the southern Palaearctic region. We recognize *Arsapnia* as a valid genus for eight West Nearctic species. Ninety-six species are retained in the artificial, obviously polyphyletic group of *Capnia* sensu lato. Additional studies of the East Palaearctic taxa are required for resolution of the proper placement of these species. Our studies indicate that the European species previously placed into in *Capnia* belongs to three genera: *Capnia* s.s., *Zwicknia*, and a yet unnamed taxon within *Capnia* s.l.

Drumming signals. Our results show that the described four Central European *Zwicknia* species are clearly distinguishable from each other on the basis of their drumming male calls. An explorative analysis of the measured characters of male calls showed that using two dimensional scatter plots, call duration and mean beat intervals are the two characters along which the signals of the four species show the clearest separation (Fig. 191). In addition, box plot series presenting the duration of each successive mean inter-beat interval of male calls also suggest that the male calls of the examined species clearly differs from each other (Fig. 190). Both of those figures show that the four species may be arranged into two groups: one containing *Z. bifrons* and *Z. acuta*. These species use longer calls with longer inter-beat intervals; the other group includes *Z. rupprechti* and *Z. kovacsi* which produce short calls with very short mean beat intervals. Our findings about the clear separation of the latter two species are uncertain because of our small sample from the male calls of *Z. kovacsi*. However the extent of difference between *Z. rupprechti* calls and calls of the two examined *Z. kovacsi* specimens is clearly larger than the intra-specific variation observable in *Z. rupprechti* calls (Fig. 191). Our study involved 13 populations of the four bioacoustically examined *Zwicknia* species and interestingly we could not find conspicuous intra-specific, inter-population differences in any of the four species regarding the examined five drumming parameters. This suggests that the inter-specific differences are relatively stable over the geographic area sampled in this study. The mosaic pattern of the geographic location of *Z. acuta* and *Z. bifrons* populations (Fig. 197) also provides strong support for treating these sets of populations as different species.

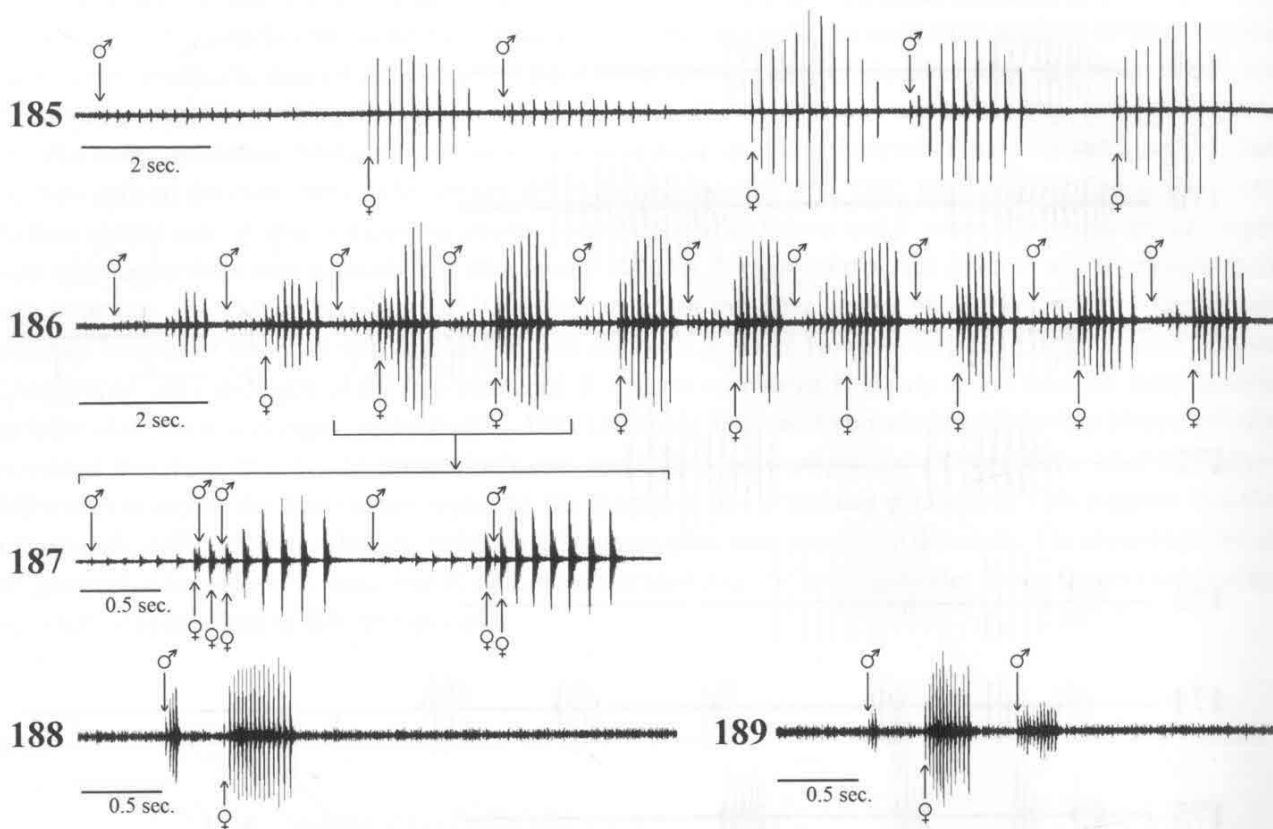


FIGURES 165–168. Slow oscillograms of male calls of four *Zwicknia* Murányi, **gen. n.** species, showing call sequences versus sporadic call production—165: two call sequence of *Z. bifrons* (Newman, 1838), “//” indicates where 2 minutes 23 seconds of silence was cut out from the recording; 166: three call sequences of *Z. acuta* Murányi & Orci, **sp. n.**; 167: sporadic calls of *Z. rupprechti* Murányi, Orci & Gamboa, **sp. n.**; 168: sporadic call production in *Z. kovacsi* Murányi & Gamboa, **sp. n.**—time scale is the same for the four oscillograms; for detailed data on the animals and recording circumstances, see Table 9.

Male signals present only the sender’s side of the pair forming acoustic communication of these animals. To know more about the specificity of female signal recognition and preferences would be equally important when using signal differences to estimate species boundaries. Rupprecht (1982) found that female answer ratios were dependent on interbeat intervals of the artificial male signals he played back to the females. He found that the response ratio of females of a Danish population, which likely belong to *Z. bifrons* was strongly dependent on the interbeat intervals of male signals and showed an unimodal preference function, with a maximum close to the population mean of that character. Those results suggest that beat repetition frequency must be an important male signal parameter in species recognition or mate choice in these stoneflies. One of the signal characters which shows the clearest separation among drumming signals of the four *Zwicknia* species described is mean the beat interval, which is the reciprocal value of mean beat frequency. Therefore, we suspect that difference to play a role in the pre-mating isolation of those four species. However, it will be important to examine female preferences against male signal characters of these species during a subsequent study using play-back experiments with artificially modified male signals.



FIGURES 169–184. Male drumming calls of *Zwicknia* Murányi, **gen. n.**—169–173: *Z. bifrons* (Newman, 1838); 174–178: *Z. acuta* Murányi & Orci, **sp. n.**; 179–182: *Z. rupprechtii* Murányi, Orci & Gamboa, **sp. n.**; 183–184: *Z. kovacsi* Murányi & Gamboa, **sp. n.** (see detailed data on the animals and recording circumstances in Table 9)—Oscillograms in Figs. 169–179, 181, 183 have the same time axis resolution (time scale bar is presented in Fig. 169 for all of them), an other time scale is used in the faster oscillograms of Figs. 180, 182, 184 (time scale bar for them can be found in Fig. 184), those are zoomed sections of Figs. 179, 181, 183, respectively.



FIGURES 185–189. Male-female drumming duets of three *Zwicknia* Murányi, **gen. n.** species.—185: *Z. bifrons* (Newman, 1838) from Hungary, Pilis Mts., Bükkös Stream, recorded at 16.9 °C; 186–187: *Z. acuta* Murányi & Orci, **sp. n.** from Slovakia, Krupinská Planina, Stará Rieka, recorded at 18.2 °C; 188: call-answer duet in *Z. rupprechti* Murányi, Orci & Gamboa, **sp. n.** from Hungary, Mecsek Mts., Völgységi Stream, recorded at 18.2 °C; 189: call-answer-reply duet in *Z. rupprechti* Murányi, Orci & Gamboa, **sp. n.** from Hungary, Mecsek Mts., Völgységi Stream, recorded at 17.9 °C—arrows with a gender sign point to the beginning of a section of the oscillogram containing the beats of that gender.

In the present study we focused on investigating the rhythmic features of male drumming calls. We made only some occasional recordings of female drumming answers. Oscillograms showing the pattern of male-female drumming duets are included here only as preliminary results (Figs. 185–189). Rupprecht (1997) found that a Swiss population similar in male call pattern to *Z. rupprechti* differed mostly in the timing of female answer from another population from central Germany using basically the same male signal. That example indicates that in these capniids not only the male signal, but also the timing of female answer may show significant divergences. A similar condition was reported in a phaneropterid bush cricket species (Orci & Heller 2004), where acoustic duetting during pair-formation was also of crucial importance. Our preliminary results suggest that the *Z. rupprechti* population from Mecsek mountains uses a female response timing similar to the German population examined by Rupprecht (1982, 1997), but further studies could yield interesting results e.g. it will be important to examine whether or not female response timing is different comparing *Z. rupprechti* and *Z. kovacsi*, where male signals are relatively similar.

Generally capniid drumming signals are simple monophasic beat series with little inter-beat interval variation (Stewart & Sandberg 2006; Tierno de Figueroa *et al.* 2009, 2011) (however examples for more complex call patterns may also be found in the family: Abbott & Stewart 1997; Sandberg 2011b). Drumming signals in the genus *Zwicknia* showed considerable inter-beat interval (Fig. 191) and beat peak amplitude modulation (Figs. 169–184), and in two of the four *Zwicknia* species described here, male calls are produced in characteristic sequences (Figs 165–166.). That drumming complexity seems to be a parallel phenomenon with the relatively derived characters of the morphology of *Zwicknia*. However, the drivers for morphological and drumming signal evolution may be different, and to form hypotheses about the selection pressures acting on drumming signals more information on female drumming signal preferences would be necessary.

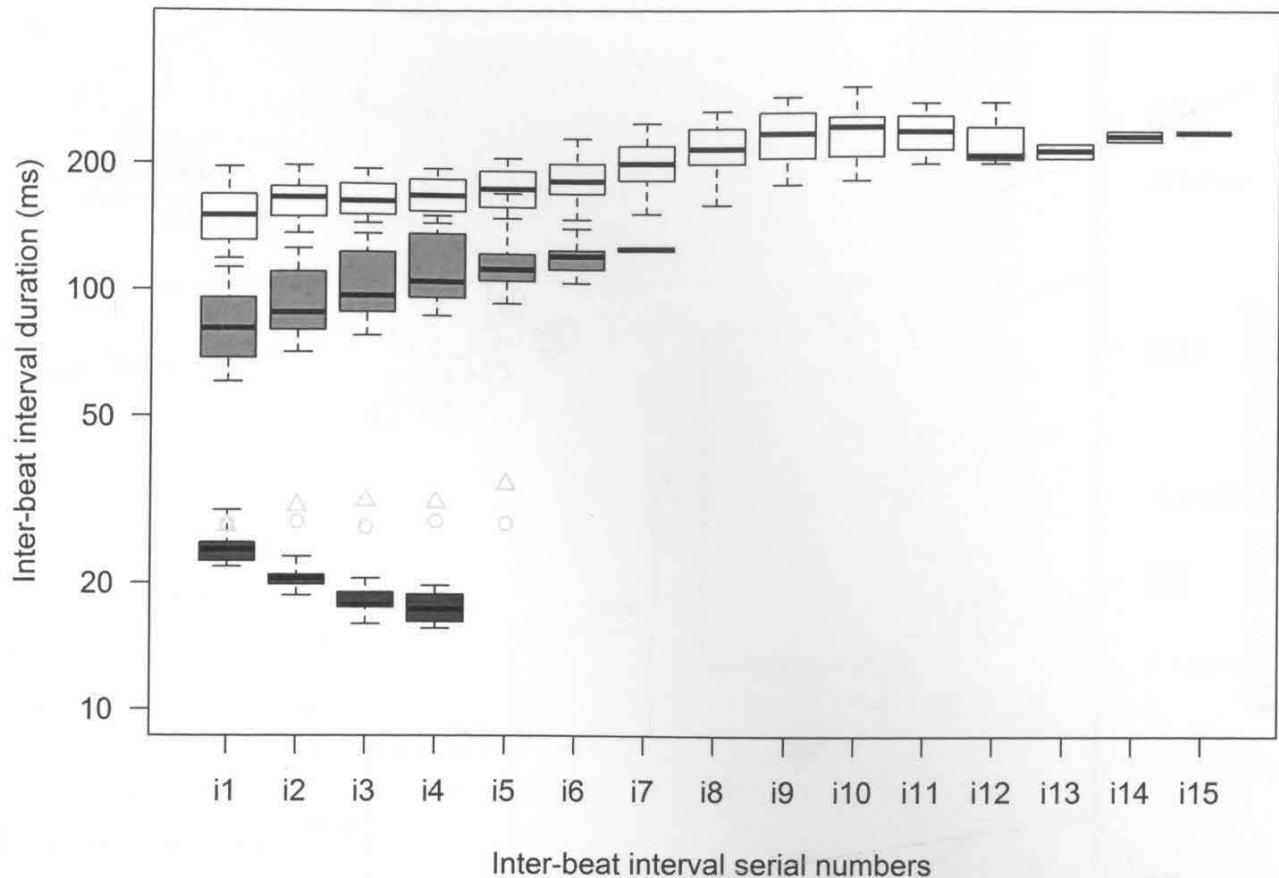


FIGURE 190. Inter-beat interval variation during male calls in the four examined *Zwicknia* Murányi, **gen. n.** species.—Box plot colors: white—*Z. bifrons* (Newman, 1838), red—*Z. acuta* Murányi & Orci, **sp. n.**, blue—*Z. rupprechtii* Murányi, Orci & Gamboa, **sp. n.** In *Z. kovacsi* Murányi & Gamboa, **sp. n.** we have drumming samples only from two specimens therefore in the case of that species two simple mark series are used to show inter-beat intervals in their calls (circles for specimen 1, and triangles for specimen 2). i1, i2, i3 and so on are labels containing the serial number of inter-beat intervals counting them from the beginning of each call. Box plots show the duration values measured in 7 specimens in *Z. bifrons* and *Z. acuta*, and 5 specimens in *Z. rupprechtii*. Vertical axis has a logarithmic scale. Only calls recorded at an ambient air temperature of 17–19 °C were used. (see the measurement data in Appendix Tables 1–4).

Phylogenetic analyses. Mitochondrial DNA analyses indicated four clades that corresponded to *Z. acuta*, *Z. bifrons*, *Z. kovacsi* and *Z. rupprechtii*, a closely related cluster of species, but genetically distinct from *C. s.l. vidua*. Haplotypes of *Z. bifrons* and *Z. acuta* appear to more closely related (Fig. 192). It is noted that morphologically and drumming evidence supported the recognition of these two taxa, but haplotypes of *Z. bifrons* collected from the Maljen Mts. in Serbia, exhibited close molecular similarities with individuals of *Z. acuta* from other locations. Presence of non-monophyletic lineages can be attributed to interspecific hybridization (Boyce *et al.* 1994; Sota & Vogles 2001). Hybridization has been found previously in stoneflies (Hanson & Mass 1960; Ross & Feytag 1967), but has not been demonstrated with molecular techniques. Other explanations could be the inheritance of allelic polymorphism from ancestral populations with persistence in descendants (Avice & Ball 1990) or incomplete lineage sorting. However, we could not test for incomplete lineage sorting with our data set. It would be expected to find more mixing of lineages than was observed in our study (e.g. Paul *et al.* 2009). Use of nuclear markers may provide answers to these two hypotheses.

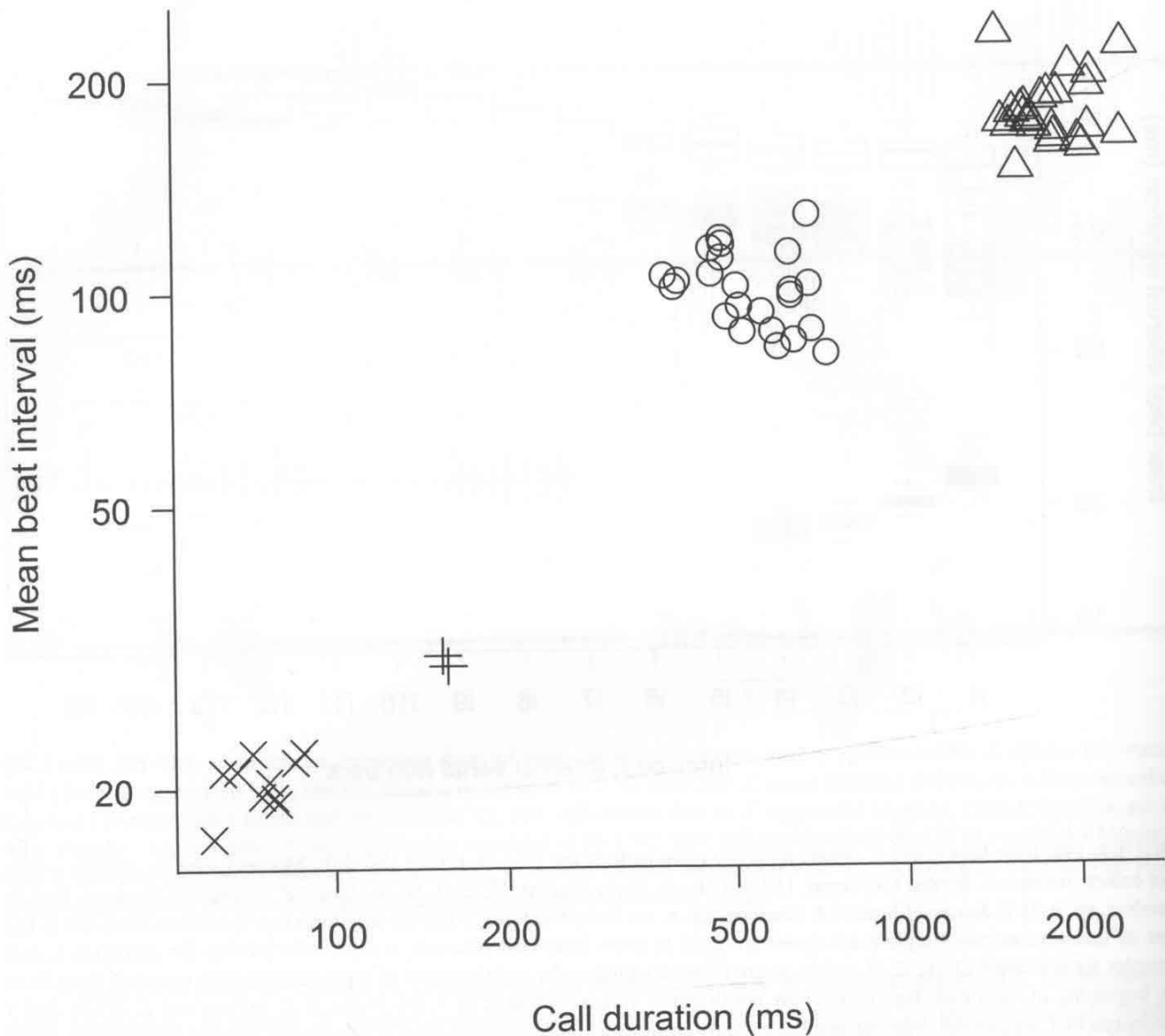


FIGURE 191. A scatter plot showing the clear separation of male calls of *Zwicknia* Murányi, **gen. n.** along two drumming signal characters—*Z. bifrons* (Newman, 1838): triangles; *Z. acuta* Murányi & Orci, **sp. n.**: circles; *Z. kovacsi* Murányi & Gamboa, **sp. n.**: +; *Z. rupprechti* Murányi, Orci & Gamboa, **sp. n.**: X—Each mark represents the mean values of the characters for a given specimen. Note that both axes have logarithmic scale. Air temperature varied between 15–21 °C in every species (for details see Tables 6–8).

TABLE 8. Descriptive statistics for the examined rhythmic characters of the male drumming calls of *Zwicknia rupprechti* Murányi, Orci & Gamboa, **sp. n.**, and also for the ambient air temperature during the sound recordings.—“n” is the number of male specimens examined. In each character data points where mean values obtained for each examined male on the basis of 1-10 signal measurements per specimen. Number of examined specimens per population: Hungary: Mecsek Mts—7; Croatia: Ivanščica Mts—3.

	n	mean	SD	min	max
Call duration (ms)	10	74.43	8.82	61	78.9
Number of beats per call	10	4.65	0.396	4	5.17
Mean beat interval (ms)	10	20.48	1.727	17	22.5
Air temperature (°C)	10	17.73	1.259	16.2	19.9

p-Distance		1	2	3	4
1	<i>Z. bifrons</i>				
2	<i>Z. acuta</i>	0.010			
3	<i>Z. kovacsi</i>	0.018	0.023		
4	<i>Z. rupprechtii</i>	0.047	0.051	0.034	
	Outgroup	0.062	0.074	0.116	0.094

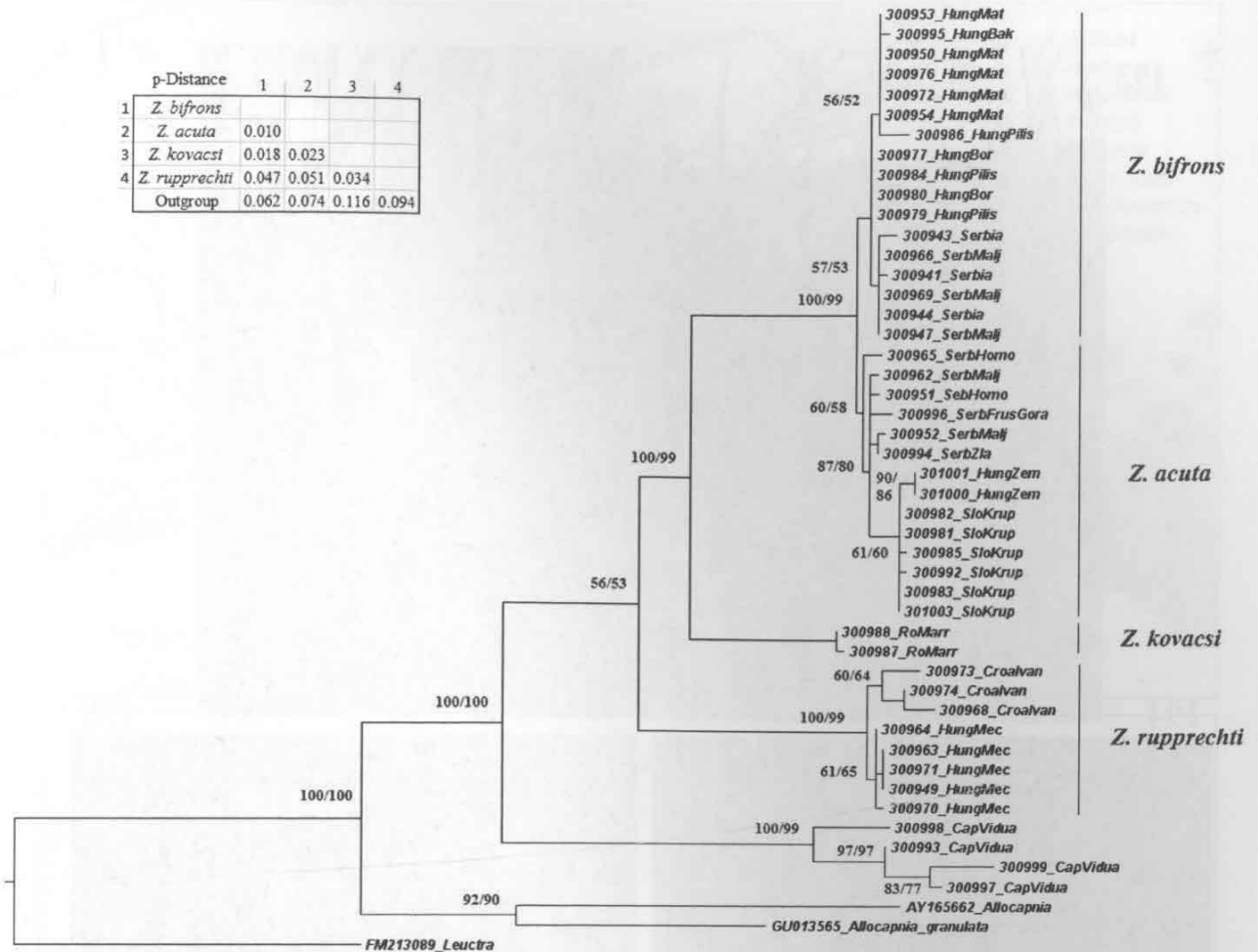


FIGURE 192. Phylogenetic tree of *cox1* including *Zwicknia* Murányi, gen. n. with our accession codes (300941-301003), and GenBank closest species (with alphanumeric accession codes) as outgroup. MP and ML had same topology. Numbers on braches are ML/MP bootstrap values >50%. Species names right to the tree refer to morphological species. P-Distance table is showed.

TABLE 9. Data for the oscillograms presented in Figs. 165–184.

Species	Figure	Collecting site	Specimen id	Ambient air temperature
<i>Z. bifrons</i>	165, 169	Hungary, Pilis Mts, Dömörkapu, Bütkös Stream	2011/No.4	20.4°C
	170	Hungary, Bakony Mts, Bakonybél, Gerence Stream	2011/No.1	17.2°C
	171	Hungary, Börzsöny Mts, Királyrét, Szén Stream	2011/No.3	18.2°C
	172	Hungary, Mátra Mts, Gyöngyössolymos, Monostor Stream	2011/No.2	18.2°C
	173	Serbia, Maljen Mts, Brajkovići, stream N of the village	2011/No.2	17.4°C
<i>Z. acuta</i>	174	Hungary, Zemplén Mts, Kishuta, Kemence Stream	2011/No.4	18.3°C
	166, 175	Slovakia, Krupinská Planina, Pötor, Stará Rieka	2011/No.4	20.1°C
	176	Serbia, Fruska Gora, Vrdnik, stream NW of the village	2011/No.1	18.1°C
	177	Serbia, Homoljske Planina, Krepoljin, stream N of the village	2011/No.1	18.3°C
<i>Z. rupprechtii</i>	178	Serbia, Zlatibor Mts, Crni Rzav Stream	2011/No.3	18.2°C
	167, 179–180	Hungary, Mecsek Mts, Zobápuszta, Völgységi Stream	2010/No.7	17.6°C
	181–182	Croatia, Ivanščica Mts, Stari Golubovec, Reka Stream	2010/No.2	18.7°C
<i>Z. kovacsi</i>	168, 183–184	Romania, Rodna Mts, Stațiunea Borșa, Cimpoiș Stream	2011/No.1	17.7°C

193



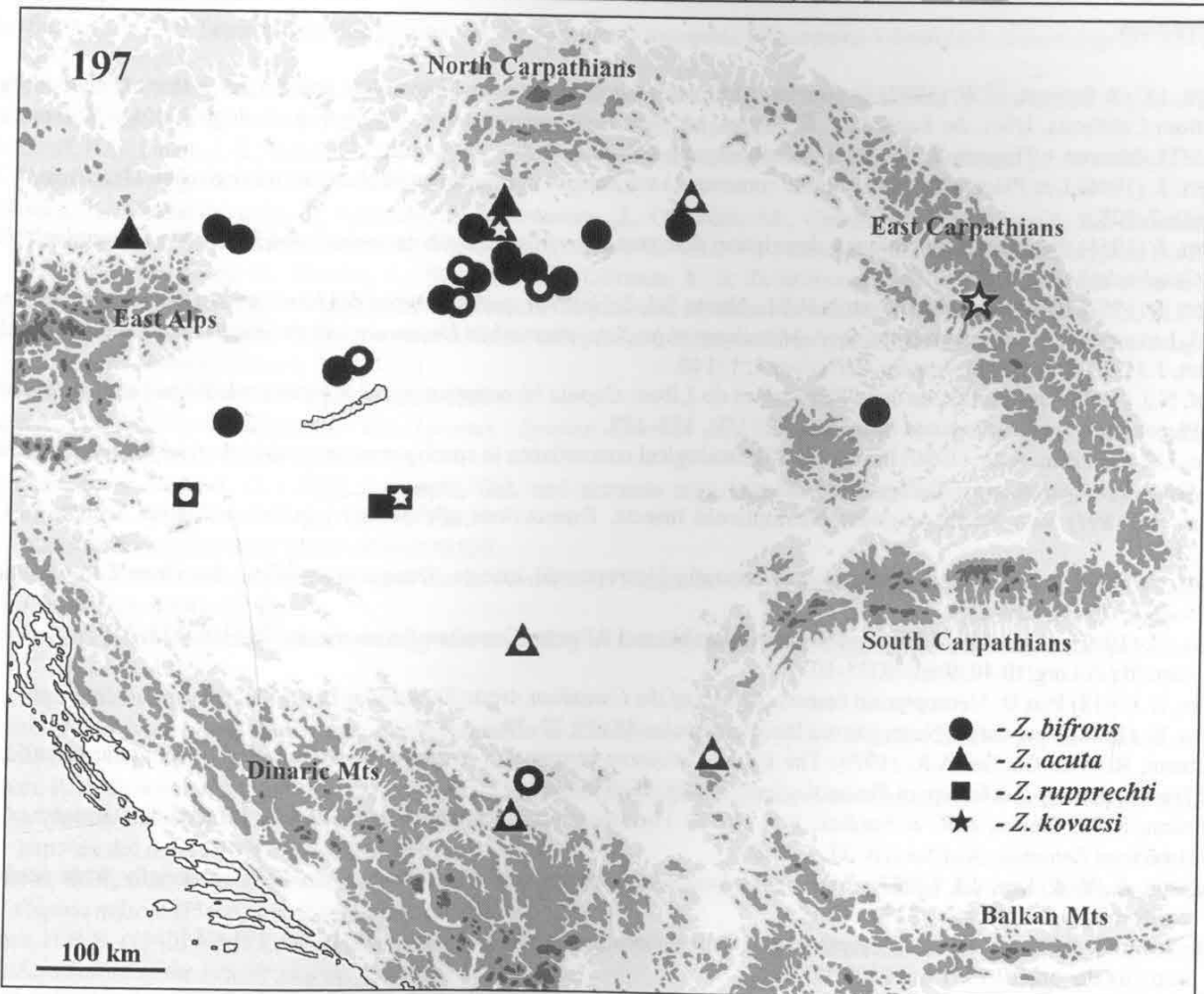
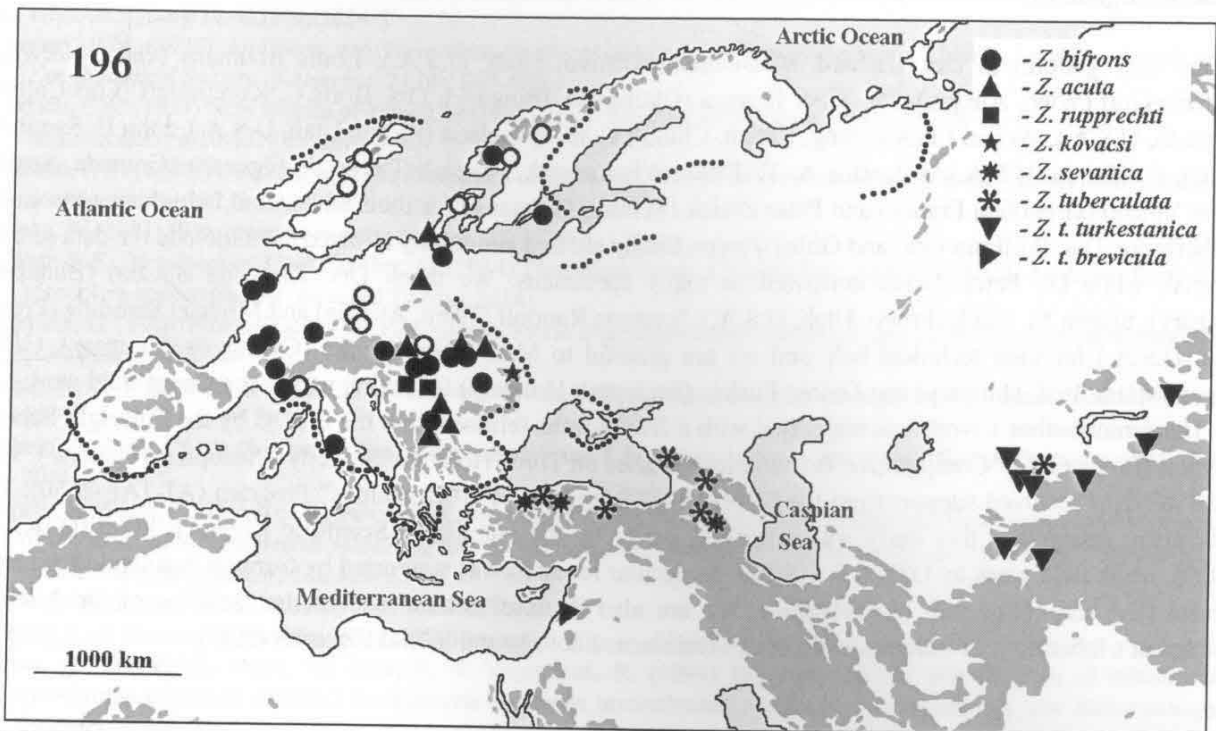
194



195



FIGURES 193–195. Type localities of the new species described in *Zwicknia* Murányi, **gen. n.**—193: *Zwicknia acuta* Murányi & Orci, **sp. n.**: Stará rieka, Slovakia, Banskobystrický Region, Krupinská Planina, Pôtor; 194: *Zwicknia kovacsi* Murányi & Gamboa, **sp. n.**: Cimpoies Stream, Romania, Maramureş County, Rodna Mts., Borşa-Staţiunea Borşa; 195: *Zwicknia rupprechtii* Murányi, Orci & Gamboa, **sp. n.**: Völgységi Stream, Hungary, Baranya County, Mecsek Mts., Komló-Zobákpusztá.



FIGURES 196–197. Distribution of *Zwicknia* Murányi, gen. n.—196: global distribution; 197: studied populations of the Carpathian Basin and the northern Balkans—in Fig. 196, white dot on *Z. bifrons* symbols indicate populations studied by Rupprecht (1997), dotted lines indicate limits of s.l. *Z. bifrons* literature reports; in Fig. 197, white dot on symbols indicate populations where drumming signals were studied by us, white star indicate type localities.

Acknowledgements

We are very grateful to Drs. Richard W. Baumann (Provo, Utah, U.S.A.), Louis Boumans (Oslo, Norway), Wolfram Graf (Wien, Austria), Mr. Tibor Kovács (Gyöngyös, Hungary), Drs. Boris C. Kondratieff (Fort Collins, Colorado, U.S.A.), Weihai Li (Xinxiang, Henan, China), C. Riley Nelson (Provo, Utah, U.S.A.), John B. Sandberg (Chico, California, U.S.A.), Valentina A. Teslenko (Vladivostok, Russia), Tierno de Figueroa (Granada, Spain), Gilles Vinçon (Grenoble, France) and Peter Zwick (Schlitz, Germany) for their advice and help during the study. Furthermore, Drs. Wolfram Graf and Gilles Vinçon kindly studied and kindly allowed us to include the data of their material, while Dr. Peter Zwick borrowed us many specimens. We thank Drs. Krisztina Buczkó (Budapest, Hungary), Shawn M. Clark (Provo, Utah, U.S.A.), Susanne Randolph (Wien, Austria) and Michael Standing (Provo, Utah, U.S.A.) for their technical help and we are grateful to Mrs. Tibor Kovács (Gyöngyös, Hungary), Gábor Magos (Mátrafüred, Hungary) and Gellért Puskás (Budapest, Hungary) for taking part in the recent field work.

The senior author's work was supported with a five months fellowship to the BYUC by the Fulbright Scholar Program (Project title: 'Comparative Taxonomical Studies on Three Holarctic Stonefly (Plecoptera) Genera'). Visit to the WNHM received support from the SYNTHESYS Project, FP7 "Capacities" Program (AT-TAF-2660). The bioacoustic research in this study was supported partly by the Hungarian Scientific Research Fund (OTKA K 81929), while field work by OTKA K 100369. Molecular research was supported by German Academic Exchange Service (DAAD) fellowship (A/09/94531). We are also thankful for the use of the facilities of Dr. Michael Monaghan's laboratory of Leibniz-Institute of Freshwater Ecology and Inland Fisheries (IGB).

References

- Abbott, J.C. & Stewart, K.W. (1997) Drumming of three *Mesocapnia* species (Capniidae) and *Soliperla thyra* (Peltoperlidae) from California, USA. In: Landolt, P. & Sartori, M. (Eds.), *Ephemeroptera & Plecoptera, Biology-Ecology-Systematics*, MTL-Mauron + Tinguely & Lachat SA., Fribourg, pp. 88–92.
- Aubert, J. (1946) Les Plécoptères de la Suisse romande. *Mitteilungen der Schweizerischen Entomologischen Gesellschaft*, 20 (1), 7–128.
- Aubert, J. (1951) Plécoptères helvétiques; description de larves nouvelles. *Mitteilungen der Schweizerischen Entomologischen Gesellschaft*, 24 (3), 281–298.
- Aubert, J. (1952) Plécoptères décrits par le R.P.L. Navas S.J. 2. Note sur quelques types des Muséums de Barcelone et de Paris 3. Les espèces de la peninsula ibérique. *Mitteilungen der Schweizerischen Entomologischen Gesellschaft*, 25 (3), 239–250.
- Aubert, J. (1959) Plecoptera. *Insecta Helvetica*, 1, 1–140.
- Alouf, N.J. (1992) Description de deux Plécoptères du Liban: *Capnia bicornata* n. sp. et *Siphonoperla libanica* n. sp. (Insecta: Plecoptera). *Senckenbergiana Biologica*, 72 (1/3), 173–177.
- Avise, J.C. & Ball Jr., R.M. (1990) Principles of genealogical concordance in species concepts and biological taxonomy. *Oxford Surveys in Evolutionary Biology*, 7, 45–67.
- Banks, N. (1897) New North American Neuropteroid Insects. *Transactions of the American Entomological Society*, 24 (1), 21–31.
- Banks, N. (1900) New genera and species of Nearctic Neuropteroid Insects. *Transactions of the American Entomological Society*, 26 (3), 239–259.
- Banks, N. (1907) A list of Perlidae from British Columbia and Alberta. *Canadian Entomologist*, 39 (10), 325–330.
<http://dx.doi.org/10.4039/ent39325-10>
- Banks, N. (1918) Part B: Neuropteroid Insects. *Report of the Canadian Arctic Expedition 1913–18*, 3, 3–5.
- Banks, N. (1938) New native Neuropteroid Insects. *Psyche*, 45 (1), 72–79.
- Baumann, R.W. & Gaufin, A.R. (1970) The *Capnia projecta* complex of Western North America (Plecoptera: Capniidae). *Transactions of the American Entomological Society*, 96, 435–468.
- Baumann, R.W., Gaufin, A.R. & Surdick, R.F. (1977) The stoneflies (Plecoptera) of the Rocky Mountains. *Memoirs of the American Entomological Society*, 31, 1–208.
- Baumann, R.W. & Lee, J.J. (2007) *Paracapnia humboldta* (Plecoptera: Capniidae), a new winter stonefly from northern California, U.S.A. *Illiesia*, 3 (3), 17–19.
- Berthélemy, C. & Dia, A. (1982) Plécoptères du Liban (Insecta). *Annales de Limnologie*, 18 (2), 191–214.
<http://dx.doi.org/10.1051/limn/1982009>
- Boyce, T.M., Zwick, M.E. & Aquadro, C.F. (1994) Mitochondrial DNA in the bark weevils: phylogenetic and evolution in the *Pissodes strobi* species group (Coleoptera: Curculionidae). *Molecular Biology and Evolution*, 11, 183–194.
- Brinck, P. (1949) Studies on Swedish stoneflies (Plecoptera). *Opuscula Entomologica*, Supplement 11, 1–250.
- Brinck, P. (1952) Bäcksländor. Plecoptera. *Svensk Insektafauna*, 15, 1–128.

- Claassen, P.W. (1924) New species of North American Capniidae (Plecoptera). *The Canadian Entomologist*, 56, 43–48, 54–57.
<http://dx.doi.org/10.4039/ent5654-3>
- Claassen, P.W. (1928) Additions and corrections to the monograph on the Plecoptera of North America. *Annals of the Entomological Society of America*, 21 (4), 667–668.
- Claassen, P.W. (1937) New species of stoneflies (Plecoptera). *The Canadian Entomologist*, 69, 79–82.
<http://dx.doi.org/10.4039/ent6979-4>
- Claassen, P.W. (1940) A Catalogue of the Plecoptera of the World. *Memoirs of the Cornell University Agricultural Experiment Station, Ithaca*, 232, 1–235.
- Despax, R. (1951) Plécoptères. *Faune de France*, 55, 1–280.
- DeWalt, R.E., Neu-Becker, U. & Steuber, G. (2014) Plecoptera Species File Online. Version 5.0/5.0. Available from: <http://plecoptera.speciesfile.org> (accessed 12 May 2014)
- Enderlein, G. (1909) Klassifikation der Plecopteren, sowie Diagnosen neuer Gattungen und Arten. *Zoologischen Anzeiger*, 34 (13/14), 385–419.
- Enting, K. & Rupprecht, R. (2001) Zur Kenntnis der Steinfliegenfauna (Insecta: Plecoptera) im Taunus. *Lauterbornia*, 41, 63–77.
- Fochetti, R. (Ed.) (2004) Plecoptera. Fauna Europea version 1.1. Available from: <http://www.faunaeur.org> (accessed 12 May 2014)
- Fochetti, R., Sezzi, E., Tierno de Figueroa, J.M., Modica, M.V. & Oliverio, M. (2009) Molecular systematics and biogeography of the western Mediterranean stonefly genus *Tyrrhenoleuctra* (Insecta, Plecoptera). *Journal of Zoology Systematics and Evolutionary Research*, 47 (4), 328–336.
<http://dx.doi.org/10.1111/j.1439-0469.2008.00508.x>
- Fochetti, R. & Tierno de Figueroa, J.M. (2008) Plecoptera. *Fauna d'Italia*, 43, 1–339.
- Folmer, O., Black, M., Hoeh, W., Lutz, R. & Vrijenhoek, R. (1994) DNA primers for amplification of mitochondrial cytochrome c oxidase subunit I from diverse metazoan invertebrates. *Molecular Marine Biology and Biotechnology*, 3, 294–299.
- Gaufin, A.R. (1970) Type-species designation for the subgenus *Utacapnia* (Plecoptera: Capniidae). *Entomological News*, 81, 197.
- Gaufin, A.R. & Jewett, S.G. (1962) New Capnias from Utah (Plecoptera). *The Wasmann Journal of Biology*, 20 (1), 69–71.
- Goloboff, P. (1999) *NONA ver. 2*. Published by the author, Tucumán, Argentina.
- Goloboff, P.A., Farris, J. & Nixon, K. (2008) TNT, a free program for phylogenetic analysis. *Cladistics*, 24, 774–786.
<http://dx.doi.org/10.1111/j.1096-0031.2008.00217.x>
- Golonka, J., Aleksandrowski, P., Aubrecht, R., Chowanec, J., Chrestek, M., Cieszkowski, M., Florek, R., Gaweda, A., Jarosiński, M., Kepińska, B., Krobicki, M., Lefeld, J., Lewandowski, M., Marko, F., Michalik, M., Oszczytko, N., Picha, F., Potfaj, M., Slaby, E., Slaczka, A., Stefaniuk, M., Uchman, A. & Zelazniewicz, A. (2005) The orava deeo drilling project and post-paleogene tectonics of the northern Carpathians. *Annales Societatis Geologorum Poloniae*, 75, 211–248.
- Gray, J.E. (1869) Notes on the fleshy Alcyonoid Corals (Alcyonium, Linn., or Zoophytaria carnosia). *The Annals and Magazine of Natural History*, Series 4, 3, 117–131.
<http://dx.doi.org/10.1080/00222936908695893>
- Guénée (1852) *Histoire Naturelle des Insectes. Species Général des Lépidoptères V.7 (Noctuérites, V.3)*. Librairie Encyclopédique de Roret, Paris, 442 pp.
- Guindon, S. & Gascuel, O. (2003) A simple, fast, and accurate algorithm to estimate large phylogenies by maximum likelihood. *Systematic Biology*, 52, 696–704.
<http://dx.doi.org/10.1080/10635150390235520>
- Hanson, J.F. (1943) Descriptions of new North American Plecoptera, II. *Proceedings of the Entomological Society of Washington*, 45(4), 85–88.
- Hanson, J.F. (1946) Comparative morphology and taxonomy of the Capniidae (Plecoptera). *The American Midland Naturalist*, 35(1), 193–249.
<http://dx.doi.org/10.2307/2421354>
- Hanson, J.F. & Mass, A. (1960) A case of hybridization in Plecoptera. *Bulletin of the Brooklyn Entomological Society*, 55 (2), 25–34.
- Hebert, P.D., Cywinska, A., Ball, S.L. & de Waard, J.R. (2003) Biological identifications through DNA barcodes. *Proceedings of the Royal Society B: Biology Science*, 270, 313–321.
<http://dx.doi.org/10.1098/rspb.2002.2218>
- Heinold, B.D., Gill, B.A. & Kondratieff, B.C. (2013) Recent collection and DNA barcode of the rare Coffee pot snowfly *Capnia nelsoni* (Plecoptera: Capniidae). *Illiesia*, 9 (2), 14–17.
- Hynes, H.B.N. (1940) A key to the British species of Plecoptera (Stoneflies) with notes on their ecology. *Freshwater Biological Association of the British Empire, Scientific Publication*, 2, 1–39.
- Hynes, H.B.N. (1941) The taxonomy and ecology of the nymphs of British Plecoptera with notes on the adults and eggs. *The Transactions of the Royal Entomological Society of London*, 91(10), 459–557.
- Hynes, H.B.N. (1955a) The nymphs of the British species of *Capnia* (Plecoptera). *The Proceedings of the Royal Entomological Society of London*, 30 (7/9), 91–96.

- Hynes, H.B.N. (1955b) A note on the Stoneflies of Iceland. *The Proceedings of the Royal Entomological Society of London*, 30 (10/12), 164–166.
- Hynes, H.B.N. (1958) A key to the adults and nymphs of the British Stoneflies (Plecoptera) with notes on their ecology and distribution. *Freshwater Biological Association, Scientific Publication*, 17, 1–87.
- Illies, J. (1955) Steinfliegen oder Plecoptera. *Die Tierwelt Deutschlands*, 43, 1–150.
- Illies, J. (1978) Plecoptera. In: Illies, J. (Ed.), *Limnofauna Europea*, 2nd edition, Fischer, Stuttgart, Germany, pp. 264–273.
- Jewett, S.G. (1965) Four new stoneflies from California and Oregon. *The Pan-Pacific Entomologist*, 41, 5–9.
- Jewett, S.G. (1966) Some species of *Capnia* from western North America (Plecoptera). *The Wasmann Journal of Biology*, 24, 101–108.
- Kawai, T. (1955) Studies on the Holognathous stoneflies of Japan II. Descriptions of two new genera, one new subgenus and three new species of the family Capniidae. *Mushi*, 28 (2), 5–11.
- Kawai, T. (1967) *Plecoptera (Insecta)*. Fauna Japonica, Biogeographical Society of Japan, Tokyo, pp. 1–211.
- Khoo, S.G. (1964) Studies on the biology of *Capnia bifrons* (Newman) and notes on the diapause in the nymphs of this species. *Gewässer und Abwässer*, 34/35, 23–30.
- Kimmins, D.E. (1946) New species of Himalayan Plecoptera. *The Annals and Magazine of Natural History*, 11 (13), 721–740. <http://dx.doi.org/10.1080/00222934608654596>
- Kimmins, D.E. (1947) A note on *Capnia nigra* Pictet (Plecoptera). *Entomologist (London)*, 80, 261–262.
- Kimmins, D.E. (1950a) Some new species of Asiatic Plecoptera. *The Annals and Magazine of Natural History*, 12 (3), 177–192.
- Kimmins, D.E. (1950b) Plecoptera (Stone-flies). *Handbooks for the identification of British Insects*, 1 (6), 1–18.
- Kis, B. (1974) Plecoptera. *Fauna Republicii Socialiste România*, 8 (7), 1–271.
- Klapálek, F. (1896) Über die Geschlechtsteile der Plecopteren, mit besonderer Rücksicht auf die Morphologie der Genitalanhänge. *Sitzungsberichten der kaiserlichen Akademie der Wissenschaften in Wien*, 105, 683–738.
- Klapálek, F. (1904) Zpráva o výsledcích cesty do Transsylvanských Alp a Vysokých Tater. *Věstniku České Akademie císaře Františka Josefa pro vědy, slovesnost a umění*, 13, 1–12.
- Klapálek, F. (1909) II. Plecoptera, Steinfliegen. *Die Süßwasserfauna Deutschlands*, 8, 33–95.
- Klapálek, F. (1914) Resultats scientifiques de l'expédition des frères Kuznecov à l'Oural Arctique en 1909, sous la direction de H. Backlund. *Plecoptera. Mémoires de l'Académie Impériale des Sciences de St. Petersbourg*, 28 (5), 1–10.
- Klapálek, F. (1920) Neue Plecopterenarten aus der Familie Capniidae. *Časopis, České Společnosti Entomologické*, 17, 3–6.
- Kondratieff, B.C. & Baumann, R.W. (2002) A review of the stoneflies of Colorado with description of a new species of *Capnia* (Plecoptera: Capniidae). *Transactions of the American Entomological Society*, 128 (3), 385–401.
- Kondratieff, B.C. & Lee, J.J. (2010) A new species of *Paracapnia* from California (Plecoptera: Capniidae). *Illiesia*, 6 (13), 206–209.
- Koponen, J.S.W. & Brinck, P. (1949) Neue oder wenig bekannte Plecoptera. *Annales Entomologici Fennici*, 15 (1), 1–21.
- Lee, J.J. & Baumann, R.W. (2011) *Mesocapnia aptera* (Plecoptera: Capniidae) a new wingless winter stonefly from northern California, U.S.A. *Illiesia*, 7 (20), 192–196.
- Li, W. & Yang, D. (2009) Synopsis of the genus *Capnia* (Plecoptera: Capniidae) from China. *Zootaxa*, 2112, 47–52.
- Li, W., Kong, F. & Yang, D. (2011) A new species of *Capnia* (Plecoptera: Capniidae) from China. *Zootaxa*, 2943, 63–68.
- Lillehammer, A. (1965) Capture of *Capnia bifrons* (Newman) at Øverland in Bærum (Plecoptera, Capniidae). *Norsk Entomologisk Tidsskrift*, 13 (1/2), 47–51.
- Lillehammer, A. (1972) Notes on the stonefly *Capnia vidua* Klapálek from Fennoscandia. *Norsk Entomologisk Tidsskrift*, 19 (2), 153–156.
- Lillehammer, A. (1974) Norwegian stoneflies I. Analysis of the variations in morphological and structural characters used in taxonomy. *Norsk Entomologisk Tidsskrift*, 21, 59–107.
- Lillehammer, A. (1988) Stoneflies (Plecoptera) of Fennoscandia and Denmark. *Fauna entomologica Scandinavica*, 21, 1–165.
- Lillehammer, A., Johannsson, M. & Gislason, G.M. (1986) Studies on *Capnia vidua* Klapálek (Capniidae, Plecoptera) populations in Iceland. *Fauna Norvegica, Series B*, 33, 93–97.
- Maketon, M., Stewart, K.W., Kondratieff, B.C. & Kirchner, R.F. (1988) New Descriptions of Drumming and Evolution of the Behavior in North American Perlodidae (Plecoptera). *Journal of the Kansas Entomological Society*, 61 (2), 161–168.
- Morton, K.J. (1896) New and little-known Palaearctic Perlidae. *The Transactions of the Entomological Society of London*, 1896 (1), 55–63.
- Navás, L. (1909) Neurópteros nuevos de la fauna ibérica. In: *Actas y Memorias del Primer Congreso de Naturalistas Españoles*, Zaragoza, 143–158.
- Navás, L. (1917) Neurópteros nuevos o poco conocidos (Novena serie). *Memorias de la Real Academia de Ciencias y Artes de Barcelona*, 3 (13), 393–406.
- Nebeker, A.V. & Gaufin, A.R. (1965) The *Capnia columbiana* complex of North America (Capniidae: Plecoptera). *Transactions of the American Entomological Society*, 91, 467–487.
- Nebeker, A.V. & Gaufin, A.R. (1967) New *Capnia* from the Rocky Mountains (Plecoptera, Capniidae). *Transactions of the American Entomological Society*, 93, 235–247.
- Nelson, C.R. & Baumann, R.W. (1987) The winter stonefly genus *Capnura* (Plecoptera: Capniidae) in North America: systematics, phylogeny, and zoogeography. *Transactions of the American Entomological Society*, 113, 1–28.

- Nelson, C.R. & Baumann, R.W. (1989) Systematics and distribution of the winter stonefly genus *Capnia* (Plecoptera: Capniidae) in North America. *The Great Basin Naturalist*, 49 (3), 289–363.
- Nelson, C.R. & Baumann, R.W. (1990) New winter stoneflies (Plecoptera: Capniidae) from the Coast Range of California. *Pan-Pacific Entomologist*, 66 (4), 301–306.
- Nelson, C.R. & Kondratieff, B.C. (1988) A new species of *Capnia* (Plecoptera: Capniidae) from the Rocky Mountains of Colorado. *Entomological News*, 99 (2), 77–80.
- Newman, E. (1838) Entomological notes. *The Entomological Magazine*, 5 (4), 372–402.
- Newman, E. (1839) On the synonymy of the Perlites, together with brief characters of the old, and of a few new species. *The Magazine of Natural History, New Series*, 3 (25/26), 32–37, 84–90.
- Nixon, K.C. (1999) *WinClada ver. 1.0*. Published by the author, Ithaca, New York, USA.
- Okamoto, H. (1922) Zweiter Beitrag zur Kenntnis der Japanischen Plecopteren. *Bulletin of the Agricultural Experiment Station, Government General of Chosen*, 1 (1), 1–46.
- Orci, K.M. & Heller, K.-G. (2004) A description of the song of *Isophya modesta* with notes on its relationship to *I. rossica* (Orthoptera: Tettigonioidae). *Journal of Orthoptera Research*, 13 (2), 211–219.
[http://dx.doi.org/10.1665/1082-6467\(2004\)013\[0211:adotso\]2.0.co;2](http://dx.doi.org/10.1665/1082-6467(2004)013[0211:adotso]2.0.co;2)
- Park, D.S., Suh, S.J., Oh, H.W. & Hebert, P.D. (2010) Recovery of the mitochondrial COI barcode region in diverse Hexapoda through tRNA-based primers. *BMC Genomics*, 11, 423.
<http://dx.doi.org/10.1186/1471-2164-11-423>
- Pauls, S.U., Theissinger, K., Ujvarosi, L., Balint, M. & Haase, P. (2009) Patterns of population structure in two closely related, partially sympatric caddisflies in Eastern Europe: historic introgression, limited dispersal, and cryptic diversity. *Journal of North American Benthological Society*, 28 (3), 517–536.
<http://dx.doi.org/10.1899/08-100.1>
- Posada, D. & Crandall, K.A. (1998) Modeltest: testing the model of DNA substitution. *Bioinformatics*, 14, 817–818.
<http://dx.doi.org/10.1093/bioinformatics/14.9.817>
- Pictet, F.J. (1833) Mémoire sur les Métamorphoses des Perles. *Annales des Sciences Naturelles*, 28, 44–65.
- Pictet, F.J. (1841) *Histoire naturelle des insectes Névroptères. Famille des Perlides*. Kessmann-Baillière, Genève-Paris, pp.1–423.
- R Core Team (2012) *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. Available from: <http://www.R-project.org/> (accessed 12 May 2014)
- Raušer, J. (1968) 67. Plecoptera. Ergebnisse der zoologischen Forschungen von Dr. Z. Kaszab in der Mongolei. *Entomologische Abhandlungen*, 34 (5), 329–398.
- Ricker, W.E. (1943) Stoneflies of southwest British Columbia. *Indiana University Publications, Science Series*, 12, 1–145.
- Ricker, W.E. (1959) The species of *Isocapnia* Banks (Insecta, Plecoptera, Nemouridae). *Canadian Journal of Zoology*, 37, 639–653.
<http://dx.doi.org/10.1139/z59-067>
- Ricker, W.E. (1965) New records and descriptions of Plecoptera (Class Insecta). *Journal Fisheries Research Board of Canada*, 22 (2), 475–501.
<http://dx.doi.org/10.1139/f65-045>
- Ricker, W.E. & Scudder, G.G.E. (1975) An annotated checklist of the Plecoptera (Insecta) of British Columbia. *Syesis*, 8, 333–348.
- Ris, F. (1905) Zwei Notizen über schweizerische Perliden. *Mitteilungen der Schweizerischen entomologischen Gesellschaft*, 11 (2), 93–97.
- Ross, H.H. & Freytag, P.H. (1967) Remarkable sympatry in the winter stoneflies *Allocaupnia indianae* and *A. ohioensis*, a pair of sister species. *The Ohio Journal of Science*, 67 (4), 228–232.
- Ross, H.H. & Ricker, W.E. (1971) The classification, evolution, and dispersal of the winter stonefly genus *Allocaupnia*. *Illinois Biological Monographs*, 45, 1–166.
- Rostock, M. (1892) *Capnodes schilleri*, eine neue deutsche Perlide. *Berliner Entomologische Zeitschrift*, 37 (1), 1–5.
<http://dx.doi.org/10.1002/mmnd.18920370103>
- Rupprecht, R. (1965) „Trommeln“ als Verständigungsmittel bei Steinfliegen (Plecoptera). *Zeitschrift für Naturforschung*, 20 (12), 1258–1260.
- Rupprecht, R. (1968) Das Trommeln der Plecopteren. *Zeitschrift für Vergleichende Physiologie*, 59, 38–71.
<http://dx.doi.org/10.1007/bf00298810>
- Rupprecht, R. (1969) Zur Artspezifität der Trommelsignale der Plecopteren (Insecta). *Oikos*, 20, 26–33.
<http://dx.doi.org/10.2307/3543742>
- Rupprecht, R. (1976) Struktur und Funktion der Bauchblase und des Hammers von Plecopteren. *Zoologische Jahrbücher*, 95, 9–80.
- Rupprecht, R. (1982) Drumming signals of Danish Plecoptera. *Aquatic Insects*, 4 (2), 93–103.
<http://dx.doi.org/10.1080/01650428209361089>
- Rupprecht, R. (1997) An attempt to explain different drumming signals within *Capnia bifrons*. In: Landolt, P. & Sartori, M. (Eds.), *Ephemeroptera & Plecoptera, Biology-Ecology-Systematics*. MTL-Mauron + Tinguely & Lachat SA., Fribourg, pp. 93–98.

- Sandberg, J.B. (2011a) Vibrational communication of *Isoperla* Banks from California and Oregon (Plecoptera: Perlodidae). *Illiesia*, 7 (1), 1–23.
- Sandberg, J.B. (2011b) Vibrational communication of nine California stonefly (Plecoptera) species. *Western North American Naturalist*, 71 (3), 285–301.
<http://dx.doi.org/10.3398/064.071.0313>
- Shimizu, T. (1997) Designation of lectotypes for three Japanese stoneflies (Plecoptera), with reference to the genus *Apteroperla* Matsumura. *Japanese Journal of Entomology*, 65 (3), 531–535.
- Sivec, I. (1980) Plecoptera. *Catalogus Faunae Yugoslaviae, Ljubljana*, 3 (6), 1–30.
- Sota, T. & Vogler, A.P. (2001) Incongruence of mitochondrial and nuclear gene trees in the carabid beetles *Ohomopterus*. *Systematic Biology*, 50, 39–59.
<http://dx.doi.org/10.1093/sysbio/50.1.39>
- Stark, B.P. & Baumann, R.W. (2004) The winter stonefly genus *Paracapnia* (Plecoptera: Capniidae). *Monographs of the Western North American Naturalist*, 2, 96–108.
<http://dx.doi.org/10.3398/1545-0228-2.1.96>
- Stewart, K.W. (2001) Vibrational communication (drumming) and mate-searching behavior of stoneflies (Plecoptera); evolutionary considerations. In: Dominguez, E. (Ed.), *Trends in Research in Ephemeroptera and Plecoptera*. Kluwer Academic / Plenum Publishers, New York, pp. 217–225.
- Stewart, K.W. & Sandberg, J.B. (2006) Vibratory communication and mate searching behaviour in stoneflies. In: Drosopoulos, S. & Claridge, M.F. (Eds.), *Insect sounds and communication: Physiology, behaviour, ecology and evolution*. Taylor & Francis, CRC Press, pp. 179–186.
- Stewart, K.W. & Stark, B.P. (2002) *Nymphs of North American stonefly genera (Plecoptera)*. 2nd Edition. The Caddis Press, Columbus, Ohio, pp. 1–510.
- Strand, E. (1935) Miscellanea nomenclatorica zoologica et palaeontologica VII. *Folia Zoologica et Hydrobiologica*, 7 (2), 300–306.
- Tamura, K., Dudley, J., Nei, M. & Kumar, S. (2007) MEGA4: Molecular Evolutionary Genetics Analysis (MEGA) software version 4.0. *Molecular Biology and Evolution*, 24, 1596–1599.
<http://dx.doi.org/10.1093/molbev/msm092>
- Thompson, J.D., Higgins, D.G. & Gibson, T.J. (1994) Clustal W: Improving the sensitivity of progressive multiple sequence alignment through sequence weighting, position-specific gap penalties and weight matrix choice. *Nucleic Acids Research*, 22, 4673–4680.
<http://dx.doi.org/10.1093/nar/22.22.4673>
- Tierno de Figueroa, J.M., Luzón-Ortega, J.M. & López-Rodríguez, M.J. (2009) First record of male drumming call of the genus *Capnioneura* Ris, 1905 (Plecoptera, Capniidae). *Entomological Science*, 12, 359–362.
<http://dx.doi.org/10.1111/j.1479-8298.2009.00346.x>
- Tierno de Figueroa, J.M., Luzón-Ortega, J.M. & López-Rodríguez, M.J. (2011) Intraspecific and interspecific variation in drumming signals in the genus *Capnioneura* (Plecoptera: Capniidae). *Aquatic Insects*, 33 (4), 335–341.
<http://dx.doi.org/10.1080/01650424.2011.640334>
- Tierno de Figueroa, J.M., Sánchez-Ortega, A., Membiela Iglesia, P. & Luzón-Ortega, J.M. (2003) Plecoptera. *Fauna Iberica*, 22, 1–404.
- Vinçon, G. & Sivec, I. (2011) Contribution to the knowledge of the Capniidae (Plecoptera) of Turkey. *Illiesia*, 7 (11), 118–126.
- Winkler, O. (1957) Plecoptera Slovenska (Faunisticko-systematická štúdia). *Biologické Práce*, 3 (7), 1–95.
- Westermann, F. (1993) Wing polymorphism in *Capnia bifrons* (Plecoptera: Capniidae). *Aquatic Insects*, 15 (3), 135–140.
<http://dx.doi.org/10.1080/01650429309361510>
- Zapekina-Dulkeit, J.I. (1975a) K faune vesnianok (Plecoptera, Insecta) rek vasseina Ozera Baikal. *Trudy Gosuda zapovednika "Stolbij"*, 10, 199–217.
- Zapekina-Dulkeit, J.I. (1975b) Novie vidi vesnianok (Plecoptera) iz Juznoi Sibiri. *Revue d'Entomologie de l'USSR*, 54 (2), 378–382.
- Zapekina-Dulkeit, J.I. & Zhiltzova, L.A. (1973) Novii rod vesnianok (Plecoptera) iz Ozera Baikal. *Revue d'Entomologie de l'USSR*, 52 (2), 340–346.
- Zeigler, D.D. & Stewart, K.W. (1977) Drumming behavior of eleven Nearctic stonefly (Plecoptera) species. *Annals of the Entomological Society of America*, 70 (4), 495–505.
- Zenger, J.T. & Baumann, R.W. (2004) The Holarctic winter stonefly genus *Isocapnia*, with an emphasis on the North American fauna (Plecoptera: Capniidae). *Monographs of the Western North American Naturalist*, 2, 65–95.
<http://dx.doi.org/10.3398/1545-0228-2.1.65>
- Zetterstedt, J.W. (1840) Famil. 5. Perlariae Latr. In: Zetterstedt, J.W. (Ed.), *Insecta Lapponica descripta*. Lipsiae, pp. 1055–1060.
- Zhiltzova, L.A. (1964) K poznaniu vesnianok (Plecoptera) Kavkaza. VI. Novie vidi Taeniopterygidae, Nemouridae i Capniidae. *Revue d'Entomologie de l'USSR*, 43 (2), 347–362.
- Zhiltzova, L.A. (1969) Novie I redkie vidi vesnianok sem. Capniidae (Plecoptera) iz Srednei Azii. *Revue d'Entomologie de l'USSR*, 48 (3), 593–611.
- Zhiltzova, L.A. (2001) Plecoptera fauna of Capniidae of Russia and adjacent territories (within the limits of the former USSR).

- In: Dominguez, E. (Ed.), *Trends in Research in Ephemeroptera and Plecoptera*. Kluwer Academic / Plenum Publishers, New York, 423–429.
- Zhiltzova, L.A. (2003) Plecoptera, Gruppe Euholognatha. *Fauna of Russia and Neighbouring Countries, New Series*, 145, 1–538.
- Zhiltzova, L.A. & Levanidova, I.M. (1978) Novie vidi vesnianok (Plecoptera) s Dalnego Vostoka. *Novie Vidi Zivotnih, Akademia Nauk SSSR Trudy Zoologiceskogo Instituta*, 61, 3–29.
- Zhiltzova, L.A. & Varykhanova, K.V. (1987) Novii vid vesnianok roda *Capnia* Pictet (Plecoptera, Capniidae) iz Mongolii. *Revue d'Entomologie de l'USSR*, 66 (1), 102–104.
- Zwick, P. (1971) Plecoptera aus Anatolien und benachbarten Gebieten. *Mitteilungen der Schweizerischen entomologischen Gesellschaft*, 44 (3/4), 233–264.
- Zwick, P. (1973) Insecta Plecoptera. Phylogenetisches System und Katalog. *Das Tierreich, Berlin*, 94, 1–465.
- Zwick, P. (1975) Weitere Plecoptera aus Anatolien. *Mitteilungen der Schweizerischen entomologischen Gesellschaft*, 48 (3/4), 387–396.
- Zwick, P. (1978) Steinfliegen (Plecoptera) aus Griechenland und benachbarten Ländern. *Mitteilungen der Schweizerischen Entomologischen Gesellschaft*, 51, 21–38, 213–239.
- Zwick, P. (1984) Geographische Rassen und Verbreitungsgeschichte von *Capnopsis schilleri* (Plecoptera, Capniidae). *Deutsche Entomologische Zeitschrift*, 31 (1–3), 1–7.
- Zwick, P. (2004) A key to the West Palaearctic genera of stoneflies (Plecoptera) in the larval stage. *Limnologica*, 34, 315–348. [http://dx.doi.org/10.1016/s0075-9511\(04\)80004-5](http://dx.doi.org/10.1016/s0075-9511(04)80004-5)
- Zwick, P. & Sivec, I. (1980) Beiträge zur Kenntnis der Plecoptera des Himalaja. *Entomologica Basiliensia*, 5, 59–138.

APPENDIX 1. Capniidae species studied for the present work; most of them are stored in the BYUC collection, otherwise indicated in the list.

<i>Allocaupnia aurora</i> Ricker, 1952	U.S.A.: North Carolina, Virginia
<i>A. curiosa</i> Frison, 1942	U.S.A.: Virginia
<i>A. forbesi</i> Frison, 1929	U.S.A.: Kentucky
<i>A. frumi</i> Kirchner, 1982	U.S.A.: West Virginia
<i>A. fumosa</i> Ross, 1964	U.S.A.: Virginia
<i>A. granulata</i> (Claassen, 1924)	U.S.A.: Oklahoma, Arkansas, Pennsylvania
<i>A. harperi</i> Kirchner, 1980	U.S.A.: Virginia
<i>A. jeanae</i> Ross, 1964	U.S.A.: Arkansas (Paratypes)
<i>A. malverna</i> Ross, 1964	U.S.A.: Arkansas
<i>A. maria</i> Hanson, 1942	U.S.A.: New Hampshire
<i>A. minima</i> (Barnston, 1848)	U.S.A.: New York
<i>A. mohri</i> Ross & Ricker, 1964	U.S.A.: Oklahoma
<i>A. mystica</i> Frison, 1929	U.S.A.: Illinois, Missouri
<i>A. nivicola</i> (Fitch, 1847)	U.S.A.: Pennsylvania, Virginia
<i>A. peltoides</i> Ross & Ricker, 1964	U.S.A.: Oklahoma
<i>A. pygmaea</i> (Burmeister, 1839)	U.S.A.: New Hampshire
<i>A. recta</i> (Claassen, 1924)	U.S.A.: Kentucky, Illinois
<i>A. rickeri</i> Frison, 1929	U.S.A.: Arkansas, Pennsylvania, West Virginia
<i>A. sandersoni</i> Ricker, 1952	U.S.A.: Arkansas
<i>A. stannardi</i> Ross, 1964	U.S.A.: Virginia
<i>A. virginiana</i> Frison, 1942	U.S.A.: Virginia, South Carolina
<i>A. vivipara</i> (Claassen, 1924)	U.S.A.: Oklahoma, Missouri
<i>A. wrayi</i> Ross, 1964	U.S.A.: Virginia
<i>A. zola</i> Ricker, 1952	U.S.A.: Tennessee
<i>Arsapnia arapahoe</i> (Nelson & Kondratieff, 1988)	U.S.A.: Colorado (Paratype)
<i>A. coyote</i> (Nelson & Baumann, 1987)	U.S.A.: California (Paratypes)
<i>A. decepta</i> Banks, 1897	U.S.A.: Arizona, Colorado
<i>A. pileata</i> (Jewett, 1966)	U.S.A.: Oregon, California
<i>A. sequoia</i> (Nelson & Baumann, 1987)	U.S.A.: California (Paratypes)
<i>A. teresa</i> (Claassen, 1924)	U.S.A.: California
<i>A. tumida</i> (Claassen, 1924)	U.S.A.: California
<i>A. utahensis</i> (Gaufin & Jewett, 1962)	U.S.A.: Utah (Paratypes), California
<i>Baikaloperla elongata</i> Zapekina-Dulkeit & Zhiltzova, 1973	Russia (females only)
<i>B. kozhovi</i> Zapekina-Dulkeit & Zhiltzova, 1973	Russia (females only)
<i>Bolshecapnia gregsoni</i> (Ricker, 1965)	Canada (Paratypes)
<i>B. maculata</i> (Jewett, 1954)	U.S.A.: California
<i>B. milami</i> (Nebeker & Gaufin, 1967)	U.S.A.: Montana (Paratypes), Colorado
<i>B. missiona</i> Baumann & Potter, 2007	U.S.A.: Montana (Paratypes)
<i>B. sasquatchi</i> (Ricker, 1965)	U.S.A.: Washington
<i>B. spenceri</i> (Ricker, 1965)	U.S.A.: Montana
<i>Capnia s.s. atra</i> Morton, 1896	Norway, Sweden, Finland
<i>C. s.s. khubsugulica</i> Zhiltzova & Varykhanova, 1987	Mongolia
<i>C. s.s. nearctica</i> Banks, 1918	Canada, U.S.A.: Alaska
<i>C. s.s. nigra</i> (Pictet, 1833)	Spain, Switzerland, Romania (HNHM), Mongolia
<i>C. s.s. pygmaea</i> (Zetterstedt, 1840)	Norway
<i>Capnia s.l. arensi</i> Zhiltzova, 1964	Russia
<i>C. s.l. barberi</i> Claassen, 1924	U.S.A.: California
<i>C. s.l. californica</i> Claassen, 1924	U.S.A.: California, Arizona
<i>C. s.l. caryi</i> Baumann & Jacobi, 2002	U.S.A.: Arizona (Paratypes)
<i>C. s.l. cheama</i> Ricker, 1965	Canada, U.S.A.: Montana
<i>C. s.l. coloradensis</i> Claassen, 1937	U.S.A.: Utah, Colorado
<i>C. s.l. confusa</i> Claassen, 1936	U.S.A.: Idaho, Utah
<i>C. s.l. elongata</i> Claassen, 1924	U.S.A.: California, Washington
<i>C. s.l. excavata</i> Claassen, 1924	Canada, U.S.A.: California
<i>C. s.l. femina</i> Kawai, 1968	Nepal (females only)
<i>C. s.l. flalai</i> Nelson & Baumann, 1990	U.S.A.: California (Paratypes)
<i>C. s.l. glabra</i> Claassen, 1924	U.S.A.: California (Paratypes), Idaho
<i>C. s.l. glacilaria</i> Claassen, 1924	Canada, U.S.A.: Utah

- C. s.l. hitchcocki* Nelson & Baumann, 1987 U.S.A.: California (Paratypes)
C. s.l. inyo Nelson & Baumann, 1987 U.S.A.: California (Paratypes)
C. s.l. jewetti Frison, 1942 U.S.A.: Oregon
C. s.l. kersti Nelson, 2004 U.S.A.: Oregon (Paratypes)
C. s.l. lacustra Jewett, 1965 U.S.A.: Nevada (Paratypes), California
C. s.l. licina Jewett, 1954 U.S.A.: Oregon, Washington
C. s.l. lineata Hanson, 1943 U.S.A.: Idaho
C. s.l. mariposa Nelson & Baumann, 1987 U.S.A.: California (Paratypes)
C. s.l. melia Frison, 1942 Canada, U.S.A.: Oregon
C. s.l. mono Nelson & Baumann, 1987 U.S.A.: California (Paratypes)
C. s.l. n. nana Claassen, 1924 Canada, U.S.A.: Idaho
C. s.l. nana wasatchae Nebeker & Gaufin, 1967 U.S.A.: Utah
C. s.l. nelsoni Kondratieff & Baumann, 2002 U.S.A.: Colorado
C. s.l. oregona Frison, 1942 U.S.A.: Oregon
C. s.l. palomar Nelson & Baumann, 1987 U.S.A.: California (Paratypes)
C. s.l. pedestris Kimmins, 1947 Pakistan (male only)
C. s.l. petila Jewett, 1954 U.S.A.: Oregon, Idaho
C. s.l. prolongata Zhiltzova, 1969 Kazakhstan (Paratypes)
C. s.l. promota Frison, 1937 U.S.A.: Oregon, Washington
C. s.l. quadrituberosa Hitchcock, 1958 U.S.A.: California (Paratypes)
C. s.l. regilla Nelson & Baumann, 1987 U.S.A.: California (Paratypes)
C. s.l. saratoga Nelson & Baumann, 1987 U.S.A.: California (Paratypes)
C. s.l. scobina Jewett, 1966 U.S.A.: California (Paratypes)
C. s.l. sextuberculata Jewett, 1954 U.S.A.: Oregon, Montana
C. s.l. shasta Nelson & Baumann, 2009 U.S.A.: California (Paratypes)
C. s.l. shepardii Nelson & Baumann, 1987 U.S.A.: California (Paratypes)
C. s.l. spinulosa Claassen, 1937 U.S.A.: California
C. s.l. uintahi Gaufin, 1964 U.S.A.: Utah (Paratypes), Idaho
C. s.l. umpqua Frison, 1942 U.S.A.: Oregon, California
C. s.l. valhalla Nelson & Baumann, 1987 U.S.A.: California (Paratypes)
C. s.l. ventura Nelson & Baumann, 1987 U.S.A.: California (Paratypes)
C. s.l. vernalis Newport, 1848 Canada, U.S.A.: Utah, Wyoming
C. s.l. v. vidua Klapálek, 1904 France, Switzerland, Italy, Slovakia (HNHM)
C. s.l. vidua rilensis Raušer, 1962 Romania (HNHM), Greece (HNHM)
C. s.l. willametta Jewett, 1955 U.S.A.: Oregon
C. s.l. yosemite Nelson & Baumann, 1987 U.S.A.: California (Paratypes)
C. s.l. zukeli Hanson, 1943 U.S.A.: Idaho
Capnionera b. balkanica Baumann & Kačanski, 1975 Montenegro (Paratypes)
C. balkanica macedonica Ikononov, 1978 Greece
C. brachyptera Despax, 1932 France
C. caucasica Zhiltzova, 1964 Russia (Paratypes)
C. libera (Navás, 1909) Portugal
C. mitis Despax, 1932 Portugal, Spain, France
C. nemuroides Ris, 1905 France (HNHM), Germany
Capnopsis s. schilleri (Rostock, 1892) Germany, Norway, Italy
C. schilleri balcanica Zwick, 1984 Croatia
Capnura anas Nelson & Baumann, 1987 U.S.A.: Oregon (Paratypes), Idaho
C. elevata (Frison, 1942) U.S.A.: Oregon, Washington
C. fibula (Claassen, 1924) U.S.A.: Arizona, New Mexico
C. intermontana Nelson & Baumann, 1987 U.S.A.: Oregon (Paratypes), Idaho (Paratypes)
C. manitoba (Claassen, 1924) Canada
C. venosa Banks, 1900 U.S.A.: Idaho, Montana
C. wanica (Frison, 1944) U.S.A.: California, Oregon, Colorado
Eucapnopsis brevicauda (Claassen, 1924) Canada, U.S.A.: Utah, Arizona
E. stigmatica transversa Aubert, 1959 Russia
Isocapnia abbreviata Frison, 1942 U.S.A.: California
I. agassizi Ricker, 1943 Canada
I. crinita (Needham & Claassen, 1925) U.S.A.: Alaska, New Mexico
I. eichlini Zenger & Baumann, 2004 U.S.A.: California (Paratypes)
I. grandis (Banks, 1907) U.S.A.: Oregon, Montana
I. guentheri (Joost, 1970) Mongolia

- I. hyalita* Ricker, 1959
I. integra Hanson, 1943
I. kudia Ricker, 1959
I. mogila Ricker, 1959
I. palousa Zenger & Baumann, 2004
I. rickeri Zenger & Baumann, 2004
I. sibirica (Zapekina-Dulkeit, 1955)
I. spenceri Ricker, 1943
I. vedderensis (Ricker, 1943)
Mesocapnia altaica (Zapekina-Dulkeit, 1955)
M. arizonensis (Baumann & Gaufin, 1969)
M. autumnata (Baumann & Gaufin, 1970)
M. bulbosa Nelson & Baumann, 1990
M. frisoni (Baumann & Gaufin, 1970)
M. lapwae (Baumann & Gaufin, 1970)
M. oenone (Neave, 1929)
M. porrecta (Jewett, 1987)
M. projecta (Frison, 1937)
M. silvatica Raušer, 1968
M. variabilis (Klapálek, 1920)
M. wernerii (Baumann & Gaufin, 1970)
M. yoloensis (Baumann & Gaufin, 1970)
Nemocapnia carolina Banks, 1938
Paracapnia angulata Hanson, 1961
P. boris Stark & Baumann, 2004
P. disala (Jewett, 1962)
P. ensicala (Jewett, 1962)
P. humboldti Baumann & Lee, 2007
P. opis (Newman, 1839)
P. sikhotesensis Zhiltzova, 1978
Utacapnia columbiana (Claassen, 1924)
U. distincta (Frison, 1937)
U. imbera (Nebeker & Gaufin, 1965)
U. lemoniana (Nebeker & Gaufin, 1965)
U. logana (Nebeker & Gaufin, 1965)
U. nedia (Nebeker & Gaufin, 1966)
U. poda (Nebeker & Gaufin, 1965)
U. sierra (Nebeker & Gaufin, 1965)
U. tahoensis (Nebeker & Gaufin, 1965)
U. trava (Nebeker & Gaufin, 1965)

- U.S.A.: Montana (Paratypes), Colorado
 Canada
 Mongolia
 U.S.A.: California, Oregon (Paratypes)
 U.S.A.: Washington (Paratypes), Idaho (Paratypes)
 U.S.A.: Oregon (Paratypes)
 Russia (Syntype), Mongolia
 U.S.A.: California, Washington
 U.S.A.: Alaska, Idaho
 Mongolia
 U.S.A.: Arizona (Paratypes)
 Canada, U.S.A.: Washington (Paratypes)
 U.S.A.: California (Paratypes)
 U.S.A.: California, Utah (Paratypes), Texas
 U.S.A.: California, Washington
 U.S.A.: Washington, Montana
 U.S.A.: California, Washington
 U.S.A.: California, Washington
 Mongolia
 Mongolia, Canada
 U.S.A.: Arizona (Paratypes)
 U.S.A.: California
 U.S.A.: Florida, Virginia
 Canada, U.S.A.: Colorado, New York
 U.S.A.: California (Paratypes)
 U.S.A.: California, Oregon
 U.S.A.: Oregon, Washington
 U.S.A.: California (Paratypes)
 Canada, U.S.A.: New Jersey
 Russia
 Canada, U.S.A.: Montana
 U.S.A.: Idaho, Wyoming
 U.S.A.: Oregon (Paratypes)
 U.S.A.: Utah (Paratypes), Idaho
 U.S.A.: Utah, Wyoming
 U.S.A.: Oregon, Idaho
 U.S.A.: Colorado, Wyoming
 U.S.A.: California
 U.S.A.: California
 U.S.A.: Oregon, Montana

APPENDIX TABLE 1. Inter-beat interval measurement data in *Zwickenia acuta* Murányi & Orci, sp. n. male calls. — i1, i2, i3 and so on are labels containing the serial number of inter-beat intervals counting them from the beginning of each call.

specimen ID	Population	Ambient air temperature	Call ser. numb. in call sequence	inter beat interval (ms)						
				i1	i2	i3	i4	i5	i6	i7
23	Slovakia: Krupinská Planina	18,3	1	68,8	73,4	77,5	86,5	93,1	104,5	
			2	85,1	91,1	96,4	107,2	112,9		
			3	72,5	87,2	94,0	102,2	110,7		
29	Slovakia: Krupinská Planina	18,2	1	68,6	77,6	82,2	89,7	97,0	110,6	124,7
			2	80,5	92,3	98,6	105,2	113,0	125,0	
			3	75,2	85,8	93,2	99,7	107,3	112,6	127,4
30	Slovakia: Krupinská Planina	18	1	89,5	87,8	112,9	107,8	125,2	141,0	
			2	106,1	122,2	135,8	143,4	170,6		
			3	112,5	124,9	124,3	150,3	141,4		
55	Hungary: Zemplén Mts	17,7	1	98,1	109,9	126,6	144,8			
			2	91,3	109,9	122,8	138,0			
			3	84,4	105,7	119,3	133,1	148,5		
56	Hungary: Zemplén Mts	18,3	1	97,8	110,5	128,6				
			2	98,8	119,8	132,7	145,8			
			3	95,5	105,6	120,7	134,0			
59	Serbia: Zlatibor Mts	18,2	1	60,2	71,2	79,0	96,0	113,9		
			2	66,1	81,5	89,9	102,4	119,3		
			3	60,5	70,8	80,3	91,8	106,4	122,6	
57	Serbia: Zlatibor Mts	17,4	1	62,3	75,1	83,3	93,4	104,6	118,5	
			2	74,7	86,8	93,9	103,5	111,7	127,9	
			3	63,7	79,9	88,1	95,4	103,8	121,0	
Mean			81,53	93,76	103,80	113,49	117,45	120,40	126,02	
Sd			15,97	17,52	19,94	21,96	20,25	10,71	1,91	

APPENDIX TABLE 2. Inter-beat interval measurement data in *Zwicknia bifrons* (Newman, 1838) male calls. — i1, i2, i3 and so on are labels containing the serial number of inter-beat intervals counting them from the beginning of each call.

specimen ID	Population	Ambient air temperature	Call ser. numb. in call sequence	inter beat interval (ms)						
				i1	i2	i3	i4	i5	i6	i7
1	Hungary: Pilis Mts	18,1	1	170,2	170,0	167,7	172,5	183,2	200,0	218,5
			2	147,5	173,1	167,2	172,6	175,2	180,9	189,9
			3	144,3	173,5	164,1	167,9	173,6	182,3	198,2
2	Hungary: Pilis Mts	17,1	1	178,2	197,0	194,0	194,8	206,4	230,3	242,2
			2	176,9	191,2	190,8	190,4	192,9	200,6	210,2
			3	175,9	175,5	190,3	190,5	186,9	192,1	201,2
9	Hungary: Börzsöny Mts	17,6	1	150,9	135,8	147,1	151,6	158,3	166,5	177,8
			2	124,7	148,7	150,8	146,7	153,9	161,1	169,9
			3	119,1	141,8	144,0	146,3	151,3	155,8	165,1
11	Hungary: Börzsöny Mts	18,2	1	168,1	165,3	168,2	183,4	199,7	226,3	244,0
			2	144,7	161,4	162,4	167,5	178,7	192,7	221,0
			3	151,8	166,3	160,8	168,0	174,8	190,8	221,4
32	Serbia: Majjen Mts	17,4	1	149,8	144,6	149,9	154,1	152,9	170,5	183,4
			2	123,4	146,6	148,8	144,2	149,5	150,9	159,8
			3	118,3	146,8	149,1	148,2	148,7	148,1	152,8
38	Hungary: Mátra Mts	17,3	1	137,0	163,6	156,5	159,6	172,7	182,7	206,6
			2	130,7	157,8	157,5	160,1	165,0	174,9	194,6
			3	127,3	154,2	153,9	154,3	161,2	171,8	187,5
61	Hungary: Pilis Mts	18,9	1	195,4	184,2	187,0	193,6	206,7	228,8	250,4
			2	165,8	183,3	182,7	186,9	195,9	200,8	225,6
			3	161,6	186,5	178,8	183,7	196,1	205,9	225,0
Mean				150,6	165,1	165,3	168,4	175,4	186,4	202,1
Sd				22,14	17,42	16,03	17,21	19,28	24,23	28,16

... continued on the next page

APPENDIX TABLE 2. (Continued)

specimen ID	Population	Ambient air temperature	Call ser. numb. in call sequence	inter beat interval (ms)													
				i8	i9	i10	i11	i12	i13	i14	i15						
1	Hungary: Pilis Mts	18,1	1	241,0	263,9												
			2	210,8	238,9	253,5											
			3	220,2	237,8	274,9											
2	Hungary: Pilis Mts	17,1	1	267,1	288,4												
			2	221,4	240,5	259,0	279,6										
			3	211,5	227,9	244,6	260,8	280,4									
9	Hungary: Börzsöny Mts	17,6	1	196,9	208,5												
			2	186,9	198,7	208,6											
			3	179,5	191,2	211,8	231,5										
11	Hungary: Börzsöny Mts	18,2	1	257,2	282,7												
			2	243,6	264,6	305,2											
			3	244,6	265,5	303,4											
32	Serbia: Maljen Mts	17,4	1	203,6	204,1	205,6	239,0										
			2	169,1	178,6	201,8	200,9	200,4	223,0	239,0							
			3	160,1	179,0	182,9	200,0	209,2	205,7	225,8	237,0						
38	Hungary: Mátra Mts	17,3	1	224,8	234,4												
			2	213,3	232,7	244,9											
			3	214,5	232,0	248,6	259,4										
61	Hungary: Pilis Mts	18,9	1														
			2	246,9	265,9												
			3	242,5	266,7												
Mean				217,8	235,1	241,9	238,7	230,0	214,4	232,4	237,0						
Sd				29,28	33,29	38,51	30,45	43,86	12,20	9,38	NA						

APPENDIX TABLE 3. Inter-beat interval measurement data in *Zwickenia rupprechtii* Murányi, Orci & Gamboa, sp. n. male calls. — i1, i2, i3 and so on are labels containing the serial number of inter-beat intervals counting them from the beginning of each call.

specimen ID	Population	Ambient air temperature	inter beat interval (ms)			
			i1	i2	i3	i4
19	Croatia: Ivanščica Mts	18,7	24,9	20,5	17,5	16,7
48	Hungary: Mecsek Mts	17	21,9	19,8	19,0	17,8
49	Hungary: Mecsek Mts	17,6	22,5	23,1	17,7	
51	Hungary: Mecsek Mts	17,6	24,0	20,9	20,5	19,7
52	Hungary: Mecsek Mts	17,6	29,8	18,7	16,0	15,6
Mean			24,62	20,58	18,10	17,44
Sd			3,14	1,63	1,70	1,75

APPENDIX TABLE 4. Inter-beat interval measurement data for *Zwickenia kovacsi* Murányi & Gamboa, sp. n. male calls. — i1, i2, i3 and so on are labels containing the serial number of inter-beat intervals counting them from the beginning of each call.

specimen ID	Population	Ambient air temperature	inter beat interval (ms)				
			i1	i2	i3	i4	i5
44	Romania: Rodna Mts	17,7	27,6	28,0	27,1	28,0	27,7
45	Romania: Rodna Mts	17,4	27,3	30,5	31,3	31,1	34,4

This document ***DOES***
NOT contain ***COLOR***
figures/plates.

Best available copy.
