OPUSCULA ZOOLOGICA

Revision of Drusinae subfamily (Trichoptera, Limnephilidae): divergence by paraproct and paramere: speciation in isolation by integration

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Abstract. In the last few years we have described over 70 new incipient sibling limnephild species applying the discovered Trichoptera speciation traits of the paraproct and paramere for species recognition and delimitation. In this revision on Drusinae subfamily, comprising 177 species, we have applied these subtle, but rapid and stable speciation traits and described 49 new sibling species from the "well studied" European mountain ranges. Discussing the theoretical background we have elaborated and adapted a new character state ranking system of phenomics to revise the long-neglected taxonomy of the Drusinae subfamily and synonymised the *Cryptothrix*, *Monocentra*, *Metanoea*, *Leptodrusus*, *Anomalopterygella*, *Hadimina* genera with the *Drusus* genus. These old genera of artificial constructs were established exclusively by divergences of secondary sexual traits known already to have only species level ranking value. According to our new character ranking system in the Drusinae subfamily, beside the *Drusus* genus, only the *Ecclisopteryx* genus has been retained having robust generic level divegences of paraproct loss and ancestral duplication of spine organising centre on the paramere pattern. Speciation trait function of the peg-packed surface on the paraproct head in *Drusus* genus moved to the gonopod apices and integrated into variously shaped stimulatory organ in the *Ecclisopteryx* genus. In the *Drusus* genus the ancestral divergence of the single spine organising centre has integrated 11 species groups with remarkably stable paramere spine pattern. Based upon ancestral divergences in the paraproct architecture we have differenciated 28 species complexes inside the 11 species groups. The delineation of the 163 mostly incipient siblings species, inside the 28 species complexes with 44 new *Drusus* species, was based primarily on the divergences of speciation trait, that is in the stimulatory head shape of the apical arms on the dorsal branches of the paraproct. In the *Ecclisopteryx* genus with 14 species we have established two independent lineages both with a single species, as well as two species complexes with five new species applying the speciation trait of the genus, that is the shape divergence of the stimulatory organ on the dorsoapical surface of the gonopods.

Based on the Darwinian natural selection, we do not understand how the discovered 70+49 new European incipient phylogenetic species of limnephilid caddisflies have been evolved in the isolated sky island habitats of high mountain ranges. This isolation induced speciation represents a challenge to the mechanistic reductionist concept of the natural selection. Our first trial to extract information from various disciplines to answer this question is presented in a brief theoretical discourse: (1) rethinking the status of natural selection towards postdarwinism; (2) teleology or teleonomy; (3) limits and potentials in understanding reality; (4) organisation of universe by integration; (5) what are and how the organising *force*s are *power*ed to *work* in the emerging *energy* mechanisms; (6) divergence by integration; (7) divergence in isolation; (8) reproductive isolation by sexual selection; (9) shape divergence; (10) speciation traits; (11) generic ranking characters. Assessing the limits and potentials, the humility and hybris attitudes towards understanding reality, we hypothesise an integrative power of organisation, instead of simplistic natural selection, that works both in isolated and sympatric populations to maintain the

integer state of the integrated autonomic entities against mutations, permutations, transmutations and perturbations. The permanent flux of these adverse, neutral or advantegous external and internal effects generates and gives rise to a responsive and balancing integrative mechanisms with comparative magnitude and multitude. This permanently balancing organisation process develops and drives a large number of interactions along various patterns of supervenient emergent mechanisms in order to integrate them into an oscillating autonomy. In isolation of the sky-islands on high altitudes, the divergences of new taxa are the adaptive autonomic byproducts of this integrative organisation. Integration and not the selection is the real force mechanism that harmonises the concerted flux of stochastic processes into reproductive isolation by sexual selection. The primacy of integration is clearly demonstrated by empirical evidences in the causes and consequences of the integrated speciation traits. Any kind of selection, artificial, natural, social or sexual, is only an emergent perturbating mechanism forced to integrate into the autonomy of an entity. This is how the entanglement of the quantum world and any supervenient integer work together through energeticism of the interactive realism. This is a must in the ontic, epistemic and semantic structural realism.

INTRODUCTION

We have elaborated and applied the delicate procedures of the fine structure analysis on the discovered speciation traits in order to construct the diverged trait matrices for sampled populations. These trait matrices were used to differentiate and describe over seventy new European incipient phylogenetic limnephilid species in the last few years (Oláh 2010, Oláh 2011a, b, c, d, Oláh & Kovács 2012, Oláh *et al.* 2012, Oláh *et al.* 2013a, b, c, Oláh & Kovács 2014, Oláh *et al.* 2014, Oláh *et al.* 2015, Vitecek *et al.* 2015, Oláh *et al.* 2016, Oláh & Ibrahimi 2016). From our limited collecting effort and from the pattern of the discovered speciation mechanisms we have predicted that much more caddisfly sibling species are still waiting to be described in southern European glacial refugia, that is in the mountain ranges where the Pleistocen ice effect was not so severe. Our prediction is perfectly supported by describing another 49 new species in this paper.

Our sibling species delimitation relies exclusively on contemporary diverged or diverging speciation traits with subtle, but stable shape divergences. The stability of these subtle trait divergences is integrated by analogy of collective cooperation of many genes and organised by the whole genome and phenome (Anderson 2001, Oláh *et al.* 2015). These subtle traits are perfectly detectable empirically at higher microscopic resolution without virtual procedures of geometric morphometrics. This fine structure phenomics is still not much practiced in routine taxonomy. The discovered speciation traits of the paraproct, paramere, aedeagus and the coevolved vaginal sclerite complex are the primary products of speciation processes driven by sexual selection and integrated almost exclusively in allopatry of high mountain crenon or epicrenon environment on the endemic hotspots of the sky islands. These contemporary speciation events have been realised in strict orographic isolation and organised under rather similar abiotic and sociodemographic environments.

This isolation induced speciation represents a challenge to the reductionist concept of the natural selection. Fully saturated and impregnated by this naive, simplistic dictate of the Darwinian industry it is really a great burden for us to understand and to evaluate how these entities have been developed in these sky islands! Our provoking findings inspire us to examine and to outline the potential of an unified integrative organising power, that is acting hidden under the terms of evolution, adaptation, selection, emergence, self-organisation, self-assembly, cooperation, closure of constraints and working reactive to the multitude of desintegrating disturbance mechanisms of entropy. This integrative power of organisation works both in isolated and sympatric populations to maintain the integer state of the integrated autonomic entities against mutations, permutations, perturbations and transmutations. This permanent flux of the externally and internally generated adverse, neutral or advantegous effects generates a balancing comparative magnitude and multitude of responsive integrative mechanisms. This is how the entanglement and integer work together through energeticism of interactive realism. This is a must in the ontic, epistemic and semantic structural realism.

In contrary, the simplified reductionism of the selection theory is based upon a single advantageous mutation according to the original mathematical formalism of beanbags. Once upon a time this was a naive belief of the modern hybris. Natural selection is not a dominant process! Rather it is an apparent epistemological byproduct of the integration! There is no single isolated mechanism of natural selection to produce a new character state, there is a "naturally integrated" character state, embedded in the autonomy of sibling species created by integrative organisation! The integration as an intrinsic state of interactive reality is powered ultimately by the energy of coherence-decoherence cycling of the poorly undetstood fluctuating quantum states through the emergence of classicality, what we examine in taxonomy, that is along various mechanisms on the increasing complexity or ranking of organisation.

Has natural selection (Darwin 1859) any role in species formation here in these sky island habitats? Are the sexual selection, the second evolutionary theory (Darwin 1871) more important in speciation than natural selection? Has mate selection a real challenge to the theory of natural selection? Are the abiotic and biotic (social, sexual) selections simply particular mechanisms among the many other phenomic and genomic effects and constraints triggering pressures and generating genetic, epigenetic and regulatory variations as well as developmental compulsions to integrate into the building process of a state adaptation in order to maintain organismic authonomy (Oláh *et al*. 2015)? Is the divergence of species, the descent with modifications, not selective, but rather an integrative process powered by state integration to survive? Is entity divergence an evolutionary process? Does evolution mean anything more than organisation intentionally obscured or ignorantly confused by human teleology? Does simply the organising process of integration dominates the universe powered by fundamental interactive forces from einselection at quantum level (Zurek 2003) to idea flux in human communities? This organisation is getting realized in concerted integration of negentropic mechanisms to compensate the flood of entropy generated mutation, permutation, perturbation and transmutation effects.

To answer these questions we are faced with spectres of mechanistic reductionism and materialism dominating the evolutionary ideology, still haunting around in the European culture. They are scattered in various theoretical and philosophical disciplines and hard to validate and naturalise them. Pure meditations, speculations, "thought" experiments and models are coherent trials in theoretical and philosophical journals, permanently expressed alone, but forming together a firm virtual show. Without accompanying empirical reality of structural realism these virtual attempts are vainly and painfully beating the air (paraphrased from Winkler *et al.* 2007). Nevertheless we are determined to search understanding or at least to get some insight into the reality of the above questions, posed by the discoveries of so many new European incipient species under similar condition and contradicting to the reductionist and naive evolutionary theory of natural selection. Our first trials, to find and extract information to these questions for taxonomists, are presented in the theoretical discourse of this paper.

Instead of pure speculation we follow our reality tradition and try to compensate the formidable and indigestible quantity of *a priori* evolutionary theories, models and speculations with our empirical *a posteriori* evidences. We describe here more new autonomous phylogenetic species organised by integration, and not simply evolved by natural selection. We examine, under high resolution microscope, the fine structure of the speciation traits of the European Drusinae subfamily and prepare their drawings of fine details for all examined species in order to present a paraproct and paramere atlas with simplified shape reality for routine taxonomy of caddisflies. We summarise our experiences about the use, abuse, advantages and limits of the paraproct and paramere fine structure examination. We review a theoretical discourse on the ontic, epistemic and semantic aspects of the integrative organisation as the potential divergence mechanism of the speciation processes dominating the scenario in the sky islands of the isolated crenon and hypocrenon habitats. Relying on the discovered speciation traits we complete our empirical studies and:

(1) elaborate a new character ranking system for the Drusinae subfamily;

(2) re-evaluate the generic, species group, species complex and species characters, the critical nodes in cladistics;

(3) elaborate the coalescence linegae structure from incipient species to genera;

(4) re-examine the taxonomic status of all unsettled taxa in the subfamily;

(5) describe 44 new species in the *Drusus* and five new species in the *Ecclisopteryx* genera;

(6) revise the natural taxonomic structure of the entire Drusinae subfamily.

THEORETICAL DISCOURSE

Based on the genuine Darwinian principles of evolution and natural selection, we do not understand how the discovered limnephilid incipient phylogenetic species were diverged in the isolated sky island habitats of high mountain ranges. In perspectives of understanding we rewiev relevant topics from virtual to empirical: (1) rethinking the status of natural selection towards postdarwinism; (2) teleology or teleonomy; (3) limits and potentials in understanding reality; (4) organisation of universe by integration; (5) what are and how the organising forces are powered to work in energy mechanisms; (6) divergence by integration; (7) divergence in isolation; (8) reproductive isolation; (9) shape divergence; (10) speciation traits; (11) generic characters.

Recent findings of molecular genetics presume that multigenic speciation traits are encoded by very complex networks of quantitative trait loci with small effect sizes and expressed under very complex mechanisms of epistasis, epigenetic, regulatory processes, developmental pathways and environmental constraints. These young species are integrated under divergent sexual selection, as a kind of social selection in cooperation with very complex stochastic genomic mechanisms. These concerted random processes have integrated into reproductive isolation under sexual selection and locally adapted by integration without detectable abiotic natural selection. Speciation traits, the products of powerful sexual selection do not need *a priori* additional natural selection pressures to create reproductive isolation. This is why for speciation paraproct or paramere is really super,

not simply magic. As we have recorded before, many *Drusus* species evolved in geographic isolation and through sexual selection of speciation traits of both the paramere and the paraproct (Oláh *et al.* 2015). These phenotypes are integrated by concerted organisation and completed in sexual selection mechanisms. This is why parameres and especially the paraprocts are very diverse and stable in the *Drusus* genus.

Long series of contemporary caddisfly divergences discovered in the last few years remained unexplained when we tried to understand how these incipent phylogenetic species were organised in isolation of identical habitats. Relying upon the accumulated virtual arsenal of molecular theories and models of evolution with natural selection our trials have failed to give explanation! Similar controversies have been accumulated in the genome universe by simplistic genic view of evolutionary processes dominated with myth-perceptions of only matter matters, fittest survival, gene determination, and random evolution (Lipton & Bhaerman 2009). Staggering in this Darwinian jungle we realise a hope on the horisont, an innovative Holon trend of coding (environment) − encoding (phenome) − decoding (genome) universe of the environmentally triggered and universally integrated interactions of entangled entities backed by both the ontic and epistemic structural realism (Oláh *et al.* 2015). Based upon this Holon approach and against the old traditional reductionism here we are forced to outline a more natural view of universe. This is the theory of organisation with integration as a holistic *versus* the old theory of evolution with natural selection as a reductionist world view. Arguments for integration *versus* selection, organisation *versus* evolution are presented here by reviewing particular relevant knowledge.

Towards postdarwinism

Uniformitarianism of Lyell (1830−1833), Lamarckianism and Malthusianism inspired or rather preprepared or even directed Darwin to compile his basic concepts: (1) descent with modification for the diversity pattern and (2) natural selection for the form-function dilemma. Neo-Darwinism appeared when Wallace and Weismann removed all the Lamarkian inheritance of acquired characteristics from the original

darwinism (Pigliucci 2007). The fusion of form (taxonomy) and gene (genetics) into the Modern Synthesis was elaborated later by mathematicians, Fischer-Haldane-Wright and by taxonomists, Dobzhansky-Huxley-Mayr. This funny cooperation for this virtual adventure opened a wide gate into the study of molecular mechanisms of speciation. However everything was promised and nothing was delivered as was briefly summarised in an evaluation on missing heritability (Maher 2008). Moreover in the last half century, powered by concentrated finance, there was progress in theoretical modelling and sequencing, but the population mathematics, dominated by simplistic genic view of genome, has left taxonomy alone without resources. Awe-inspiring model building and speculations as well as formidable body of mathematical theories both based on virtual foundation say little or almost nothing about the formidable molecular data accumulated in the last years (Orr 2005) and represent neither real value to the taxonomy of biodiversity. As a result the causation of speciation processes was restricted into the genotype space without real effort to generate related empirical knowledge on the phenotype space.

This overly gene-centric theory of evolution culminated in the Modern Synthesis failed to feed progress in the empirical realities of taxonomy, nature conservation, gene manipulation and medicine: (1) described only a very small fraction of biodiversity; (2) accelerated extremely the desintegration of natural habitats; (3) engineered gene manipulated random entities of low quality with unkown and uncontrolable future; (4) created misconceptions on cancer treatment. The ongoing revision of the Modern Synthesis is accelerating. Extended Evolutionary Synthesis necessitates an extension in order to ground a limited survival of the neo-Darwinian Modern Synthesis (Mesoudi *et al.* 2013). Important drivers, others than genes must be woven into the fabric of evolutionary theory. Beside genes, processes regulating the growth and development of organisms are recognised as causes of evolution. Inheritance of epigenic effects, phenotypic plasticity, cultural transmission, niche construction and the entire complex fabric of eco-evo-devo mechanisms represent the full scale of processes that replace evolution paradigm with organisation. Organisms are const-

ructed in development, co-constructed with their environment, and not simply programmed by genes. Species are not evolved to fit into pre-existing environment of the genome (Laland *et al.* 2014). The current evolutionary theory of genes must reunite with Darwin's theory of form (Pigliucci 2007). Otherwise this simple genic view continues to propagate an overal simplistic nature view suggesting that the eco-evo-devo, the entire phenom is reduced to proximate status, calibrating organisms to environmental stochasticity and only genes represents ultimate status (Dickins & Rahman 2012). This is a dogmatic insistence on invalidated equation of "ultimate causation = gene-based selection" and everything ontogenetic or phenotypic treated as solely a proximately causal process (Mesoudi *et al.* 2013).

Genomics based natural selection needs a rethink! After more then half century of selective and genic view of nature, the empirical achievements in human practice is disappointing. In taxonomy we have no any multigenic morphological traits available for complex lineage studies with known genomic structure. Studies on elite organisms revealed that the genetic architecture of just the bristle number and position on *Drosophila* mesonotum is surprisingly complex, covering substantial genomic fraction with pervasive pleiotropy among the large number of loci, often with sex- and environment-specific effects (Mackay & Lyman 2005). Similarly in medicine, no disease phenotype and its treatment including cancer is understood by this simpistic genic strategy. What we have, the unrelated and isolated sequence-based genotype studies seem insufficient to elucidate the phenomena of species and speciation by natural selection (Houle 2010) or the disease phenotypes and their treatment. Listing trait-unrelated genes or even gene-trait associations in the far future tells us little about how diverging organisms or sick human beings that carry the genes are put together (paraphrased from Hooker 2015).

Phenotypic studies going back almost a century estimated that the human height is 80−90% heritable. Look at the mirror and at your mate to predict how tall your children might one day be. At the same time with detailed genome wide association studies we were able to predict only little more than 5% of height's heritability (Maher

2008). Sequence studies alone are not sensitive enough to quantify mechanisms of epistasis, epigenetics, and regulatory gene expressions, the most important processes modifying the continuous traits with small effect sizes. Faced with climate change, global warming and biodiversity crisis, the taxonomy, that is the science of empirical phenotypic reality of our planete remained without resource. Similar reductionist phylosophy failed to help healing practice in medicine. The traditional phenotypic risk factors, like obesity for diabetes, remained more effective predictors than multitudes of single nucleotide polymorphism associations (Houle *et al.* 2010). Similarly, genomic war failed on cancer phenome (Spector 2010, Davies & Lineweaver 2011, Davies 2013, Lineweaver *et al.* 2014).

Genetics, medicine, ecology and conservation are stagerring in agony without sound taxonomy of phenomics. Taxonomy was an integrative well-supported discipline synthetizing all the phenomics before the scenario of the "new systematics" of "modern synthesis" took over all the available resources. The present desparate state of taxonomy valorizes the recent discovery of adaptive speciation traits of incipient phylogenetic species. These selective traits are sensitive enough to detect early stages of reproductive isolation ongoing in geographic isolation under self-demonstrating selective sexual pressure. Self-demonstrating by evident diversity gradient along non-sexual and sexual structures (Oláh *et al.* 2013a). Sensitivity is ensured by fine structure analysis of information rich traits and realized by simple and reliable empirical observations or, if requered, further sensitized with procedures of geometric morphometrics.

Natural selection: self-evidences? Darwin's theory of evolution is the widely held evident notion that all life is related and has descended from a common ancestor: (1) "descent with modification", (2) "complex creatures evolve from more simplistic ancestors". The main driving force of evolution is the natural selection, the *central tenet*, the *ideologized idea*, the *political project*, that is the "*survival of the fittest*" inherently extended to social darwinism and later to the painful eugenics.

Natural selection acts to preserve and gradually accumulate minor advantageous mutations. How this oversimplified reductionist theory works? A specimen of a species developed an advantage, "it grew wings and learned to fly". Its offspring would inherit that advantage and pass it on to their offspring. The disadvantaged members of the same species would gradually die out, leaving only the advantaged members of the species. Natural selection is the preservation of a functional advantage that enables a species to compete better. Natural selection is the naturalistic equivalent to domestic breeding. Traits that enhance survival and reproduction become more common in successive generations of a population. It has often been called as a "self-evident" mechanism because it necessarily follows from evidences: (1) phenotypic variation: variation exists within populations of organisms; (2) differential fitness: different traits have different rates of survival and reproduction; (3) heritability of fitness: these traits pass from generation to generation.

Natural selection: molecular contradictions. However these self-propagating, "self-evident" notions of natural selection are not supported by ontology neither by epistemology nor by the practice in the microcosm of moleucules. Here we cite just a few molecular disproofs. Nonsynonymous substitition rate elevated above synonymous rate would be an evidence for darwinian positive selection of molecular adaptation, or adaptive molecular evolution. But well established cases of molecular adaptation by natural selection are very rare (Yang & Bielawski 2000). The majority of amino acid substitutions in proteins are neutral or nearly neutral, not selective (Kimura 1983). Gene expression levels in primates evolve largely in the absence of selective constraints (Gilad *et al.* 2006). The majority of gene expression differences within and between species are not functional adaptation, in spite of fact that environmental and physiological stimuli are clearly responsible for changes in expression levels of many genes. Organisms switch transcriptional states with high plasticity and transcriptional phenotypes cluster by life history strategy and not by genetic differentiation. Environment can dramatically alter gene expression without selection. Single trascription factors can regulate the activity of hund-

reds of target genes; this is how development is integrated and orchestrated (Gibson 2006). This power of transcriptome to regulate expression level of genes has undermined the historical and morphological idealistic concept of homology: in spite of the fact that the pre-Darwinian term of homologue (Owen 1843) became the basic concept of the evolution. The homologous structures in taxa are structures derived from the same structure in their latest common ancestor. In molecular genetics the traditional morphological characters of the homology was extended to morphology of molecules. Recently the homology concept was further extended to characters which are organised through the expression of homologous genes. This usage has created ambiguity due to the regulatory power of expression. In the *Cis*-regulatory apparatus and *trans*-acting factors various inputs of gene responds are integrated during development with significant potential to alter the expression pattern of specific genes. The new term of homocracy (from Greek: same government) was suggested for caharcters which are organised through the expression of identical patterning genes (Nielsen & Martinez 2003). The majority of expression differences are selectively neutral or nearly neutral caused by integration of stochastic processes and not by Darwinian selection. Neutral model is the null model for transcriptome evolution. Further work is needed to reveal whether proteome evolution is also dominated by selectively neutral changes (Khaitovich *et al.* 2004). The driving force of phenotypic evolution is the random mutation (Nei 2007). This is again a simplified, reductionist, poorly grounded slogan for the infinite complexes of perturbations. Natural selection is only one of the endless mechanisms operating among integrative processes to maintain the self-determination of organisational closure in the biological autonomy (Moreno & Mossio 2015), powered by the fundamental interactive forces exerted below the molecular level of organisation.

The power of the words. During this discourse on the virtual findings of the evolutionary theories we apply technical terms of various disciplines without any additional explanations. This condensed style of presentation relies upon our belief in the self-explanatory nature of the words. Unfortunately many of the terms in European science are not organic words, their majority is virtual immagination without self-explanatory power. They are rather dubious artificial and mostly personal human construct with weak explanatory power, making more difficult and more demanding to follow and to understand our presentation of limited English. Reader has to realize that many terms we apply, without any explanation in our theoretical discourse, are backed by an entire book of mathematician, philosopher, theoretical physicist, biochemist, geneticist to understand its technical details. Moreover during text formulation we frequently and irregularly replaced the word *evolution* with the world of *organisation* to test whether the young word of evolution has any indispensable content detectable by confusion or by poor understanding compared to the older word of organisation. The known use of the word "evolution" goes back to 1622 and Lyell (1832) was the first who used it for scientific purposes.

Organic words in fractal languages have self-explanatory power. At least until "Babel", during the golden age of the less limited resources, the language was organised by integration on the fractal pathway. Words were developed organic in the fractal factory of primordial language. Human in close harmony with external and intenal worlds has produced birth of voice, words, and sentences similarly as the trees grow. Anything is organic if starts growing from a centrum, organised by natural rules, and is fractal if the new outhgrowths are proliferating by the same principle, like river network, plant trees, animal phylogenetic trees or human vascular system. The organic fractal worlds contain and reflect their own meaning, they are self-explanatory, this is why they are fractal (Varga 2003, Oláh 2005). Language built by an organic culture has followed nature's deepest essence along nature's path of creation. The organic and fractal structure of the primordial language is realized by the core of a few roots expanded by agglutination, similarly how the tree is growing with annual whorl of branches. Words are organised by nature and human interaction in memory encoding while encoder stores and recalls information. The fractal nature of language reflects the fractal pattern of memory processing. The word starts with the basic root (root morpheme) expressing the deepest sense of meaning and is extended by fractals of suffix agglu-

tination. The core is a whole, a closed and self-improving system. This living petrifaction reflects the metaphysical view of our earliest ancestors. The roots and world are the coded expression of primordial pattern in our mind. The word of the stone age man is a picture. They told pictures of nature to each other, loudly expressed pictures of reality.

The Hungarian language preserved most fractal structures, rules and words of the archaic proto-nostratic language, the language of stone age (Varga 2010). Big part of the English vocabulary has more similarity to the Hungarian (Varga 2007, 2012). It is not surprising since once, developing in and following the stone age, an organic and fractal archaic root-language was spoken by everybody in Eurasia.

We emphasise the power of words just in order to compare the similar dictate of the words of "evolution" and "organisation". Here we compare the innate meaning of the young word *evolution* of Latin origin with the older word *organisation* of Greek origin. The meaning of evolution is based on the Latin worlds "$e(x) =$ out"and "*volvere* = to roll". The meaning of organisation is based on the Greek world "*organon* = an instrument, an organ of more complex structure". This wonderful fractal world diversified from the Greek world "*ergon* = work", elaborating or organising and being organised. Without a detailed analysis here, we rely on the self-explanatory power of the two words. Our idea is supported by formidable data accumulated in coding-encoding-decoding holon and in the eco-evo-devo disciplines.

The universe is elaborating, organising by integration under the four fundamental interactive forces, not just unrolling or outrolling something by chance of selection in evolution. The divergence of a new species, generating a new autonomy of self-determination is not an accident! It is based on the Holon principle, and functions like the memory with integrated ability to encode, store and recall or decode information. Organisation integrates particles (entities) by interactive forces. In contrary to Setrov (1971) the words of "organisation" and "evolution" are almost synonymous epistemologically. Except the word evolution, being a recent artificial construct, unin-

tentionally incorporates some idea of directedness, directivity, progress, a positive component, a hope of better future governed by nature law, by unknown natural powers or by Nature God expressed and simplified by archaic pantheism and later latinized by deism. The universe is teleological as dictated and organised, and not evolved, by the integrativ mechanisms of the fundamental interactive forces operating against the power of entropy. Living systems are inherently teleological and the organisms, as a cyclically organised system of interdependent causal processes, their identity, unity and their functional operation are understood through a teleological perspective (Moss & Nicholson 2012).

Teleology or teleonomy?

Darwin did not like the word evolution. It contains meaning for some kind of process getting better, best to perfection, leaving a room for an ultimate creator and perfect creation. He did not even use the word evolution in his book until the last line (Darwin 1859). Darwin's devotion against perfect creation fabricated the principle of random evolution. Nevertheless in spite of enormous effort to reject teleology the evolutionary process remained complicated by function purposiveness and by antichance process of natural selection, but teleology remained dogmatically refused. There are popular slippery slogans that natural selection (1) is not goal-directed; (2) has no long-term goals; (3) no genetic mechanism is known to produce goal-directed evolutionary process; (4) orthogenesis is refuted; (5) evolution is not deterministic (Mayr 2001). Presenting and reducing teleology as being purposeful, and the goal-directedness of structures and functions in living organisms as being created by divine intention, are outdated tricks in the Darwin industry.

These ideas are overly and firmly tied to the divine dogma of evolution by natural selection, disregarding conflicts in careful function analysis: the function is a contribution to a goal that is integrated into the autonomy of entities. Function is an ambiguous and increasingly sophisticated concept due to its teleological dimension, a sensitive issue in the liberal ideology. Mysteries sur-

round functional discourses. Adequate definition of function may help in naturalization of normative properties without the extrinsic evaluative decision of the observer: (1) why hearts are supposed to pump blood; or through teleology (2) how intentionality can arise in the world of causes; (3) how slight difference in the definition of function can modify our understanding of the reality (Artiga 2011). The teleological or goal-directed dimension of function became a philosophical problem, difficult to handle in evolutionary context. During the last half century significant philosophical resources were directed and spent to cope with the apparent ontological or epistemological contradictions present or created between the principles of evolution by natural selection and teleology. Various, poorly understandable theories have been fabricated and widely discussed to discard the teleological dimension of functional attributions in order to replace the divine *telos* of ultimate creator with scientifically acceptable causal explanation.

In spite of these efforts there is no sharply defined functional concept achieved which supports evolution with or without teleology. Etiological, dispositional approaches have been elaborated, with focus on justifying functional discourse through naturalisation. Etiological definitions try to explain why a trait has a function in evolution and dispositional theories focus on why traits operate as something in taxonomy (Artiga 2011). These trials are mostly debated, but a new autonomous perspective, perhaps a vindication or a new and refined version of dispositional theories, advocates an organisational approach with integrated systemic framework (Moreno &Mossio 2015).

Etiological approach. The functions of entities are identified by reasons for their existence. The most accepted and popular theory to function is the etiological approach formulated by Wright (1973): the function of X is Z means (1) X is there because it does Z; (2) Z is the consequence of X is being there. Canonical etiological theory of functions tries to identify processes of components in a system with a role and associate functions with those parts. Functions are past effect of traits causally explaining their present existence. A trait function is determined by its recent history and explains why it is present. Etiological approach is

a backward looking, evolutionary theories of function. Nagel (1961) and Hempel (1975) have shown that self-regulated systems are teleological, directively organised systems, but without finalism: (1) "X has a function Z" equals with (2) "Z possible if X is present". With this trick of equivalence the first teleological (functional) statement has been reversed to the second statement less conflicting with Darwinism. This is an eliminativist approach denying teleology model, that functions play an explanatory role, and reducing functional statement to the deductive-nomological model. The heart functions to pump blood because pumping blood was the effect that heart was selected for and contributed to the survival of the ancestors. Further speculation states that function of a trait is its effect produced by natural selection, a process that explains its presence, attributed to its past selective value and not to its current properties. This is the selected-effect version, a historical etiological account of teleofunctions (Delancey 2006), appealing to selection as the causal process. This is also the *proper function* originates through reproduction as well as the derived proper function as the product of some prior device. The history of an item determines its proper function rather than its present properties or dispositions (Milliken 1989). But this is inconsistent with the concept of non-historical current function at least in physiology (Roux 2014) and in taxonomy. Godfrey-Smith (1993) tried to solve this inconsistency by arguing that there is no a unified concept for function; instead there are distinct notions of functions that are appropriate to different entities. Evolutionary etiological theories suffer from major problems: (1) loaded with epiphenomenalism: function is based on the trait's causal history and the trait's current activity is superfluous; (2) failed to account for exaptations: adapted traits may change their original functions (Artiga 2011).

Dispositional approach. According to the dispositional theories the function of a device is determined by the contribution it makes to a system. This systemic approach restricts functional attributions to hierarchically organised entities. Cummins (1975) ascribes a function to a system component if it has a capacity that contributes to the system capacity. He has suggested a dispositional

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approach considering functional statement to components of a structure, identifying constituent causal contributions in complex processes and explaining in terms of capacities of the components it contains and how they are organised. Ascribing a function to something it is to ascribe a capacity to it which is singled out by its role in an analysis of some capacity of a containing system. The Cummins-function of an entity is always relative to the overall capacity of a system, targeting the role of functions in the explanation of complex capacities. There is no special trial to distinguish teleological or proper functions from other, non-teleological functions. Cummins' functional analysis does not contribute to the understanding of the teleological functions and many of his functions are not proper function (Griffiths 1993). Functional ascriptions had nothing to do with the past history of a system, and should be understood exclusively from the viewpoint of the present organization of a system. Decomposition of complex organic function and to recognise how it is discharged could be integrated into the etiological approach. The function of an entity S is what S is designed to do. Each functional attributions rest on some presupposition about design and stem from the intentions of a cognitive agent or from the operation of selection (Kitcher 1993). However this concept of design is threatened with circularity being undefinable without using the notion of function (Artiga 2011). Brown's speculation (2012) suggests that Descartes frequently engaged in functional explanation resembling modern causal functional analysis while eschewing non-normative, non-teleological position by emphasizing the interdependency of parts of biological systems. This is one kind of dispositional approach of Cummins (1975). Main problems with the dispositional account: (1) difficulties to determine the system of reference; (2) difficulties to select between essential and accidental effects; (3) difficulties, like malformation in the actual state of the traits.

Organisational approach. Functionality includes dimensions of teleology, normativity and organisation. Organisation, closure and functionnality are mutually related concepts of the same causal system. The process dynamics of normative function is based on Aristotle: "The hand separated from the body is not a true hand"

(Christensen & Bickhard 2002). The etiological theory answers "what it is for a part of a system to have a function", the autonomy theory of organisational account focuses on "what it is to be an adaptive system". Organisational approach seems to be accounted for teleological loop between a trait's performance and the trait's existence without far-removed historical causal relation, avoiding epiphenomenality and provides observer-independent criteria for function attribution (Artiga 2011).

Teleonomy instead of teleology. How and why the *telos* concept was basic for Plato and Aristotle, uncomfortable for Darwin, regulative for Kant, speculative for Hegel and dialectical for Marx. According to Kant the regulative teleology is ontic by interactions of cause/effect, target/tool, whole/part relations (Setrov 1971). Teleology is purpose as consequent to a phenomenon: future determines the present. Ontologically the teleonomy is a purpose antecedent to the phenomenon, attributed to the organism's history of consequences and integrated in organisation by natural law. Epistemologically it avoids the time-reversal problem of teleology: history or its trace is antecedent to current responding. However, it is a regulative rather than a constitutive principle (Rees 1994). Adapted system serves a purpose, but can be explained by the paradigm of organisation by integration. The theory of organisation by integration is based on *teleonomy*, an apparent purposefulness, goal-directedness in both abiotic and biotic universe brought about by "deism" of the natural laws, a nomic model of explanation.

Selection or integrationon? The organisation process drives a large number of interactions along various patterns of supervenient emergent mechanisms to integrate. This is an apparent teleological adaptive strategy realised through stochastic processes organised and powered by specific, emergent-dependent mechanisms of the ultimate interactive forces against the permanent and complex external and internal actions of mutations, permutations, perturbations and transmutations coupled with sexual selection producing reproductive isolation with subtle shape divergences of speciation traits. The concept of single random mutation induced speciation by natural selection, the central neo-darwinian tenet

of the "Modern Synthesis" is a mechanistic simplification, a reductionist approach. Natural selection is rather a misconcept, a nonsense mechanism to govern speciation processes in isolation. The selection of better adapted individuals with adaptive traits of better characters is unlikely a mechanisms that created the 159 *Drusus* species in the isolation of the European sky islands. During a careful examination we have found no any natural selected traits, at least in the adult stage! In turn we have discoved sexually selected and integrated traits with subtle shape divergences in all of these species. They diverged in isolation by integrative organisation of the sexual selection. We acknowledge however that these visible and touchable empirical findings may have various explanatory context to understand reality. Proper epistemology have decisive function in evolutionary research especially after the "modern synthesis" when the virtual theory and model buildings supported by slippy and tricky target philosophies started to dominate over the empirical phenomic findings of taxonomy. Here we briefly survey the epistemic constraints, structure and property theories, laws of nature, humility and hybris in research. We focus on the fundamental forces powering and energizing the integration mechanisms at quantum level and emerging to macroscopic entities, for instance to species of biodiversity.

Understanding reality

Epistemic constraints. Understanding how reality is organising itself is determined and limited (1) by capacities of observer's sensual experiences, (2) by his mental processes and (3) by his interest. A finite cognitive capacity is limited by the observer's context, every cogniser has a different relative being of anything. We meditate in order to understand both the entities of observer dependent relative being and the entities of absolute being. The absolute real beings (Kant's Ding-an-sich=thing-in-itself) are independent of observer, but necessarily correlated to relative beings. Therefore, even these absolute beings could be observed from an infinity of perspectives and could be described by an infinity of potential properties or aspects. Moreover probabilities are relative to the level of observation and to the degrees of order quantified by entropies of the same entity down to quantum level. Stochasticity depends on the level of observation as well as on the observer, how we set the boundaries between empirical and quantum states (Gershenson & Heylighen 2003). How can we be certain that our perception of these entities are true picture of reality? Both class of entities are operational, epistemic, semantic and semiotic in explanation trials of speciation mechanisms and processes. Our basic experience of the world can offer only an assessment of perception and science is an explanation between scientific concepts and our everyday experience. As a result both the matter and energy are abstract. They are notions, conceptions or beliefs about something. They do not reflect our everyday experiences. Concepts of science reveal a deeper layer of reality beyond the range of our immediate perception. Energy, one of the concepts of modern physics must reflect cause and effect relations at Planck's level of reality by relying on the interacting superficial levels.

Are the reality, entities, our eyes, brains, mind and our sense qualia just interactive forms of energy? How the aggregated light, the wave function of the objects we see, distinguishable from the light which reaches our eyes? These various waves, the forms of energy interacting with each other into a holistic composite perception are as substantial and immediate as the less composite forms of energy at a lower level of complexity? Our experince is nothing more nor less than an energetic vibrancy of structures. The coolness, smoothness, loadness, sweetness, darkness or redness as packets of qualia as well as stable, subtle characters of speciation traits are qualitative differences of sensation. However, we never feel warmth alone but in relation to the total system of interconnecting reality. Even mathematical numerical description is a distinctive type of interacting. During centuries we have tried to qualify and to quantify observational events of distinctive types of interactings in a coherent whole of the Newtonian physics. But Newtonian materialism was unable to account for the perception of experience and for the human thought. For today Newtonian explanatory power become suspect or even invalidated by quantum and relativity theories. Energeticism and energy with its quantum nature offers a unified world of experience, a holistic context of interactions for a new kind of coherent theory with the ontology of interactivity or with

the ontic structural realism. The world itself, our senses, perceptions, experiments, hypotheses and scientific knowledge are all organised types of interacting and they are all interactively connected by the fundamental interactive forces (Sonnier 1993). We generate knowledge via causal relations, through energy interactions down to causal-cum-structural evidences. We cannot explore or even see categorical or purely intrinsic properties (Esfeld 2009). We can explore the fine structure of any entities only by interactive dual and relational nature of photon.

Integration at quantum level. We gain our knowledge via causal relations with the basal matrix of quantum entanglement. All in the world is structure with variously entangled densities of node aggregates interacting to integrate some types of apparent objects against desintegration by entropy. There is an interaction picture of treating Hamiltonian quantum mechanics with operators in a perturbative fashion for creating decoherence, that is a certain collapse of wavefunction along increasing levels of organisation through speciation to consciousness. How this reduction of state vector, the quantum measurement problem, this discontinuous process of reduction is realised when the quantum state becoming entangled with a measuring apparatus operated by a physicist with his own quantum state integrated into his environment. The entire interacting quantum state is unitary organised (evolved) continuously according to the Schrödinger equation of wave function. Upon measurement the state vector is reduced by (1) probabilities according to the most influential "Copenhagen interpretation"; (2) Einstein's hidden variables explaining non-locality; (3) the unitary organisation (evolution) of an approximation; (4) the possible macroscopic alternatives remain superposed co-existing in reality of "many worlds" or "many minds"; (5) gravity having an unstabilising role in state vector reduction by macroscopic quantum superposition of two different mass distributions triggering state decay (Penrose 1996). The emergence of classical behavior, the classical description of reality from quantum dynamics is realised through decoherence leading to the environment-induced super-selection (einselection). That is justified by the existence of the preferred pointer states, less perturbated by decoherence and remained stable despite environmental interactions. The emerged or integrated einselected states lack coherence and do not exhibit the quantum behaviours of entanglement and superposition.

Human consciousness is operated by more complex integration of coherent quantum states. Along the organised pattern of microtubules of the brain neuron, the energy is also organised into the integration phase of integrate-and-fire sequence. This implies the reduction of uncertainty, merging and consolidating multiple possibilities to one: selecting conscious perceptions and actions. This final moment of the mental property emergence is realised in the orchestrated objective reduction with collapse of quantum superposed-state. Consciousness is initiated from these discrete physical events playing an intrinsic role in the universe, not just a product of brain adaptation, it is an action of the universal quantum space (Hameroff & Penrose 2014).

Ontic, epistemic and semantic structural realism. Belief in the unobservable entities posited by scientific theories and underpinned by no miracle argument is the scientific realism. Belief that the reality is ontologically independent of our perceptions and concepts is our philosophical realism. Structuralism posits that reality is best understood in terms of empirical scientific constructs of entities and their relations, rather than in terms of concrete entities in themselves. *Epistemic structural realism* posits that all that we know is structure (Worrall 1989). The retention of structure across theory changes goes back to Poincaré (1905) (1) to overcome the pessimistic metainduction, that theories are proved to be sooner or later as false; (2) to respond to the metaphysical implications of quantum physics with regard to the ontological status of object. Objects including individual organisms, like our incipient phylogenetic species, are no more than temporarily stable nexuses in the flow of the upward and downward causal interactions (French 2006). *Semantic structural realism* posits that the contents and terms of scientific theories refer to structures. *Ontic structural realism*, focusing on the relationships between entities suggest that all that there is in reality, is structure. The *eliminative ontic structural realism* posits that there is only relations and no relata. The *non-eliminative ontic*

structural realism posits that there are relations and relata, but relatum is represented by the relations in which they stand. The ontology of interactivity is further supported by structures of entanglement instead of object with an intrinsic identity in the domain of quantum physics as well as by metrical structures including gravitational energy instead of space-time points with an intrinsic identity in the domain of the theory of general relativity. These fundamental physical structures possess a causal essence. Their modal nature is force. In reality there are structures only. Objects are only nodes of structures, instead of structures requiring objects that stand in them (Esfeld 2009).

Causal and categorical theories of properties. Let start with an apparent final conclusion that properties are causal, and not categorical. Categorical position would underdetermine the causal and nomological relations in our world: the causal theory of properties, and the causal structuralism. Properties are disposition in the sense of power to produce certain effects.

In contrast, Humean metaphysics suggests the prominent conception of categorical and intrinsic properties. Objects have intrinsic properties irrespective of wherther or not there are other contingent objects. Properties are purely qualitative, what they are is independent of the causal and nomological relations. The world is a vast mosaic of primitive local particulars, space-time points, matter or fields with local arrangement of qualities, all else supervenes on this. If properties are categorical and intrinsic, how can we know them? There is no a single photon connecting us to them. Yes, we see objects without direct interaction, but by intercepting scattered photons that encode information about the object's spatial structure. We can know anything only through their causal-cum-relational nature. They are undetectable if there is no difference in causal and nomological relations. According to the Humean metaphysics there are different particulars because they differ in intrinsic properties, rejecting any necessary connections between distinct existences. Properties possess primitive qualitative characters (quiddity = whatness), they are indiscernible for observers, grounding an epistemic humility (Esfeld 2009).

Canonical debate over laws. Humean and non-Humean interpretations of laws, grounded by their property theories, represents the canonical debate over laws of nature formalised in opposite modal accounts of the nature of fundamental properties (McKenzie 2013). In Humean accounts the laws consist of metaphysically contingent connections between properties. Humean categorical properties assume an account of law (1) not appropriate for elucidating fundamental properties; (2) having no place for quantum mechanics formalism; (3) a given kind of particle could behave differently. Laws are only axioms for the description of Humean point particles in a background space-time. Laws are not made true by locally instantiated properties, on the contrary, propertties are discovered and determined by the laws (Dorado & Esfeld 2015). Particulars of particles are primitive since the laws supervene only on their entire distribution. Particles determine the laws, not opposite, laws determine the particles.

In non-Humean account (both dispositionalist and structuralist) the laws consist of metaphysically necessary connections between properties and laws are necessary. Fundamental properties are essentially dispositional, a given species of fundamental particle defined by given set of fundamental properties can act with one law across different possible worlds. There are difference between dispositionalist and structuralist where we situate modality: in the laws or in the properties. There are strong reasons to reject dispositionalism since it fails to accord with modern physics and accept structuralism since it does (Cei & French 2014).

Humility and hybris. It is impossible to test a scientific hypothesis in isolation. According to the Duhem-Quine thesis testing requires multitudes of background assumptions or auxiliary hypotheses. Without background knowledge the hypothesis remains underdetermined and even the principle of transient underdetermination does not help much. To cope with pessimistic induction and underdetermination the Ramsey sentence would eliminate theoretical terms, applying only observational terms while retaining the empirical content of the theory. Reductionism of modern human hybris tries to deduce a property, concept or

explanation from knowledge gained at lower level organisations. How classical genetics can be reduced to molecular genetics? Why phenome is irreducible to genome? The answer may come from ontological, methodological and theory reductionisms. Hempel's deductive-nomological account is intended to capture a form of deterministic scientific explanation (*explanans*, *explicans*) of events (*explanandum*, *explicandum*) from true propositions including sientific laws, but less from causal relations. You need to produce a deductive argument why that particular shape of speciation trait has been integrated and not an other alternative shape. Hempel's inductive-statistical account of probabilistic explanation of a trait integration requres inductive argument conferring high probabilty. Unification theory of explanation enhances understanding the causal structure of nature by unifying disparate phenomena.

How can we sense the intrinsic properties of particulars, the shape divergences of speciation traits? The answer depends on metaphysical considerations about the nature of properties and laws. The metaphysics of philosophy explains the fundamental nature of beings through ontology and epistemology. How class, type, category and set theories are inteconnected? How to distinguish the categories of entities by Aristotelian realism, Kantian conceptualism, Husserlian descriptivism or by scepticism? How transcendentals, like being, thing, one, unity, good, true and beauty relate to the categories with or without transcendence? How to keep epistemic balance between the *a priori* (before sense observation) and the *a posteori* (based on sense observation)? Is a substance distinct from its properties? Is the problem of universals real? The question is whether properties exist at all?

The objects or events of noumenon ("something that is thought") known without the use of ordinary sense-perception is constrasted with phenomenon, with the objects of senses, the physiological capacity of organisms that provides data for perception. Empiricism, along with rationalism and skepticism, generates knowledge only or primarily from sensory experiences emphasizing the role of experience and evidence. Sensory experiences have priority over the notion of innate ideas. All speculations, hypotheses and theories must be tested *a posteriori* against observations, rather than relying on *a priori* reasoning and intuition. In modern hybris, *a priory* reasonings and speculations dominate the contemporary evolutionary theories superimposed and oversaturated by endless model buildings of genomics. Phenomenology studies the structure of experiences and the consciousness of something and its effects. But epiphenomenalism suggest that mental buildings of genomics have no effect in the real world: after more than half a century of molecular genetics still we are not trained how to delineate incipient sibling species in biodiversity and we are far to treat cancer.

Liebniz's identity of indiscernibles works not only in quantum level, but also in taxonomy. There cannot be separate objects or entities having all their properties in common. We have to find fine structures or the molecules separating entities in biodiversity. However still we are troubled with "thisness" (haecceity) sometimes called essences. The property of being is identical with a certain particular individual, with the individualising difference between the concept of incipient sibling species, a particilar species of guiddity ("whatness") and a specimen ("thisness"). Quiddity refers to more general qualities of a thing: "whatness" may be shared with a genus of things (Adams 1979). The substance of bare particular is a substratum with all its qualitative properties of universals "subtracted". But a particular or an individual can lack all qualitative properties, but still have its thisness. Objects may be Hume's bundles of properties (togetherness) consisting of properties, relations or tropes. Tropes are abstract particulars and concrete universals. They are particular instances of a property, therefore universals are unnecessary. Kant's central tenet, that humility is the only appropriate epistemic attitude (White 2006) both in phenomic and genomic research is further justified by particular properties liable to permute with actual, alien or idler properties.

Organisation by integration

The conceptual framework of evolutuionary theory is staggering between mathematical theories of information and operational definitions superimposed by the reductionist application of

principles between organisational levels. Neither the reams of data generated by reductionist perspecives on molecular genetics, nor the arsenal of research algorithms and analytical models or the endless phylosophical speculations on evolutionary theories provide the anticipated understanding. Moreover the application of mathematical modeling has not helped much either. The Darwin's theory of descent with modification by natural selection operates on a long time frame of the phylogeny, but lacks a theory of organisms on a shorter time frame of ontogeny from conception to death (Longo *et al.* 2015). Simplified concept of the reductionist materialism seems to support definite demarcation between ontogeny and phylogeny: stongly distinguishing between evolution, the historical origin of life and organisation, the systemic essence of life. They do not represent and do not explain each others, boths are principal and equal property of material (Setrov 1971). During the last half century the evolutionary dimension has been so dominant that the organism has become almost dispensable. The idea of an unifying treatment originates from Bogdanov (1912)'s tectology, from the science of construction, known today as the general theory of organisation. This systemic approach brings together ontogeny and phylogeny by constructing elements into a functional entity with development of holistic, emergent phenomena. Unfortunately the first publication of general system theory under the name of tectology was completely neglected by Bertalanffy's general systems theory (1969). A recently renewed complex theory of biological autonomy provides a more sophisticated perspectives for a more unified treatment of ontogeny and phylogeny (Moreno & Mossio 2015).

Based on this authonomy approach here we specify the paradigm of integrative organisation (1) operating with level specific mechanisms along the complexity gradient; (2) representing an ultimate and unified universal creator and operator behind both the ontogenetic and phylogenetic processes; (3) and powered by fundamental interactive forces. First we summarise some basal principles of authonomy in order to give formulation of potential terms connected to integrative processes operating against the desintegrative entropic mechanisms of mutation, permutation, transmutation and perturbation.

These principles are collected and presented here in an undisciplined format and content, just to provide the first framework for further, more sophisticated and comprehensive treatment of the integrational approach to speciation.

Integrational approach. This approach emphasizes the inherent integrative nature of organisation to create, maintain and repair the autonomy of living systems. Living entities retain their integrity over time with internal recovery and self-repair realised by regenerating processes in which the parts and the whole are mutually involved. This self-regeneration as an integrative process of self-maintaining structures determines the function of the participants (Artiga 2011). Autonomous entities are far from equilibrium, but cohesive, coherent and causally integrated by the system itself through the capacity to perform work and repair itself. Intended (adaptive, non-neutral) and unintended (non-adaptive, neutral) traits got together and work as an integrated liveable package, functions as an integrated viable system. Without explaining design or functional norms adaptive systems function as integrated systems under actual interactions. Understanding integrated adaptive systems is a functional issue does not collapse to design. If functional relations can be normative at all, the functional usefulness to an autonomous system should be considered normative. Cohesion with interdependencies is involved in adaptively successful normative functioning. Autonomy is a highly process oriented concept avoiding structurally defined entities like the molecular gene concept. Developmental systems theory rejects the essential link between genes and heritability. Instead developmental processes generate traits through diverse interactions that are heritable (Christensen &Bickhard 2002). Shifting to process oriented theories on concepts in biology is based on plurality, treating any particular process as adaptation with its contributing factors such as development, but again with complex variables. Pattern of process interdependence is the key for understanding normative function. Integrity and functional integration of biological entities is the result of process oriented functional integration interrelated with evolution, and not derived from it (Christensen & Bickhard 2002). Process interdependency relations of functions determine the nature of viable

cohesive system. Individual parts and processes exhibit normative functions within autonomous systems.

Organisation. The theory of organisation by integration operates both on long and shorter time frames. Organisation is the general process of integration producing complex from simple, emerging higher levels of hierarchies with emergent properties and maintaining higher degrees of order of an organised system. The level of organisation is best indicated by the intensity of integration (Setrov 1971). Organisational complexity increases by new emergence properties in each level of hierarchy. Organisation is more than low entropy, it is also structure that has function or purpose. Depending on the purpose of the entity, organisation can be seen as disorder, like the human purposed melting ice cream (Gershenson & Heylighen 2003).

Integration. The ontology of integration suggest a complex system of mechanisms, a syntax to organise, to maintain and to protect more information into a whole integer system, into the autonomy. The simple sum of information in the composing members of the integer is much less without integration: whole is more than just the sum of its part. Integration is the complex mechanisms to organise autonomy. In epistemology the generation of authonomy must be interpreted within an integrative systems approach. Integrative organisation works against entropy, but producing diversification as a by-product of mutations, permutations, perturbations and transmutations.

Autonomy. Autonomous systems are thermodynamically open and operationally closed. The closure as an emergent regime of causation is maintaned by the mutual dependence between constraints of constituents and their collective capacity to self-regulate. According to concept of supervenience this irreducible emergence is determined by the properties of, and relations between, its realisers. This distinctive regime of causation emergent from and irreducible to the lower level physical or chemical systems. According to the principles of non-deducibility (Kim 2006) or non-derivability the emergent properties of the whole cannot be predicted, explained or deduced from the properties of the realisers. The

self-determination by closure of constraints at thermodinamical openness is the conceptual core of autonomy.

Self-organisation. Originally, the term self-organizing was used by Kant arguing that teleology is a meaningful concept. Self-organisation was adopted in general systems theory and further developed from cybernetic (Ashby 1962) to dissipative thermodynamic concept of Prigogine (1962). Self-organisation, the order formation in complex dynamic systems is "order from noise", or order "through fluctuation". According to the "science of complexity" systems organise themselves without external direction, manipulation or control while produce an increase in the structure or in the order of the system and change its own organisation, rather than being changed by an external entity or by any auxiliary agent outside. Self-organisation is an adaptive process where entities acquire and maintain structures themselves without an external agent while developing towards an attractor of a single organised behaviour or towards chaotic attractor allowing large variety of behaviours. Once there, the further organisation of the system is constrained to remain in the attractor realising robustness against perturbations. Self-organisation is dynamic arising in time and robust due to adaptability to change and its ability to maintain the increased order (DeWolf & Holvoet 2005).

The principle of self-organisation goes back to the "laws of form". It seems there are invariant platonic natural forms specified by physical law. Physical laws must have had a far greater role in the evolution of the biological form than is generally assumed (Denton & Marshall 2001). After all, what are the mechanisms behind the integrative self-organisation that direct the processes of the evolution? Four physical fundamental interactive forces direct the universe through integrative organisation. These interactive and integrative forces are building a finit set of natural forms through constructional, supervenient, emergent structural mechanisms. These are the ultimate forces powering the works and organising energy mechanisms for integration against entropy, starting with the einselection building in the quantum states, through strings, quarks, protons, atoms, molecules, supramolecules, crystals, to protein folds, cells and species building.

Emergence. Emergence is the appearance of a new observable that cannot be derived from the root theory (Longo *et al.* 2015). Reductionism states that a system can be reduced to the sum of its parts, like in most of the theories and models in "molecular taxonomy". However during emergence the lower micro-level inputs are transformed to the higher macro-level outputs and reaching a certain degree of complexity and the emergence begins to exhibit novel properties not possessed by its simpler constituents (Kim 2006). This basic emergence principle is not utilised yet properly to understand boundaries between quantum and empirical levels. In emergent systems there is a bidirectional, two-way link between micro-level and macro-level: lower level initiates emergence and higher level produces downward causation. According to deWolf & Holvoet (2004) (1) in complex adaptive systems theory the emergence of macro-level pattern arises from interacting agents; (2) in nonlinear dynamical systems and chaos theories the central concept is the attractors, the specific behaviour to which the system evolves; (3) emergents arrive when the system organises itself in time with attractors to divergent state as coherent interacting parts under decentralised control; (4) this decentralised control plus the fact that no single entity can have a representation of the global emergent implies that such a single entity cannot be a single point of complete failure ensuring a relative insensitivity to mutations, permutations, perturbations and transmutations; (5) emergence is dynamic arising in time and robust due to flexibility in the specific parts that cause the emergent properties; (6) especially in very complex multi-agent adaptive community systems emergence and self organisation occur together.

Agency. Autonomy includes agency, the interactive dimension of the relations between the organism and its environment, characterized as a set of constraints subject to closure (Moreno & Mossio 2015). Multiple, extensive and complex feedback systems of constraints regulate and modulate their organisation to cope with challenges of mutations, permutations, disturbances and transmutations.

Cooperation. Fundamental activity of cells beyond self-organisation is to form cooperative associations in a plurality of froms. It seems that the organisation of life is determined not by competion but by the ability to cooperate in complex single- or multi-species communities (Dupré & O'Malley 2007).

Organising forces of integration

Fundamental forces. What are the ultimate universal forces organising the authonomy of emergent hierarchies at increasing complexity levels and acting also behind the delicate divergences organised by integration in the speciation processes? In biology we used to speak about forces like polymerization force of ratchet models behind the cell movement (Ananthakrishnan & Ehrlicher 2007) or evolutionary forces of founder effect, genetic drift, migration, mutation and selection (Sober 1984). These are misleading reductionist analogies between the forces powering works with energy in the Newtonian mechanics and the driving mechanisms of the evolution. These reductionist analogies between forces causing the movement of bodies and mechanisms causing changes in gene and genotype frequencies have debating advocates and proponents even today (Hitchcock & Velasco 2014; Earnshaw 2015, Luque 2016). "Biological forces" on the organisation levels of cell and species are not forces they are only force analogies or force metaphores of the real "forces" in the traditional Newtonian sense. Why philosophers are speculating with these surrogates? In reality these are mechanisms! They are supervenient, emergent structural mechanisms organised and operated by adequate emergent patterns of the fundamental interactive forces, similarly for instance to friction and elastic mechanisms (routinely called as friction and elastic forces) operating on the physical level of organisation. The interconnected dual development of structure and energy organisation (particle and interactive force) as an inherent and innate combined nature of reality are constrained by the great survival of Cartesian dualism. The rise and fall of the three fashionable expectations of electromagnetic, energetic and phenomenalist reductionisms of reality (Blackmore 1982), the Heisenberg's claim that energy is the single substance of reality, the concepts of energy and interactionism (Sonnier 1993), and the debate between Oswald-Mach's energeticism and Boltz-

mann's atomism (Blackmore 1985) has been survived and followed today by the concept of mass and energy dualism. The old Cartesian ontology was challanged by the single substance of the energeticism, but the particle-energy (res extensa/res cogitans) concept seems to be survived. This particle and interactive force dualism (Oláh 2005b) has ben compromised by Einstein's relativity and by the Planck's quantum.

Force mechanisms. At the very early universe there has been a fused, unified single force and with dropping temperature and with spontaneous symmetry breaking the gravity force has been separated first, followed by the separation of strong, weak and electromagnetic forces. The forces of these fundamental interactions or forces of integration have realised intense integrative work powered with energy and started to aggregate proton, atom, nitrogen, helium, stars, larger molecules, up to organic molecules, organisms and communities. The intrinsic interactive nature of this reality has organised the four interactive fundamental forces into various integrative mechanisms along complexity gradient of the aggregating entities from quarks to living organisms and further to ecosystems and to the human communities. The basic physical and chemical organisational levels of power and energy mechanisms have been further organised into novel emergences of integrative mechanisms at the increasing organisational levels (Oláh 2005a):

(1) reproductive mechanisms organised first to integrate a living entity;

(2) concurrence mechanisms to integrate individuum;

(3) competition mechanisms to integrate communities and

(4) idea flux mechanisms of consciousness to integrate human interest.

Various observer specific epistemic mechanisms of physics, chemistry, biology and sociology are thought to preserv the integrated autonomy at each level of organisations.

Divergence by integration

The neutral theory of molecular evolution has demonstrated that majority of polymorphism within and among species are selectively neutral or nearly neutral (Kimura 1983). Divergence is not selective! Neutralists emphasize repeatedly that majority of nondeleterious mutations are neutral or nearly neutral and very few are advantageous. This new mutation scenario gives more importance to random genetic drif and downgrade the importance of selection in the evolution. As a consequence we have to accept that natural selection and other phenomena or scenarios of population structure, like divergence and migration are simply perturbation of the standard neutral model, that is of the natural null model or the neutral null model of the nature (Nordborg & Innan 2002).

Divergence is a byproduct of the integrative organisation operating against the permanent flux of environmental processes of mutation, permutation, perturbations and transmutations powered by entropy. Different genotypes may respond differently to the environment and changes are unpredictable, but integration is organised by similar principles of interactions and mechanisms, powered ultimately by the fundamental interactive forces. For instance, integration of a similar phenotype could be very complex: (1) retained from common ancestry in homology; independently derived in homoplasy (2) by convergence and (3) by parallel organisation or (4) by gene reuse reversal in repeated organisation (Wake *et al.* 2011).

The diversity of integrative mechanisms is increasing along the complexity gradient. Following the paradigm of the ontic structural realism an increase in structural complexity is realised by an increase of relational complexity, that is by an increase of energy pathway complexity manifesting and powering structures and structural nodes of energy aggregates. Moreover the organisation of complexity by integration is further structured by emergence mechanisms leading to increasing levels of organisation up to the developed incipient sibling species integrated contemporary and further to the human consciuosness. Below just for demonstration we list some integrative or desintegrative mechanisms again in an undisciplined format and content, just to provide the first framework for further, more sophisticated and comprehensive treatment of the integrational approach to speciation. We have picked, by random collection, some types of selection mecha-

nisms, as well as some mechanisms of molecular genetics as representative modalities of integrative organisation. All these mechanisms need a comprehensive evaluation in order to specify their integrative nature. There are countless integrative mechanisms organised along the complexity gradients of structure and energy from quantum decoherence to the emergence of human consciousness.

Background selection. The loss of genetic diversity at a non-deleterious locus due to negative selection against linked deleterious alleles. It is one form of linked selection, where the maintenance or removal of an allele from a population is dependent upon the alleles in its linkage group. The genetic background and the environment of a neutral mutation has a significant impact on whether it will be preserved or eliminated in the integrative organisation.

Balancing selection, in contrast, preserves polymorphism, that is, keeps alleles from drifting to low frequencies and being lost by chance. As a result the selectively different alleles/traits will be older than alleles at loci without balancing selection. Older alleles accumulates selectively neutral shape differences in the flanking regions (Nordborg & Innan 2002). It may happen that the locus or site under selection is surrounded by a peak of increased polymorphism. As an analog and result of integration high shape variation is frequently observable at the periphallic genital structures as compared to the stable adaptive phallic structures.

Directional selection is limited to a selected site but leaves a trace in the surrounding chromosomal region resulting in a local loss of variation.

Negative selection or purifying selection is the selective removal of alleles that are deleterious. This can result in stabilizing selection through the elimination of deleterious variations.

Concerted evolution is a universal biological phenomenon, a complex process homogenising DNA sequences in repetitive families by recombination, repair and replication mechanisms of unequal crossing-over, gene conversion and gene amplification. Member genes in the multigene family evolve as a unit in concert, acting more effectively than purifying selection. Elimination or fixation of alleles and mutations by concerted

evolution may take various length of time depending on selection and drift. The cooperative homogenisation of concerted evolution influences both selection and selfish genetic elements in meiotic drive. Concerted evolution of modular genetic architecture is canalized by mechanisms of parcellation, integration, pleiotropy, differential epistasis, and epigenetics as well as balanced by recombination, segregation, selection, drift and gene flow as well as realised through linkage disequilibrium (Oláh *et al.* 2015).

Repeated evolution. Organisation may integrate similar phenotypes at several biological levels. Nature often repeats itself with independent organisation of similar features in two lineages. Similar traits in distinct lineages frequently produced by gene reuse, involving mutations in the same gene: (1) either by several independent causative mutations or (2) by subsequent sorting process of a single original mutation. These are genomic hotspots of phenotypic variation with repeated *de novo* mutations at orthologous loci. Aggregation of multiple small-effect mutations at the same hotspot locus may organise alleles with large-effect. A new phenotype organised once may be subsequently reverted to the ancestral state, however reversions with a single gene mutation is scarce. Gene death and resurrection or birth and death can also be interpreted as forms of reversion. Ancestral polymorphisms of adaptation from standing genetic variation and from incomplete lineage sorting as well as lateral transfers of introgression by secondary hybridization and by gene transfer between distant species are independent origins of derived variants (Martin & Orgogozo 2013).

Paracentric inversion polymorphism. The impact of inversion on evolution has been revisited recently (Hoffman & Rieseberg 2008). Both inversions that differentiate species and inversion polymorphisms within species tend to accumulate at different rates in lineages. Selection on inversion polymorphism may facilitate speciation by reducing recombination and protecting genomic regions from introgression. Recombination might be completely suppressed. Inversion maintains nonrandom association among alleles at loci located within or near inversion and have epistatic effects on fitness facilitating the spread of the

coadapted alleles. Inversion facilitates the accumulation of alleles responsible for reproductive isolation between populations connected by gene flow. As a result of reduced recombination the Bateson − Dobzhansky − Muller incompatibilities accumulate at species boundaries. Inversion support sympatric or parapatric speciation if association develop by epistasis or pleiotropy between alleles under divergent natural selection and directional sexual selection. Increasing number of traits have already been associated with inversion, but their genetic basis is still poorly known.

Morphogenes. Morphological traits are more enriched with transcriptional regulators than physiological traits, more likely to be pleiotropic and evolve faster in expression profile (Liao *et al.* 2010).

Antagonistic pleiotropy. The ability of a gene to affect two or more phenotypes among multiplied phenotypes in opposite directions where no single mutation can be advantageous for all phenotypes in all environments (Yadav *et al.* 2015). The genome-wide association study approach has discovered, hundreds of genetic variants associated with quantitative traits. This may have implications on the rates and limits of adaptation by shaping its processes, and thus modulating phenotype variance. Detrimental mutations are not torelated and hence integrated out of the evolving populations or compensated by other mutations mitigating the trade-offs by reducing the associated fitness cost.

Linkage disequilibrium. The nonrandom association of alleles at different loci, is a sensitive indicator of the population genetic mechanisms that structure a genome. Increasingly used to map genes that are associated with quantitative characters in order to understand the joint evolution of linked sets of genes. It constrains the mechanism in which haplotype frequencies respond to selection, but selection alone can increase linkage disequilibrium and balancing selection persist and stabilise it indefinitely (Slatkin, 2008).

Reduced recombination. Low recombination rates can facilitate the accumulation and maintenance of isolation genes in partially isolated populations, increasing the effect of selection in the face of gene flow. In large panmictic populations, linkage disequilibrium rapidly erodes except in area of reduced recombination.

Selective sweep. An allele increases the fitness and increases rapidly in frequency due to selection. Sweeps can be categorized: (1) *Hard selective sweep* occurs when once a beneficial mutation has occurred it increases in frequency rapidly, thereby drastically reducing genetic variation in the population; (2) *Soft selective sweep* from standing genetic variation occurs when a neutral mutation that was present in a population becomes beneficial; (3) *Multiple origin soft selective sweep* occurs when mutations are common occurring on different genomic backgrounds such that no single genomic background can hitchhike to high frequency.

Genetic hitchhiking, or genetic draft. An allele changes frequency because it is near another gene that is undergoing a selective sweep on the same DNA chain. Neutral and slightly deleterious alleles that happen to be close by on the chromosome 'hitchhike' along with the sweep. In contrast, effects on a neutral locus due to linkage disequilibrium with newly appeared deleterious mutations are called background selection. Both genetic hitchhiking and background selection are stochastic, random evolutionary forces, like genetic drift.

Cooperative functions. Phenome, and through phenome, the genome is the perpetual object of permanent beneficial and deleterious effects and impacts. New biology suggests that contrary to the basic principles of the modern synthesis the genomes are not tidy libraries or abstract assemblages of numerous alleles of small effect. Rather, genomes show the imprint of accidents laden with mechanistic and historical details, more baroque then elegant, and implicate biochemical, cellular, organismal, ecological and evolutionary machineries simultaneously. The genomic foundation of new biology may suggest more functions to integration through cooperation than to selection (Rose & Oakley 2007): (1) abundant DNA sequences without apparent benefit, (2) proliferation of DNA sequences within genome, not benefit organisms, (3) ancient protein-coding DNA sequences older than species, (4) multiple level rapid genome changes with transposition, mutation and recom-

bination, (5) complex and shifting patchwork of genome subject to constraints and pressures.

Birth-and-death model of evolution of multigene families is also a kind of cooperation process interacting with different mechanisms, like pseudogene formation, gene loss, genomic drift, selection and concerted evolution. In this model some duplicate genes stay long in the genome; others are inactivated or deleted (Eirín-Lopez *et al.* 2012).

DNA duplication is an important mechanisms acting on evolution. Duplicated regions are due to errors in meiosis, but transposable elements and reverse transcription also amplify redundancy. Gene duplication, modification, degeneration, complementation accompanied by processes of non-functionalization, neo-functionalization, sub-functionalization and sub-neofunctionalization complicate genomic cooperative constraints in multigene families. More than third of the human genome consists of interspersed repetitive DNA and 10% of tandemly repeated DNA. The majority of the repetitive sequences are nongenic. The function of noncoding repetitive sequences remains still elusive. Both the coding and noncoding sequences of repetitive families evolve in a concerted cooperation, at least greater sequence similarity is found in paralogous regions within a species than in homologous regions between species (Liao 1999).

Intragenomic conflicts, an intrinsic process to every organism getting more importance in the evolution of reproductive isolation (Crespi & Nosil 2012). Various conflictual mechanisms form a central role in driving mutation order speciation, imposing more selective pressure than ecological speciation to organise divergences among populations and incompatibilities between them, especially in isolated populations. Hybrid incompatibility genes: remnant of a genomic battleield? The answer to this question raised by Johnson (2010) is a definite no. Incompatibilities are rather the best possible genomic pattern of genomic cooperation built by constructive interactive mechanisms against conflictual genomic events, driving divergence. Intragenomic conflicts are antagonistic interactions between DNA sequences, but reorganised by intragenomic coo-

peration transforming conflictual speciation into a symbiotic speciation.

Selfish genetic elements. Are genes selfish? No! Multitude of selfish genetic elements in genetic conflict is transformed to innovation through complex mechanisms of genomic cooperation. Some empirical and more theoretical or conceptual development have overemphasized a simplistic, reductionist gene-centric view of the evolution, as a symbolic by-product of the Western World View. In pharisaic political correctness the influential tale of selfish replicators (Dawkins 1976) has triumphed over science. Selfish gene became a symbol of the basic competitive ideology to promote, advertise and to sell practices and machineries of the liberal empire of the "Modern Economic Man". However, epistemology suggests just the opposite. Shelfish genes represent negative agency in the biological autonomy (Moreno & Mossio 2015). The particular selfish elements behave as disturbing agents of the internal perturbation powered by entropy, but supervised by the order of negentropy. They are under a permanent control of integrative organisation in the genomic space powered by ultimate phenomic constraints. In contrary to Dawkins, the phenome is the "replicator" and molecule complexes are the "vehicles". Are genes selfish? Yes! There are a few "selfish", but controlled by the dual nature of reality. Repetitive DNA replicators and self-promoters forming a variety of the selfish genetic elements and enhancing their own transmission to the rest of genome: (1) transposable elements, jumping genes moving around the chromosome; (2) segregation distorters and meiotic drivers increasing their transmission during meiosis; (3) biased gene converters preferentially insert themselves into homologous uninserted sites; (4) heritable organelles and microbes having preferential transmission through female.

Selfish genetic elements are components of the evolutionary change and innovation, but as a consequence of their existence rather than the cause (Werren 2011). Genomic cooperation mechanisms harmonise, concert and integrate their conflicting genomic processes in shaping the structure and function of genetic novelty. Phenotypic reality through genome and epigenome creates, modifies, aggregates, cooperates, orchestrates and

organises entities in a single hierarchy of dual reality under the attractive, constructive and repulsive, destructive mechanisms of the four fundamental interactive forces. Traits are mostly quantitative, encoded by multitude of genes of small effects with combined pleiotropy, epistasis and epigenetic cooperation on the quantitative trait loci. Major genes with large effect play a role in species differences only occasionally (Orr 2001). The effect size of genes, that is the magnitude of increment of genes to the total reproductive isolation is small, genes seldom work alone. The quantum terminal of this organising complex works on the analogy of "orchestrated" coherent superposition quantum state of unitary evolution theorised in conscious processes (Hameroff & Penrose 2014). All the mechanisms, selfish or altruist, cooperative or selective, constructive or destructive, experienced by any deductive rational or inductive empirical observer are only a variety of "objective reduction" of this quantum superposition.

Divergence in isolation

In order to learn achievements of various evolutionary disciplines, we review some theoretical aspects of the speciation processes in geographic isolation. How our species described from the European sky islands are created in allopatry with or without mass selection (Fisher 1930), shifting balance (Wright 1931, 1932) or founder effect (Mayr 1942)? Which kind of evolutionary mechanisms, if any, might produce our newly discovered limnephilid species in these isolated crenon habitats?

Reductionist theories and models. The present "ontology" or rather the "metaphysics" of most evolutionary theorists are based primarily on endless sophistication of the basic mathematical models of beanbag genetics. This virtual speculation about reality manipulates ideas, theories and models on genes as independent units suffering by indetermination of the underdetermination and debated by pessimistic metainduction. Reading the newest publications with promising titles and subjects in the rapidly proliferating journals it is painfull, for a taxonomist, to realise that theories and models are mere speculations without empirical support. This reductionist paradigm is meaningless both from physiological and evolutionary viewpoint (Mayr 1963). The two beanbag mathematicians of this virtual evolutionary paradigm, S. Wright and R. A. Fisher, themselves fought bitterly on their own speculative scenarios of fundamental theorem (large population size theory) and adaptive landscape (shifting balance theory) during over thirty years (Frank 2012).

Large population size theory. Fisher's early model of evolution, the large population size theory, the fundamental theorem is based upon large, randomly mating or panmictic populations and driven by Darwinian mass natural selection and realised by average effects of single allele changes of weak effect at single loci independent of other loci, that is without any epistasis. Fisher's view of evolution, the large population size theory suggests that evolution occurs in large, randomly mating or panmictic populations and is driven primarily by natural selection, or mass selection, at low levels acting on the average effects of single allele changes (of weak effect) at single loci independent of all other loci.

Shifting Balance Theory. Wright's shifting balance theory is summarized basically as the evolution proceeds via a shifting balance processes through three phases: (1) random genetic drift causes subpopulations semi-isolated within the global population to lose fitness; (2) mass selection on complex genetic interaction systems raises the fitness of those subpopulations; (3) interdemic selection then raises the fitness of the large or global population.

Founder effect. Founder effect functions when a subgroup, not fully reperesenting the entire genetic structure of the parental population colonizes previously uninhabited territory. Founder effect intensity relates to the size of the colonizing subgroup. Smaller subgroup has greater chance to under- or over-represents or to lose completely genes of the parental population. Founder effect is based on observation that morphologically deviant or aberrant populations are peripherally isolated and the widespread and contiguous species has less geographic variations and evolutionary inert. Their alleles require long period of time to get fixed in the large species range. The establishment of a new population by a few original founders is based only on a small fraction of the total genetic

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variation of the parental population. The founder effect creates a severe bottleneck situation and accompanying genetic drift condition that results in a reduction of genetic variability. This genetic revolution of Mayr (1963) is realised in significant rearrangements of the coadapted gene complexes. The evolutionary significance of founder effects has been questioned frequently, but it pesists, in spite of adaptive differentiation, as was demonstrated recently in a field experiment with lizards (Kolbe *et al.* 2012).

In contrast to the combined Wright-Fisher population model still widely applied in molecular genetics: (1) most of the population has two sexes; (2) mating is non-random due to sexual selection; (3) reproductive success is non-random; (4) population size vary in time; (5) population is subdivided into demes of local populations; and deterministic mechanisms of (6) selection and stochastic mechanisms of (7) recombination, (8) genetic drift and (9) gene flow are all variously present (Charlesworth 2009). Random mating has been long a basic assumption in theoretical population genetics ignoring the old and recent finding that mate and/or gamete choice are the major selective mechanism driving genetic change in sexual populations (Carson 2003).

*Speciation in allopatry.*The empirical evidence detected at the incipient phylogenetic species, that is the speciation traits are the products of the sexual selection integrated into phenotypes in random processes of isolation without gene flow. Much of what mathematical evolutionists of the modern synthesis theoretized about the species problem and speciation was wrong (Coyne 1994). Our modern knowledge of speciation derives from a taxonomist, Ernst Mayr (1942). One of his major contribution to the modern synthesis is the theory of allopatric speciation supported by Dobzhansky's (1937) genetic expertise. He arrived to a conclusion that geographic speciation in allopatry seems the only speciation mechanism in mammals and birds (Mayr 1963, Mayr & Diamond 2001).

All our incipient limnephilid species evolved in the isolation of allopatry. Therefore, here we do not review the present confused state and the potential future of the sympatric speciation. How proponents of the ecological speciation try to support the basic Darwinian mechanisms of natural selection? What, if anything, is sympatric speciation? Sympatric speciation is probably the infinitesimal end point of a continuum. Better to measure than speculate about discrete categories like sympatric and allopatric speciation (Fitzpatrick *et al.* 2008). More productive is to study how "genomic islands or even continents" may develop in parapatry or sympatry with gene flow (Michel *et al.* 2010).

Instead, we summarise Mayr (1942)'s insistence on the primacy of allopatric speciation and critiques of sympatric speciation. Most speciation proceeds via geographic isolation. Populations become geographically isolated, either by vicariance (*dichopatric speciation*) due to a barrier dividing the range of the species, or by dispersal due to colonists founding a new disjunct population. The sibling populations in allopatry may diverge in their reproductive behavior, and complete the speciation in secondary sympatry by reproductive isolation, by ecological segregation (Mayr 1942) or by reinforcement (Dobzhansky 1940). The reinforcement of hybridization may rarely promote speciation (Servedio *et al.* 2013), in spite of the multitude of interactions between hybridization and speciation (Abbott *et al.* 2013). When a population becomes geographically isolated, its genetic similarity is no longer maintained by gene flow, but subject to divergent genetic processes: (1) new mutations; (2) loss of alleles by drift; (3) novel genotypes by recombination; and (4) differential survival of different genes. The population becomes a distinct species, incapable of breeding with the parental species. If populations are reproductively isolated but not ecologically distinct, they establish "parapatric contact" with minimal interbreeding at the contact border.

Why speciation is rapid in isolation? The recently discovered and described young incipient sibling limnephilid species remained undetected by the inherent resolving limits of the traditional gross morphology and by the blind neutral DNA markers. We have recognised them by fine structure analysis of their genitalic traits, the products of contemporary sexual selection. If differentiation in phenotypic traits exceeds that in neutral marker genes, it suggests a predominant role of

selection over drift (Leinonen *et al.* 2005). A meta-analysis on comparative divergences of quantitative traits (Q_{ST}) and neutral markers (F_{ST}) measured by geometric morphometrics and by microsatellites and allozymes has demonstrated the utility of Q_{ST}-F_{ST} comparison as a practical tool for inferring selection processes (Leionen *et al.* 2008). In the case of the differentiated incipient limnephilid species the divergence arrive through selection of primary sexual traits of paramere, paraproct and aedeagus, leading to reproductive isolation. These young phylogenetic species evolved almost exclusively in isolated spring-fed habitats of high elevations or of karst fragmentations along the Carpathian Basin s.l., that is on the inner slopes of the Carpathians, the Alps and mountain ranges of the Western Balkan Peninsula. Some of them were described form similar isolated spring habitats of the Iberian and Apennine peninsulas. Why this contemporary speciation is limited to these isolated habitats and which kind of speciation processes forms this rapid evolutionary rate?

Two alternatives have been emerged as isolation mechanisms: (1) vicariance by fragmentation of widespread ancestor with only *a posteriori* dispersal and (2) dispersal across a pre-existing barrier into newly colonized isolated habitats with both *a priori* and *a posteriori* dispersal. Dispersal-variance analysis and more complicated geological history revealed multiple speciation events of vicariance and dispersal processes in east-west Mediterranean disjunction (Sanmartin *et al.* 2003). Previsic *et al.* (2014) have discussed that vicariance on very small geographic scale, through landscape alteration, might enforced allopatric diversification of microendemic *Drusus* species without pattern of major admixture events of secondary contact clines, in contrast to the widely distributed *Drusus discolor* having such a contact zone pattern in other regions. Unfortunately both the dispersal-vicariance analysis combined with coalescent method and the estimation of divergence time is computed, in every step of calculations, by multitude of subjective or even manipulated theoretical model networks and algorithms. This theory and model ladden procedure is very far from the validity to substitute empirical reality. The results, the major divergences among

regional populations dated to 2.0 to 05 Mya, seem unrealistic.

Both the vicariance and the dispersal alternatives of isolation mechanisms realise an allopatric type of speciation. In isolation with restricted gene flow speciation is rapid and frequent (Mayr 2001). Reproductive isolation can evolve within tens, hundreds or thousands of generations (Hendry *et al.* 2007), especially in allopatric or in founding populations. Contrary, ecological trait divergence under a balance between selection and gene flow may exhibit only weak reproductive isolation (Nosil 2008).

The high mountain isolated spring habitats of the described incipient limnephilid species can harbour only small and isolated populations or subpopulations of metapopulation. In small populations the genetic drift that is the random elimination of genes may be a more successful process than selection and recessive mutations have more chance to become homozygous. In small populations the sampling error or "accidents of sampling" in genetic drift may reduce genetic variability producing gene loss, genetic homogeneity and bottleneck effect. In this context the range of small population is several hundreds of individual or even less. In populations of several thousands to tens of thousands individuals, rapid speciation may proceed without selection by mutation pressure. If effective breeding population is still greater, around panmixia, speciation will slow down considerably (Wright 1931).

According to Mayr (1942) the reduced variability and high speciation rate due to genetic drift in small and geographically isolated populations may develop also in founder populations, as an auxiliary mechanism. The isolated limnephilid populations in limited spring habitat resources are exposed to allopatric, bottleneck effect and also to the founder principle under both vicariance and dispersal or combined isolation mechanisms. We need to repeat and emphasize that speciation almost always occurs in allopatry (Mayr 1976).

Reproductive isolation

Sexually selected speciation traits. Species are separated both by reproductive isolation and by "ordinary" non-sexual differences in morphology

and behaviour (Orr 2001). Rapidly diverging genitalia, the primary sexual traits are the most important structures applied in taxonomy to distinguish among closely related caddisfly species suggesting directly and empirically that speciation is initiated, driven and completed more by sexual selection and less by natural selection. Postcopulatory sexual selection is regarded as an evolutionary engine. Prezygotic isolation established in sexual selection or in assortative mating, by its very nature, might contribute more to the total barrier to gene flow, than might postzygotic isolation (Butlin *et al.* 2012) or ecological trait evolution. Ecological speciation is frequently overemphasized by pharisaic political correctness and by interpretational bias to support Darwinian ideology. Ecological speciation without reproductive isolation remains liable to the disruptive effects of gene flow, genetic drift and recombination. Traits that are divergent adaptations and also generate assortative mating, the magic traits, can reduce this effect by reproductive isolation avoiding recombination (Boughman 2013). Occasionally divergent selection on genes affecting ecological traits can be transmitted via pleiotropy or linkage disequilibrium to genes causing reproductive isolation (Rundle & Nosil 2005). Genes under divergent selection are usually different from the genes causing reproductive isolation. There are some empirical evidences that ecological divergent selection promotes the evolution of reproductive isolation (Nosil 2008). However it is rather an incident then a rule. It seems that sexual selection has higher potential of generating reproductive isolation than ecological speciation alone, especially in isolated allopatric or founder populations. At the same time sexual divergence might be ephemeral in sympatry without ecological concerted reinforcement (Butlin 2012) and traits influencing mating success are also subject to viability selection.

Divergence in the secondary sexual traits of pheromone communication covers multigene families of chemosensory systems. The birth-and-death evolutionary mechanism of multigene families has relatively high gene turnover rates for proteins of odorant chemoreception in olfactory system of hair-like sensilla. Black hair-like alar androconial sensilla present in many caddisfly groups, including *Drusus* genus, represent power-

ful mechanisms of reproductive isolation. The size of these multigene families differs markedly across many insect species (Eirín-Lopez *et al.* 2012). The structure and function of the alar androconia present on the hindwing of *Drusus* species and its molecular genetics as well as its concerted or birth-and-death evolutionary mechanisms have not been examined by molecular geneticists.

Directional sexual selection is thought to create positive allometric scaling, especially in secondary sexual traits and leading to extreme sexual dimorphism like runaway selection of deer antler and peacock tail. In caddisflies neoformations, bizarre modifications of sexual dimorphism appear very frequently as secondary sexual traits and develop usually on palps, scapes, legs and on wings. Most of these unusual structures are developed to facilitate certain forms of stimulatory or sensory functions in runaway directional sexual selection and are integrated from stochastic processes of mutations, genetic drift, and gene flow directly or through accumulated standing and cryptic genetic variation (Oláh *et al.* 2015). These bizarre neoformations with stimulatory and sensory functions communicate signals to females in order to assess three possible prominent models of sexual selection: (1) signal of species identity assessing population for species recognition to avoid hybridization; (2) signal of indicator trait to assess quality of male; (3) Fisherian or Lande-Kipatrick model, that is the run-away signal of ornamental trait to assess sexy males (Hill 2015).

The lek paradox, that persistent female choice for particular male trait value depletes genetic variation in male trait, is resolved by genic capture hypothesis (Tomkins *et al.* 2004). The genetic variation in male sexually selected traits in the face of strong female preference is maintained by capturing part of the additive genetic variance for condition. In genic capture there is covariance between sexual traits and offspring fitness and the condition dependence is developed, affected and maintained by many loci with high coefficients of additive genetic variation in local adaptation. The condition dependence may be enforced by environment to phenotypic variation. In turn offspring environments may be shaped by maternal phenotype effect, like habitat selection behaviour and

may be combined with genetic basis of the indirect genetic effects (Miller & Moore 2007).

Natural versus sexual selection. A theoretical counterintuitive role of sexual selection is suggested especially operative in allopatric speciation. Contrary to common-sense expectation, the model of strong Fischerian sexual selection may reduce ecological trait divergences between populations (Servedio & Bürger 2014). This theory has supportive experimental tests. Mexican spadefoot toad tadpoles, *Spea multiplicata* (Cope, 1863) has "omnivore" and "carnivore" ecomorphs and this divergence in disruptive and directional natural selection is weaker in treatment with sexual selection (Pfennig *et al.* 2015). The explosive adaptive radiation of Hawaiian Drosophilidae is accompanied by a greater role of sexual selection in the evolution of this group (Kaneshir, 2006). A growing body of data demonstrates the rapid evolution of sex and reproduction related genes, rapid divergence of sexual traits, faster rate of DNA sequences divergence, the evidence of novel traits/genes in sexual functions (Singh & Kulathinal 2000). Time is here for more comparative mapping studies on genes affecting viability *versus* fertility to elucidate the genetic basis of speciation.

Shape divergence

Today the phenomics, a renewed empirical research trend, a revived old paradigm of realism, the promising by-product of genomic fiascos give new perspectives for evolutionary and medical research. It enlarges our capacity to extract information from phenomes applying the arsenals of higher resolution with fine structure analysis (Houle 2010, Houle *et al.* 2010, Oláh *et al.* 2015). Painful failures of modern hybris force us to learn that phenomics, a comprehensive study of phenotype with high resolution is essential to understand reality. Time is here to change how we describe biodiversity or how we study the processes of speciation (Deans *et al.* 2011).

There is multitude of taxa with diverse patterns of subtle shape divergences. These evolutionary signatures of speciation processes are waiting to be explored. Biodiversity represent an unexplored huge resource to enlarge our narrow scenario produced by the model organisms, by the elite

objects of limited imagination. Reference organisms have value as experimental systems, but they represent only small part of the huge phenotypic diversity. We need non-reference organisms to be identified and described with subtle shape divergences, like our contemporary diverging caddisflies in sky-islands, in order to widen the scope of the studies on speciation processes. Rapid developments both in sequencing and phenotyping technologies would provide data and information on genome, transcriptome, proteome and phenome associations and interactions to identify genomic structures and mechanisms underlying the rapid, subtle, but stable shape divergences in speciation microstructures.

Rapid, subtle and stable divergences. All the examined incipient sibling species of caddisflies have been detected and delimited by fine structural divergences of the speciation traits (Oláh *et al.* 2015). The discovered species complexes exhibit rapid and subtle, but stable divergences in the fine structure of the speciation trait. Speciation structures defining species boundaries develop rapidly under sexual selection.

Rapid, stable and subtle shape alterations seem to be a rule, rather than exception in initial lineage splitting evolved under selective, adaptive pressures in non-random, non-neutral phenomic processes of sexual selection. This subtle initial morphological divergence is canalized by resource polymorphisms (Pfennig *et al.* 2015), reinforced in secondary contact clines and maintained by strong stabilizing selection with or without gene flow. We need to understand why are the speciation traits diverging rapidly, stably and subtly in sexual selection and what is the genetic architecture underlying this widespread process in millions of species?

Rapid sexual selection. Male genitalia diverge more rapidly than any other morphological traits. There are millions of species with rapid genital divergence. The rapid evolution of animal genitalia testified by extraordinary high diversity is an empirical evidence of the divergent sexual selection. The diversified genitalia may play essential role in speciation whether acting at the onset of the lineage splitting process or after disruptive ecological selection to reinforce gene flow barriers. Variation in male fertilization success and

shape variation in male genital structure seems interrelated. Earlier explanation of sexual selection favouring mating barriers between species, that is the premating isolation by female choice is slowly replaced by growing evidence of sexual selection acting in post-copulatory processes responsible for rapid divergence in genital shape pattern, like postmating, prezygotic isolation by postcopulatory cryptic female choice. In sexual antagonist coevolution the male genitalia evolve to prevent females from mating with other males. Two different types of sexual selection can operate with various mechanisms after male and female genitalia have come into contact: sperm competition and the cryptic female choice. The later mechanism is getting importance; more than 20 female processes could result in cryptic female choice (Eberhard 2011).

Is the inability to interbreed an integrated signature effect, the by-product of selection or it is the primary cause of speciation. Is the rapid, subtle and stable shape divergence of speciation trait a by-product of the selection or it is the speciation engine itself? Is the divergence of reproductive barriers detected in the form of rapid, subtle and stable shape alterations initiated and created by ecological or sexual selection? We have found that the most influential mating, internal courtship or copulatory actor, the phallic organ or the paraproct have diverged and evolved as a speciation trait in most of the discovered new caddisfly taxa (Oláh *et al*. 2015). This mere fact suggests the importance of the sexual selection in these isolated sky-island habitats. Early diversification of parameres has been reported already in genus *Eocosmoecus* Wiggins & Richardson, 1989: the differences in periphallic organs were minor, but the parameres of the phallic organ diversified clearly by changes in the number and pattern of spines.

Experimental evolution demonstrated that sexual selection can generate rapid divergences in genital morphology. Similarly in nature aedeagal divergence evolved very rapidly among native and exotic allopatric populations of dung beetle *Onthophagus taurus* (Schreber, 1759) (Simmons 2014). There are processes, like founder effect and interaction of natural and sexual selection, capable of generating such rapid subtle changes

also in genital pattern of *Enallagma* Charpentier, 1840 damselflies (McPeek *et al*. 2008). Founder effect operates when a species colonizes a new location, that might happened when *Enallagma* were faced of punctuated climate change associated with glacial advances and retreats throughout the Pleistocene.

Diverging genital structures. The product of the directional sexual selection, the diverged genital structure or microstructure incorporates rich amount of information about the processes or mechanism that produced the diverged traits. The subtly and stably diverged traits of fine structures are sensitive indicators of early divergences. They are integrated under sexual selection with potential stochastic processes of genetic drift, recombination and mutation or under the influence of gene flow. This focus of recently derived traits can help us to select among the multitude of morphological details of genitalia, which has real importance in species delimitation in the early stages of speciation. These adaptive, non-neutral traits are stable enough compared to non-adaptive, neutral traits those varying under various stochastic processes.

In the grasshopper genus *Melanoplus*, non-intromittent structures exhibit less divergence than do intromittent structures (Márquez & Knowles 2007). Generalisation seems reasonable that non-intromittent genitalia evolve in sexual selection mostly through their effects on mating success, while intromittent genitalia are subject to selection through their effects on fertilisation success (Simmons 2014).

Stable shape divergence. Male genital structure in general is known to have low phenotypic and genetic variations (Takahara & Takahashi 2015). The detected striking divergences in the speciation traits across species suggests directional sexual selection acting on these structures. Following initial divergence, between speciation events, stabilising selection favours intermediate values of the diverged trait. Stabilising selection reduces trait variation, generates negative allometry with pattern of canalised growth protected from environmental perturbations and results in highly invariant, stable genital traits (Simmons 2014). The degree of fluctuating assymetry, easily

detectable on parameres, indicates disturbances in the development of this canalised growth.

In primary sexual traits, like in the speciation trait of paraproct of Drusinae subfamily, some analogue of directional selection creates the initial split in shape divergence. The subtly diverged paraproct is evolved by directional selection and balanced into stabilized shape through condition-dependent trait expression and certain genetic variation maintained in stabilizing selection. Most traits change little over splitting due to reinforcement as well as to stabilizing selection thought to be the most common selection mechanisms in most populations.

Standing genetic variation. Allelic variation that is currently segregating within a population; as opposed to alleles those appear by new mutation events. Does it mean that in adaptation the allelic variation is already present, not created by mutations, and in adaptation it prevails over the others? Standing genetic variation is the presence of more than one allele at a locus in a population. When an allele goes to fixation there is no standing genetic variation at the locus until new mutations occur. Loci where alleles are not fixed are described as having standing genetic variation. The polymorphisms contributing to adaptation can either be present as standing genetic variation at the onset of selection or emerge through mutations. A longstanding challenge in quantitative and evolutionary genetics has been quantification of the relative contributions from standing and emerging variation to long-term selection response.

Polymorphism. The definition of polymorphism for widely distributed and greatly varying species is incorrect. This strongly violates the basic historical synpatry concept of polymorphism. The widespread synpatry concept of polymorphism is based on discontinuous variation, that requires polymorphic developments inside a panmictic population and not between geographically isolated populations. Although the epistemology of the widely accepted and applied sympatry concept of polymorphism is not well established, it is routinely used both by traditional taxonomy and by molecular genetics. In principle the polymorphism could be the very beginning of various speciation processes both in synpatry or in allopatry and may represent early stages of spe-

ciation combined/coupled or not by reproductive isolation. To correct the incorrect polymorphism concept here we repeat some premises and details of the presently accepted sympatry concept of polymorphism.

Divergence in isolation is not polymorphism. Descriptions of polymorphism emphasize the occurrence of more than one kind or form of organisms of the same species that exists together in one locality in contrast to monomorphism: (1) Polymorphism, the discontinuous genetic variation, dividing the individuals of a population into two or more sharply distinct forms is the occurrence of two or more different morphs as alternative phenotypes in the same population of a species. (2) Polymorphism is the coexistence of two or more distinct forms independent of sex. (3) Sex itself as dimorphism is a form of polymorphism of the same species; the most common example of polymorphism is the sexual dimorphism. (4) Polymorphic forms of discontinuous variation must occupy the same habitat at the same time in the same panmictic (randomly mating) population. (5) There are two basic mechanisms in the organisation of polymorphism *sensu lato*. Polyphenism appeares, if different morphs arise from the same genotype by environmental interaction. Polymorphism *sensu stricto* is the genetic polymorphism evolves if different forms are created by certain mutations, alterations and integration in the genotype. (6) Genetic polymorphism, the occurence together in the same population of two or more genetically determined phenotypes in such proportion that the rarest cannot be maintained merely by recurrent mutation.

However, this distinction between environmental polyphenism and genetical polymorphism is highly artificial, epistemological and often far from reality. Molecular genenicists define frequency of the less common allele in genotype between populations. Taxonomists are interested in determining differences in phenotype between individuals. In reality the existence of a species in several forms of phenomics, existence of genes in several allelic forms of genomics/transcriptomics or the existence of a molecule in several forms of proteomics is rather a rule than an exception and they are under the pressure of permanent integrative organisation in complex interactive processes.

All these omics is, in emerging systems approach, under the direct or indirect impact of the ecome of ecomics (Kikuchi *et al.* 2011) and of the biome of biomics through trans-omics networks by interactome of interactomics (Janga *et al.* 2011). As a result of interactome most polyphormism is transient and governed by the processes of spreading or supressing in a population, or balanced by selective agencies. Balanced polymorphism is an equilibrium mixture of homozygotes and heterozygotes maintained by integration against both homozygotes through selective advantage.

In routine practice the reference to phenomenon of polymorphism, similarly to the cryptic species concept, is frequently and unconsciously an epistemological product used to camouflage our limited knowledge or simply a trial to delineate our narrow horisont. According to the cryptic species concept the species are cryptic because our phenotypic resolution is insufficient and our knowledge on fine structure of phenotype is limited due to the deprived state of taxonomy, the badly depressed science of biodiversity. The so called highly variable widespread species are frequently composed of populations with large amount of undetected phenotypic divergences. Their morphology or phenotype is only superficially indistinguishable. Many of these polymorphic and cryptic species are pseudo-polymorphic or pseudo-cryptic, they are perfectly diverged incipient siblings simply undetected due to the inadequate study of morphological features, limited knowledge of ecology, unknown behaviour in nonvisual sound, vibration, pheromones and electric mating signals. They are cryptic or polymorphic simply because we are blind. We apply inadequate phenotypic resolution (Oláh *et al.* 2015).

Incipient species or polymorphism? Allopatric divergences and not sympatric polymorphism have been demonstrated in species complexes of the *Potamophylax* Wallengren, 1891 genus (Oláh & Kovács 2012, 2014, Oláh *et al.* 2015). Similarly the six subspecies in the *Potamophylax cingulatus* complex evolved in allopatry of geographical isolation along almost all the European mountain ranges. The diverged taxa in *P. cingulatus* complex need a detailed population study by fine structure analysis of the speciation traits.

Population trait matrices will demonstrate how stable the diverged traits are. In this species complex the phallic organ, especially the paramere divergence is very pronounced and possibly resulted in contemporary speciation processes producing incipient sibling species of the phylogenetic species concept. In caddisfly taxonomy we used to work with gross structures of neutral, non-adaptive, random traits strongly exposed to both gene flow and genetic drift. The time has come to rely more on the non-neutral, non-random but adaptive traits creating reproductive isolation in contemporary speciation processes and resulting in the rapid formation of subtle and stable speciation traits in incipient sibling species of the phylogenetic species concept.

Minor shape modification. In alpha taxonomy we are frequently faced with unresolved difficulties how to evaluate minor shape modifications. We are frequently forced to decide without real molecular knowledge behind, whether these alterations represent ranges of (1) neutral genomic variation; (2) epigenetic variation; (3) phenomic plasticity; or (4) they are sign of developmental instability; (5) early adaptive signatures of diverging populations; or (6) they are already products of non-neutral, non-random adaptive genomic processes, representing diverged reproductive barriers of closely related incipient sibling taxa; indicating some (7) incomplete lineage sorting or (8) hybrid effects in secondary contact clines under reinforcement.

Neutral versus adaptive traits. According to the Hardy-Weinberg principle genotype frequencies in a population will remain constant from generation to genartion in the absence of other evolutionary influences, like mate choice, mutation, genetic drift, gene flow, meiotic drive, and effective population size. However natural populations are dynamic under the effects of such influences. Natural populations are permanently exposed to varying as well as fluctuating complex multitudes of both abiotic and biotic perturbations. Neutral, adverse and benefitial perturbating effects modify both their phenome and genome. Therefore neutral traits are exposed to high genetic variations and in alpha taxonomy we are permanently faced with wide variabilities of neutral traits. In contrary, the adaptive traits of the di-

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verged genital structures are under various integrative processes and mechanisms stabilizing and protecting the adapted values of the speciation traits.

Subtle shape divergence. Interspecific morphological differences in the adaptive traits seem subtle for human eye of limited capacity, but have sensible stimulatory effect in the copulation processes of *Drusus* mates. This initial split of speciation divergence appears subtle for routine practice. Is it really subtle? It is subtle compared to the inadequate resolution level that traditional taxonomy applies routinely in delimiting species, but robust enough for mate recognition in building the reproductive isolation. Imagine the stimulatory robustness of a rigid sclerotized structure if would develop or appear on the phallic organ to operate in human mate! In contemporary taxonomy we used to apply robust genital structural differences of old splitting in determining or differentiating between species and not prepared to subtle contemporary divergences of young sibling species.

Genomics behind subtle divergences. The combination of phenomics and genomics, the mutual support of observability and virtuality, the relevant combined evidence of speciation, the background empirical knowledge necessary for molecular cladistic inferences liable to and testable by falsification, are still almost lacking in taxonomy. The assignement of trait identity classes to specific types and combinations of mutation, recombination, genetic drift and gene flow would produce more perspective to a real breakthrough in diversity research. Taxonomy works with empirical reality of phenomics. Our knowledge is especially limited on linkages of molecular genetic to the mechanisms of shape transformation. Its fundamental potential to interpret the phylogenetic information content of morphological traits is not utilized yet.

Especially little is known about the genetic architecture or the specific genome structure underlying the evolution of male genitalia. Our knowledge is very limited even in the model genetic systems like *Drosophila*. Time and methodology are here to search the causal relationship between phenotypic differences and the genetic polymorphism observed both within species and among closely related incipient siblings. Searching quantitative trait loci and candidate genes of speciation traits in natural population is just started, but molecular tools are increasingly available (1) for quantitative trait loci mapping; (2) for mapping by pattern of gene expression; (3) for population genomics approach. Quantitative trait loci mapping remains a powerful, but tedious procedure to identify genomic regions co-segregating with a complex traits. However, only allelic diversity that segregates between parents of the particular F2 cross or within the recombinant inbred line population can be assayed. Moreover the amount of recombination occurring during the creation of the recombinant inbred line population limits the mapping resolution (Korte & Farlow 2013). A complementary and powerful tool became available to connect the phenotype-genotype map. This is the genome wide association study, that overcomes the limitations of the quantitative trait loci mapping. Its basic approach is to evaluate associations between each genotyped marker and the complex phenotype, like the diverged shape of paraproct in *Drusus* scored across a large number of individuals.

Sax (1923) showed first that quantitative trait loci could be mapped by linkage to visible markers. With variation of this approach, candidate loci or genes of large effect with naturally occuring allelic variation and contribution to quantitative variation in *Drosophila* bristle (sensillum!) number have been identified. Sex specific effect and epistatic interaction, comparable to additive effects were observed between the mapped genetic factors (Long *et al*. 1995).

Subtle shape divergences have been regularly detected at young incipient sibling species in several limnephilid caddisfly genera (Oláh *et al.* 2015). Similar shape divergences are well documented at elite model organisms in the *Drosophila* genus. *D. melanogaster* and its sibling species, *D. simulans*, *D. mauritania*, and *D. sechellia* are morphologically very similar, distingishable only by the posterior lobe of the genital arch. But it is suprising how complex genetic network of elaborated quantitative trait loci has produced these minor adaptive shape divergences in directional sexual selection and preserved in intermediate range of the stabilizing selection. Applying advanced intercross mapping design

three quantitative trait loci were identified having influence on shape divergence of the posterior lobes among siblings of *Drosophila melanogaster* complex (McNeil *et al.* 2011).

Slight shape variation in genital sructures is a striking empirical tool to describe biodiversity. Subtle or even tiny shape divergences in the genital structure, creating reproductive isolation, frequently characterises closely related sibling species with very complex underlying genetic structures with many quantitative trait loci and thousand of candidate genes. Siblings of *Drosophila* species in the *D. buzzatii* cluster well differentiated by genetic markers was morphologically detectable only by quantitative variations in aedeagus curvatures. The differences are indiscernible empirically, that is the shape differences either variable or small, not distingishable by visual magnification, but measurable reliably only by geometric morphometry (Franco *et al.* 2006). The distophallus, the most prominent sclerotized structure of the males intromittent organ diverged subtly, but in a highly species-diagnostic manner at species of the *Drosophila virilis* group. Owing to lack of reliable landmarks, elliptic Fourier analysis was applied in geometric morphometry and principal component analysis together with composite interval mapping to localise quantitative trait loci. Intraspecific variation involves multiple quantitative trait loci with largely additive small effects (Schafer *et al.* 2011).

Divergence in the size and shape of genital posterior lobe serves as the most reliable morphological character to distinguish among sibling species in the *D. melanogaster* complex. Siblings of this complex mate each other to produce steril F1 hybrid males and fertile F1 hybrid females. Backcross generated F2-like genotypes, together with introgression lines with large effect sizes were applied for quantitative trait locus mapping and transcriptome analysis. Experiments identified a minimum of 20 loci underlying morphological differences with hundreds to thousands of genes. Genetic causes for rapidly diverging posterior lobe morphology include species specific differences both in protein coding sequences and in gene expression levels. The genital structures in *Drosophila* develop from larval genital imaginal disc. Among the detected 8000 genes 2261 genes

were differentially expressed between *D. mauritiana* and *D. sechellia* (Masly *et al.* 2011).

Posterior lobe morphology of F1 hybrid was modified into various intermediate shapes of the two parental species. A common, but usually neglected phenomena in alpha taxonomy. Specialist are frequently faced with hybrid specimens of intermediate shape variations seriously challenging species delimitation and delineation of siblings. Intermediate shape variation accumulating during reinforcement processes in the contact zones or clines is a clear indicator of the recent, contemporary divergences. These shape variations are frequently observed phenomena occuring in contact populations of contemporary diverged young incipient species in the *Drusus* genus.

Speciation traits

Among all the genital structures the paramere is the most direct structure functioning in close cooperation with the aedeagus during copulation while performing various courtship, titillating, stimulating, harm, cleaning, anchor, mate assessment, ejaculate guarding and plug device functions. Diversity of parameres evolves along these various functions and under their interactions. The diversification of genital fine structures, like parameres, directly involved in mating, are not yet accounted reasonably in taxonomy. The discovery and the application of speciation traits of paramere, paraproct and aedeagus in caddisfly taxonomy (Oláh *et al.* 2015) provide powerful tool with high resolution ability to delimit boundaries of the phylogenetic incipient sibling species in the early stages of reproductive isolation.

Phenotypic sophistication in Drusus taxonomy. In our studies on speciation trait during the description of the 70 incipient phylogenetic limnephilid species, by fine structure analysis, we have experienced that the neutral DNA markers frequently failed to detect any differences between species having evolved well diverged fine structures on the speciation traits. These easily observable phenotypic differences of morphological characters are highly valued new tools in taxonomy (Oláh *et al.* 2014, 2015). Instead of remaining on the old pathway in *Drusus* taxonomy (Pauls *et al.* 2006; 2009; Previsic *et al.* 2009; Vitecek *et al.* 2015) and repeating to couple un-

related entities, that are the phenotypes of traditional gross morphology with the inherently blind neutral markers masked applicable by multitudes of theoretical model manipulations, it is more prospective to rely more upon the immense empirical information evolved into the fine structure of phenotypes on parameres and paraproct or on other speciation traits of the genitalia. These tiny, but stable divergences are sensitive enough to quantify both interspecific and intraspecific genetic variations in biodiversity.

The inductive sensory empiricism of direct observation on fine structure pattern differs ontologically and radically from the rationalism of the deductive theoretical models elaborated in model masking industries in order to cloak and obfuscate inconvenient data by pruning rogue data and applying various types of data-smoothing algorithms and techniques to manipulate discordant, ambiguous data of the reality (Tomkins & Bergman 2013). Molecular data are used reasonably in phylogenetics to reconstruct species trees based on the coalescent theory (Lorusso 2011). However tree of life is more complex, at least four phenomena complicate bifurcations: (1) horizontal transfer, (2) symbiogenesis, (3) differential lineage sorting, (4) frequent gene duplication. Moreover coalescence times of alleles among species are highly variable (Rose & Oakley 2007). The long lasting fashionable and dressy trials with neutral markers in taxonomy developed into a kind of nightmare for the mathematical theory of evolution, also known as population genetics (Rao *et al*. 2010). Did population genetics contribute anything beyond the obvious? This fundamental issue raised by Mayr (1959) was first answered by one of the beanbag founder (Haldane 1964) by listing his oversimplifying assumptions, his mechanistic and reductionist vision of reality: (1) population is infinite, (2) generations are separated, (3) mating is random, (4) gene is completely recessive, (5) segregation is perfect, (6) and selection acts constant. Haldane himself said that the mathematical theory of evolution was quite primitive, in spite of struggling with Fisher's mathematics (Cro, 2007). Are the abstract figures, formulas, equations or models more valid than the abstracted empirical reality? Can anyone imagine evolutionary theory without mathematics? The

answer is clearly "yes" produced by Darwin (Ewens 2008). The reductionist single-locus theories of the "Modern Synthesis" were followed recently by mathematical multi-locus theories. These multi-locus models have revealed and incorporated some complexities but not lead to paradigm-changing conclusion (Ewens 2008). Dead parts of the Modern Synthesis are not revived yet (Rose & Oakley 2007). They will be buried deep, sooner rather than later: (1) genome is a well-organised library of genes, (2) genes have single function, (3) species are finely adjusted to environment, (4) durable units of evolution are species, (5) adaptive machinery can be modelled.

Taxonomist separate species and establish boundaries mostly by empirical phenotypic morphological traits created by many loci under environmental effects, further complicated by dominance, epistasis, and pleiotropy as well as by complex regulatory mechanisms in expression of the polygenic traits and by developmental constraints. Quantitative traits do not exhibit discrete phenotypes, but vary continuously. We have to give one more reason to the limits listed earlier (Oláh *et al*. 2015): why neutral molecular markers are blind in meaningful taxonomy. The correlation between molecular and quantitative measures of genetic variation is low, weak, nonsignificant. These markers have only very limited ability to predict quantitative genetic variability (Reed & Frankham 2001). These nonlinear molecular interactions complicate genotype-phenotype mapping through pervasive epistasis of additive variance and result in missing heritability (Mackay 2014). The neutral markers have limited capacity to detect morphological divergences of speciation traits. These mitochondrial and nuclear sequences have only indirect contact to processes governing the shape divergence of the polygenic paramere, paraproct or aedeagus. How can we expect any real and causal correlation between the neutral markers and the non-neutral, adaptive polygenic speciation traits in the contemporary divergences? These traits integrated by complex interactions of several quantitative trait loci have already demonstrated their phenomic power in detecting and delineating incipient phylogenetic sibling species.

Phenotypes of morphology, ecology and behaviour drive most research in life sciences. It is a must to cope with the genotype by combining information from genomes, transcriptomes, proteomes, phenomes and biomes with the help of emerging informatics standards (Deans *et al.* 2012) as well as of the high-tech and high-throughput phenotyping (Sozzani & Benfey 2011). The unexplored landscape of phenotype data based on ontology terms and entity-quality formalism is available to process by cyber-infrastructure (Deans *et al.* 2015).

Generic characters

Phylogenetic concept of higher taxa. The revolutionary concept of evolution, the descent with modification has not realised Darwin's prediction to convert taxonomy into genealogy, the line of descent. Instead, existing taxonomies were re-interpreted in evolutionary terms and previously recognised taxa, both species and higher or lower categories, were taken granted. However, during the Modern Synthesis species was accepted as fundamentally different from taxa of higher and lower levels. The biological species of Mayr (1942, 1963) are outcome of evolution, functioning in a direct way as gene pools, exist as whole, as real things, but the higher or lower taxa are viewed as subjective and arbitrary (deQueiroz 1985). The widely accepted conclusion of the modern synthesis was that species are fundamentally different from taxa of lower or higher categorical level.

In his phylogenetic systematics Hennig (1966) has radically changed the role of evolution in formulating higher taxa. In spite of the view that evolution is not a necessary assumption of cladistics, that is the assumption of descent with modification is not required to justify cladistics (Brower 2000). The product of evolution above species level are monophyletic groups composed of ancestral species, a complete system of common ancestry, clades, the natural outcome of the process of evolutionary descent. Higher taxa like genera are real, existing as a whole, outside of the mind of taxonomists (deQueiroz & Donoghue 1988). One way of determining branching order, hierarchy of higher levels, is the character ranking system in taxonomy, that can be realised through

principle of generality (Winther 2009). More general character provides the basis for a larger group.

*Specific and generic characters.*Characters are the characteristics of an organism. The trait is the specific expression of a characteristic, rooted in the genotype.Trait indicates the inherent qualities that are present in an individual from birth. Trait is the phenotypic variation on a character. For instance in the *Drusus* genus the paraproct head shape is a character, the truncate head shape is a trait. Character is to be understood in the sense of quality. Such qualities can either be inherited or acquired over a period of time, with interaction between intrinsic and extrinsic environment. A phenotypic trait, or simply trait, is a distinct variant of a phenotypic characteristics of an organism; it may be either inherited or determined environmentally, but typically occurs as a combination of the two. A trait is a characteristics or a feature of a species that is inherited normally genealogically**.**

All the species of a genus resemble each other, and in which they differ from allied genera, are called generic characters. Traits in which species differ from other species of the same genus are called specific characters. Specific characters are more variable than generic. Parts which have recently and largely varied being more likely still to go on varying than parts which have long been inherited and have not varied. Secondary sexual characters are highly variable. It will also be admitted that species of the same group differ from each other more widely in their secondary sexual characters, than in other parts of their organisation.

Characters and character states. In speech the word "feature" refers to those objects or entities which an observer recognises as separable elements of attributes, traits, characteristics or characters comprising of the organisms. Taxonomic characters are the basic unit of taxonomic description, fundamental data of cladistics and an organising power in systematic analysis. Characters are features expressed as independent variables. Character states are mutually exclusive conditions of a character (Sereno 2007). Some systematics equated character and homology, being homologies the characters of monophyletic taxa (Patter-

son 1982). Cladistic analysis starts with data matrix of homologous, informative character findings for phylogenetics, continues with character analysis and completes with phylogenetic analysis with final product of monophyletic clades. Are taxonomic characters, the data matrix for cladistics natural units or artefacts of observation and description? Character reality depends how these characters are abstracted, verified or falsified. The diversity of taxonomic approaches as well as phylogenetic questions in systematics hinders the precise understanding of what kind of data represent true characters.

Character typing. Attributes are converted to characters by fixing it in one observed taxonomic unit and by recognising its transformational differences relative to other taxonomic unit. There are two fundamental character patterns: (1) neomorphic pattern of *de novo* appearance or loss without trace; and (2) transformational pattern from one state to another comparable state (Sereno 2007). There are discrete or discontinuous attributes with non-overlapping state values and continuous attributes with overlapping state values. There are several ways to establish and order the attribute states of taxa or entities: (1) present or absent states of binary discrete attributes; (2) morphological attributes with three states: absent, small, large; (3) four-state discrete attributes are the states of G,A,T,C in DNA sequences; (4) multi-state discrete attributes are amino acid residues in proteins.

Character processing. Our practice applies the same characters to describe and organise species in an objective, repeatable and operational way in taxonomy, but also to organise the attributes of the entities in a hierarchical context of phylogeny, including species and lower or higher level taxa. First (1) we sample entities densely enough to capture its range of variation; (2) decide character homology and state homology; (3) code characters; (4) choose outgroups to provide root for polarity; (5) establish character weighting scheme (deSalle 2006).

Distance based phenetic clustering phenograms of numerical taxonomy represent matrices of distance data but not represent a true hierarchy. In these phenograms the hypothetical taxonomic units at nodes have no any attributes. The cha-

racter based phylogenetic trees may represent real hierarchy, because the hypothetical taxonomic units have reconstructed attributes at internal nodes of the cladogram, demonstrating transformation of characters.

Character obscuring. Subjective processes, terminological controversies, unstable, unorganised character selection and delimitation, theory-laden assumption-domination and model-manipulation obscure both epistemic and semantic character perception and application in taxonomy and phylogenetics. Character selection and identification are highly subjective and depend on the background knowledge of the specialists. The identification, individuation, and measurement of any taxonomical character are based on subjective theory-laden abstraction. This is true for all kind of characters, but especially for molecular characters which are seriously permeated and saturated by theory and model speculations. This deformed reality becomes all too easy to inappropriately reify characters and all too difficult to distinguish real from artifactual characters. In cladistics the recognition of character similarity, the "same but different" for homology, starts with empirical observation, but operates behind with conceptual elements of abstraction. This is a subjective grounding in character delimitation. Subjective processes of abstraction include (1) abstract away character variation; (2) abstract the core properties; (3) abstract the sameness or character identity; (4) abstract specimen distortion to find identity (Winther 2009).

From proper background knowledge specialists of taxa have ideas that certain state changes are impossible, highly unlikely; others are possible but more or less probable; some attributes are better than others; some attributes are more informative. Therefore character weighting is commonly required, even equal weights is a form of weighting. However, the relative weight of cetain classes of attributes, the process partitions, has been subject of intensive debate. For instance there is especially severe pointed debate around the weighting of morphological and molecular attributes.

Phylogenetic concept of species. In biological systematics we need theories to guide our everyday taxonomic practice in constructing biological

classifications. Systematics is dominated by phylogenetic perspectives, the evidence that evolutionary history is of primary importance when delimiting and ranking taxa. Unfortunately non-phylogenetic, non-history based species concepts, like the biological species concept lead to errors. The existing Linnaean species taxa having common morphologies and ecologies were not taken as given (deQueiroz & Donoghue 1988). The biological species concept, as a fundamental evolutionary unit and with focus on reproductive isolation, is a byproduct of the Modern Synthesis but violates the proper understanding of evolutionary mechanisms (Valesco 2008): (1) conflicts with evolutionary thought; (2) distorts evolutionary history; (3) reproductively isolated groups might be non-monophyletic; (4) can be paraphyletic, composed only of some of the descendants of some ancestral population; and (5) can be not an exclusive group, not more closely related to each other than any of them is to anything outside the group.

In the biological species concept populations of one species could be more closely related to another species than to other populations in the same species; this paraphyly is produced when reproductive isolation evolves in one population of phylogenetically distinct biospecies. This paraphyly problem is less important if confuses population history, but it does not lead to mistaken inferences in species delineation. It becomes more severe if mislead us about interspecific relationships. But splits between groups, like switching to new ecological niche or diverging in morphology takes place without building reproductive barriers. If we separate organisms by single property other than genealogical history, paraphyletic group could be easily formed, even if we calculate with the history of reproductive isolation. The combined concept of phylogenetic species is based both on the diagnosable combination of character states of initial splits and on trait histories.

Monophyletic concept of phylogenetics. Following Linnaeus and after Darwin the desire to form groups of organisms upon evolutionary relationships has led to develop evolutionary taxonomy, numerical taxonomy and cladism. Hennig's cladistic analysis of morphological data established the phylogenetic systematics inferring evolutionary relationships from shared derived characteristics of evolutionary novelties. The branching point or node on the cladogram represents the initial split; the point where shared derived morphological characters arose. Diverged taxa branching from a common node are closely related sister groups. The monophyletic group or clade, the similarity of common ancestry arise from a single ancestor and include all the living and fossil descendants. Members of a monophyletic group share at least one derived character. Paraphyletic group is a taxon that include some, but not all of the descendants of a common ancestor.

Phylogenetic species tree might be defined as the pattern of branching of species lineages via the process of speciation, but gene trees are produced by gene replication (Maddison 1997). Phylogenetic taxon tree is a containing tree descending and branching while within its branches a contained tree, the gene tree itself descends and branches. However multitude of tangled gene trees is present within a species, one for each nonrecombined locus and superposed recombination brings together gene regions with different phylogenies. Even without recombination and to find the simple unrooted best trees topologies with 55 sequences, the number of possible tree topologies is around 1×10^{79}, more than the total number of electrons in the observed universe (Doyle & Gaut 2000). Whether or not a particular gene tree agrees with the species tree may highly depend on what gene copies have been included and what models and methods are applied.

Phylogeny reconstruction by model-level understanding of nucleotide substitution processes and applying parsimony, distance, maximum likelihood or any methods faces the same problem how to find the optimum among the vast number of possible gene trees. Unfortunately empirical characters are replaced by virtual models that dominate how gene phylogenies are inferred from nucleotide sequences. As a result phylogeny is best illustrated as a cloud of gene histories, a history what happened in micromorphology of molecules or even better to view phylogeny as a history of what could have happened, that is as a model of probabilities of interbreeding (Doyle & Gaut 2000). The calculated optimal trees may not

reflect the relationships of organisms. This discord, the incongruences between gene trees and taxon trees might be produced by (1) mixing paralogous and orthologous sequences, by (2) horizontal transfer of genes among species through vectors or introgressive hybridization and by (3) sorting of ancestral polymorphisms and deep coalescence (Maddison 1997).

Character ranking. Evolutionary taxonomy (Darwin 1859, 1871, Huxley 1940, Mayr 1942), numerical taxonomy (Sokal & Sneath 1963) and phylogenetic systematics (Hennig 1950, 1966) were all developed while forming the new discipline of systematics, a combination of traditional taxonomy, phylogeny and biogeography, in an attempt to uncover evolutionary relationships among taxa, that is to discover the branching tree of life. Phylogenetic systmatics (and the later cladistics) directly establishes character ranking based upon shared derived characteristics or evolutionary novelties. Phylogenetic trees depict lineage splits through time supplying visual character ranking for establishing hierarchies of taxa. Phylogenetic tree building is both the process and the result of character ranking in taxonomy.

However, pervasive mistakes obscure the character ranking in tree inferences as well as compromise its epistemic utility in pessimistic meta-induction about changes in individual characteristics. Misconceptions are still popular and published regularly in manuals and in journals with the highest impact factors (Omland *et al.* 2008): (1) looking ancestors in the tops of trees among extant species, (2) reading trees "left to right"along ladder of progress, (3) describing extant species as "primitive", (4) celebrating living fossil taxa or lineages (5) one species is ancestral to other extant species, (6) primitive lineage fallacy of attributing ancestry for early branching or (7) for basal species-poor lineages. These are misleading concepts because evolution or organisation generally has not stopped in any lineages. Even living fossils continue to accumulate many molecular changes. New mutations, permutations, perturbations as well as neutral processes of genetic drift combined with gene flow lead to better adaptation by integration between organisms and environmental factors. All

extant species and genes are a mix of ancestral and derived characteristics and not the extant organism or gene itself that is ancestral/"primitive"/branched early or derived/young/branched off last. Phylogenies of extant species or genes show relatioships among evolutionary cousins, better to use "sister group" whenever possible when describing trees and determine which characteristics are ancestral.

Character ranking creates understanding in structural realism of living hierarchies. Every day taxonomy faces the routine questions how to distinguish character combinations in order to delineate taxa and to establish species complexes, species groups, species, genera and higher hierarchies. Which character state is more ancestral and which have higher ranking value? Complete, simple or complex? In caddisfly phylogeny Ross (1956) prefered the simple, Schmid (1958) argued for the complex. We think that popular intuitive search prefers to work with complete structural integrity pertinent to a particular level of organisation. To distinguish between present-day descendant and long-dead ancestors remained a permanent unresolved reverent task of taxonomy. What were the characteristics of extinct ancestor, which characters are more ancestral (earlier organised) or more derived (recently organised), how to establish reliable character ranking? There is a need to answers the simple question still unresolved in the evolution of paramere and paraproct complexity: do these speciation traits evolve from simple to complex or the opposite? Sophisticated, assumption based model building helps to reconstruct the ancestral features of the organisms in character ranking, but remains virtual if not supported by empirical information, that is by phenomic reality of taxonomy, functional morphology, genetics, development and ecology. In order to understand what is simple and complex or which character state is ancestral plesiomorphic or derived apomorphic we need to outline some basic relations in complexity theory. Most surveys oversimplify the ever-changing and complicated understandings and speculations about entities and interactions inside the self-organising complexity (Oláh *et al.* 2014).

Early branching lineages without empirical data do not signify ancestral traits (Crisp & Cook

2005). Speciation rates differ and are most frequently individual in lineages, therefore morphological differences do not reflect time differences. Slow rates of certain characters do not mean that speciation in a lineage as a whole slows down. Gene tree building complicates further lineage ranking. Relation between gene trees and their containing species trees magnify difficulties how to reconstruct species trees from gene tree ranking with a cloud of gene histories (Maddison 1997). This gene cloud might disagree with the species phylogeny produced by discordant processes of horizontal transfer, hybridization, introgression, lineage sorting, undetected gene duplication and extinction. Incomplete lineage sorting inversed in deep coalescence might fail to coalesce until deeper than previous speciation events. Ancestral polymorphysms persist through several speciation events. The biological species concept permits paraphyly, distorts character ranking when historical splits take place by shifting to new ecological niche and diverged in morphology, without reproductive isolation (Velasco 2008). This appropriate ranking is further complicated by attribution of these "biospecies" properties to higher taxa.

Genome complexity is correlated with morphological complexity and driven primarily by non-adaptive stochastic mechanisms, rather than by adaptive evolution (Lynch 2006, Yi 2006). These questions emerged important for paraproct and paramere structures, especially, when their non-neutral, adaptive sexual selection driven evolution become more documented (Oláh *et al.* 2012, Oláh & Ito 2013a, Oláh *et al.* 2013b, Oláh *et al.* 2013c). Titillating or harming speciation traits of the phallic organ directly involved in sexual selection processes diverge into variously complex structural patterns fitting to perform their multiple and complex functions in the initial stage of divergence (Oláh *et al.* 2013c). Nevertheless species delimitation and character ranking in tree inferences are especially difficult in recent divergences when different loci/structures have different histories (Meara 2010).

According to the Williston's law the structures tend toward reduction: structural parts are reduced by loss and fusion (Williston 1914). A general evolution-pattern of reduction in structural parts

was demonstrated by Gregory (1935). An ancestor must be constituted by the integration of the largest possible number of characters (Schmid 1979). Based upon these considerations we have selected the structurally most complex parameres for the ancestral plesiomorphic state both in the *Potamophylax nigricornis* species group (Oláh et al. 2013b) and in the *Allogamus* genus (Oláh *et al.* 2014). Our decision is confirmed by the simple fact that the ancestral species with the most complex paramere has the largest distributional area, compared to large series of diverged peripatric sibling species with reduced complexy of parameres and with small distributional area. Nevertheless we have considered that the terms simple, complex, primitive, generalized, specialized, are all strictly comparative (Ross 1956, Schmid 1958).

However, reduction in the number of structural parts could be associated with increasing complexity (Esteve-Altava *et al.* 2013). Complexity may increase with complementary qualities associated to the decrease of structural units. Reduction of elements is compensated (1) by anisomerism, that is by specialization of the structures (measured by dissimilarity of connectivity and heterogeneity); (2) by the number of unpaired structures as a side-measure of anisomerism (fusion of two or more pre-existing structures, representing the most modified, specialized ones); (3) by density of connections (more connected is more complex); (4) by characteristic path length (speed of information flow), (5) by cluster development (loops of connections, integration, modularity). Specialization by simplification could be an inherent complexity increase. Parts tend toward reduction in number, with the fewer parts greatly specialized in function. Early excessive complexity followed by adaptive reduction is a possible route to adaptation. More advanced structures can have fewer parts.

Downgrading secondary sexual characters. At the dawn of Drusinae taxonomy the male secondary sexual characters have been used almost exclusively as generic characters to establish new genera. In a revision of generic concepts of Hawaiian Drosophilidae the secondary sexual characters proved to be not valid to warrant generic groupings. Rather, these bizarre characters have

provided misleading interpretation of evolutionary divergences (Kaneshiro 1976).

Earlier we have also recorded and evaluated the vague generic characters in Hydroptilidae family (Oláh & Johanson2011). Differences in wing venation, head, ocelli, antennae, maxillary palps and tibial spurs have been used traditionally for generic discrimination in adult Trichoptera. In Hydroptilidae family the venation characters have been substituted and the head, leg and especially the thoracic characters proved to be a satisfactory basis for generic separation (Ross 1944). In a taxonomic review of the genera of the Hydroptilidae, Ross's thoracic characters, the shape of mesoscutellum and metascutellum were placed in the centre of higher level classification of the hydroptilid family (Marshal 1979). The number of tibial spurs and the highly variable reduced or compressed wing venation, although considered diagnostic in the past proved to be rather unreliable in genus discrimination of many hydroptilids (Wells & Huisman 1993). At such reduced dimensions venational features are not constant in genera and species (Marshal 1979). The real diagnostic value of generic characters is complicated further by secondary sexual structures.

Discoveries of unusual structures and neoformations on head, antennae, wing and legs developed to facilitate sensory functions in sexual selection have initiated the proliferation of genera in Leucotrichiini (Oláh & Flint, 2012): *Leucotrichia*, *Celaenotrichia* (Mosely 1934), *Costatrichia*, *Zumatrichia* (Mosely, 1937), as well as *Abtrichia*, *Acostatrichia*, *Betrichia* (Mosely, 1939) genera have been erected mostly on neuration and on these unusual structures. Later modifications on tibia (Harris&Bueno-Soria 1993) erected new genera in Leucotrichiini tribe. *Anchitrichia* was established and separated from *Zumatrichia* by rooflike holding of forewing and its transverse green pattern, unmodified antennae and the general structure of the male genitalia (Flint 1970). *Byrsopteryx* without any head or antennal modifications is almost identical with *Celaenotrichia* and its genitalia are very similar to both *Celaenotrichia* and *Alisotrichia* (Flint 1981). *Ascotrichia* was described and related to *Abtrichia* from which it differs in the form of head, antennae and forewing (Flint 1983). *Ceratotrichia* was

established by bizarre sexual modifications of the head and antennae (Flint 1992). The elevation of *Alisotrichia quemada* species group to the generic level of *Scelobotrichia* is based on the presence of tibial lobe on the foreleg (Harris & Bueno-Soria 1993). The plesiomorphic state of tibial spur present, although greatly reduced on foreleg initiated the creation of *Cerasmatrichia* genus (Flint 1994). Modified forewing with the presence of jugal lobe, reduced spur number and vestigial gonopods created *Mejicanotrichia* (Harris & Holzenthal 1997). This unsatisfactory classification of tribe Leucotrichiini was admitted already by Marshall (1979) and many genera were considered very heterogeneous by Flint (1992). In a study on the Neotropical Hydroptilidae (Oláh & Johanson 2011) we have found various modifications present or absent together with rather similar genital structures. This suggests that these bizarre modifications, the secondary sexual structures of sexual dimorphism, are species specific rather than genus specific.

MATERIAL AND METHODS

In this revision of the Drusinae subfamily we have given priority to character ranking in order to re-evaluate the generic, species group, species complex and species characters and to elaborate the coalescence linegae structure from incipient species to genera as well as to revise the natural taxonomic structure of the entire Drusinae subfamily based on phenomic characters. The delimitation and description of new incipient sibling species is based primarily on the adaptive shape and pattern divergences of the paraproct and paramere. In descriptions of new species we have prepared and discussed the detailed fine structure drawings without repeating body or wing neutral characters, those which are presented in details in the original description of their sibling species.

As a standard we have faced four basic bottlenecks in material and methods during the five years of intensive concentrated research on the revision of the Drusinae subfamily: (1) lack of population sampling; (2) the empirical and virtual limits in resolution of fine phenomics; (3) variability ranges and fluctuating asymmetry in the spine pattern on the parameres; (4) lack of cooperation between phenomics and genomics.

Population sampling

Working on fine structure of the speciation trait to delineate young incipient species we need to sample many population and many specimens in order to distinguish between subtle shape divergences and to quantify the ranges of trait variations. Population sampling for fine structure analysis is a bottleneck to realise subtle, cryptic phenomics in the new taxonomy. It is mostly prohibitive due to various limits of reality (Hillis 1987): (1) the overal resource deprived state of taxonomy in the present state of western culture resulted almost in a complete lack of financial resources for meaningful sampling of biodiversity; the revision of Drusinae subfamily would have not been possible without searching and compromising historical specimens scattered in various collections; without the accumulated specimens in private collections of the authors of the present revision; without the special private financial effort of the first author to realise targeted field sampling during the last eight years; (2) lack of trained and experienced collectors; the resource limited collection practices permit to cover only universal collection strategies to sample as many groups of organisms as possible, not specialised for particular group of organisms; (3) rarity of species; most of the contemporary diverged incipient sibling species are represented by small effective population size in limited habitats exposed to various environmental perturbations; (4) inaccessibility of habitats; small and vulnerable populations of the young incipient species evolved in specialised or highly specialised habitats which survived mostly in remote, inaccessible localities, frequently in high elevations of isolated mountain ranges; (5) destruction of habitats, a dominating process of the profit oriented western culture; (6) legal protection of habitats or species; national laws emerging worldwide to limit the collection of specimens. These regulations are legitimized to protect natural populations and species, but impeding professionals to carry out taxonomic research (Oláh et al. 2015), but how to protect what is still unknown (Dubois 2010); (7) increasing cost of procurement and acquisition.

Population thinking in the new taxonomy requires more elaborated field collecting strategies (Oláh et al. 2015). To collect many specimens from many populations are the prime target of any research project aimed to find the first signatures of reproductive isolation, to search species boundaries, to delimite closely related incipient taxa, and to recognize the young phylogenetic species. Biodiversity research and conservation are badly limited by the lack of population field sampling. Staggering in the deprived discipline of taxonomy and suffering the lack of adequate collecting we have been forced to outline the principles and practice of cooperation how to put together what we have (Oláh et al. 2013c). There are historical materials scattered in museum, university and private collections. Taxonomy has to survive somehow the two-faced European science and environmental policies: speaking nice and killing biodiversity twice: with economy and pharisaism! We have laboured an idea of cooperation how to realise comprehensive studies when funding is removed from taxomomy to "modern" disciplines of genetics, ecology and conservartion and no resource remained available even for adaequate population sampling. A limited effort with fine structure analysis on speciation traits disclosed how meager is our knowledge on the European aquatic biodiversity.

Theories, algorithms, methods and procedures of population sampling are the basis of the New Taxonomy. Today under the present course of resource disposing policy we have to rely upon caddisfly specimens already collected in various research projects and deposited in various collections. If money limits our efforts in alpha taxonomy we have to put together what we have. To bring together these scattered specimens we need a specialist who is interested in that particular species complex. He will initiate and organise this collective effort. We have to understand clearly that the collected, sorted and determined material incorporates already significant scientific work and has high primary value for such a joint surveys. Adequate population sampling is a key component of any fine structure analysis of phenotypic speciation traits. Therefore we practice that colleagues who contribute to the survey with their collected, sorted, prepared and identified specimens and agree with the final findings become coauthor of the paper and/or of the species automatically. It was a great challenge and required sustained effort to bring together all

the necessary specimens to revise the Drusinae subfamily, including new collecting trips by many of the authors between the years of 2009 and 2016.

Empirical limits

Examination of fine structures of *Drusus* parameres and paraproct is not easy. It can be very difficult to visualise and understand its fine structures with reasonable accuracy. Published paramere drawings are mostly rough, not detailed enough and not consistent. Exploring and presenting only a very small ratio of the phenotypic information content of the paramere. Inconsistencies arrive by poor visibility of low magnification of stereomicroscope and by angle distortion of higher resolution of compound microscope. As a result the examination of the setal pattern present on *Drusus* paramere could be very embarrassing, misleading and resulting false, incorrect conclusions even in meaningful taxonomic studies. At the same time the purposeful, careful and experienced examination, utilising advantages and avoiding disadvantages of both the stereomicroscopy and the compound microscopy, can generate multitude of valuable phenotypic information more sensitive than any of the neutral molecular markers.

At the magnification range of stereomicroscopy we can observe only the basic architecture of the setal pattern. This satisfies targets of routine serial examination of specimens in population studies, but only in that case if the detailed structure is already understood, described and known to the observer. Usual observation with stereomicroscope gives no access to details. Without compound microscopy setal shape, setal articulations, setal alveoli, setae adhered to shaft surface, smaller setae and the types of surface texture remain undetected.

At the higher magnification of compound microscopy the high resolution induces smaller depth of field and smaller working distance. However, the higher magnification potential of the compound microscope may help to detect and understand fine structures of the genitalia. To recognise properly the shape, connections, interactions and articulations of the small and frequently weakly pigmented structures requires

practice and experience. Permanent movement and maceration with fine tipped pins and forceps of the properly cleared and denuded parameres under the stereomicroscope, as well as under inverted compound microscope with large working depth, help us to detect the otherwise indiscernible structures of various setal articulations.

A high quality stereomicroscope under highest resolution is required to be able to observe important three-dimensional structures, instead of using the higher magnification of compound microscope. Stereomicroscope uses 2 separate optical paths to provide different viewing angles to the left and right eyes. It therefore produces a three-dimensional visualization of the genital structures with great working distance and sufficient depth of field. However, higher resolution induces smaller depth of field and working distance. The stereo microscope should not be confused with a compound microscope equipped with double eyepieces. In a compound microscope, both eyes see the same image, and the binocular eyepieces simply provide greater viewing comfort. However, the higher magnification potential of the compound microscope may help to detect and understand finer structural details of the genitalia.

Positive identification is possible only with teasing out of the entire phallic organ, not only the phallic tip. In practice teasing the entire phallic organ either anterad or posterad may injure or distort those parts of the parameres which are directed in opposite of teasing. Especially when teasing the phallic organ anterad, the complex arm of the paramere is usually detached and hooked in its original position. Imitating the natural movement of the phallic organ as it functions by teasing out the aedeagus and paramere from the phallocrypt, while kept together, posterad, it results in perfectly visible structure without significant injuries. It is advisable to examine several specimens with properly withdrawn phallic organ to understand in detail the structure and function of an unknown paramere with possible operational artefacts. The in situ paramere position is highly dependent on the pre or postcopulatory state of the animals. Moreover, only a little plane change creates significant alteration how we see the very complex structure of paramere under microscope.

To distinguishe between taxa of species complexes we rely upon the shape of paraproct and the setal pattern of the paramere both in left lateral view. In *Drusus* genus we find the paraproct rather divergent among taxa and stable both inside and between populations. This mere finding suggests that paraproct may have an important direct function in copulatory processes and diverged in selective, non-random, non-neutral mechanisms. The setal pattern of the paramere is stable with a range of variation. Variability is caused by two types of artefacts. First type of variation is the result of functional injuries, distortions or even damages accumulated during copulatory actions. The actual setal pattern depends on whether the parameres of the specimens what we examine was collected before or after the copulation. The second source of variation is subjective. On the high resolution a tiny alteration in the view of examination significantly changes the pattern of this fine structure. Such subjective source of variation is very pronounced also in the dorsal or caudal view of the paraproct. These views are unstable, very difficult to reproduce similar drawings even from the same specimen. Moreover, sometimes the paraproct in caudal view is poorly visible in front of the black spinulose area of tergit VIII.

Paramere asymmetry

Fluctuating asymmetry is the variation in the differences between right and left sides of bilateral traits, like parameres and easily used by quantification to assess developmental instability (Oláh *et al.* 2016). These usually small differences are random imprecisions in developmental processes deviating from the expectation of target phenotype and expressed under genomic and environmental control. However normal distribution would require many small additive and independent random effects, but fluctuating asymmetries are rather nonlinear, non-additive with mutual interdependences although random in their directions. Fluctuating asymmetry is effectively applicable to study the developmental origin of integration within and between morphological structures. Development is not completely deterministic.

Most paramere exhibit fluctuating asymmetry with imprecision measures of developmental in-

stabilities correlated or caused either by adverse environmental conditions or by genetic challenges. Genomic molecular integration with chromosomal rearrangement rather than selection influences this fluctuating asymmetry in polygenic mechanisms comprised of pleiotropic, epistatic, dominance and various "selfish" genetic processes. Gene flow, genetic drift, mutations, recombination and standing genetic variation all may further influence the effective power of the integrative mechanisms in asymmetry. Developmental processes are inherently stable and could be remarkably precise depending on balance between genomic or environmental noise and buffering by developmental stability and canalization (Klingenberg 2015).

There is no exatly copied parameres; every individual is slightly different, as we have experienced during the examinations of many thousands of parameres. This follows also from Leibniz's principle of identity of indiscernibles. But we have experienced very high stability in the complex structure of the parameres in all European populations of the spring-dwelling caddisfly species *Potamophylax nigricornis* (Oláh *et al.* 2013) as well as in other limnephilid genera (Oláh *et al.* 2014, 2015). At the same time we have recorded significant fluctuating asymmetry in the count of terminal setae on the parameres of the *Chaetopteryx rugulosa* species group (Oláh *et al.* 2012). Similarly less species specific stability and more fluctuating asymmetry was experienced during our studies on parameres in the *Drusus bolivari* (Oláh *et al.* 2015) and in the *Drusus discolor* (Oláh *et al.* 2016) species complexes. In the present study we have recorded variously developed asymmetry in several species complexes and here we present some examples (Fig. 1).

Cooperation asymmetry

In a long series of papers we have documented that species delimitation with subtle, but stable trait divergences seem to be a rule in endemic hotspots of sky-islands in the mountain ranges embracing the Carpathian Basin *sensu lato*. In these habitats mostly in allopatry with limited secondary contact we have discovered and described 70+49 new closely related endemic caddisfly species usually with small, but stable

Figure 1. Fluctuating asymmetry in the spine pattern between right and left parameres in various *Drusus* species and in *Ecclisopteryx alkon* sp. nov.

and consistent morphological divergences (Oláh *et al*. 2015, present paper). Unfortunately most of these populations have low effective population size very liable to extinction by contemporary climate change.

All the discovered incipient sibling species have exhibited surprisingly rapid, subtle but stable morphological divergences in the shape of the speciation traits, an actor of sexual selection. Traditional phenomics of alpha taxonomy relies on gross structural divergences and suffers of inadequate tradition, experience and knowledge

how to detect, visualize and describe these "tiny" divergences. In alpha taxonomy we are even more unprepared to understand the molecular mechanism and processes underlying the evolution of the "tiny" shape divergences of the speciation traits. Unfortunately the molecular mechanisms of shape divergences is poorly studied. A limited knowledge is slowly accumulating on genomic processes of the subtle shape divergences, pertaining exclusively to some reference elite organisms like *Drosophila*, but highly deteriorated by virtuality (Franco *et al*. 2006, Masly *et al*. 2011, Mc Neil *et al*. 2011, Schafer *et al*. 2011).

In alpha taxonomy we must be interested in the molecular mechanisms underlying the speciation processes, like the integration of speciation traits. Taxonomists must apply the basic achievement generated on reference and model organisms. However, most of these results are highly theoretical and virtual, that follows from the simplified reductionist philosophy of the present-day molecular genetics, even more of the "molecular taxonomy". These results are generated mostly by theoretical models. Moreover the so called "factual" measured molecular information is abstracted and interpreted by several powers of model algorithms. In addition, data are limited to some highly manipulated laboratory organisms and detected in highly artificial and simplified experiments far from the environmental condition of natural populations.

We slowly realize how huge task is waiting for the betrayed taxonomy without resources to collect and quantify biodiversity and to describe millions of unknown taxa and how virtualized is the supporting molecular genetics of phylogeny, full of theories and model constructs and far from reality. How to cooperate? The phenomics and the genomics are two independent disciplines huge enough alone and far from each other and both have own independent scope. Taxonomists are not sophisticated in genomics and molecular taxonomists have limited knowledge in molecular genetics other than processing the blind neutral markers.

Nevertheless taxonomy needs genomic explanations of some basic phenomics to improve the practice of taxonomy in delineating closely related taxa. The two disciplines, phenomics and genomics, are tightly interwoven in the entangled Holon and there are unresolved practical questions which may require joint effort to answer. For instance how to delimit and delineate diverging incipient sibling species with fine structure analysis of the speciation traits? Which evolutionary and molecular mechanisms form the subtle shape alterations? Neutral DNA markers have indetermined as well as underdetemined sensitivity, conceptual and practical limits. Moreover they are blind for non-neutral, non-random trait divergences, like the speciation traits under sexual selection. However rapid innovations in mapping by quantitative trait loci, by pattern of gene expression and by population genomics, especially by genome wide association studies offer new perspectives (Oláh *et al.* 2015). An urgent need to bridge some deep gaps between taxonomy and molecular genetics must inspire us to speculate about the theoretical background and to understand at least the molecular genetics of the initial shape divergences in the subtle and stable traits of the speciation process.

Depositories

Cantonal Museum of Zoology Laussane, Switzerland (CMZL)

Constantin Ciubuc Private Collection, Sinaia, Romania (CCPC)

Coppa Private Collection, France (CPC)

Department of Biology, Faculty of Mathematics and Natural Sciences, University of Prishtina, Prishtina, Kosovo (DBFMNSUP)

Moretti Collection, Department of Chemistry, Biology, and Biotechnology, University of Perugia, Italy (MC)

Museo Civico di Scienze Naturali "E. Caffi", Bergamo, Italy (MCSNBG)

Cianficconi Collection, Italy, deposited at the Museo Civico di Scienze Naturali "E. Caffi" Bergamo, Italy (CC)

Moretti Juvenile Collection, deposited at the Museo Civico di Scienze Naturali "E. Caffi" Bergamo, Italy, (MJC)

Museo Friulano di Storia Naturale di Udine, Italy (MFSNU)

Museo Civico di Storia Naturale di Genova, Italy (MCSNG)

Museum der Natur, Gotha, Germany (MNG)

Museum for Natural History of the Humbolt University of Berlin, Germany (ZMB).

National Museum, Prague, Czech Republic (NMPC)

National Museum of Natural History, Sofia, Bulgaria (NMNHS)

Oláh Private Collection, Debrecen, Hungary, under national protection by the Hungarian Natural History Museum, Budapest (OPC).

The Natural History Museum, London, England (NHM)

Wien Museum , Austria (WM)

Zoologische Staatssammlung, München, Germany (ZSM)

Zoological Institute, St. Petersburg, Russia (ZIN)

RANKING IN DRUSINAE SUBFAMILY

In the present system of the Drusinae subfamily most of the genera are artificial construct established by giving unjustified upgraded taxonomic ranking value to structures of secondary sexual characters appearring as sexual dimorphisms mostly on the forewing or on the hindwing. Secondary sexual characters are species specific and not the characters of generic ranking

(Oláh & Flint 2012). Schmid (1955) has introduced the term of neoformation for these unusual structural modifications into the trichopterology. These neoformations appear very frequently as secondary sexual traits and develope usually on palps, scapes, legs and on wings in the form of setal bunch (pencil of hairs of McLachlan, accomodated in a pouch on hindwings). However, neoformations might also evolve as bizzare shape transformations in any body structures and could be initiated by stochastic genomic processes and fixed/reinforced by sexual selection. They are less common in lineages with primitive character states and more common in lineages with specialized characters. These bizarre modifications, even brachypterism appear throughout the caddisfly taxa from *Rhyacophila* to *Limnephilus*. Most of these unusual structures are developed to facilitate certain forms of sensory functions in sexual selection and produced through stochastic speciation processes including mutations, genetic drift and gene flow. The first discoveries of these secondary oddities have initiated the proliferation of genera in hydroptilids and lepidotomatids (Mosely 1934, 1937, 1939). We have found such modifications, present or absent while coupled with rather similar genital structures (Oláh & Johanson 2011, Oláh & Flint 2012). This finding suggests that these bizarre modifications are species specific. The taxonomic value of the secondary sexual traits was downgraded long ago in Lepidostomatidae family and 25 genera have been synonymized with the genus *Lepidostoma* (Weaver 2002).

Without these secondary sexual modifications the *Drusus* genus is highly homogenous, similarly to the entire subfamily. The first species grouping in the *Drusus* genus was elaborated by Schmid (1956). He has established six species groups based almost exclusively on the shape and position of the paraproct. However, he has emphasized that both his species grouping in the *Drusus* genus, and the six genera revised and retained in the subfamily, are only artificial constructs. Schmid's basic conclusion was repeated, but no new grouping idea or any ranking system was suggested in a recent cooperative complex study, that was based on larval morphology, larval feeding strategy and sequence data from two mitochondrial loci and from one nuclear gene (Pauls *et al.* 2008). A more comprehensive and complex species grouping in the *Drusus* genus as well as an evaluation of genus downgrading in the Drusinae subfamily was suggested, that shuold focus rather on adult morphological traits (Oláh *et al.* 2015). Selection principles for character ranking should rely on traits of varying diversity, stability rates and of different splitting ages in order to establish a natural phenomics for taxon ranking.

Unreliable generic characters. The taxonomic history of the genera in Drusinae subfamily is based on two unreliable charcaters (see at the taxonomic history of *Drusus* genus): (1) the alterations in tibial spur formula as well as (2) the presence or absence of some secondary sexual characters: scales on the wings, wing brachyptery, and first of all, the presence or absence of "pencil pouch" on the male hindwing.

Varying spur numbers. Specific alteration of spur formula, that is the change in the number of spurs present on tibiae is a very frequent phenomenon in caddisflies. The generic diagnostic value of spur formula has been rejected due to their high variability (Oláh 1914). Alterations in spur number from the basal formula of the particular taxon is realised by neutral stochastic processes, produced by genetic drift and gene flow, highly influenced by effective population size through regular recombination modified by irregular impacts of mutations, permuations and perturbations and fixed by integration mechanisms.

Secondary sexual traits. The specific and not generic alterations in secondary sexual characters, like "pencil pouch", wing scales, wing brachyptery, can be initiated by stochastic processes and fixed by sexual selection. Its taxonomic ranking value have been misused in several groups of organisms. The pencil pouch present on the male hindwing is a setal bunch or pencil of hairs composed of long setae (or scales in *Drusus improvisus*) with alveoli adhered together in resting position thus forming this "pencil-like" structure accommodated in a deep pouch between or along the veins of A2 and A3. In the taxonomy of Drusinae subfamily its ranking value has been overestimated during the dawn of caddisfly research by establishing several new genera or underestimated, for instance in the taxonomic evaluation of the *Drusus rectus* and *Drusus nigro-*

rectus siblings (Malicky 2005a). The presence of scales on the male forewing induced the erection of the genus *Monocentra*, the discovery of whitish scales in the pouch of *Drusus improvisus* transferred this species into a new genus *Monocentra* and the absence of pouch initiated the erection of genus *Metanoea*, as well as the presence of unusually broad pouch led to the erection of genus *Cryptotrix*. At the same time, as an absurd position, the lack of pouch on the hindwings of *Drusus nigrorectus* was not enough to accept its specific status as compared with the *Drusus rectus* having pouch on hindwings. Based on the specific and not generic nature of these secondary sexual traits and developing new ranking criteria (see below!) here we revise the existing genera in the Drusinae subfamily and synonymise all the genera with the *Drusus* genus and retain only the genus *Ecclisopteryx* having significant generic modification in its periphallic structures and in its paramere pattern.

Generic ranking in Drusinae subfamily. Lineage sorting in deep coalescence, that is looking backward in time, is frequently complicated by failure of a trait to coalesce back into a common ancestral character state until deeper than previous speciation events. Nevertheless, common ancestry remained a basic inference principle for phylogenetic analysis and for character ranking practice in taxonomy. However incomplete lineage sorting may hinder further this procedure. Therefore it is more workable to replace the secondary sexual characters and to find more reliable generic characters if we rely simply upon the universal principles of diversity, hierarchy, parsimony and generality (Winther 2009).

For generic ranking we have recognised the importance of ancestral architectural divergences in the adaptive paraproct and paramere structures. The periphallic organ of gonopods, cerci and paraprocts have been variously exposed to previous historical sensory and stimulatory functions and have been liable either to adaptive processes of sexual selection or to neutral stochastic mechanisms. In the Drusinae subfamily *Ecclisopteryx*, the only genus has modified radically the basic architecture of the ancestral periphallic organs, diverged from *Drusus* and represents only the single taxon to deserve the generic level of ranking. All the other taxa in the subfamily we have synonymised here with the *Drusus* genus. *Drusus* genus is a very compact lineage which has retained the variously shaped, but complete structure of paraproct with full stimulatory function. The heavily sclerotized head on the dorsal branch of the paraproct roughened with densely spaced short pegs serves as stimulatory organ in copulatory processes.

In contrary the paraproct of *Ecclisopteryx*, both its ventral and dorsal branches, have almost completely disappeared, rather vestigial, reduced to a pair of narrow sclerotized bands shifted ventrad and sunken and hidden deep between the enlarged cercal complex and the phallobase. During these studies we have recognised graduality in the character state transformation of paraproct reduction. How the complete paraproct character state of *Drusus* is modified gradually to the almost complete lack of paraproct in the *Ecclisopteryx* genus. (1) The unique species of *Ecclisopteryx malickyi* is characterized with mixed character states of the *Drusus* and *Ecclisopteryx* genera. Its compact, not reduced, non vestigial paraproct relates this species to *Drusus* genus but its gonopod with peg packed roughened surface relates it to the *Ecclisopteryx* genus. (2) The dorsal branches of the paraproct is already lost, but the ventral barches of the paraproct is still present at *Ecclisopteryx madida*. (3) all the other species of the *Ecclisopteryx* genus has only vestigial paraproct in the form of narrow stipes or bands

The stimulatory function of the lost paraproct at the *Ecclisopteryx* genus has been taken over by the modified head of the gonopods. The gonopod head of the *Ecclisopteryx* genus has modified significantly to the same roughened surface, covered by the same densely packed heavily sclerotizede pegs as the paraproct head has in the *Drusus* genus.

Besides the vestigial paraproct, the generic status of *Ecclisopteryx* is also supported and correlated by an ancestral divergence in the paramere structure. The ancestral setal/spine pattern on the paramere is produced by a single organising centre in the *Drusus* genus, but it is organised by two organising centres in the *Ecclisopteryx* genus.

Species group ranking. For species group ranking inside the *Drusus* genus we have discovered the importance of ancestral divergences in paramere structures. Our species grouping in the enlarged *Drusus* genus is based on the ancestral divergence in spine pattern of parameres. These divergences have followed an earlier split in prepattern which resulted in the duplication of organising centre in *Ecclisopteryx*.

In Trichoptera the paramere (titillator) is a true appendages, accompanying the aedeagus, primitively paired and inserted on the endotheca in a lateral inferior position and never present when aedeagus is lost. Paramere is derived from paired ectodermal outgrowts, from the primary phallic lobes which contain the terminal ampullae of the vasa deferentia. In higher insects the primary lobes are divided into a pair of secondary lobes (phallomeres). The mesal secondary lobes are the mesomeres and the lateral secondary lobes are the parameres. The aedeagus is formed by the fused mesomeres containing the gonopore of the ductus ejaculatorius, the joined common tube of the paired vasa deferentia. According to an alternative explanation the lateral secondary lobes or parameres might have produced the gonopods also in Trichoptera and the paramere of the phallic organ is developed from gonapophyses, that is from the median process of the coxopodite of the gonopod or from paraphyses.

The paired parameres in Drusinae subfamily have variously developed spine pattern on the slender paramere shaft of at least partially setal origin. In several species groups or complexes the vestigial alveolus of the modified setal structure are still discernible, but the overall setal origin of paramere spines still has to be confirmed. The tertiary spines are most probably noncellular processes of cuticular origin. The development of sensory setal structures is organised by a prepattern of field centres of mophogenes and substrate concentration (Maynard Smith & Sondhi 1961, Simpson & Marcellini 2006). Sensory setal structures of bristle typed macrochates are usually constant in number and distributed with stereotyped pattern for a species. Microchaetes are more numerous, but show no fixed number and only some regularity in spacing. We have found similar trend in the spatial pattern in the number and spacing of the primary, secondary and tertiary spines on the paramere shaft. It was really a great experience to realise first how stable and conservative are the basic spatial spine pattern permitting to establish natural lineages with species group ranking among the existing confused species groups in the *Drusus* genus. The first trial of species grouping was based exclusively on paraproct pattern (Schmid 1956).

Species complex ranking. The ancestral divergence in basal pattern of the *Drusus* parameres has been integrated after or separate of the ancestral split completed between *Drusus* and *Ecclisopteryx* genera. This ancestral divergences are very stable in every species groups. The species complexes of incipient siblings are detectable mostly by ancestral divergences in the architecture of basal shape formation of the entire paraproct. Apparent architectural shape formation of paraproct is realised by reduction, enlargement, pattern alteration or fusion of the dorsal and ventral branches, detectable both in lateral, dorsal and caudal profiles. Species complexes could be specific for particular paraproct profiles having the most pronounced divergences. Species complexes could be also specific for what are the most indicative paraproct profiles offering the most stable and reliable detection and demonstration.

Species ranking. Species ranking is based on the contemporary subtle divergences in the shape of the paraproct head. This roughened surface of peg-armed structure is most exposed and most intimately involved in the direct stimulatory contact with the female during the various processes of the cryptic female choice. Confirming this sexual communication we have detected that the rapid, subtle and stable divergences are usually localised on the very top of the dorsal branch of the paraproct.

Revised lineage structure in Drusinae subfamily. Based on our theoretical discourse and on detailed evaluation of the principles of generic ranking here we present our revised lineage structure of the Drusinae subfamily. First we have downgraded the following false generic character state to species character states: (1) the stochastic body modifications, the results of inadequate integrative power against internal and external random effect; (2) the varying spur numbers; the

secondary sexual characters: (3) the brachyptery; (4) the scales developed on forewing; (5) the pencil pouches present along the anal veins on the hindwings. Applying this basic ranking rule here we downgrade the generic status of the genera *Anomalopterygella*, *Chryptotrix*, *Hadimia*, *Leptodrusus*, *Metanoea* and *Monocentra* and synonymise them with the *Drusus* genus. We have placed them in appropriate species groups based upon the types of the ancestral paramere patterns they have. The species groups have been established by the basic ancestral pattern of paramere setal arrangement. In species group we have established species complexes based upon the types of paraproct architecture. The incipient species inside the species complexes was delineated and delimited mostly by subtle, but stable shape divergences on the head of the paraproct dorsal branches. Below we list the genera, species groups, species complexes and the species of the revised lineage structure in the Drusinae subfamily:

Genus *Drusus*

Drusus annulatus species group:

Drusus amanaus species complex: *amanaus, kumanskii, zhiltzovae.*
Drusus annulatus species complex: *annulatus, aprutiensis, berthelemyi, cantabricus, ingridae, marinettae, morettii, nigrorectus, rectus, thibaulti, vinconi.*
Drusus bolivari species complex: *bolivari, carmenae, estrellensis, gonzalezi, grafi, gredosensis, jesusi, pyrenensis.*
Drusus trifidus species complex: *brunneus, erimanthos, franzressli, rizeiensis, trifidus.*

Drusus caucasicus species group:

Drusus caucasicus species complex: *baksan, bayburti, botos, caucasicus, fuesunae, kazanciae, ketes.*
Drusus simplex species complex: *aranos, armeniacus, barajan, bolhos, hassankif, iranicus, nultas, polur, quruk, simplex, zanus.*

Drusus bosnicus species group:

Drusaus bosnicus species complex: *arbanios, bosnicus, crenophylax, dacothracus, gombos, illiricus, klapaleki, kovacsi, lepcos, medianus, ostot, paros, pelasgus, plicatus, radovanovici, ramae, septentrionis, vespertinus.*
Drusus discophorus species complex: *discophorus,*

juliae, kerek, komanus, krusniki, popovi, sharrensis, vernonensis.
Drusus graecus species complex:
Drusus graecus siblings: *graecus, lakmos.*
Drusus lepidopterus siblings: *apuanensis, dudor, lepidopterus, liguriensis, piemontensis, savoiensis, Drusus sp.*
Drusus improvisus species complex: *camerinus, improvisus, konok, cianficconiae, Drusus sp.*
Drusus muranyorum species complex: *goembensis, ilgazensis, kazdagensis, muchei, muranyorum.*

Drusus discolor species group:

Drusus chapmani species complex: *chapmani, letras.*
Drusus chrysotus species complex: *chrysotus, lapos, noricus, sarkos, slovenicus.*
Drusus discolor species complex: *discolor, ferdes, kupos, leker, visas.*
Drusus macedonicus species complex: *krpachi, macedonicus, malickyorum.*
Drusus muelleri species complex: *arkos, horgos, magas, muelleri.*
Drusus romanicus species complex: *ekes, meridionalis, pirinensis, romanicus.*
Drusus siveci species complex: *fortos, puskasi, siveci, vekon, fabbrii.*

Drusus monticola species group:

Drusus balcanicus species complex: *balcanicus, bureschi, concolor, dardanicus, discophoroides, osogovicus, pallidus, rhodopaeus, tovises, Drusus sp.*
Drusus destitutus species complex: *croaticus, destitutus, kronion, melanchaetes.*
Drusus monticola species complex: *monticola, neltel, nigrescens.*

Drusus mixtus species group:

Drusus flavipennis species complex: *apados, flavipennis, malickyi, rhaeticus, vercorsicus.*
Drusus mixtus species complex: *biguttatus, mixtus.*
Drusus spelaeus species complex: *buscatensis, spelaeus, valserinensis.*

Drusus tenellus species group: *botosaneanui, schmidi, tenellus, vargai.*

Drusus budtzi species group: *budtzi, maculosus.*

Drusus alpinus species group:

Drusus alpinus species complex: *alpinus, carpathicus, franzi.*
Drusus nebulicola species complex: *euphorion, nebulicola.*

Drusus chauviniana species group: *chauviniana.*

Drusus torosensis species group: *torosensis.*

Unplaced *Drusus* species: *anatolicus, demirsoyi, gueneri, hackeri, serbicus.*

Genus *Ecclisopteryx*

Ecclisopteryx asterix.
Ecclisopteryx dalecarlica species complex: *aksu, alkon, dalecarlica, ivkae, keroveci, loudai, oylat.*
Ecclisopteryx guttulata species complex: *guttulata, kunkor, legeza, tolda*
Ecclisopteryx madida.

Unplaced *Ecclisopteryx* species: *malickyi.*

TAXONOMY

Family Limnephilidae Kolenati, 1848

Subfamily Drusinae Banks, 1916

Drusinae Banks, 1916: 117: Type genus: *Drusus* Stephens, 1936.

Limnephilidae and Drusinae subfamilies are distinguished by presence (Limnephilinae) or absence (Drusinae) of spines on the last joint of hind tarsus or on the base of first tibia."

Genus *Drusus* Stephens, 1837

Drusus Stephens, 1837:231: in section *Anabolia.* Type species: *Anabolia testacea* Stephens *nec* Gmelin, syn. of *annulatus* Stephens (subsequent selection of Westwood, 1840:49).

Stathmophorus Kolenati, 1848:60:"Character essentialis: Tegminibus oblique rotundatis, cubito pilis molibus adpressis, areolis et arcis laevibus et pubescentibus, areola apicali prima ad fundum longiori et acutiori. Theca supra et infra surculis gravata. Tibiae: 1. 3.4." *S. destitulus* listed in the new genus as species 1. Ulmer, 1907b:64: synonymised with *Drusus* genus.

Peltostomis Kolenati, 1859:37: "Spornzahl beim ♂ 1.3.3., beim ♀ 0.3.3. Die stirne mit 2 Langsfurchen, zwischen welchen die gewölbte Stelle ein Schild hervorragt. Die Palpen des Mannchens 3-, des Weibchens 5gliederig. Bei Mannchen am Grunde der Hinterflügen zwischen costula gemina antica und postica eine lange Faltentsche, in welcher ein langer Haarpinsel liegt. Flügel an der Spitze parabolisch, die Nervatur wie bei *Ecclisopteryx* Kolenati." Type species *Peltostomis sudetica.*

Peltostomis Kolenati, 1859: McLachlan, 1876:179: "Spurs 0, 3, 3, ♂, 1, 3, 3, ♀. Otherwise as in *Drusus.* The few words given above sufficiently characterize this genus, which, in fact, is only an offshoot of *Drusus* in which ♂ has no spur on the anterior tibiae; the first joint of the anterior tarsi in the ♂ shews no perceptible modification (It is usually the case that when the anterior tibiae are spurless, the 1st joint of the tarsi is shortened). I am aquainted with two very different species. Their existence shows how necessary it is to exercise great caution in discriminating the spur-foprmula." Species listed and described: *P. sudetica* Kolenati, *P. graeca* n. sp. Ulmer, 1907b:64: synonymised with *Drusus* genus.

Potamorites McLachlan, 1867:54-55: "Palpi maxillares glabri, in ♂ 3-articulati, in ♀ 5-articulati. Ocelli adsunt. Alae anticae angustae, elongatae, ad apicem oblique truncatae; pipis brevibus sparse vestitae; cellula discoidali elongata. Alae posticae anticis breviores, latiores, glabrae. Tibiae tarsique spinosi. Calcaria in ♂♀ 1. 32. 2. Forma paulo robusta" Type species: *Potamorites biguttatus* Pictet.

Potamorites McLachlan, 1867: McLachlan, 1876: "Spurs 1,2,2, ♂♀. Otherwise much allied to *Drusus,* by the pouch and "pencil" in the posterior-wings of the ♂, but the anterior-wings are narrower and more elongate, and obliquely truncate at the apex (as in most species of Limnophilus); hairs in pouch of posterior-wings of ♂ strong and stiff. The anal parts of the ♂ are fashioned as in *Drusus,* but in a less pronounced manner. The habits are as in *Drusus.* A Limnophiliform satellite of *Drusus,* having no connection with Enoicyla, in which it was provisionally placed on account of the four posterior tibiae being bicalcarate." Schmid, 1956: 4: synonymised with *Drusus* genus.

Cryptothrix McLachlan, 1867:56-57: "Eine sehr bemerkenswerthe Gattung; Dieses Genus kömmt warscheinlich vor *Apatania* zu stehen."

Cryptothrix McLachlan, 1867: McLachlan, 1876: 181-182: "Allied to *Drusus,* but differing in several details. Anterior-wings clothed with short but very dense pubescence which almost conceals the neuration. Posterior-wings … in the ♂ have a very broad fold in the anal portion towards the base, the pouch broad, widely open, and extending to the margin, the "pencil" composed of very long erect silky hairs."

Cryptothrix McLachlan, 1867: Schmid, 1956:4: "est aussi légitime à cause de la forme des ailes et de sa nervulation très particulière." 73: "Dans la grande homogénéité de la sous-famille des Drusinae, *Cryptothrix* parait, à première vue, assez aberrant; en realité, il n'est caractéristique que par un petit nombre de caractères." 74: "*Cryptothrix* est une genre plus primitif que *Ecclisopteryx* et *Monocentra* et n'a pas subi de reduction du Xe segment. Il ne se différencie de *Drusus* que par sa nervulation dont il est difficile de dire si elle est plus primitive ou plus évoluée que celle des espèces de ce dernier genre."

Cryptothrix McLachlan, 1867: Pauls et al. 2008: 781: "topologies show a basal clade with *Cryptothrix nebulicola, Drusus muelleri, D. romanicus, D. chrysotus* and *D. discolor.* Within this clade, *C. nebulicola* is basal to a highly supported clade comprising members of the genus *Drusus.*" 785: "The current genetic concept is not supported in our analysis. The genera *Anomalopterygella, Cryptothrix, Ecclisopteryx* and *Metanoea* are nested in *Drusus.*"**New Synonym**!

Monocentra Rambur, 1872:489: "Les quatre tibias postéri-eurs n'ayant qu'un seul éperon vers le milieu de leur longueur. Ailes légérement couvertes de poils et d'écailles entremélés."

Monocentra Rambur, 1872: McLachlan, 1876:177-178: "Almost entirely similar to *Drusus*, but in the ♂ the anterior-wings and the greater part of the posterior (excepting only the anal portion) are clothed with short inflated hairs (simulating scales, mixed (in the anterior-wings) with ordinary pubescence; the pouch in the posterior wings is very deep and long, extending almost to the margin, and (I n lieu of the pencil of fine hairs) furnished on either side with decumbent long clavate "scales"."

Monocentra Rambur, 1872: Schmid, 1956:70: "Le genre *Monocentra* est un très proche parent de *Drusus*. Le principal caractère des *Monocentra* réside dans la présence d'écailles sur les ailes." " Le genre *Monocentra* est donc basé principalement sur un caractère sexuel secondaire." "Nous avons déja vu que *improvisa* McLachlan est un vrai *Drusus*." **New Synonym**!

Anomalopteryx Stein, 1874:251:"Alae anticae sine verrucis piliferis, maris subabruptae, apice cuspidatae, feminae spatulato-rotundatae; calcaribus maris = 0 − 2 -2, feminae = 1 − 2 − 2." Type species *Anomalopteryx chauviniana* Stein (monobasic). Under Chaetopterygini.

Anomalopterygella Fischer, 1966: 131. New name for *Anomalopteryx* Stein, 1874. Preoccupied by Reichenbach, 1853 in Aves. Type species: *chauviniana* Stein (replacement). **New Synonym**!

Catadice McLachlan, 1880:40: "Spurs 1,2,3, ♂ ♀. The ♂ without a pouch and pencil of hairs in the posterior-wings; the inferior appendages of the ♂ is very broad. Otherwise as in *Drusus*. Founded on a single species, the anal structure of which shows so much analogy with that of the curious *Anomalopteryx chauviniana* (p. 202) as to convince me that (as already hinted) *Anomalopteryx* is a genus of the group of *Drusus*." This new genus established as monotypic with type species *Catadice bolivari*. Mosely 1933: 498: synonymised with *Drusus* genus.

Stasiasmus McLachlan, 1880:42: "Spurs 0,2,3, ♂ (probably 1,2,3 ♀). Characters otherwiseas in *Drusus* (vide p. 162)." This new genus was erected for *Drusus rectus* McLachlan, 1868. Mosely, 1933: 498: synonymised with *Drusus* genus.

Metanoea McLachlan, 1880:40: Type species: *Metanoea flavipennis* (Pictet, 1834). "Characters as in *Drusus*, but the ♂ has no pouch and pencil of hairs in the posterior-wings. The position of the single species of this genus in *Halesus* is unnatural, and I have therefore decided upon removing therefrom. It is practically a *Drusus*, excepting in the absence of the pouch and pencil in the posterior-wings of the ♂." *Metanoea chapmani* Morton, 1914:49-51: "Three males and one female, Lauteret, Alps of Dauphiné (Chapman, July 22nd, August 5th). Also occurs in Val Bedretto (Ris, September 6th, 1896; July 20th, 1906): Splügen (Ris, July 16th 1897), uncertain whether from the Swiss or the Italian side, probably the latter; Madonna di San Martino (July 29th and August 1st, 1889, Nageli in Ris coll.)." "Differs from *H. flavipennis*, especially in the direction of the blackened processes of the last dorsal segment."

Metanoea flavipennis (Pictet, 1834): Schmid, 1956:67-69: "R. McLachlan a confondu sous le nom de *flavipennis*: la vraie *flavipennis* de Pictet et une autre espèce. Malheureusement, il a figuré et décrit cette dernière. La vraie *flavipennis* a été ultérieurement redécrite par K. J. Morton sous le nom de *chapmani*. Aujourd'hui, il convient donc de mettre les choses au point: *chapmani* Morton entre en synonymie de flavipennis Pictet et je donne à la *flavipennis* de R. McLachlan (nec Pictet) le nouveau nom de rhaetica. Je n'ai pas vu les types de Pictet, ni chassé dans la localité typique, mais l'absence en Suisse romande de la flavipennis de R. McLachlan suffit à trancher la question." **New synonym**!

Leptodrusus Schmid, 1956:81-82: "En décrivant *Potamorites budtzi*, G. Ulmer, qui avait conscience de ce qu'a d'artificiel un classement générique basé sur les formules calcariennes, déclara que cette espèce n'était pas un "echte *Potamorites*" et préconisa, pour elle, la création d'un genre distinct. Aujourd'hui, j'établis donc le genre *Leptodrusus*, dont les caractéristiques sont les suivantes." *Diagnosis.* "Il n'y a pas de repli, mais les cellules thyridiale et troisième anale portent une rangée de fortes soies." "Après *Anomalopteryx*, est le genre le plus aberrant de la sousfamille. Par son armature genitale, la forme des ailes et la nervulation, il est très caracteristique. Par la longueur des antennes, des palpes et des pattes, il se rapproche d'*Anomalopteryx*, mais il s'agit probablement d'une évolution parallèle. La ♀ est malheureusement inconnue et il serait très intéressant de voir s'il existe un dimorphisme sexuel comme chez ce dernier genre." **New synonym**!

Hadimina Sipahiler, 2002:239: "Type species: *Hadimina torosensis* sp. nov. "Maxillary palps of males three segmented, of females four segmented. Apical segments of the antennae are crenate. In the male genitalia, tergite 8 has bifurcated lobes on the posterior margin, developing dorsally and ventrally. Preanal appendages are sclerotized and located caudally; the aedeagus is short and curved, lacking the parameres." **New Synonym**!

Species grouping in the Drusus genus. Based upon the principles discussed above we have established eleven species groups in the *Drusus* genus. The genus was enlarged by synonymising the five old historical genera established by secondary sexual characters. As discussed above our species grouping was based excusively on ancestral divergences in the paramere setal pattern (Fig. 2). Ancestral divergence of paramere setal pattern followed the older split of the paramere pattern of the *Ecclisopteryx* genus. The *Drusus*

Figure 2. Lateral profile of the spine pattern on left parameres indicating the ancestral divergences giving rise to genera of *Drusus* and *Ecclisopteryx* and to species groups in Drusinae subfamily. The ancestral paramere divergence is one of the basic genus ranking character between the *Drusus* genus with a single spine pattern organising centre and the *Ecclisopteryx* genus with two spine pattern organising centres as well as the only species group ranking character in the *Drusus* genus. *Drusus* species groups: (1) *annulatus*, (2) *caucasicus*, (3) *bosnicus*, (4) *discolor*, (5) *monticola*, (6) *mixtus*, (7) *tenellus*, (8) *budtzi* with *Drusus maculosus*, (9) *alpinus*, (10) *chauviniana*, (11) *torosensis*, missing in the drawings because paramere is lost. *Ecclisopterys* paramere with two spine pattern organising centres.

genus retained the single organising centre of setal pattern opposed to *Ecclisopteryx* genus, that was diverged by duplicating the ancestral setal organising centre, probably by gene duplication. Here we enlist the eleven species groups of the *Drusus* genus by their most prominent characters of the setal pattern on the parameres integrated by a single organising centre. (1) *Drusus annulatus* species group is integrated through ancesteral divergence by recumbent primary and secondary paramere spines. (2) *Drusus caucasicus* species group is integrated through ancestral divergence by recumbent primary spine and secondary spines reduced in size and by inflated apical paramere shaft. (3) *Drusus bosnicus* species group is integrated through ancestral divergence by a single robust erected primary paramere spine accompanied by secondary or tertiary spines anterad. (4) *Drusus discolor* species group is integrated through ancestral divergence by the reduction of setal pattern to a single subapical spine without

any secondary or tertiary spines. (5) *Drusus monticola* species group is integrated through ancestral divergence by multidivision of the single subapical spine into spines of a single bunch composed of various number of smaller spines. (6) *Drusus mixtus* species group is integrated through ancestral divergence by subapical spine bunch having at least one larger primary upward arching spine and a stout abbreviated apical shaft. (7) *Drusus tenellus* species group is integrated through ancestral divergence by firm basal fusion of the paramere pair with spine pattern similar to the *D. mixtus* species group. (8) *Drusus budtzi* species group is integrated through ancestral divergence by shifting all the spines to the very top of the paramere and as a consequence the lost of the apical shaft of the paramere that is preserved and present in all the other species groups. (9) *Drusus alpinus* species group is integrated through ancestral divergence by the complete loss of all the spines, but preserved the entire paramere

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shaft without any spines. (10) *Drusus chauviniana* species group is integrated through ancestral divergence by the miniaturization of the entire paramere. (11) *Drusus torosensis* species group is integrated through ancestral divergence by the complete loss of the parameres.

Lineage ancestry of the Drusus species groups. The lineage history of the *Drusus* species groups needs further study. To designate ancestry ranking among the *Drusus* species groups we have followed the Williston's law (1914), according to which all structures tend toward reduction, as was also demonstrated by Gregory (1935), suggested by Schmid (1979) and applied for *Potamophylax nigricornis* species group (Oláh *et al*. 2013b) and for the *Allogamus* genus (Oláh *et al*. 2014). We have found at *Potamophylax* and *Allogamus* genera that the most complex paramere was present at the putative ancestral species having as well the largest distributional area, surrounded by small area of sibling species of less complex paramere that diverged in peripatry or parapatry with simplification.

In the *Drusus* genus we have designated the paramere pattern of the *Drusus annulatus* species group as the most complex, the less specialized ancestral structure. This species group, together with the similar *Drusus caucasicus* sibling species group has the largest distributional area inhabiting the entire distributional range of the subfamily from Spain to Iran. All the other species group have more limited distribution.

Drusus annulatus species group

This species group is integrated through ancestral divergence by the recumbent primary and secondary paramere spines. Based upon the complexity principles discussed in details in the theoretical discourse as well as upon the large distributional area, this species group together with the closely related *Drusus caucasicus* species group having the most complex paramere pattern is the most ancestral lineage in the *Drusus* genus. Comprised of four species complexes with 27 species. The delineation of all the species complexes in the species group is based on divergenses in the paraproct architecture.

(1) *Drusus amanaus* species complex has dorsal branch of the paraproct with straight apical arms of slightly diverging shapes in lateral view, widely bifid in caudal view;
(2) *Drusus annulatus* species complex has dorsal branch of paraproct with blunt apical arms in lateral view, mesally fused broad plates in caudal view;
(3) *Drusus bolivari* species complex has dorsal branch of the paraproct with straight apical arms of variously shaped heading in lateral view, mesally completely fused digitiform shape in caudal view;
(4) *Drusus trifidus* species complex has dorsal branch of the paraproct with hook-shaped or anterad angled apical arms in lateral view, variously dorsad or laterad directed in caudal view.

Drusus amanaus species complex

This species complex has dorsal branch of the paraproct with straight apical arms of subtle diverging shapes in lateral view, widely bifid in caudal view. Yellowish, middle sized species known as distributed in allopatry in the Western Caucasus. Three sibling species belong to this complex: *D. amanaus*, *D. kumanskii* sp. nov., D. *zhiltzovae*.

Drusus amanaus Mey & Müller, 1979

(Figures 3−9, 23−28)

Drusus amanaus Mey & Müller, 1979:176−177: „Holotypus ♂ und Allotypus ♀: 11. X. 1978, Amanaus-Schlucht südlich von Dombai (Westkaukasus), leg Mey et Müller. Die typen werden im Museum der Natur, Gotha, aufbewahrt. 3 Paratypen von gleichen Fundort in coll. Mey."

Material examined. Holotype and allotype from Museum der Natur, Gotha, Germany. 2 paratypes from Amanaus-Schlucht südlich von Dombai (Westkaukasus) from the collection of Mey, deposited in the Museum für Naturkunde der Humboldt Universitat zu Berlin, Germany.

Figures 3–9. *Drusus amanaus* Mey & Müller, 1979. Holotype: 3 = male genitalia in left lateral view, 4 = paraproct in caudal view, 5 = apex of the apical arms of the dorsal branches of paraproct in dorsal view, 6 = parameres in left lateral view. Allotype: 7 = female genitalia with vaginal sclerite complex in left lateral view, 8 = tergite IX and vaginalsclerite profile in dorsal view, 9 = vulvar scale in ventral view.

Diagnosis. Mey & Müller, 1979:176–177, „*D. amanaus* n. sp. ist mit *D. simplex* Martynov verwandt."

Additional diagnosis. In the paramere spine pattern the secondary spines located anterad to the recumbent primary spine, they are less developed and reduced both in size and in number to 1–2 on the examined holotype and paratypes; apical shaft of the paramere 4 times longer than the lenght of the primary spine. The most easily visible and stable shape divergence, distinguishing this species from its sibling *D. zhiltzovae*, is the head shape of the apical arms of the dorsal branch in perpendicular view. Perpendicular to the largest surface of the arms; arms themselves are located oblique lateromesad plane, therefore the largest surface is visible from a view between lateral and caudal view. The perpendicular shape of the arm head is parallel-sided, truncate therefore quadrangular.

Drusus kumanskii **Oláh sp. nov.**

(Figures 10–16, 29)

Material examined. Holotype: Caucasus Teberda or Baksan river system, code 374 (male, OPC). Allotype: same

as holotype (female, OPC). Kumanski (1980) has examined several specimens of *Drusus amanaus* from 16 isolated populations sampled in the Teberda and Baksan rives valleys of the western Caucasus. Among the 105 specimens of *D. amanaus* he has found a male and female specimen deviating from all the examined *D. amanaus*. This pair was labeled as *Drusus* sp. ? with a code of 374K. Unfortunately Kumanski's code list with explanation has been lost. We are unable to find the collection details of these specimens. However applying the fine structure analysis we have found this interesting couple worth to describe as a new sibling species in the *D. amanaus* species complex.

Diagnosis and description. In the paramere spine pattern the 3 secondary spines located anterad to the recumbent primary spine are more developed compared to its sibling *D. amanaus* and even to *D. zhiltzovae*; apical shaft of the paramere robust dilated and 2 times longer than the lenght of the primary spine. The most easily visible and stable shape divergence, distinguishing this species from its sibling *D. amanaus* and *D. zhiltzovae*, is the head shape of the arms of the dorsal branch in perpendicular view. The perpendicular shape of the arm head is broad based with quadrangual apical half at the holotype, not parallel-sided, and not triangular. Beside this perpendicular view there are also stable diver-
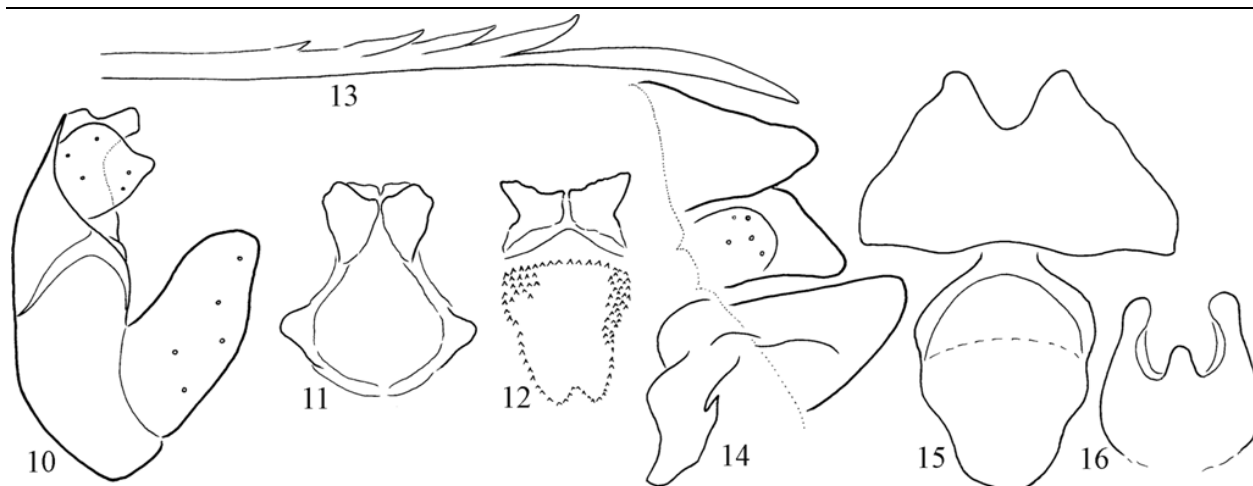
Figures 10–16. *Drusus kumanskii* Oláh sp. nov. Holotype: 10 = male genitalia in left lateral view, 11 = paraproct in caudal view, 12 = apex of the apical arms of the dorsal branches of paraproct with the pegged spinulose area on tergite VIII in dorsal view, 13 = paramere in left lateral view. Allotype: 14 = female genitalia with vaginal sclerite complex in left lateral view 15 = tergite IX and vaginal sclerite profile in dorsal view, 16 = vulvar scale in ventral view.

gences distinguishing this new species from its siblings in the paraproct head shape also in the dorsal, lateral and caudal view, but again highly observer dependent to reproduce the exact viewing and drawing angles.

Female genitalia. Tergite of segment IX forming short tube, open ventrally, with V-shaped mesal excision; lateral lobes triangular in dorsal view; the lateral setose lobe of sternite IX rounded. Segment X membranous and embedded inside segment IX and encircling anus; supragenital plate of segment X well-developed and quadrangular in lateral view with downward elongated angle. Median lobe of the vulvar scale (lower vaginal lip) present and short triangular. Dorsal profile of the vaginal sclerite complex narrowing anterad.

Etymology. We dedicate this new species to our colleague Krassimir Kumanski who has made great contributions to the knowledge of Trichoptera of the Balkan, Cuba, Korea and New Guinea.

Drusus zhiltzovae Oláh & Malicky, 1979 stat. restit.

(Figures 17–22, 30–37)

Drusus zhiltzovae Oláh & Malicky, 1979 in Malicky & Oláh, 1979:829–831. Holotype and paratypes: Caucasus,

Georgia, Svanetia, stream below Zagarski Pass, 5. VIII. 1957, leg. L. A. Zhiltzova (7 males, 3 females). Paratypes: Caucasus, Georgia, Svanetia, spring of Inguri stream, 3. VIII. 1957, leg. L. A. Zhiltzova (3 males, 1 female). Caucasus, Abhazia, stream on the road to Ancho Pass, 1800 m, 26. VIII. 1958, leg. L. A. Zhiltzova (3 males). Kavkazski zapovednik, r. Beloe, 6. VII. 1936 leg. Teplova (4 males). Kavkazski zapovednik, r. Beloe, 3. VII. 1936 leg. Teplova (1 male).

Drusus zhiltzovae Oláh & Malicky, 1979 in Malicky & Oláh, 1979, Malicky 2005a, 567: synonym of *Drusus amanaus* Mey & Müller, 1979. Based upon the additional diagnosis here we reinstate its species status, **stat. restit**.

Material examined. Holotype: Caucasus, **Georgia**, Svanetia, stream below Zagarski Pass, 5. VIII. 1957, leg L. A. Zhiltzova (1 male, ZIN). Allotype: same as holotype (1 female,ZIN). Caucasus, **Abhazia**, stream on the road to Ancho Pass, 1800 m, 26. VIII. 1958, leg. L. A. Zhiltzova (12 males, OPC).

Diagnosis. Malicky & Oláh 1979:833, "The species is well characterized by the shape of most pieces of the copulatory armature of males and females, but closer relationships to any particular other species are not evident. It is relatively close to many other species from Central Europe and from the Balkan Peninsula."

Additional diagnosis. In the paramere spine pattern the secondary spines located anterad to the recumbent primary spine are more developed compared to its sibling *D. amanaus*; apical shaft
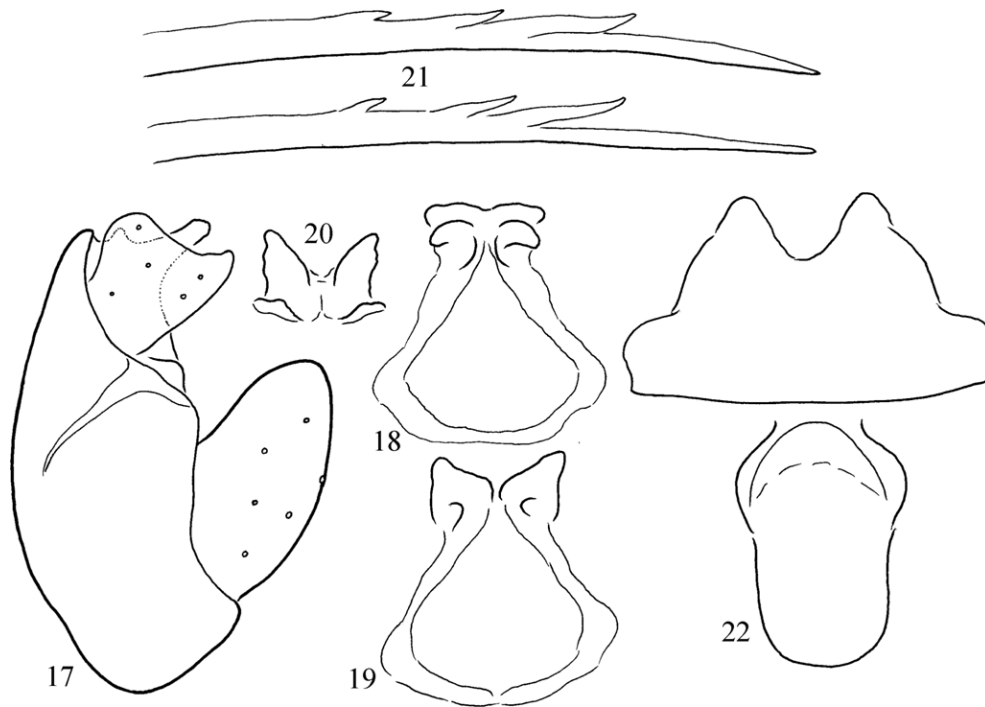
Figures 17–22. *Drusus zhiltzovae* Oláh & Malicky, 1979.Holotype: 17 = male genitalia in left lateral view, 18 = paraproct in slightly dorsocaudal view, 19 = paraproct in caudal view, 20 = apex of the apical arms of the dorsal branches of paraproct in dorsal view, 21 = paramere in left lateral view. Allotype: 22 = tergite IX and vaginal sclerite profile in dorsal view.
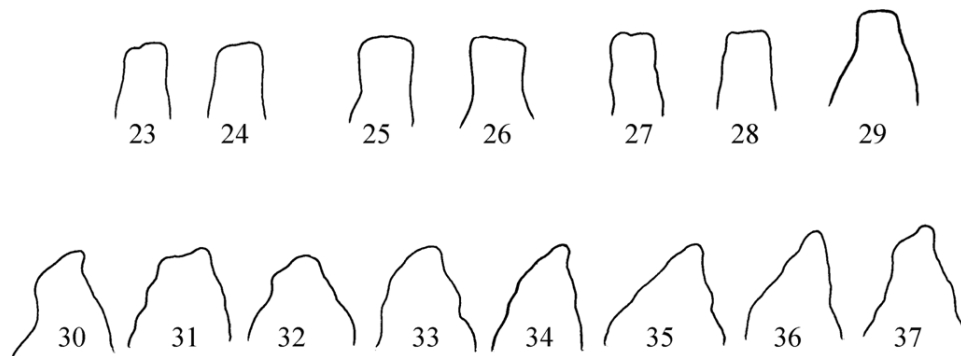
Figures 23–37. Apical arms of the dorsal branches of paraproct in lateral perpendicular view at higher magnification.
23–28 = *Drusus amanaus*Mey & Müller, 1979, 29 = *Drusus kumanskii* Oláh sp. nov.,
30–37 = *Drusus zhiltzovae* Oláh & Malicky, 1979.

of the paramere only 2 times longer than the lenght of the primary spine. The most easily visible and stable shape divergence, distinguishing this species from its sibling *D. amanaus*, is the head shape of the apical arms of the dorsal branch in perpendicular view. The perpendicular shape of the arm head is clearly triangular at all of the examined 12 specimens, not parallel-sided and truncate therefore quadrangular. Beside this perpendicular view there are also stable divergences between *D. amanaus* and *D. zhiltzovae* in the paraproct head shape also in the dorsal, lateral and caudal view, but highly observer dependent to reproduce the exact viewing and drawing angles. The synonymy of this species was suggested (Malicky 2005) without the examination of the

type specimens of *D. amanaus* and without any trait comparisions and evaluations. Based on the stable shape divergence in the head shape of the paraproct here we restitute the species status of *Drusus zhiltzovae*.

Drusus annulatus species complex

Drusus annulatus species complex has dorsal branch of paraproct with blunt apical arms in lateral view, mesally fused broad plates in caudal view. This species complex is comprised of 11 species: *annulatus*, *aprutiensis*, *berthelemyi*, *ingridae*, *marinettae*, *muranyorum*, *morettii*, *nigrorectus*, *rectus*, *thibaulti*, *vinconi*.

Drusus annulatus Stephens, 1837

(Figures 38–43)

Anabolia annulata Stephens, 1837:231, "Rare: found in June in Devonshire."

Anabolia testacea Stephens, *nec* Gmelin 1837:231, "Not very common: taken in July and August at Hertford; also in the New Forest and in Devonshire."

Anabolia flavipennis Stephens, *nec* Pictet 1837:231, "Apparently rare: taken, in June, in Devonshire."

Drusus annulatus (Stephens, 1837): McLachlan 1876:166–167, "England and Scotland; locally not uncommon about clear torrents in rocky and mountainous districts in summer and early autumn. But the ♀ appears to be rarely captured."

Drusus annulatus (Stephens, 1837): Schmid 1956:59, "Cette espèce est un des rares *Drusus* qui ait une large répartition en Europe; elle habite la plaine, mais, dans les Alpes suisses, s'élève jusqu'à 1.000 m environ."

Peltostomis sudetica Kolenati, 1859, Schmid 1956:6, synonymised with *Drusus annulatus* Stephens.

Material examined. **Czech Republic**, E Moravia, Bílé Karpaty Mts, Velicka river, (700 m), 28. VI. 2005, leg. P. Chvojka (4 males, 2 females; OPC). Central Bohemia, Vuznice stream NW of Nizbor (310-365 m), IX.-X.. 2006, leg. P. Chvojka (6 males, 3 females; OPC). W.Bohemia, Krusné hory Mts, Hluboky potok brook W of Dolni Nivy, (540 m), 31. VIII. 2015, at light leg. J. Sumpich (6 males, 3 females; OPC). N.Bohemia, Jizerské hory Mts, Malá klecová louka peatbog, 4. VIII. 2004, at light leg. F. Krampl (6 males, 6 females; OPC). **France**, Department Puy-de-Dôme, Massiv-central Mts., Chambon sur Lac, Ru Derrière la Dent de la Rancune ru Granit, 23. VI. 2012, leg G. Copa (1 male, 2 females; OPC). Department Cantal, Brezons, sur le Brezons Saut de la Truite, 27.VI.2010, leg G. Coppa (2 females, OPC). **Hungary**, Börzsöny Mts. Diósjenő, Kemence stream, 700m, 14.vi.2005 leg. D. Murányi (3 males, 1 female,

NHMB). **Poland**, Gorce Mts. Kamiernica stream, 26. VI. 1985, single leg. J. Oláh (1 male, 1 female; OPC). High Tatr, Chocholowska Valley,22. VIII. 1986, leg. J. Oláh (1 male, OPC). **Romania**, Valéea Cupas, Lacu Rosu, 19. VI. 1981, ,light leg. L. Peregovits & L. Ronkay (1 male, OPC). **Slovakia**. N Slovakia, Chocské vrchy Mts. spring, brook NE of Valaská Dubova, 4. VII. 1992, leg. P. Chvojka (4 males, 2 females; OPC).

Diagnosis. Stephens, 1837:231, "Reddish-ochre: eyes black; thorax rather dusky; wings very transparent, pale immaculate, yellowish-ochre, the nervures distinct and somewhat darker."

Schmid, 1956:59, "*Dr. annulatus* est très voisine de *rectus*, mais présente une coloration orange beaucoup plus claire."

Additional diagnosis. In the paramere spine pattern the recumbent primary spine is associated by a smaller joint spine and accompanied anterad by various number of 5–7 small secondary spines. We have found no significant spine pattern divergences in the examined populations from the Czech Republic, France, Hungary, Poland, Romania and Slovakia.

Drusus aprutiensis (Moretti, 1981)

(Figures 44–48)

Drusus aprutiensis Moretti, 1981: 180, "Holotype ♂, allotype ♀: Abruzzi, P. N. A., Jannanghera, 1200 m, L'Aquila, 25. VI. 1954, leg. Consiglio. Paratypes ♂♂ ♀♀ collected between 1955 and 1979, Abruzzi (several springs) 364♂ 83♀, Lazio 12♂ 43♀ + 3♂ 3♀ sent to us by Botosaneanu. In Morett's collection. Abruzzi 1♂ 1♀ in Malicky's collection."

Material examined. **Italy**: Abruzzi, Appenino Abruzzese, Mts Gran Sasso d'Italia, Pagánica, Vera springs, 3.VIII. 2005, leg. D. Murányi (1 male, HNHM). Italy, Aquila, Pacentro, Fonte Romana, 42.06N 14.03E, 1300 m, 6. IX. 1970, leg. Francescantonio (1 male, 1 female; OPC).

Diagnosis. Moretti, 1981: 180, "The central 9th segment lobe is long and arched ventrally like that of *D. monticola*. The lateral lobe of the vulvar squama are large and curve towards the shorter nedian lobe. *D. aprutiensis* is, therefore, similar to the *D.monticola* ♀ as Botosaneanu rightly supposed."

Additional diagnosis. Based upon the female genital structure Moretti has related this species to
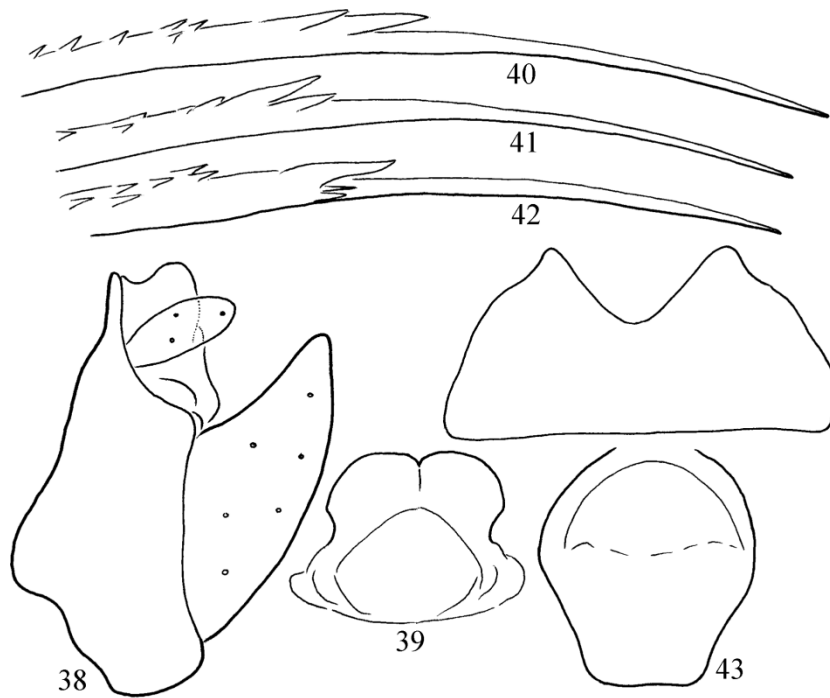
Figures 38–43. *Drusus annulatus* Stephens, 1837. 38 = male genitalia in left lateral view, 39 = paraproct in caudal view 40 = paramere in left lateral view, Hungarian population, 41 = paramere in left lateral view, Romanian population, 42 = paramere in left lateral view, Slovakian population, 43 = tergite IX and vaginal sclerite profile in dorsal view.
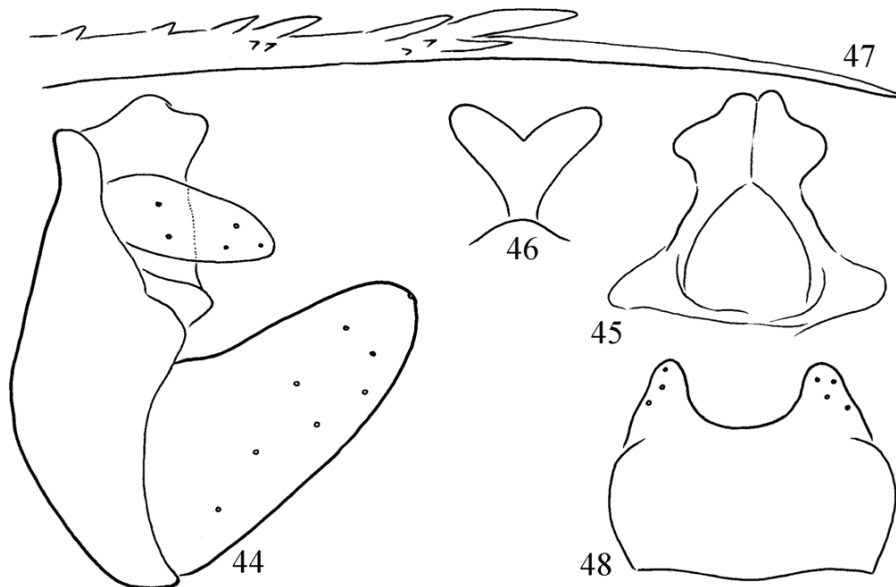
Figures 44–48. *Drusus aprutiensis* (Moretti, 1981). 44 = male genitalia in left lateral view, 45 = paraproct in caudal view, 46 = apex of the apical arms of the dorsal branches of paraproct in dorsal view, 47 = paramere in left lateral view, 48 = tergite IX in dorsal view.

D. monticola. However, *D. monticola* belongs to another completely differently diverged species group. *D. aprutiensis* female has segment IX in dorsal view a very pronounced, deep and rounded mesal excision surrounded by well developed lateral lobes. *D. monticola* female is without this deep mesal lobe and without the robust lateral lobes. Moreover,*D. aprutiensis* male of the *D. annulatus* species group has a typical ancesteral paramere divergence by the recumbent primary and secondary paramere spines. *D. monticola* is the nominate species of the *D. monticola* species group with highly differentiated paramere spine pattern integrated through ancestral divergence by the multidivision of the single subapical spines into spine bunch composed of various number of smaller spines.

Drusus berthelemyi Sipahiler, 1992

(Figures 49–52)

Drusus berthelemyi Sipahiler, 1992:287–288, "Types. Holotype ♂, allotype ♀ and paratypes (3♂): **Spain**, Sierra de la Demanda (entre Logrono et Burgos), affluent du rio Oja, a la station de ski Valdezcaray, 1800–2000 m, 4.VIII. 1987, same place and date: 1500 m, 2♂, 1♀; 900–1000 m, 1♂, 1♀; same place, Trigaza, 1800 m, 3. VIII. 1988, 1♂; leg. Vincon.

Material examined. Holotype and allotype: R-196, **Spain**, Sierra de la Demanda (entre Logrono et Burgos), affluent du rio Oja, a la station de ski Valdezcaray, 1800–2000 m, 3.VIII. 1987, leg. Vincon (1 male, 1 female; ZSM). The allotype is overcleared, completely depigmented, almost invisible. The dorsal profile of the vaginal sclerite complex is very feable, just discernible.

Diagnosis. Sipahiler, 1992:288, "*Drusus berthelemyi*, spec. nov., is closely related to *D. rectus rectus* McLachlan (Schmid 1956) and *D. rectus thibaulti* Decamps (Decamps 1972) from the Pyrenées and well distinguished from the related subspecies by the shape of the superior appendages, which are long, thin, and pointed at tips. In *D. rectus rectus* they are short, broad, and rounded at apex. In *D. rectus thibaulti* they are somewhat longer and thinner that in *D. rectus rectus*. The female genitalia of these subspecies are similar and there are no visible differences between them (Decamps 1972). *D. berthelemyi*

has remarkable differences in the females genitalia; the tubular pieces are longer and thinner than those of *D. rectus rectus*, the hairy area of the lateral pieces of segment 9 is large, whilst they are thin in *D. rectus rectus*. *D. berthelemyi* has a long median piece of vulvar scales which is only half the size of the lateral scales in *D. rectus rectus*. *D. berthelemyi* is also smaller than the related species."

Additional diagnosis. Compared to *D. rectus* and *D. nigrorectus* stat. restit. The species of *D. berthelemyi* has the ancesteral paramere divergence by the recumbent primary and secondary paramere spines differently formed having less secondary spines. Moreover the mesal excision on the female segment IX is deeper and rounded, not V-shaped.

Drusus cantabricus Schmid, 1956

(Figures 53–54)

Drusus cantabricus Schmid, 1956: 55–57, „Holotype ♂: Pena Rubia, Province de Lugo, Espagne, 22. VIII. 1950, (E. Morales-Agicino), déposé dans ma collection."

Material examined. Holotype male. After a long search at museums ,where the author, Fernand Schmid was working (Cantonal Museum of Zoology Laussane, Museum of Natural History Geneva, Canadian National Collection (CNC) of Insects, Arachnids and Nematodes, Ottawa) and following the advice by Prof. Marcos Ganzalez and Prof. Hans Malicky we have found the type in the Wiggins Collection curated at the Royal Ontario Museum, Toronto.

Diagnosis. Schmid, 1956:57, „Cette espèce ne présente aucun caractère qui soit très frappant; par la forme de ses appendices supérieurs, elle se rapproche du groupe de *monticola*, mais c'est la un caractère artificiel. La forme de ses appendices intermédiaires l'apparente apparemment à *discophorus*. A cause de la disposition et la fusion patielle de ces derniers, je place l'espèce aux cotés du groupe de *annulatus*, ce qui me parait être le plus raisonable."

Additional diagnosis. Based on cerci Schmid has related *D. cantabricus* to *D. monticola* species group, based on paraproct shape to *D. discophorus*, a species of *D. bosnicus* species group. Finally based on the disposition and the fused
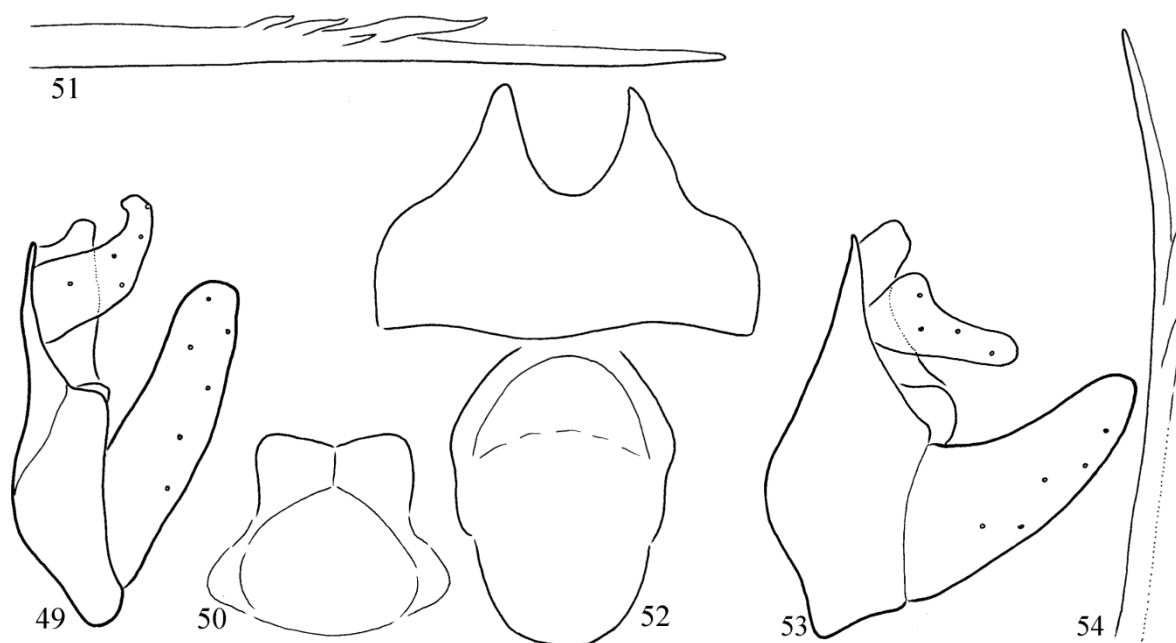
Figures 49–52. *Drusus berthelemyi* Sipahiler, 1992. Holotype. 49 = male genitalia in left lateral view, 50 = paraproct in caudal view, 51 = paramere in left lateral view. Allotype: 52 =t ergite IX and vaginal sclerite profile in dorsal view.

Figures 53–54. *Drusus cantabricus* Schmid, 1956. Holotype. 53 = male genitalia in left lateral view, 54 = paramere in left lateral view.

state of the paraproct Schmid has related *D. cantabricus* to the *D. annulatus* species group. After repeated trials there was no new material collected near to *locus typicus* for a more detailed study. The genitalia of the single holotype is embedded in permanent preparate. It was impossible to examine the caudal view of the paraproct, but the paramere pattern was partially visible with two spines of similar disposition to the parameres of the *D. annulatus* species group.

Drusus ingridae Sipahiler, 1993

(Figures 55–58)

Drusus ingridae Sipahiler, 1993:67–68, "Holotype male and 6 paratype males: France, sud du Massif Central, Aude, Montagne Noire, ruisseau affluent de l'Argent Double, 800 m, 14. X. 1989; – Montagne Noire, Citau, 11. XI. 1989 (1 male); leg. Vincon, coll. Zoologische Staatssammlung München."

Material examined. Holotype male: **France**, sud du Massif Central, Aude, Montagne Noire, ruisseau affluent de l'Argent Double, 800 m, 14. X. 1989, leg. Vincon, coll. Zoologische Staatssammlung München. New materials:

France, Department Hérault, Rosis, Amont Perpignan de la Grave Rouselle, 25. IV. 2007 leg G. Coppa (4 males, OPC). France, Department Aveyron, Cornus, Source de la Sorgue, 20. VII. 2013 leg G. Coppa (4 males, 2 females; OPC). France, Department Aveyron, Aurelle Verlac, Ruisseau du Saltou Piste, 25. V. 2011 leg G. Coppa (3 males, 2 females; OPC). France, Department Tarn, Lacaune, ru l'Abeouradou les Vidales, 20. VI. 2014 leg G. Coppa (4 males, 2 females; OPC). France, Department Pyrénées-Orientales, Font Romeu Odeilla Via, ru d'Eynes Pont D116, 24. VIII. 2011 leg G. Coppa (2 males, OPC). France, 42º57'52.01"N 0º51'50.01"E, 1278 m, 25. VII. 2012 leg. W. Graf (1 male, OPC).

Diagnosis. Sipahiler 1993: 67–68, "*Drusus ingridae* sp. nov. is closely related to *D. rectus* McLachlan, 1969 (Schmid 1956) and distinguished by the following features; In *D. rectus* the spinulose zone of tergite 9 is long and quadrangular in shape; the preanal appendages with dorsal lobe on the dorsal margin. In *D. ingridae* sp. nov. the spinulose zone is short, very large and possesses lateral dilatations; the preanal appendages are rounded. In *D. rectus* the inferior appendages are gradually directed to the sides from the base; in *D. ingridae* sp. nov. they are distinctly directed to the sides on the subdistal parts."

Additional diagnosis. The paramere spine pattern with less secondary spines and the apical shaft of the paramere is longer as compared to the *D. rectus*.

Drusus marinettae Sipahiler, 1992

(Figures 59–63)

Drusus marinettae Sipahiler, 1992: 288–289, „Types. Holotype ♂ allotype ♀ and paratype ♂: France, Pyrénées-Orientales, ruisseau d'Eyne, affluent de la Tet, 2200 m, 28. VII. 1987; same place, 2435 m, 1♂, 1♀; other paratypes: ruisseau du Cady, affluent de la Tet (massif du Canigou) 2200 m, 8. VII. 1987, 6♂; Aude, ruisseau de l'Aiguette, affluent de l'Aude, 2000 m, 10. VII. 1987, leg. Vincon."

Material examined. Holotype ♂ allotype ♀: **France**, Pyrénées-Orientales, ruisseau d'Eyne, affluent de la Tet, 2200 m, 28. VII. 1987, leg. Vincon, coll. Zoologische Staatssammlung München.. *New materials*: France: Department of Pyrénées-Orientales**,** Angoustrine Villeneuve des-Escaldes, ru du lac Sobirans, Estang Sobirans, 19.VIII.2011, leg. G. Coppa (2 males, OPC).

Diagnosis. Sipahiler, 1992: 289, „This new species of *Drusus* is well characterized by the shape of male genitalia. The large quadrangular spinulose zone of tergite 8 and the cylindrical inferior appendages somewhat resemble *D. r. rectus* McLachlan (Schmid 1956), but the structure of the intermediate appendages which

are curved dorsally in *D. r. rectus* McLachlan and form slender preanal appendages, which have something like a lobe on the dorsal edge in the related species, distinguish both species. The female genitalia of *D. marinettae* resemble *D. discolor* Rambur (Malicky 1983); both species were collected in the same place in the Pyrenees where the paratypes of *D. marinettae* was collected. Although shape of the tubular piece is clearly similar, those of *D. discolor* Rambur are longer than those of *D. marinettae* and they are close to each other with their inner margins which are U-shaped at center. In *D. marinettae* the apical margin of segment 10 is dorsally rather smooth between the tubular piece. The median piece of the vulvar scale is as long as the lateral pieces and large in *D. discolor*, but in *D. marinettae* it reaches only half the size of the lateral pieces and is narrow."

Additional diagnosis. *D. marinettae* female has completely different segment IX in dorsal view than *D. discolor*. The mesal excision on segment IX is almopst rectangular in *D. marinettae* and triangular in *D. discolor*. The male paramere of *D. marinettae* is typical for the *D. annulatus* species group and the paramer of *D. discolor* is typical for the *D. discolor* species group. The paramere spine pattern of *D. marinettae* is more reduced than the paramere pattern of *D. rectus*.
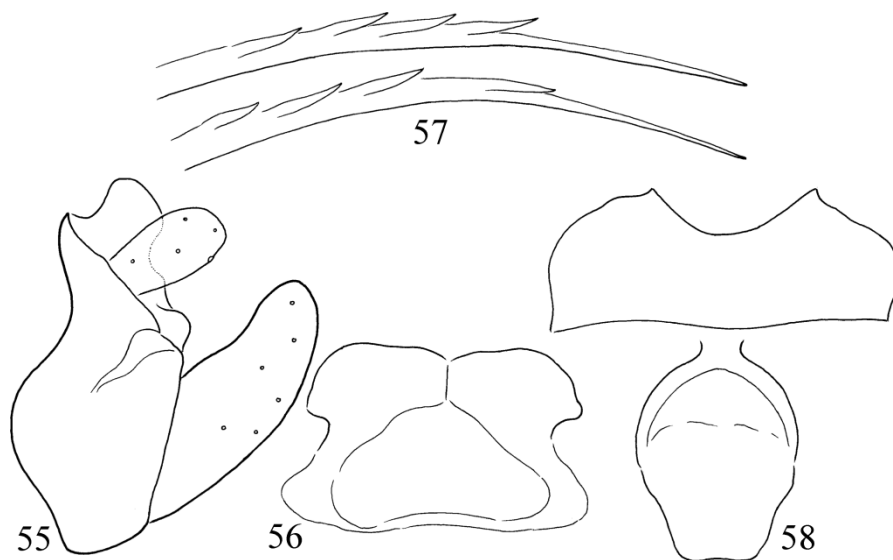
Figures 55–58. *Drusus ingridae* Sipahiler, 1993. Holotype. 55 = male genitalia in left lateral view, 56 = paraproct in caudal view, 57 = parameres in left lateral view. 58 = female tergite IX and vaginal sclerite profile in dorsal view.
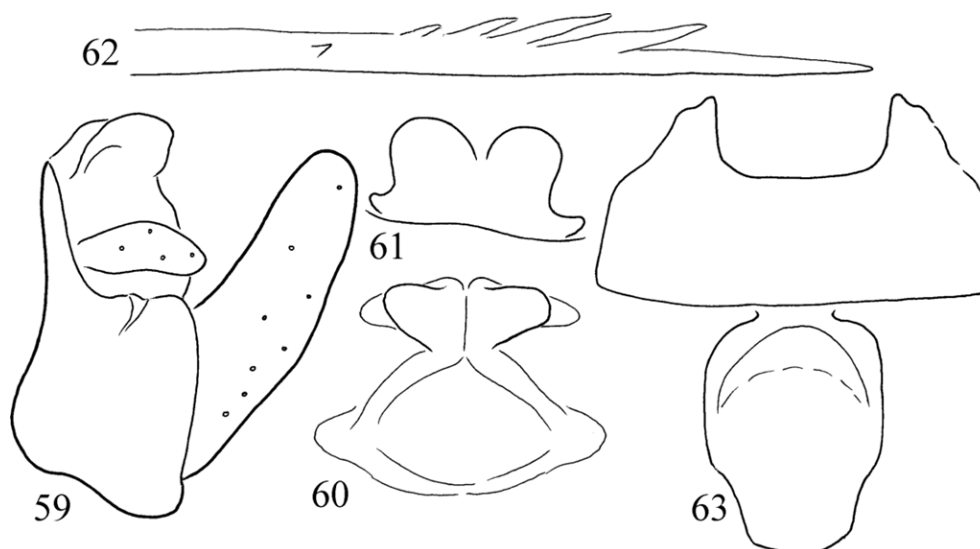
Figures 59–63. *Drusus marinettae* Sipahiler, 1992. Holotype. 59 = male genitalia in left lateral view, 60 = paraproct in caudal view, 61 = apex of the apical arms of the dorsal branches of paraproct in dorsal view, 62 = paramere in left lateral view, 63 = tergite IX and vaginal sclerite profile in dorsal view.

Drusus morettii Malicky, 2004

(Figures 64–70)

Drusus sp.n.? Moretti, 1988: 13, „Si tratta di un esemplare raccolto da Valle nell'agosto del 1978 nell'Ariege (Francia). Sconosciuto in Italia, risulterebbe appartenere ad una specie non ancora descritta, ma avendo a disposizione un solo esemplare si reputa opportuno rimandare l'istituzione della presunta specie nuova ad un esame approfondito, avvalendosi di ulteriori auspicabili rinvenimenti."

Drusus morettii Malicky, 2004: 40, „Der Holotypus ♂ aus den französischen Pyrenaen Moulis (Ariege), August 1978, leg Valle, befindet sich im Museo Civico di Scienze Naturali „E.Caffi", Bergamo."

Material examined. Holotype male on loan from Museo Civico di Scienze Naturali "E. Caffi", Bergamo, Italy: **France**, Pyrenéen, Moulis (Ariège), August 1978, leg. M. Valle (1 male, deposited in Museo Civico di Scienze Naturali "E. Caffi" Bergamo, Italy). *New material*: France, Aude Department, Escouloubre, Les Bains, 27. X. 1989, leg. G. Coppa (1 female, OPC).

Diagnosis. Malicky 2004: 40, „Diese Art hat Moretti (1988) schon beschrieben und abgebildet, aber nicht benannt. Ich gebe hier seine Abbildungen und Beschreibung wieder und benenne die Art zu seinem Gedenken."

Additional diagnosis. The species is represented only by the single holotype belongs to the *D. annulatus* species group based on ancesteral paramere divergence by the recumbent primary and secondary paramere spines and to the *D. annulatus* species comlex based on dorsal branch of paraproct with blunt apical arms in lateral view, and mesally fused broad plates in caudal view. Its very abbreviated gonopods is unique in the species complex.

Female description. The female is unknown. We have collected a single female not far from the locus typicus with some resemblence *D. vinconi*. Here we describe as the probable female of *D. morettii*. *Female genitalia*. Tergite of segment IX forming short tube, open ventrally, with rounded V-shaped mesal excision, rather shallow; very deep at *D. vinconi*; lateral lobes short triangular in dorsal view; the lateral setose lobe of sternite IX rounded. Segment X membranous and embedded inside segment IX and encircling anus; supragenital plate of segment X well-developed and quadrangular in lateral view. Median lobe of the vulvar scale (lower vaginal lip) present and sharp triangular, half as long as the lateral lobes. Dorsal profile of the vaginal sclerite complex low, narrowing anterad.

Drusus nigrorectus **Mosely, 1935 stat. restit.**

(Figures 71–74)

Drusus nigrorectus Mosely, 1935: 557–559, Described as an independent species, although first the author "determined the species with some hesitation as *Drusus (Stasiasmus) rectus* McL. a Pyrenean insect, but remarked that not only was the insect smaller and darker in colour than the Pyrenean form, but that the pouch in the posterior wing of the male was lacking the pencil of yellowish hairs which is a feature of this species"
Drusus rectus nigrorectus Mosely, 1935, Schmid 1956:61, Reduced to subspecies status.
Drusus rectus nigrorectus Mosely, 1935, Malicky 2005a: 568, Listed as synonym of *Drusus rectus* McLachlan.

Material examined. **France**, Massiv-Central, Department Puy-de-Dôme, Chastreix, ru de la Jarrige, 27.VI.2010, leg G. Coppa (6 males, OPC). France, Massiv-Central, Department Puy-de-Dôme, Chambon-sur-Lac, ru principal en aval du pont de Sainte-Anne, 21.VII.2012, leg G. Coppa (3 females, OPC). France, Massiv-Central, Department Puy-de-Dôme, Chastreix, Ru Fontaine Salèe vers le Milieu, 2.VII.2015, leg G. Coppa (11 males, OPC). France, Massiv-Central, Department Puy-de-Dôme, Mont Dor, Val de Courre, limite de la prairie en aval, 4.VII.2015, leg G. Coppa (5 females, OPC). France, Massiv-Central, Department Puy-de-Dôme, Chastreix, Ru de la Jarrige, 27.VI.2010, leg G. Coppa (6 males, 3 females, OPC).

Additional diagnosis. Due to the rather uniform genital architecture in Drusinae subfamily, most of the genera were established on modifications of secondary sexual dimorphism created by sexual selection (Schmid 1955). Such neoformations appear very frequently on hindwings in the form of setal bunch, pencil of hairs according to McLachlan (1874–1880), actually composed of long setae with alveoli sitting in various arrangements on veins A2 and A3 and adhered together in resting position thus forming this "pencil-like" structure accommodated in a deep pouch between veins of A2 and A3. We have briefly reviewed the available information (Oláh *et al.* 2015) and suggested that these bizarre modifications are species specific rather than genus specific. The specific status of the *Drusus nigrorectus* was well established by Mosely (1935) even when he has recognised that its male genitalia is not distinguishable from the genitalia of *Drusus rectus* McLachlan. He has distinguished *D. nigrorectus* from *D. rectus* by the dark body colour and by the

loss of the hair pencil on the hindwing. In his monograph Schmid (1956) has reduced its status to subspecies and recently Malicky (2005a) even synonymised *Drusus nigrorectus* Mosely, evolved in allopatry in the Massive Central, with *Drusus rectus* McLachlan of the Pyrenées.

The function of the hair pencil in the *Drusus* genus is not studied. Based on analogy of the similar structures, present on many other Trichoptera taxa and on Lepidoptera, we suppose that these structures have communication function. These alar androconia of the setal pencil evolved in sexual selection processes and may function in prezygotic sexual isolation as well as in extrinsic postzygotic isolation as direct consequence of divergent sexual selection (Seehausen *et al.* 2014). Both the gain and loss of this important phenotype is a powerful mechanism to craete and maintain reproductive isolation even in sympatry.

This reproductive isolation in allopatry created by the loss of androconia was enforced by the divergence of paramere, a sensitive speciation trait in the genus *Drusus*. The setal pattern diverged by the reduction of setae on *Drusus nigrorectus* paramere.The abbreviation of the setose paramere section was accompanied by shape modification of the female vaginal sclerite complex. This shape modification was stable at the examined 3 female specimens. Based on the divergences of the alar androconia, paramere and female vaginal sclerite we confirm Mosely's sophisticated decision and reinstate the species status of *Drusus nigrorectus* Mosely, 1935 **stat. restit.**

Drusus rectus **(McLachlan, 1868)**

(Figures 75–80)

Halesus (Drusus) rectus McLachlan, 1868: 295, "Pyrenees (Rev. T. A. Marshall), 1♂."
Drusus rectus (McLachlan, 1868): McLachlan 1876: 167–168, "One ♂ from the Pyrenees (Marshall)."
Drusus rectus rectus McLachlan, 1868: Schmid 1956: 59–61, "Cette espèce habite les Pyrénées ou elle semble être de beaucoup le *Drusus* le plus répandu."

*Material examined.***France**, Department Hautes-Pyrénées, Aragnouet, Neste de Saux, 8.VII.2009, leg G. Coppa (6 males, OPC). Haute-Garonne, Bagnère-de-Luchon, torrent
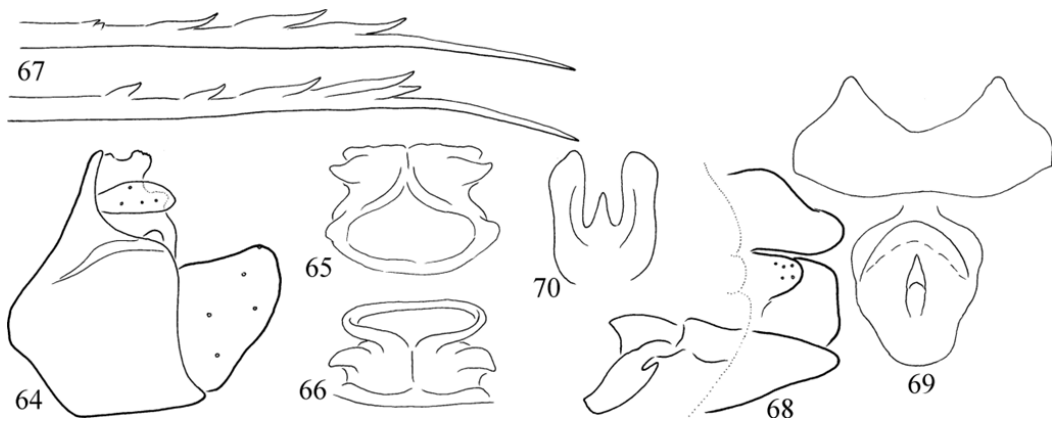
Figures 64–70. *Drusus morettii* Malicky, 2004. Holotype: 64 = male genitalia in left lateral view, 65 = paraproct in caudal view, 66 = apex of the apical arms of the dorsal branches of paraproct, 67 = parameres in left lateral view. 68 = female genitalia with vaginal sclerite complex in left lateral view, 67 = tergite IX and vaginal sclerite profile in dorsal view, 70 = vulvar scale in ventral view.

Figures 71–74. *Drusus nigrorectus* Mosely, 1935. 71 = male genitalia in left lateral view, 72 = paraproct in caudal view, 73 = parameres in left lateral view. 74 = tergite IX and vaginal sclerite profile of two specimens in dorsal view.
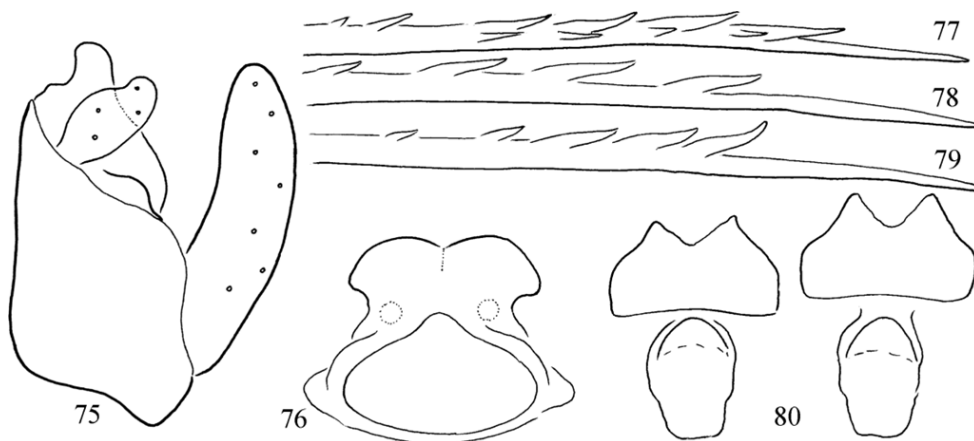
Figures 75–80. *Drusus rectus* (McLachlan, 1868) 75 = male genitalia in left lateral view, 76 = paraproct in caudal view, 77 = parameres in left lateral view from Haute-Pyrénées, 78 = parameres in left lateral view from Pyrénées-Orientales, 79 = parameres in left lateral view from Haute-Garonne, 80 = tergite IX and vaginal sclerite profile of twospecimens in dorsal view.

pont de Venasque, 10. VII. 2012, leg G. Coppa (3 males, 1 female; OPC). Department Hautes-Pyrénées, Gavarnie, amont barrage Oussous, zone de neige et pierres, 27.VII. 2010, leg G. Coppa (5 males, OPC). Department Pyrénées Orientales, Porte Puymorens, Ru de l'Orris, 21.VIII.2011, leg G. Coppa (1 female, OPC). France, 42º23'9.24"N, 2º5'45.02"E, 11. VII. 2012, leg. W. Graf (1 male, OPC). Department Hautes-Pyrénées, Aragnouet, La Gela dans le Parc, 17.VII.2012, leg G. Coppa (4 males, 2 females; OPC). Department Hautes-Pyrénées, Gèdre, Estaube avant Pont Source, 26.VII.2010, leg G. Coppa (3 males, 1 female; OPC). Department Pyrénées-Orientales, Err, Ru d'Err Aiguanein, 24.VIII.2011, leg G. Coppa (2 males, 1 female; OPC). Department Hautes-Pyrénées, Cauterets, Ru des Agudes de Deca Riv Droite du Lutour, 18.VII.2010, leg G. Coppa (3 males, 3 females; OPC). Department Hautes-Pyrénées, Loudervieille, Neste de Louron, 9.VII.2009, leg G. Coppa (2 males, 1 female; OPC). Department Pyrénées-Atlantiques, Laruns, Gave de Bious, 13.VII.2010, leg G. Coppa (6 males, 2 females; OPC). Department Hautes-Pyrénées, Tramezaigues, Rioumajou près du Parking Frecandon, 18.VII.2012, leg G. Coppa (3 males, 1 female; OPC). France: Department of Pyrénées-Orientales**,** Angoustrine Villeneuve-des-Escaldes, ru du lac Sobirans, Estang Sobirans, 19.VIII.2011, leg. G. Coppa (1 female, OPC).

Diagnosis. McLachlan, 1876:167–168, "A species with much of the aspect of *D. annulatus*, but abundantly distinct by the darker coloration of the body, the neural characters, and especially by the anal parts." Schmid 1956: 60–61, " *Dr. rectus* est très voisine d'*annulatus*, mais s'en distingue par une teinte plus sombre, par ses appendices inférieurs très proeminents et par divers caractères écologiques. J'ai étudié un grand nombre d'exemplaires capturés dans les Pyrénées francaises et espagnoles."

Additional diagnosis. See at *Drusus nigrorectus* Mosely, 1935.

Drusus thibaulti Decamps, 1972 stat. nov.

(Figure 81)

Drusus rectus thibauti Decamps, 1972: 262, "Cette espèce m'a été confiée pour étude par Max Thibault. Elle provient de plusieurs chasses à la lumiére effectuées sur le Lissuraga, petit affluent de la Nivelle , en mars-avril (2 ♂) d'un part, et en septembre-octobre-novembre (7♂, 4♀) d'autre part. Holotype ♂ et allotype ♀ dans ma collection."

Material examined. Type material was preserved in alcohol and deposited in the Decamps's collection at the Laboratory of Hydrobiology, Paul-Sabatier University, Tou-

louse. Dr. Decamps retired, a colleague who took care of his collection also retired, the Laboratory of Hydrobiology moved to a new place and the collection was possibly (!) transferred to the Museum of Natural History in Toulouse. By intensive correspondence we have tried to find the types at the museum without any success. Finally Dr. Decamps informed us that they are unable to send us any specimen because the collection is probably set aside, somewhere and nobody is directly in charge of it at the present time. It seems to us that the type material has been lost, our repeated trials to recollect specimens were unseccesfull. New specimens from two localities collected by Dr. Gilles Vincon have been studied by Sipahiler (1993) and deposited in her collection. However, our personal as well as team efforts to borrow her speciems for our fine structure studies on the speciation traits of paraproct and paramere were refused and our direct and indirect trials to establish a working cooperation remained unanswered!

Diagnosis. Decamps 1972: 262, "Suivant l'avis de L. Botosaneanu (in litt.) je considère cette forme comme une race géographique de *Drusus rectus rectus* (au même titre que *Drusus rectus nigrorectus*). Les différences morphologiques sont faible mais constantes pour les 9 ♂ observés."

Additional diagnosis. Based on drawings and species description we consider *Drusus rectus thibauti* as a distinct phylogenetic species, a sibling of *D. berthelemyi*. Here we raise its taxonomic status to species level, **stat. nov.**

Drusus vinconi Sipahiler, 1992

(Figures 82–86)

Drusus vinconi Sipahiler, 1992: 390–291, " Types. Holotype ♂, allotype ♀, and paratypes (4♀): France, Pyrenées-Atlantiques, ruisseau de Chousse, affluent du Vert d'Arette (Vallée du Gave d'Orion), en dessous de Serre de Benou, Pierre St. Martin, 1300 m, 30. VI. 1987, leg. Vincon."

Material examined. Holotype and allotype: R-190, **France**, Pyrenées-Atlantiques, ruisseau de Chousse, affluent du Vert d'Arette, 1000–1100 m, 1700 m, 7. VIII. 1987, leg. Vincon (1 male, 1 female; ZSM). Here we have given the collecting date written on the label present in the vial with the Holotype. The collecting date is 30.VI. 1987 in the published species description. The allotype is overcleared, completely depigmented. The dorsal profile of the vaginal sclerite complex is very feable, just discernible.

Diagnosis. Sipahiler 1992:291, "*Drusus vinconi*, spec. nov., is closaely related to *D. monti*
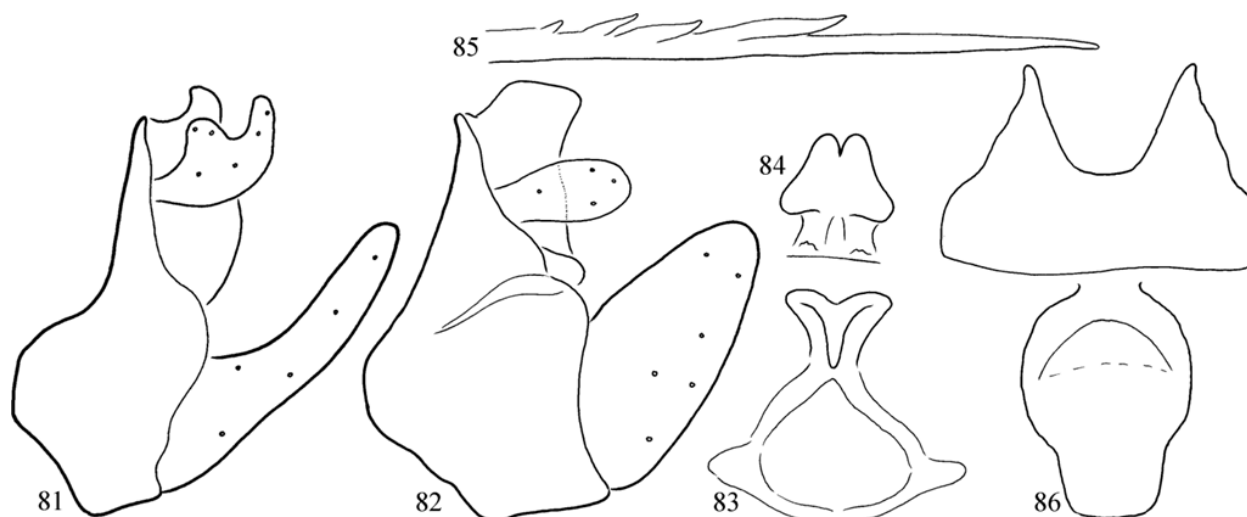
Figure 81. *Drusus thibaulti* Decamps, 1972. 81=male genitalia in left lateral view.
Figures 82–86. *Drusus vinconi* Sipahiler, 1992. Holotype: 82 = male genitalia in left lateral view, 83 = paraproct in caudal view, 84 = apex of the apical arms of the dorsal branches of paraproct in dorsal view, 85 = paramere in left lateral view.
Allotype: 86 = tergite IX and vaginal sclerite profile in dorsal view.

cola McLachlan (Schmid 1956) from the southern Alps. The main differences are in the male genitalia, especially in the structure of the intermediate appendages, which are ovoid in *D. monticola*, whilst they are clearly triangular in *D. vinconi*. The preanal appendages of *D. monticola* are small and rounded; in *D. vinconi* they are long and ovoid. Shape of segment 9, which is narrow ventrally and pointed anteriorly in *D. monticola* is also different. The differences in female genitalia are also remarkable, especially shape of tubular pieces, which are short and laterally quadrangular in *D. monticola*, and the median scale which is very short in *D. vinconi*, whilst it reaches half the length of the lateral scales in *D. monticola*."

Additional diagnosis. In the species diagnosis of the original description this species was related to *D. monticola*. However *D. vinconi* has a typical ancesteral paramere divergence by the recumbent primary and secondary paramere spines. *D. monticola* is the nominate species of the *D. monticola* species group with highly differentiated paramere spine pattern integrated through ancestral divergence by the multidivision of the single subapical spines into spine bunch composed of various number of smaller spines.

Drusus bolivari species complex

Based upon our ranking principles and criteria here we elaborated for the Drusinae subfamily *Drusus bolivar* species complex has dorsal branch of the paraproct with straight apical arms of variously shaped heading in lateral view, mesally completely fused into a digitiform shape in caudal view. *Drusus bolivari* species complex is comprised of eight species: *bolivari, carmenae, estrellensis, gonzalezi, grafi, gredosensis, jesusi, pyrenensis*.

Drusus bolivari (**McLachlan, 1876**)

(Figure 87)

Catadice bolivari McLachlan, 1876: 40–41, Described from a single male specimen collected in Spain (Sierra de Guadarrama, Navacerrada Pass, leg. Bolivar).
Drusus bolivari (McLachlan, 1876): Mosely 1933: 499, *Catadice* synonymised with *Drusus*.
Drusus bolivari (McLachlan, 1876): Schmid 1952: 680. Male and female specimens collected in Gredos Mts. Spain. Misidentification! Described as *Drusus gredosensis* Oláh, 2015 in Oláh *et al.* 2015.
Drusus bolivari (McLachlan, 1876): Schmid, 1956: 51–52, *Dr. bolivari* habite probablement tout le système montagneux qui s'étend au centre de l'Espagne et qui est composé des Sierras de Estrella, de Gata, de Gredos et de

Guadarrama. *D. estrellensis* (McLachlan, 1884) was synonymized with *D. bolivari* (McLachlan, 1876).

Drusus bolivari (McLachlan, 1876): Malicky 1983: 165, genital drawings: Misidentification! Oláh *et al.* 2015: 37, described as *Drusus gredosensis* Oláh, 2015.

Drusus bolivari (McLachlan, 1876): Malicky 2004: 197, genital drawings: Misidentification! Oláh et al. 2015: 34, described as *Drusus gonzalezi* Oláh, 2015.

Material examined. Holotype male. Deposited in The Natural History Museum, London. Cleared abdomen and rest of the body without wings are embedded in permanent slide praparate with two labels: (1) red-framed label: *Catadice Bolivari* McLach. Det. McLachlan TYPE. C/B. (2) black double-line framed label: Navacerrada, Spain Mclachlan Coll. B. M. 1938-674, BMNH(E) # 251071.

Diagnosis. Schmid 1956: 52, "Cette espèce est isolée dans le cadre du groupe par ses ailes fortement tachetées et le faible développement des appendices intermédiaires et du corps du Xe segment." "Dans ce travail, je place estrellensis en synonymie de bolivari, car ces espèces ne se distinguent que par un seul caractère qui semble varier géographiquement le long de ce système montagneux, les exemplaires provenant de la partie occidentale de l'aire de repartition (Estrella) ont des appendices intermédiaires épais et sans dent apicale et plus on s'avance vers l'Est, plus les exemplaires ont des appendices minces et recourbés."

Oláh *et al.* 2015: 33, "*Drusus bolivari*, the name bearing species of the complex has unique paraproct, its dorsal branch is almost horizontal and its dorsoapical region bifid, apex truncated, upper margin excised before apex in lateral view. Unfortunately the paramere not fully visible on the single male holtype genitalia embedded in a permanent slide preparate."

Drusus carmenae Oláh, 2015 in Oláh *et al.* 2015

(Figures 88–92)

Drusus carmenae Oláh, 2015 in Oláh *et al.* 2015:31–32,*Etymology.carmenae*, we dedicated this species to Dr. Carmen Zamora-Muñoz , who has collected this species to appreciate her significant contribution to the knowledge of Trichoptera.

Material examined. Holotype: **Spain**, Nacimiento R. Guadalquivir, Sierra de Cazorla (Jaén), 37.902273ºN-2.937723ºE, 1378 m, 9. X. 2009, leg. C. Zamora-Muñoz, (1 male, DZFCUG). Allotype: same as holotype (1 female, DZFCUG). Paratypes: same as holotype (1 male, 1 female, DZFCUG; 1 male, 1 female, OPC). Spain, Nacimiento R. Castril, Sierra de Castril (Granada), 37.895773ºN, 2.747502ºE, 1220 m, 28. XI. 2001, leg. C. Zamora-Muñoz, (1 male, DZFCUG, 1 male, OPC).

Diagnosis. Oláh *et al.* 2015: 31, "Most close to *D. grafi* sp. nov., but differs by having spinulose area on tergit VIII differently shaped; cerci short and high quadratic, not low and long triangular; paraproct dorsal branch straight and blunt not with pointed slightly recurving dorsoapical region in lateral view and more bifid in apical view; paraproct ventral branch with robust lateral section, not thin; gonopods short and robust not elongated slender; paramere with 3–4 modified setae, not with 3 spine-like setae."

Drusus estrellensis (McLachlan, 1884)

(Figures 93–97)

Catadice estrellensis McLachlan, 1884: 13–14, "Portugal (Stream south of Sabugueiro, Beira Baixa, 4092 ft., 5th June, Eaton, 3♂, 3♀)."

Drusus estrellensis (McLachlan, 1884): Mosely 1933: 499, *Catadice* synonymised with *Drusus*.

Drusus bolivari (McLachlan, 1876): Schmid 1956: 52, Synonymized with *D. bolivari*: Misidentification.

Drusus estrellensis (Mclachlan, 1884): Oláh *et al.* 2015: 33, raised to species level: stat. restit.

Material examined. Holotype male. Deposited in The Natural History Museum, London. Cleared abdomen embedded in permanent slide praparate with two labels: (1) red-framed label: *Catadice estrellensis* McL. ♂ TYPE. C/B. (2) black double-line framed label: **Portugal**, Sabugueiro 5/6/1880 A.E.Eaton Mclachlan Coll. 1938-674, BMNH(E) # 251069. Type series: *Catadice estrellensis* McL. ♂ TYPE. With seven labels: (1) brown small oblong: Type; (2) pink oblong handwritten: *Catadice estrellensis* McL.; (3) gray oblong typed: *Catadice estrellensis*, McLach. Det. McLachlan; (4) blue oblong: McLachlan Coll. B. M. 1938-674; (5) yellow short oblong: Eaton. Portugal. 1880; (6) white oblong with code: BMNH(E):1253659; (7) yellowish rounded one side: b. 5. VI.80, other side: Sabugueiro, 5/6. *Catadice estrellensis* McL. ♂ TYPE. With seven labels: (1) red small oblong: Type; (2) pink oblong handwritten: *Catadice estrellensis* McL.; (3) gray oblong typed: *Catadice estrellensis*, McLach. Det.McLachlan; (4) blue oblong:
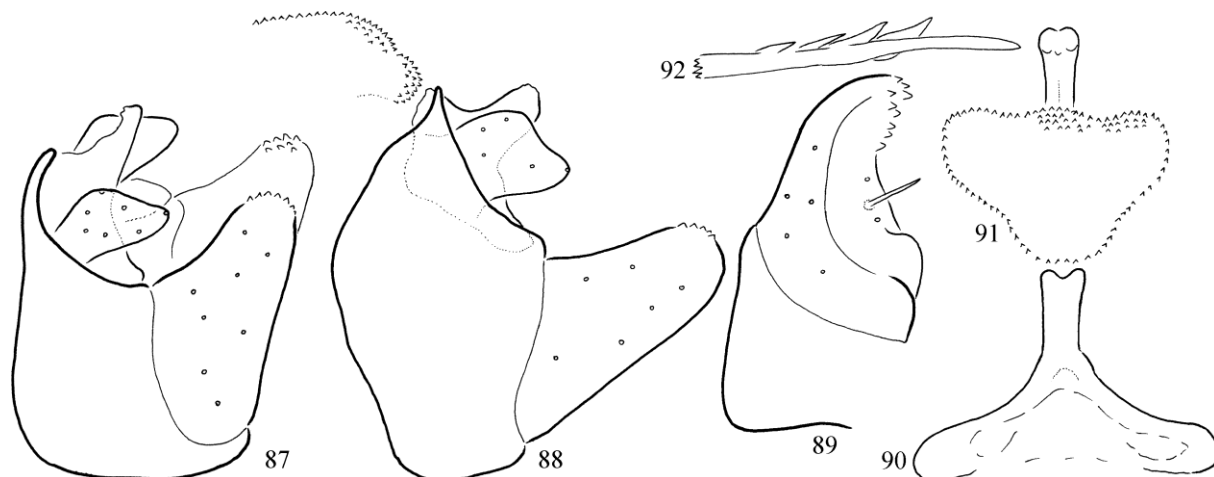
Figure 87. *Drusus bolivari* (McLachlan, 1876). Holotype. 87 = male genitalia in left lateral view.

Figures 88–92. *Drusus carmenae* Oláh, 2015. Holotype. 88 = male genitalia in left lateral view, 89 = left gonopod in ventral view, 90 = paraproct in caudal view, 91 = apex of the apical arms of the dorsal branches of paraproct with the pegged spinulose area of tergite VIII in dorsal view, 92 = paramere in left lateral view.
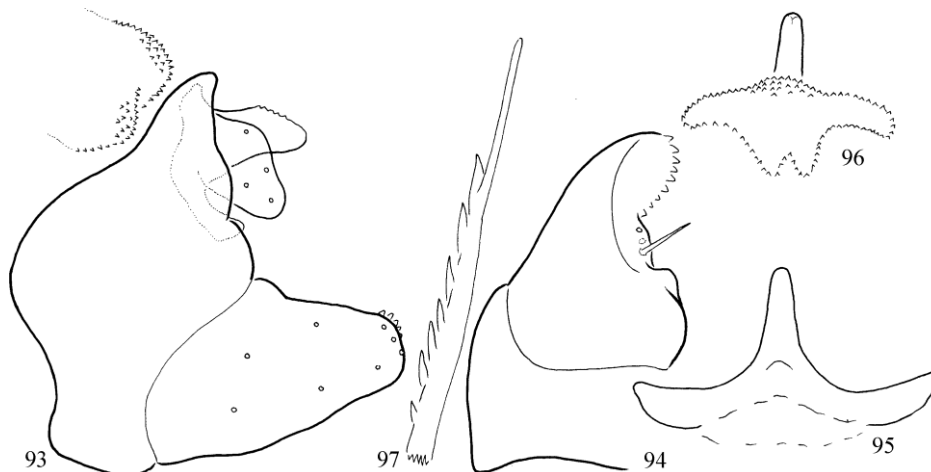
Figures 93–97. *Drusus estrellensis* (McLachlan, 1884).Holotype. 93 = male genitalia in left lateral view, 94 = left gonopod in ventral view, 95 = paraproct in caudal view, 96 = apex of the apical arms of the dorsal branches of paraproct with the pegged spinulose area of tergite VIII in dorsal view, 97 = paramere in left lateral view.

McLachlan Coll. B. M. 1938-674; (5) yellow short onlong: Eaton. Portugal. 1880; (6) white oblong with code: BMNH(E): 1253660; (7) yellowish rounded one side: b. 5. VI.80, other side: Sabugueiro, 5/6. *Catadice estrellensis* McL. ♀ TYPE. With seven labels: (1) brown small oblong: Type; (2) pink oblong handwritten: *Catadice estrellensis* McL.; (3) gray oblong typed: *Catadice estrellensis*, McLach. Det.McLachlan; (4) blue oblong: McLachlan Coll. B. M. 1938-674; (5) yellow short onlong: Eaton. Portugal. 1880; (6) white oblong with code: BMNH(E):1253661; (7) yellowish rounded one side: b. 5. VI.80, other side: Sabugueiro, 5/6. *Catadice estrellensis* McL. ♀ TYPE. With seven labels: (1) brown small oblong: Type; (2) pink oblong handwritten:

Catadice estrellensis McL.; (3) gray oblong typed: *Catadice estrellensis*, McLach. Det.McLachlan; (4) blue oblong: McLachlan Coll. B. M. 1938-674; (5) yellow short onlong: Eaton. Portugal. 1880; (6) white oblong with code: BMNH(E):1253662; (7) yellowish rounded one side: b. 5. VI.80, other side: Sabugueiro, 5/6.

Diagnosis. McLachlan 1884: 13–14, "Larger, darker, and more robust than *C. bolivari*, differing also in the form of the intermediate appendages of the ♂." "It is scarcely correct to say that *Catadice* has no "pouch" in the postertior –wings of the ♂;

there is indication of a very short pouch, but it has no pencil of hairs in it, and hence is scarcely evident."

Oláh *et al.* 2015: 33, Species described from Portugal, Estrella Mts. The lateral shape of paraproct is most close to *D. pyrenensis*, but more robust; differs also by having higher number (6–7) of modified setae on the paramere, not less number (3–5), cerci regular quadratic, gonopods short and high, not long and low in lateral view.

Drusus gonzalezi Oláh, 2015 in Oláh *et al.* 2015

(Figures 98–102)

Drusus bolivari (McLachlan, 1876): Malicky 2004: 197, genital drawings: Misidentification!
Drusus gonzalezi Oláh, 2015 in Oláh *et al.* 2015: 34–35, "*Etymology.gonzalezi*, we dedicated this species to Professor Marcos A. Gonzalez who has collected this species to appreciate his significant contribution to the knowledge of European Trichoptera"

Material examined. Holotype: **Spain**, NW Spain, Sierra de Ancares, Lugo, Rio de la Vara, Rio da Vara, N42º48'10.74" W6º53'19.90", 1230m, 14.VII.1984, leg. Marcos A. Gonzalez (1 male, OPC). Allotype: same as holotype (1 female, OPC).

Diagnosis. Oláh *et al.* 2015: 34–35. "The drawings of this species was published under the name of *Drusus bolivari* McLachlan (Malicky 2004), but differs by having simple straight and long triangular shape of paraproct dorsal branch in lateral view, not bifid and excised dorsoapicad; gonopods with tapering apex, not blunt. It is most close to *Drusus carmenae* sp. nov., but differs by having narrowing apex of the paraproct dorsal branch not blunt in lateral view, bellied laterad, not straight in caudal view; parameres with six spine-like setae".

Drusus grafi Oláh, 2015 in Oláh *et al.* 2015

(Figures 103–107)

Drusus gonzalezi Oláh, 2015 in Oláh *et al.* 2015: 36, "*Etymology.grafi*, we dedicated this species to Professor Wolfram Graf who has collected this species to appreciate his significant contribution to the knowledge of *Drusus* genus."

Material examined. Holotype: **Spain**, Sierra de la Demanda, near Ezcaray, 42.255785°N, 2.978349°E. 1371 m, 15. VI. 2013 leg. W. Graf (1 male, OPC). Allotype: same as holotype. Paratype: same as holotype (1 male, OPC).
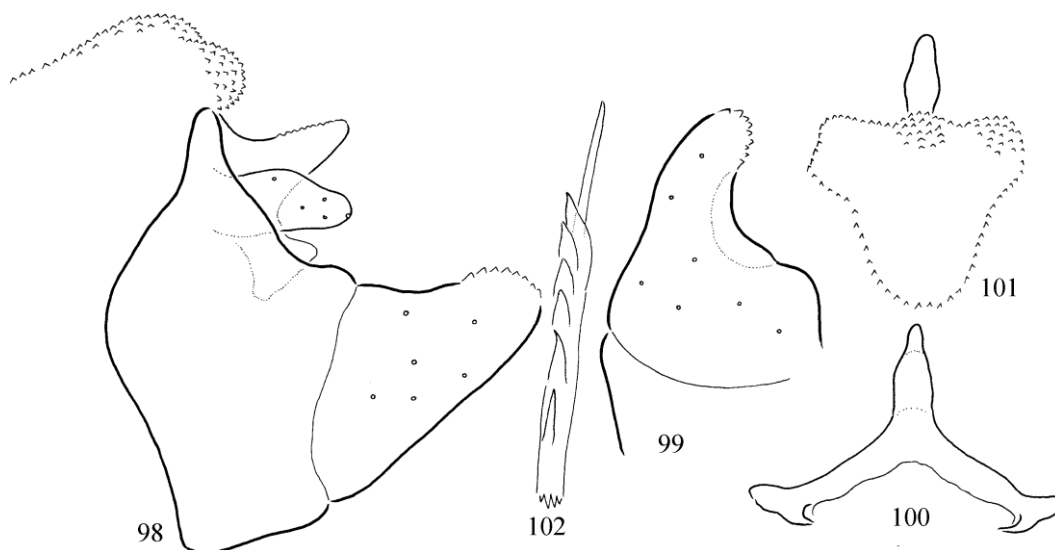
Figures 98–102. *Drusus gonzalezi* Oláh, 2015. Holotype. 98 = male genitalia in left lateral view, 99 = left gonopod in ventral view, 100 = paraproct in caudal view, 101 = apex of the apical arms of the dorsal branches of paraproct with the pegged spinulose area of tergite VIII in dorsal view, 102 = paramere in left lateral view.
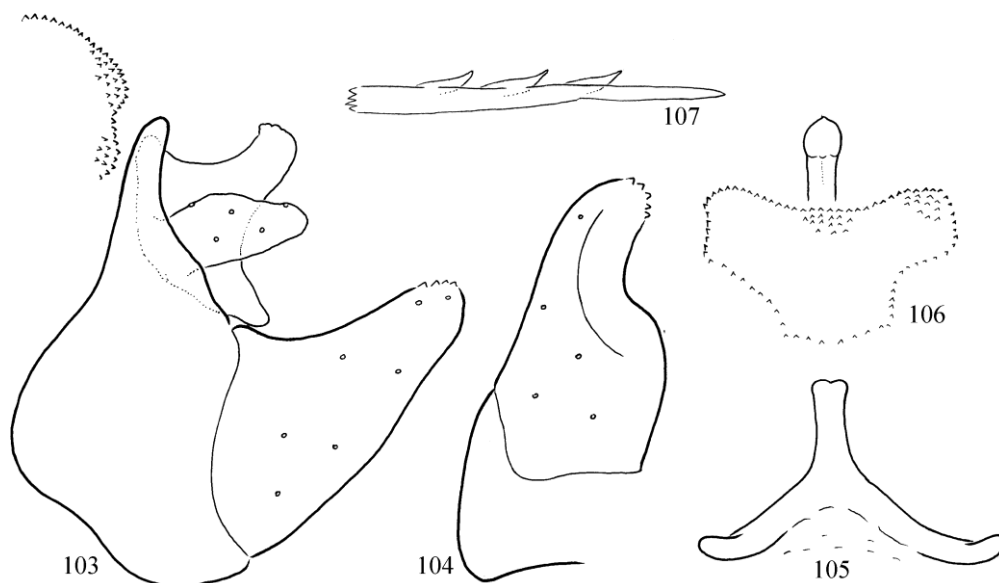
Figures 103–107. *Drusus grafi* Oláh, 2015. Holotype. 103 = male genitalia in left lateral view, 104 = left gonopod in ventral view, 105 = paraproct in caudal view, 106 = apex of the apical arms of the dorsal branches of paraproct with the pegged spinulose area of tergite VIII in dorsal view, 107 = paramere in left lateral view.

Diagnosis. Oláh *et al.* 2015: 36. "Most close to *D. carmenae* sp. nov., but differs by having spinulose area on tergit VIII differently shaped; cerci low and long triangular, not short and high quadratic; paraproct dorsal branch with pointed slightly recurving dorsoapical region, not straight and blunt in lateral view and less bifid in apical view; paraproct ventral branch with thin lateral section, not robust; gonopods elongated slender, not short and robust; paramere with 3 modified setae, not with 3–4 spine-like setae".

Drusus gredosensis Oláh, 2015 in Oláh *et al.* 2015

(Figures 108–112)

Drusus bolivari (McLachlan, 1876): Schmid 1952: 680, Spain, Gredos Mts. Misidentification.

Drusus bolivari (McLachlan, 1876): Schmid 1956: 51–52, Misidentified male and female specimens from the Gredos Mts. Moreover *D. estrellensis* (McLachlan, 1884), from Portugal, Estrella Mts. was synonymized, with *D. bolivari* (McLachlan, 1876) from Spain, Guadarrama Mts.

Drusus bolivari (McLachlan, 1876): Malicky 1983: 165, genital drawings: Misidentification.

Drusus gredosensis Oláh, 2015 in Oláh *et al.* 2015: 37, "*Etymology.* We named this species after the mountain range where the type material was collected."

Material examined. Schmid (1952a) has collected several *Drusus* specimens from **Spain** (Sierra de Gredos) and determined as *Drusus bolivari* (McLachlan). He has deposited 3 males and 1 female in The Natural History Museum, London. Holotype: Spain (Av.) Lac de Gredos, 16–23. VII. 1950, leg F. Schmid, Brit.Mus. 1951-132, BMNH(E) 1253663 (1 male, NHM). Allotype: Lac de Gredos, 16–23. VII. 1950, leg F. Schmid, Brit.Mus. 1951-132, BMNH(E) 1253665 (1 female, NHM). Paratypes: Spain (Av.) Lac de Gredos, 16–23. VII. 1950, leg F. Schmid, Brit.Mus. 1951-132, BMNH(E) 1253664 (1 male, NHM). Spain (Av.) Spain (Av.) Lac de Gredos, 16–23. VII. 1950, leg F. Schmid, Brit.Mus. 1951-132, BMNH(E) 1253666 (1 male, NHM).

Diagnosis. Oláh *et al.* 2015: 37, "*Drusus gredosensis* Oláh differs from *D. bolivari* (McLachlan) by having lateral aspect of paraproct differently formed; apex pointed and upward as well as slightly backward turning, not straight horizontal and not bifid dorsoapicad. Paraproct has slender, slightly recurving, hook-like apex in lateral view, the most slender in the species complex. Cerci are with elongated apical ventrum. Other periphallic structure, the gonopods differs

from all the other related species by having no mesad directed apex in ventral view. Number of paramere spines, the modified setae is very high 11–12. Paramere with 11 modified setae differs from all the other species in the complex; those are with much less setae. In the holotype the modified setae of the paramere are lying recumbent, probably a more virgin condition before copulation. In paratypes the setae are less recumbent, more erect, probably worn during copulation."

Drusus jesusi Oláh, 2015 in Oláh *et al.* 2015

(Figures 113–117)

Drusus jesusi Oláh, 2015 in Oláh et al. 2015: 37–38, "*Etymology. jesusi*, We dedicated this species to Dr. Jesús Martínez Menéndez who has paid desperate trials to delimit species in the *Drusus bolivari* complex with neutral DNA markers."

Material examined . Holotype: **Spain**, NW Spain, Sierra de Ancares, Lugo, Rio de la Vara, Rio da Vara, N42°48'10.74", W6°53'19.90", 1230m, 14.VII.1984, leg. Marcos A. Gonzalez (1 male, OPC). Allotype: same as holotype (1 female, OPC).

Diagnosis. Oláh *et al.* 2015: 37–38. "The single male and female specimens available for this study were collected by Prof. Gonzalez together with male and female specimens of *Drusus gonzalezi* sp. nov. in the Anceras Mts. The females were simply size-associated, need further confirmation. Most close to *Drusus bolivari* McLachlan described from the Guadarrama Mts. at least by comparing with the permanent slide praparate of the single holotype male of *D. bolivari*. The permanent preparete, although of very good quality, permits examination only in lateral view with slightly left caudal distortion. Moreover, the paramere pattern is not visible. Further studies are required to give detailed comparative trait analysis of the two species. The type locality of the single *Drusus bolivari* specimen is far from the type locality of *Drusus jesus* sp. nov. Several incipient species inhabit mountain ranges nearby to the Type Locality of *D. bolivari* in the Guadarrama Mts.: *Drusus estrellensis* McLachlan in Estrella Mts., *D. gredosensis* sp. nov. in Gredos Mts., *D. grafi* sp. nov. in Demanda Mts."
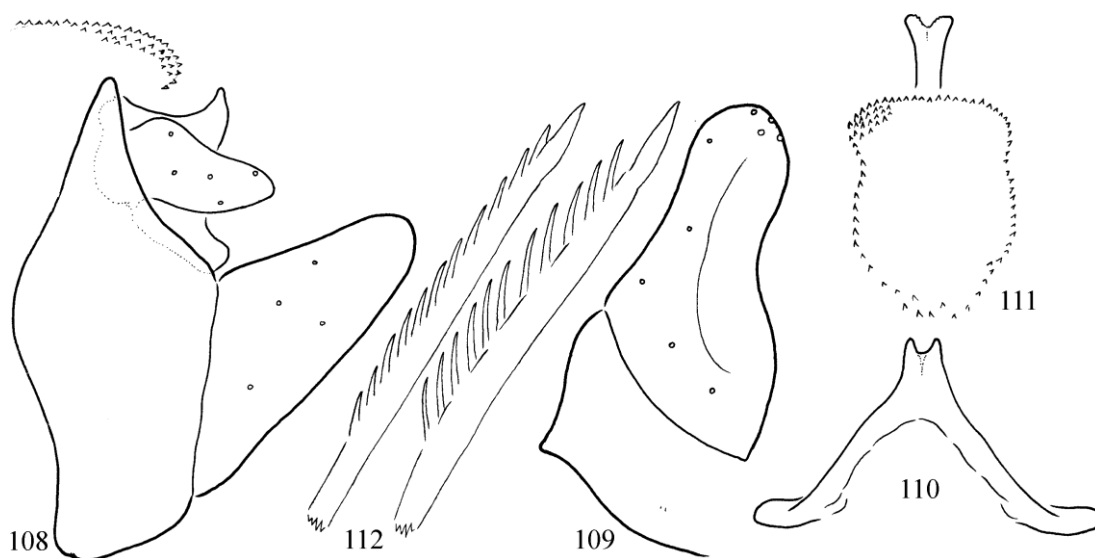
Figures 108–112. *Drusus gredosensis* Oláh, 2015. Holotype. 108 = male genitalia in left lateral view, 109 = left gonopod in ventral view, 110 = paraproct in caudal view, 111 = apex of the apical arms of the dorsal branches of paraproct with the pegged spinulose area of tergite VIII in dorsal view, 112 = parameres in left lateral view.
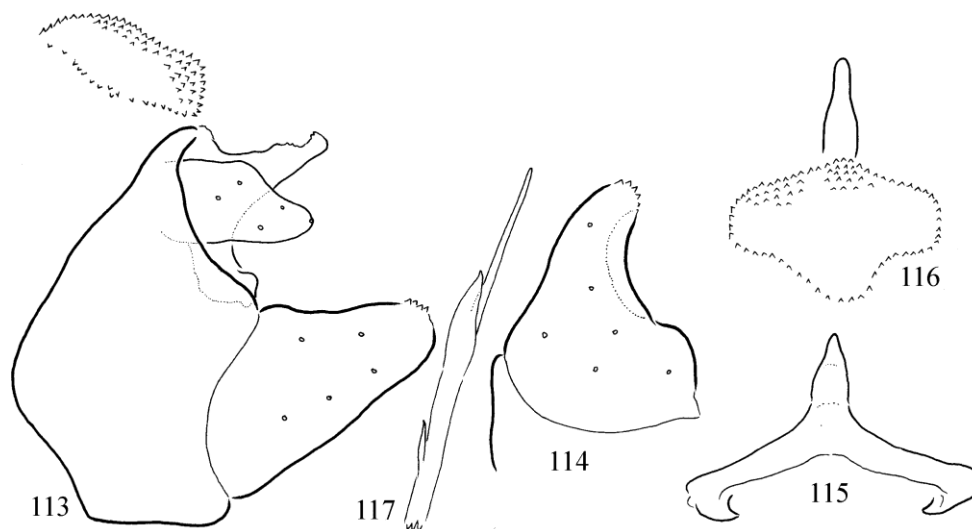
Figures 113–117. *Drusus jesusi* Oláh, 2015. Holotype. 113 = male genitalia in left lateral view, 114 = left gonopod in ventral view, 115 = paraproct in caudal view, 116 = apex of the apical arms of the dorsal branches of paraproct with the pegged spinulose area of tergite VIII in dorsal view, 117 = paramere in left lateral view.

Drusus pyrenensis Oláh & Coppa, 2015 in Oláh *et al.* 2015

(Figures 118–122)

Drusus pyrenensis Oláh & Coppa, 2015 in Oláh *et al.* 2015: 39–40, "*Etymology.* We named this species after the mountain range where the type material was collected."

Materialexamined. Holotype: **France**, Hautes-Pyrénées Province, Bagnères-de-Bigorre, Soulagnet bord du torrent, source de la Brassere, 2. VII. 2013 leg. G. Coppa, (1 male, CPC). Paratypes: same as holotype (2 males, CPC; 2 males, OPC).

Diagnosis. Oláh *et al.* 2015: 34–35. "Most close to *D. estrellensis* sp. nov., but differs by having spinulose area on tergit VIII less trilobed; cerci differently shaped, long and low, not short and high; paraproct dorsal branch less robust in lateral view and paraproct ventral branch less expanded; gonopods elongated slender, not short and robust; paramere with 3–5 modified setae, not with 6–7 spine-like setae".

Drusus trifidus species complex

Drusus trifidus species complex has dorsal branch of the paraproct with hook-shaped or at least anterad angled apical arms in lateral view, variously dorsad or laterad directed in caudal view. Typical paramere pattern with ancesteral divergence by recumbent primary and secondary paramere spines is present in this species complex, but two species, *D. brunneus* and especially *D. rizeiensis* exhibit paramere with inflated apical shaft of various pilosity, a character of the *D. caucasicus* species group. This could be the result of an incomplete or perturbated lineage sorting. *Drusus trifidus* species complex is comprised of five species: *brunneus*, *erimanthos*, *franzressli*, *rizeiensis*, *trifidus*.

Drusus brunneus Klapálek, 1898

(Figures 123–127)

Drusus brunneus Klapálek, 1898: 489. "Habituell dem *D. Muelleri* sehr ahnlich." „Hungary: Mehádia, Corniareva, Marmaros, Boroszno. 6♂, 4♀."
Drusus brunneus Klapálek, 1898: Schmid 1956: 48–49, "Cette espèce est localisée dans les montagnes de l'Europe orientale: j'ai vu une dizaine d'individus, provenant de Hongrie et de Roumanie."

Material examined. **Romania**, Maramureş county, Ignis Mts, Săpânţa, mineral water springs and their outflows in a beech forest in the lower valley of the Săpânţa, N47°56'05.5", E23°40'41.2", 408m; 30.vi.2005 leg. J. Kontschány, D. Murányi & K. Orci (2 males, NHMB). Maramureş county, Rodna Mts. Borşa - Staţiunea Borşa, spring area of the Bistriţa Aurie River under the Gargalău
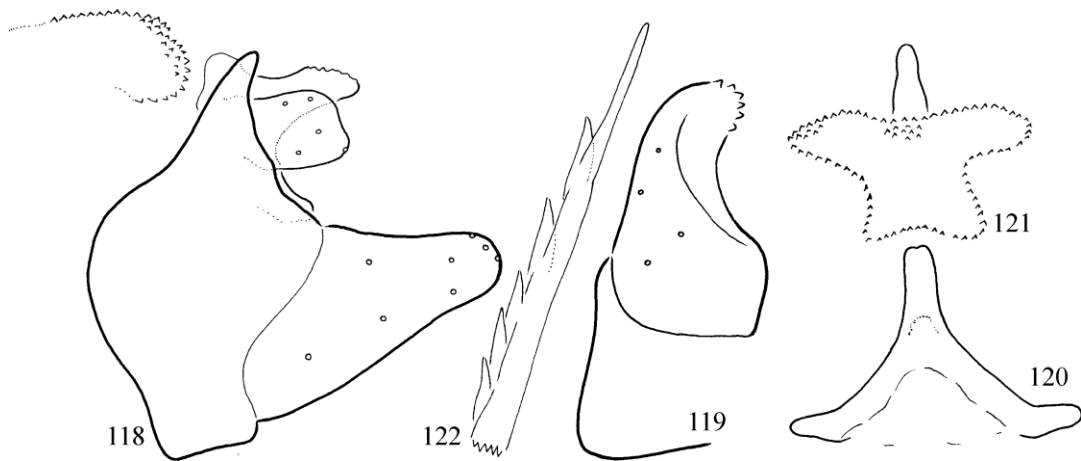
Figures 118–122. *Drusus pyrenensis* Oláh & Coppa, 2015. Holotype. 118 = male genitalia in left lateral view, 119 = left gonopod in ventral view, 120 = paraproct in caudal view, 121 = apex of the apical arms of the dorsal branches of paraproct with the pegged spinulose area of tergite VIII in dorsal view, 122 = paramere in left lateral view.
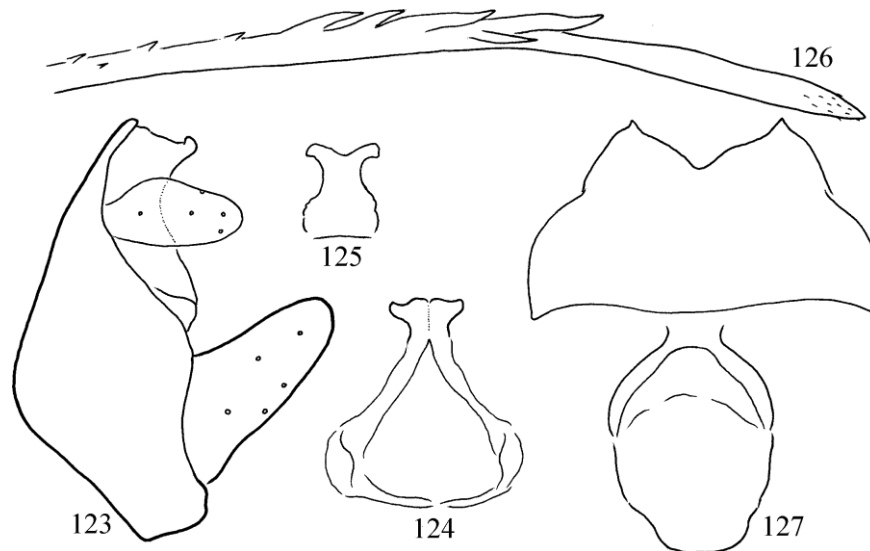
Figures 123–127. *Drusus brunneus* Klapálek, 1898. 123 = male genitalia in left lateral view, 124 = paraproct in caudal view, 125 = apex of the apical arms of the dorsal branches of paraproct in dorsal view, 126 = paramere in left lateral view, 127 = tergite IX and vaginal sclerite profile in dorsal view.

Peak, N47º34.380', E24º48.575', 1688–1711m, 29.06.2005 leg. J. Kontschány, D. Murányi& K. Orci (1 male, NHMB). Munţii Lăpuşului (Lápos), Văleni (Mikolapatak), peat bog, its inflow and outflow brooks in a beech forest, N47°42'43.2", E24°01'48.7", 987m, 23.V.2006 L. Dányi, M. Földvári, J. Kontschán & D. Murányi (1 male, NHMB). Maramureş county, Maramureş Mts, Poienile de sub Munte (Havasmező), Budescu valley, brook in mixed forest, N47º52.254', E24º36.192', 821m, 24.v.2007, leg. Cs.Csuzdi, L. Dányi, J. Kontschán & D. Murányi (1 male, NHMB). Parâng Mts, Gâlcescu Lake, 1935 m, N45.35º,E23.61º,

4.VII.2007, leg. M. Bálint (10 males, 2 females, OPC). Caraş-Severin county, Semenic Mts. Open brook E of Mt. Piatra Goznei, 1340m, N45°10.949', E22°03.967', 11.VI.2011, leg. T. Kovács, D. Murányi&G. Puskás (2 male, 1 female, HNHM). Caraş-Severin county, Ţarcu Mts. Spring and its outlet at Cuntu Meteorological Station, 1465m, N45°18.008', E22°30.059', 09.VI.2011, leg. T. Kovács, D. Murányi&G. Puskás (1 male, HNHM). Cindrel Mts. Păltiniş, stream Dăneasa, N45°39.524', E23º55.019', 1138m, 29.V.2013, singled leg. J. Oláh, E. Bajka, Cs. Balogh, & G. Borics(1 male, OPC). Apuseni Mts. Munţii Gilăului, Staţi-

unea Muntele Băişorii, three-branched stream, N46°30.701' E23°16.279', 1620m, 19.VI.2013, singled leg. J. Oláh, Cs. Balogh, & S. Fekete (1male, OPC). Apuseni Mts. Vârtop, spring streams, N46°31.045' E22°39.821', 1209m, 20.VI.2013, singled leg. J. Oláh, Cs. Balogh, & S. Fekete (1 female, OPC). Apuseni Mts. Munţii Gilăului, Staţiunea Muntele Băişorii, Lupinus stream, 18.VI.2013, singled leg. J. Oláh, Cs. Balogh, & S. Fekete (1 male, OPC). Retezat Mts., Chele Buţii, 910m, N: 45°18' 06,96" E: 22°58' 31,48" 9.VII.2013, light leg. E. Bajka, Cs. Balogh, G. Borics, P. Borics (1 male, OPC). Apuseni Mts. Bihor Mts. above Galbena village, valley Cepelor, N: 46°27' 44.01" E: 22°43' 58,88"1035 m, 13.05.2014, leg. Cs. Balogh & B.V. Béres (1 male, OPC). Apuseni Mts., Vlădeasa Mt. Stâna de Vale, Gălbenele stream, N46°40.809' E22°37.147', 1180 m, 7.VI.2015, leg. M. Kiss, J. Oláh & L. Szél (6 males, 1 female, OPC). Apuseni Mts., Vladeasa Mt. Stana de Vale, upper section of Ciripa stream, N46°40.546' E22°38.515', 1360 m, 6.VI.2015, leg. M. Kiss, J. Oláh & L. Szél (2 males, 2 females; OPC). Apuseni Mts. Muntii Gilaului, Statiunea Muntele Băişorii, three-branched stream, N46°30.701' E23°16.279', 1620m, 20.VI.2015, singled leg. J. Oláh, Cs. Balogh, & P. Juhász (4 males, 2 females; OPC). Bucegi Mts. Ialomiţa stream, 25.446274, 45.397739, 1638 m, 14. VII. 2015, leg. Z. Baczó & J. Kecskés (5 males, 2 females; OPC). Bucegi Mts. Ialomiţa stream, 25.444064, 45.425296, 1917 m, 15. VII. 2015, leg. Z. Baczó & J. Kecskés (27 males, 7 females; OPC). Bucegi Mts. Cocora stream, 25.443147, 45.3402125, 1680 m, 16. VII. 2015, leg. Z. Baczó & J. Kecskés (3 males, OPC). Bucegi Mts. Ialomiţa stream, 25.416958, 45.416957, 1837 m, 15. VII. 2015, leg. Z. Baczó & J. Kecskés (8 males, 4 females, OPC). Romania, Dâmboviţa county, Southern Carpathians, Bucegi Mountains, Brătei stream valley, Brătei stream, 45.383102N 25.385147E, 13. VII. 2016 leg. Z. Baczo & J. Kecskés (2 males, 1 female; OPC). Romania, Dâmboviţa county, Southern Carpathians, Bucegi Mountains, Brătei stream valley, Negru stream, 45.383283N, 25.350528E, 14. VII. 2016 leg. Z. Baczo & J. Kecskés (1 male, OPC).

Diagnosis. Klapálek 1899: 434–435. "Obwohl diese Art durch ihr Aeusseres stark an den *Drusus Muelleri* erinnert, so lasst sie sich durch die Genitalanhange sogleich von demselben unterscheiden."

Schmid 1956: 49, "*Dr. brunneus* est caractérisé par ses deux paires d'ailes brun-jaune foncé, par ses appendices intermédiaires armés de deux pointes très petites, par le corps du Xe segment proéminent et par ses appendices inférieurs assez petits et peu velus."

Additional diagnosis. This is a very common species and distributed in the entire Carpathian ranges from Bieszczady Mts. of Ukranine to the Southern Carpatians in Romania. Schmid (1956) has listed *D. brunneus* in his *Drusus mixtus* species group. However, its typical paramere pattern with ancesteral divergence by recumbent primary and secondary paramere spines clearly relate this species in the *D. annulatus* species group. The apical shaft of the paramere dilated and pilosity present on its apex.

Drusus erimanthos Malicky, 1992

(Figures 128–131)

Drusus erimanthos Malicky, 1992: 42–43, "Holotypus ♂ und Paratypen (1♂, 3♀): Griechenland, Erimanthos-Gebirge, Lakomata,18. IV. 1990, leg. Horvat & Sivec."

Material examined. Paratype male on loan from Malicky Private Collection.

Diagnosis. Malicky 1992: 42–43, "Diese Art ist in die Verwandtschaft von *Drusus franzressli* Malicky aus Mittelgriechenland zu stellen, von dem sich die Mannchen aber sofort durch das unpaare Borstenfeld des 8. Tergits unterscheiden. *D. franzressli* hat dort eine breite, zweilappige Borstenzone mit vorspringenden lateralen Ecken. Es ist eine auffallend kleine Art mit ungewöhnlich frühen Funddatum. Mir liegt zwar auch *Drusus franzressli* schon von 25. April (aus dem Vardusia-Gebirge) vor, aber seine Hauptflugzeit ist im Mai und Juni."

Additional diagnosis. Paramere pattern clearly relates this specie to the *D. annulatus* species group. The hook formation on the apical arms of the dorsal branch less developed, there is only an anterad directed pair of tips.

Drusus franzressli Malicky, 1986

(Figures 132–136)

Drusus franzressli Malicky, 1986: 14–16, "Holotypus ♂: Graecia, Pendayi, N 38°35', E 22°05', 900 m, 2. VI. 1973, leg. Aspöck, Rausch und Ressl; in coll. Malicky."

Material examined. **Greece**, Vardousia Gebirge, Kallion, 400 m, N38° 34' E22° 11', 20. V. 1990, leg. H. Malicky (1 male, 1 female, OPC). Greece, Phocis county, Vargiani, springs and torrent in the village, 970 m, N38° 38.499' E22° 25.515', 8.IV.2009, leg. L. Dányi, J. Kontschán & D. Murányi (1 male, HNHM).
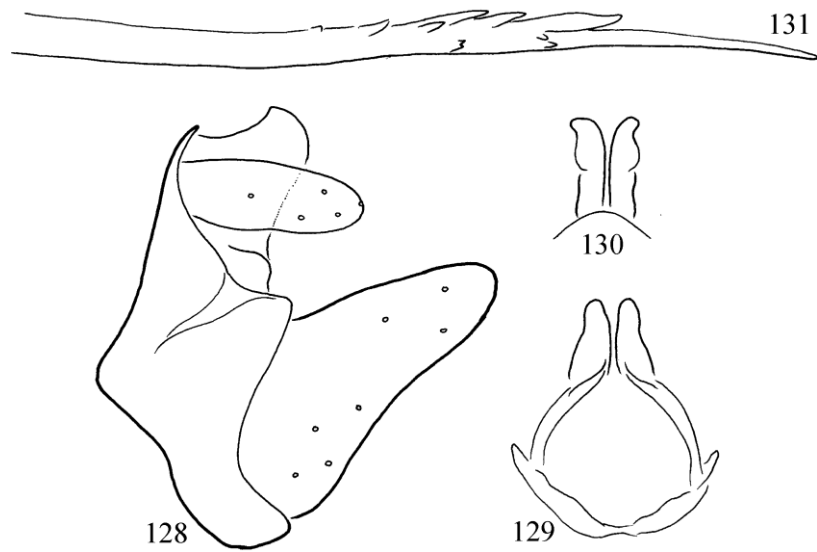
Figures 128–131. *Drusus erimanthos* Malicky, 1992. Paratype: 128 = male genitalia in left lateral view, 129 = paraproct in caudal view, 130 = apex of the apical arms of the dorsal branches of paraproct in dorsal view, 131 = paramere in left lateral view.
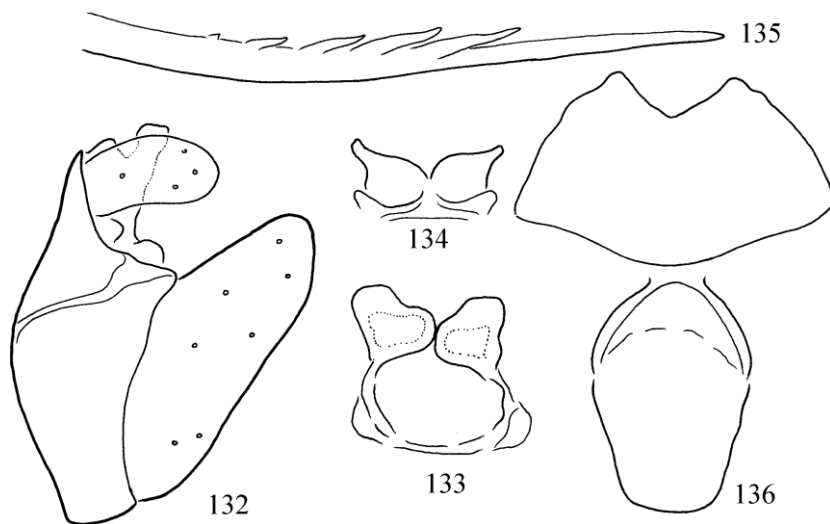
Figures 132–136. *Drusus franzressli* Malicky, 1986. 132 = male genitalia in left lateral view, 133 = paraproct in caudal view, 134 = apex of the apical arms of the dorsal branches of paraproct in dorsal view, 135 = paramere in left lateral view, 136 = tergite IX and vaginal sclerite profile in dorsal view.

Diagnosis. Malicky, 1986: 14–16, "Diese Art Fallt durch den Bau der Dörnchenzone des 8. Tergits sofort auf. Sie ahnelt verschidenen von der Balkanhalbinsel bekannten Arten wie zum Beispiel *bosnicus*, aber wahrscheinlich auch *klapaleki*, *radovanovic*i und *ramae*."

Additional diagnosis. Paramere pattern clearly relates this species to the *D. annulatus* species group and has no relations to *D. bosnicus*, *D. klapaleki*, *D. radovanovici* and *D. ramae* of the *D. bosnicus* species group. The hook formation on the apical arms of the dorsal branch somehow

modified and as a result the apical arm of the dorsal branch broad shaped in apical view.

Drusus rizeiensis Sipahiler, 1986

(Figures 137–140)

Drusus rizeiensis Sipahiler, 1986: 115–116, "Holotype ♂ and paratype ♂: Turkey, Rize, Camlihemsin, Ayder, Kaler, 1900 m. 17. VII. 1984, leg and coll. Sipahiler."

Material examined. **Turkey**, Rize province, Cat SW of Camlihemsin-springs, brooks 40°51.6'N 40°56.6'E, ca. 1290 m, 9. VII. 2013, leg. P. Chvojka (2 males, OPC).

Diagnosis. Sipahiler 1986: 115–116, "This species is closely related to *D. biguttatus* Pictet. The main differences between the two species are seen in several parts of the male genitalia. The spinulose zone of the tergite 8 of *D. biguttatus* is really different in shape and the length of this zone is shorter than *D. rizeiensis*. Superior appendages of *D. rizeiensis* larger than the related species. Dorsally intermediate appendages of *D. biguttatus* are close to each other and rather thick. But in *D. rizeiensis* they are divergent and thin. Inferior appendages of *D. biguttatus* are nearly parallel with their outer margin. In *D. rizeiensis* they diverge lateral side. Parameres of *D. biguttatus* have curved spines before apex. Such spines are not found on the parameres of *D. rizeiensis*. In addition to these differences in genitalia, the male of *D. rizeiensis* is paler than *D. biguttatus* which is nearly dark brown. And the spur formula of *D. rizeiensis* is 1.3.3 but in *D. biguttatus* is 1.2.2."

Additional diagnosis. This species was related by Sipahiler (1986) to *D. biguttatus*, a species belongs to the *D. mixtus* species group and to the *D. mixtus* species complex. However the paramere pattern clearly relate *D. rizeiensis* to the *D. annulatus* species group and its paraproct shape to the *D. trifidus* species complex. The differences between the paramere structure of *D. rizeiensis* and *D. biguttatus* was already recognised by Sipahiler (1986).
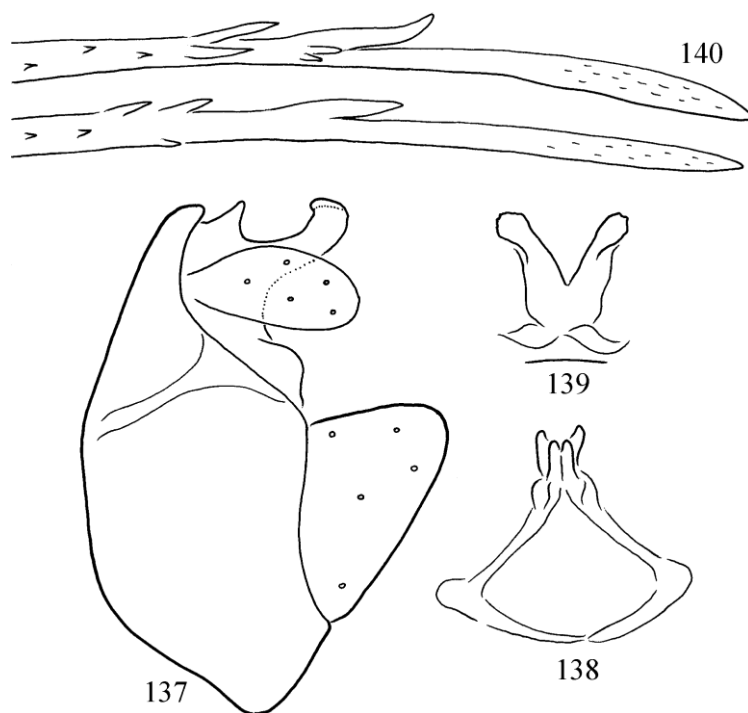
Figures 137–140. *Drusus rizeiensis* Sipahiler 1986. 137 = male genitalia in left lateral view, 138 = paraproct in caudal view, 139 = apex of the apical arms of the dorsal branches of paraproct in dorsal view, 140 = parameres in left lateral view.

Drusus trifidus (McLachlan, 1868)

(Figures 141–145)

Halesus (*Drusus*) *trifidus* McLachlan, 1868: 294, "Departement de l'Aube, France, 1 ♂."

Drusus trifidus (McLachlan, 1868): McLachlan 1876: 171–172, "My original example was recorded as from the Départemen de l'Aube, France, I have since seen the species from, Switzerland, Tyrol, Upper Austria"

Drusus trifidus (McLachlan, 1868): Schmid 1956: 51, "Cette espèce habite la plaine et les altitudes médiocres; elle pénétre dans les Alpes jusqu'a 1.800 m environ. Son aire de répartition forme une large bande à travers l'Europe moyenne: France, Suisse, Allemagne centrale et méridionale, Autriche, Bohéme et Roumanie."

Material examined. **Austria**, Mondsee, 8. VII. 1986, light leg. J. Oláh (2 males, OPC). **Czech Republic**, E Bohemia, Orlické hory Mts, Orlické Zahori, limnocren, (680 m), 14. VII. 1995, leg. P. Chvojka (3 males, 3 females; OPC). S Bohemia, Sumava Mts, pool nr. Hamersky brook (1040 m), 27. VII. 1991, leg. P. Chvojka (3 males, OPC). **Hungary**, Aggtelek National Park, Lófej spring, 31. V. 1962, singled daytime, leg. J. Oláh & Z. Varga (first record in Hungary with the present borders: 7 males, 3 females; OPC). Hungary, Aggtelek National Park, Small Tohonya spring below the VITUKI Research House, 9. V. 1983, leg. J. Oláh & Z. Varga (light: 1 male, singled daytime: 10 males; OPC). Hungary, Aggtelek National Park, Patkós spring in Ménes valley, 4. VII. 1985, singled leg. J. Oláh & Z. Varga (1 male, OPC). Hungary, Aggtelek National Park, spring along Ménes stream, 5. VII. 1985, singled leg. J. Oláh & Z. Varga (4 males, 6 females; OPC). Hungary, Borsod-Abaúj-Zemplén, Aggtelek National Park, Ménes stream, below the Medvekert springs, N48°31.994' E20°35.618', 355 m, 20. V. 2015, leg. A. Huber, T. Kovács, D. Murányi & G. Puskás (5 males, 6 females; OPC). **Poland**, High Tatra Mts., Chocholowska Valley, 22. VIII. 1986 leg. J. Oláh (31 males, 6 females; OPC). Poland, High Tatra Mts., Chocholowska Valley, Wywierzysko karstic spring, 21. VIII. 2009 leg. J. Oláh (11 males, 3 females; OPC). Poland, High Tatra Mts., Polana Bialego Potoka, 20-21. VIII. 2009 leg. J. Oláh (12 males, 2 females; OPC). **Romania**, Zavoi, Sinaia, 17. VII. 1954, leg. C. Ciubuc (2 males, OPC). **Slovakia**, Presov region, High Tatra Mts. Tatransky NP, Podbanske, Bela River, N49°08.647' E19°54.424', 945 m, 20. IX. 2014, leg. D. Murányi et al (1 female, OPC). Slovakia, Presov region, High Tatra Mts. Tatransky NP, Ticha dolina, Tributary of Tichy stream, N49°09.759' E19°55.366', 1005 m, 20. IX. 2014, leg. D. Murányi et al (10 males, OPC). High Tatra Mts., Biela voda river above Lysa Polana, (980 m), 6. VII. 1989, leg. P. Chvojka (6 males, 2 females; OPC). High Tatra Mts., Nizné Temnos mrecinské pleso lake, (1674 m), 29. IX. 1993, leg. P. Chvojka (2 males, 3 females; NMPC). Lower Tatra Mts., Biela Voda, 22. VII. 1966, singled leg. J. Oláh (1 male, 1 female; OPC).

Diagnosis. McLachlan, 1876:172, "There should be no difficulty in recognising this species, from the very singular form of the last dorsal segment of the ♂, the small size, peculiar and uniform coloration, dense pubescence of the anterior-wings, neuration."
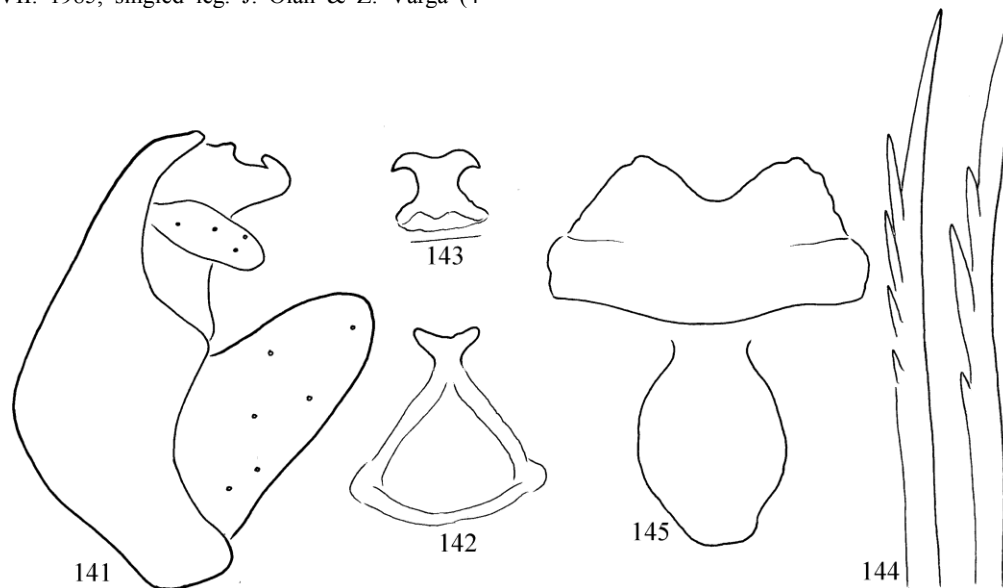
Figures 141–145. *Drusus trifidus* (McLachlan, 1868). 141 = male genitalia in left lateral view, 142 = paraproct in caudal view, 143 = apex of the apical arms of the dorsal branches of paraproct in dorsal view, 144 = paramere in left lateral view, 145 = tergite IX and vaginal sclerite profile in dorsal view.

Schmid 1956:51, "*Dr. trifidus* est la plus petit espèce du genre; elle est caractérisée par les trois lobes apicaux de VIIIe tergite très proéminents, par ses petits appendices supérieurs et ses appendices inférieurs saillants, mais obtus; elle est isolée dans le cadre du groupe; son plus proche parent est *brunneus*."

Additional diagnosis. Genital structure relates this species to *D. brunneus*, but spinulose area is trilobed; general colour pale, not dark and the apical paramere shaft is simple, not dilated and not pilosed.

Drusus caucasicus species group

Species group of the inflated paramere terminalia! *Drusus caucasicus* species group is integrated through ancestral divergence by the recumbent primary spine and secondary spines reduced in size and by inflated apical paramere shaft. This species group is characterized by further spine pattern reduction on paramere and by specialised enlargement of the paramere terminalia by inflation. Primary spine present, not perpendicular, decumbent or recumbent, seldom reduced to some vestigial structure. Secondary spines mostly present. Tercier spines seldom present. Paramere terminalia enlarged, inflated, expanded, usually thicker than the paramere shaft. Surface of the terminalia frequently piliferous, tomentose pubescent, covered with fine hairs. Top of terminalia sometimes modified into an individualised pin tip structure. Paraproct, especially the ventral arm, is strongly developed and forms a closed ring around anus with very produced triangularly shaped ventrolateral corner. The delineation of the two species complexes in the species group is based on divergenses in the entire paraproct architecture.

(1) In the *Drusus simplex* species complex the dorsal (internal, apical, horizontal) branch of the paraproct is organised into a pair of dorsolateral variously shaped and elongated knobby process;
(2) In the *Drusus caucasicus* species complex parts of the dorsal branch of the paraproct is fused to cerci as a setaless mostly digitiform process.

With this fusion the *Drusus caucasicus* species complex exhibit the most diverged character state of paraproct structure. This advanced apomorphy in the genus is realised in the partial detachment of dorsal arm of the paraproct from the ventral (inferior, basal, vertical) structure of the paraproct and in the fusion to the basomesal region of the cercus.

Taxa diverged by subtle, but stable divergences both in the *Drusus caucasicus* and *Drusus simplex* species complexes. The few available specimens from a very limited number of mountain ranges indicate a remarkable potential of high diversity of both comlexes in this eastern species group. However, more detailed population sampling and fine structure analysis of variability ranges will confirm and multiply the recognised divergences, distribution and contact/cline zones of taxa.

Yellow, stramineous or light brown animals populating the most eastern part of the distributional area of Drusinae subfamily from Turkey through the Caucasus to the Iranian Elburz and Zagros Mountain ranges. *Drusus caucasicus* species group is comprised of 18 species.

Drusus caucasicus species complex

Paramere characterized by inflated terminalia and the setaless dorsal arm of the paraproct is fused to the dorsomesal region of the setose cerci resulting in an apparent bilobed shape of the cerci. The outer plate-shaped setose lobe is the genuine cercus and the digitiform setaless inner process is the fused dorsal arm of the paraproct. Variously retained suture discernible between these fused structures of somite (paraproct) and podite (cercus) origin of the XIth abdominal segment. The discovered species of this complex populate eastern Turkey, Caucasus and Hamadan Province in western Iran. *Drusus caucasicus* species complex is comprised of seven species: *baksan* sp. nov., *bayburthii*, *botos* sp. nov., *caucasicus*, *fuesunae*, *kazanciae*, *ketes* sp. nov.

Drusus baksan Oláh, sp. nov.

(Figures 146–150)

Material examined. Holotype: Central Caucasus (northern slopes, basin of Baksan River), Dongusorun (right confluence of Baksan), between the mouth (2000 m) and the Dongusorun Lake (2500 m), 24. VI. 1974 leg. Mr. and Mrs Joost (1 male, OPC). Allotype: The Central Caucasus (northern slopes, basin of Baksan river), Baksan River, above the hotel "Itkol", 30. VI. 1972, leg. Mr. and Mrs. Joost, (1 female, OPC).

Diagnosis and description. Light brown animal with forewing length of 12 mm. Most close to *Drusus caucasicus* but differs by having the inflated terminalia on paramere more broad apicad with a subapical constriction, more tomentose, especially at and just after the principal spine region; the primary spine much more developed and the two secondary spines anterad of the primary spine absent; terciary spines present and numerous. The mesal arm of the bilobed fused structure, that is the setaless fused dorsal arm of the paraproct is sagittaly flat, arching in lateral view and straight, not S-shaped in caudal view.

Female genitalia. Tergite of segment IX forming short tube, open ventrally, with short and broad excision in dorsal view; its apical lateral lobes tiny, tapering in dorsal view; the lateral setose lobe of sternite IX rounded and continuing into setaless less pigmented downward section. Segment X membranous and embedded inside segment IX and encircling anus; supragenital plate of segment X well-developed and subquadrangular both in lateral and dorsal view, its apical margin with above middle hump. Median lobe of the vulvar scale (lower vaginal lip) present. Dorsal profile of the vaginal sclerite complex less narrowing anterad.

Etymology. named after the type locality.

Drusus bayburti Cakin, 1983

(Figures 151–155)

Drusus bayburti Cakin, 1983: 242–243, "Holotype ♂, allotype ♀ and 23 paratypes (8♂♂ + 15♀♀): Gümüshane, Bayburt, Yoncali, 3000 m, 30. VII. 1981, leg. N. Kazanci, coll. Cakin."

Materialexamined. **Turkey**, Van Province, Yuksekova Mts., 2.5 km E of Guseldere Pass, 38^o11'N 43^o56'E, 2600 m, 2.VII.2002, leg. B. Benedek & T. Csővári (1 male, OPC). Van Province, Yuksekova Mts., 2.5 km E of Guseldere Pass, 38^o11'N 43^o56'E, 2600 m, 5.VII.2002, leg. B. Benedek & T. Csővári (3 males, OPC).

Diagnosis. Cakin, 1983: 245, "Closely related to *D. caucasicus* Ulmer. (Schmid 1956), especially by the concavity of the 8th tergite, small intermediate appendages and by the superior appendages consisiting of two pieces."
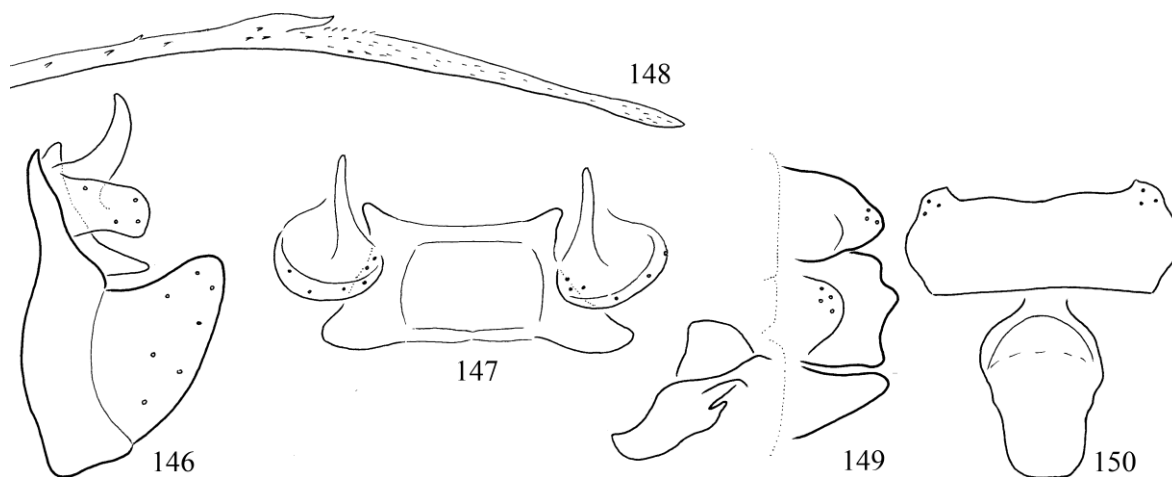
Figures 146–150. *Drusus baksan* Oláh, sp. nov. Holotype: 146 = male genitalia in left lateral view, 147 = paraproct with cerci in caudal view, 148 = paramere in left lateral view. Allotype: 149 = female genitalia with vaginal sclerite complex in lateral view, 150 = tergite IX and vaginal sclerite profile in dorsal view.
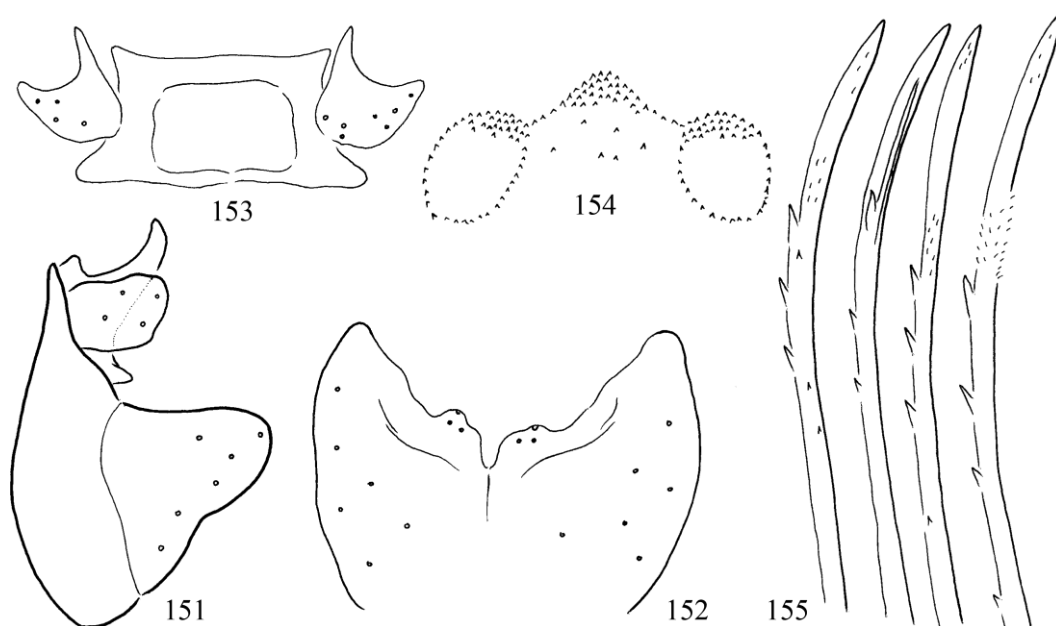
Figures 151–155. *Drusus bayburti* Cakin, 1983. 151 = male genitalia in left lateral view, 152 = gonopods in ventral view 153 = paraproct with cerci in caudal view, 154 = pegged spinulose area on tergite VIII, 155 = infrapopulational paramere variability in left lateral view.

Re-diagnosed. Most close to *Drusus ketes* sp. nov. but differs by having principal spine on paramere delicate, not robust; secondary paramere spines 2–3, not single; the outer arm of the bilobed fused structure, that is the setose cerci slender, not broad in caudal view.

Drusus botos Olah, sp. nov.

(Figures 156–168)

Materialexamined. Holotype: **Turkey**, Agri Province, Karasu-Aras Mts., 5 km SE of Sarican, 39º47'N 42º28'E, 2000 m, 10.VII.2002, leg. B. Benedek & T. Csővári (1 male, OPC). Allotype: same as holotype (1 female, OPC). Paratypes: same as holotype (2 males, 1 female; OPC). Agri Province, Karasu-Aras Mts., 5 km SE of Sarican, 39º47'N 42º28'E, 2000 m, 7-8.VII.2002, leg. B. Benedek & T. Csővári (2 males, 1 female; OPC). Erzerum Province, 8 km NW of Kop Pass, 40º02'N 40º28'E, 2000 m, 11.VII.2002, leg. B. Benedek & T. Csővári (1 male, 1 female; OPC).

Diagnosis and description. Light brown animal with forewing length of 12 mm. Most close to *Drusus caucasicus* but differs by having the inflated terminalia on paramere more broad apicad, almost club-shaped and more tomentose, less in-flated at speciemen form Erzerum. The mesal arm of the bilobed fused structure, that is the setaless fused dorsal arm of the paraproct is upward directed straight rod-shaped, not mesad curving spine-shaped. Paraproct divergence is similar at specimens both from Agri and Erzerum Provinces.

Female genitalia. Tergite of segment IX forming short tube, open ventrally, with short and broad excision in dorsal view; its apical lateral lobes tiny, tapering in dorsal view; the lateral setose lobe of sternite IX rounded elongate and continuing into setaless less pigmented downward section. Segment X membranous and embedded inside segment IX and encircling anus; supragenital plate of segment X well-developed and quadrangular both in lateral and dorsal view. Median lobe of the vulvar scale (lower vaginal lip) present. Dorsal profile of the vaginal sclerite complex narrowing anterad. Less narrowing at one specimen!

Etymology.botos, rod-like in Hungarian, refers to the diverged rod-like shape of the fused dorsal arm of the paraproct.
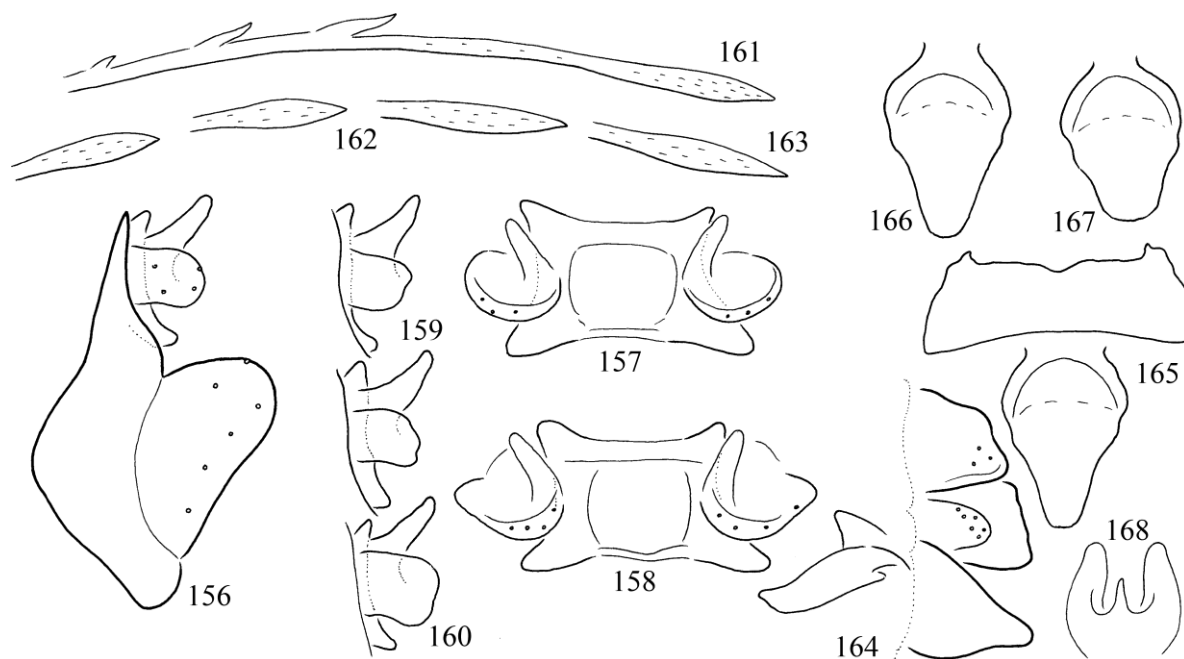
Figures 156–168. *Drusus botos* Olah sp. nov. 156 = holotype male genitalia in left lateral view, 157 = holotype paraproct with cerci in caudal view, 158 = paratype paraproct from Erzerum Province with cerci in caudal view, 159 = paraproct with cercus of paratypes from Agri Province in left lateral view, 160 = paraproct with cercus of paratype from Erzerum Province in left lateral view, 161 = holotype paramere in left lateral view, 162 = dilated paramere terminal of 3 paratypes from Agri Province in left lateral view, 163 = dilated paramere terminal of paratype from Erzerum Province in left lateral view, 164 = allotype female genitalia with vaginal sclerite complex in lateral view, 165 = allotype tergite IX and vaginal sclerite profile in dorsal view, 166 = dorsal profile of paratype vaginal sclerite complex from Agri Province, 167 = dorsal profile of paratype vaginal sclerite complex from Erzerum Province, 168 = allotype vulvar scale in ventral view.

Drusus caucasicus Ulmer, 1907

(Figures 169–175)

Drusus caucasicus Ulmer, 1907: 50–52. "Kaukasus, Passanaur bis Lars, 8–11. VII. 1900, leg. F. Karsch 2 males (Berliner Museum)."

Drusus sp. Kumanski 1980:44–45. The Western Caucasus (northern slopes, basin of Teberda river). The town of Teberda (1300 m a.s.l.), 12. VII. 1972 leg. D. Braasch, 16 females. The Central Caucasus (northern slopes, basin of Baksan river), Baksan River, above the hotel "Itkol", 30. VI. 1972, leg. Mr. and Mrs. Joost, 1 female. The Central Caucasus (northern slopes, basin of Baksan river), Adyrsu (right confluent of Baksan), between the ravine (1650 m a.s.l.) and the mountainer lager "Ullo-tau" (2400 m a.s.l.), 28. IX. 1974, leg. Mr. and Mrs. Joost, 1 female. Misidentification!

Drusus caucasicus Ulmer. Kumanski 1980:43. The Central Caucasus (northern slopes, basin of Baksan river), Dongusorun (right confluent of Baksan) between the mouth (2000 m a.s.l.) and the Dongusorun Lake (2500 m a.s.l.), 24. VI. 1974, leg. Mr. and Mrs. Joost, 1 male.

Material examined. **Georgia**, Svanetia, small stream at River Inguri, 3.VII.1957, leg. L. Zhiltzova (2 males, OPC).

Russia, Teberda, Teberda stream, light 22.VII.1954, leg. L. Zhiltzova (1 male, OPC). Teberda, Teberda stream, light 2.VIII.1954, leg. L. Zhiltzova (2 males, 38 females, 4 females MCSNBG, OPC).

Diagnosis. Ulmer, 1907:50, "Farbung wie bei den hellen Arten dieser Gattung (*Drusus discolor* Rambur, etc.), eher noch heller, wie bei *Metanoea flavipennis* Pictet."

Additional diagnosis. Most close to *Drusus botos sp. nov.* but differs by having the inflated terminalia on paramere less broad apicad and less tomentose. The mesal arm of the bilobed fused structure, that is the setaless fused dorsal arm of the paraproct is mesad curving spine-shaped, not upward directed straight rod-shaped.

Distribution. Examined specimens have been collected in the western ranges of the Caucasus Mts.: Teberda (Donbay), Svanetia, Dongusorun (Elbrus) from the upstream regions of the Teberda, Baksan and Inguri river valleys.

Drusus fuesunae Malicky, 1974

(Figures 176–179)

Drusus fuesunae Malicky, 1986: 2–4, "Material – Holotypus ♂ und mehrere Paratypen ♂ und ♀: Türkei, Provinz Trabzon, 40º39'N, 39º24'E, Karadeniz daglari, Zigana gecidi, 1600 m, 7. IX. 1985, H.Hacker leg. – In meiner Sammlung."

Material examined. **Turkey**, Prov. Irabzon, Karadeniz Gaglari, Zigana Gecidi, 1600 m, N40º 39' E39º 24', 7. IX. 1985, leg. Herm. Hacker(1 male, 1 female; OPC).

Diagnosis. Malicky, 1986: 2–4, "Diese neue Art ist insofern bemerkenswert, als sie die Tendenz der Reduction der mittleren Anhange in der *caucasicus*-Gruppe fortsetzt; sie sind bei ihr so weit reduziert, dass ihre Funktion von den Innenteilen der oberen Anhange übernommen wird."

Additional diagnosis. Most diverged in the species complex. Paramere principal spine produced, secondary spine single. Paramere terminalia less inflated and less pubescence.The top of paramere terminalia modified into a specialised pin-tipped apex. The mesal arm of the bilobed fused structure, that is the setaless fused dorsal arm of the paraproct is most elongated.

Drusus kazanciae Cakin, 1983

Drusus kazanciae Cakin, 1983: 243–245, "Holotype ♂ and allotype ♀: (**Turkey**) Hakkari, Bercalan, 3250 m, 17. VIII. 1981, leg. N. Kazanci, coll. Cakin."

MaterialExamined. No specimen has been examined. The here established taxonomic position is based on the species description and drawings. Several personal or team trials to borrow type material or any specimens from the author remained unanswered. Further study is required on paramere fine structure.

Diagnosis. Cakin, 1983:245, "Closely related to *D. caucasicus* Ulmer. (Schmid 1956), especially by the concavity of the 8th tergite, small intermediate appendages and by the superior appendages consisiting of two pieces."

Additional diagnosis. The species was placed into the *Drusus caucasicus* species complex by the original diagnosis as well as by the analysis of the original drawings.
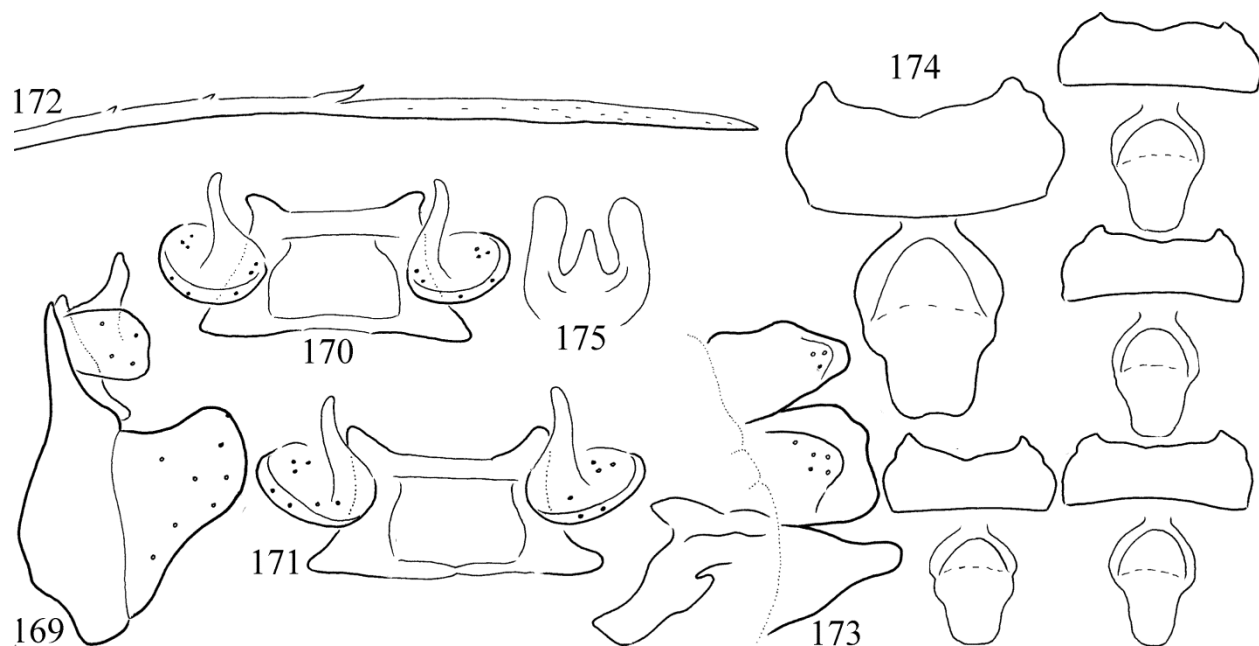
Figures 169–172. *Drusus caucasicus* Ulmer, 1907. 169 = male genitalia from Teberda in left lateral view, 170 = paraproct with cerci from Teberda in caudal view, 171 = paraproct with cerci from Svanetia in caudal view, 172 = paramere from Teberda in left lateral view, 173 = female genitalia with vaginal sclerite complex from Teberda in lateral view, 174 =tergite IX and dorsal profile of vaginal sclerite complex from Teberda in dorsal view, 175 = vulvar scale in ventral view.
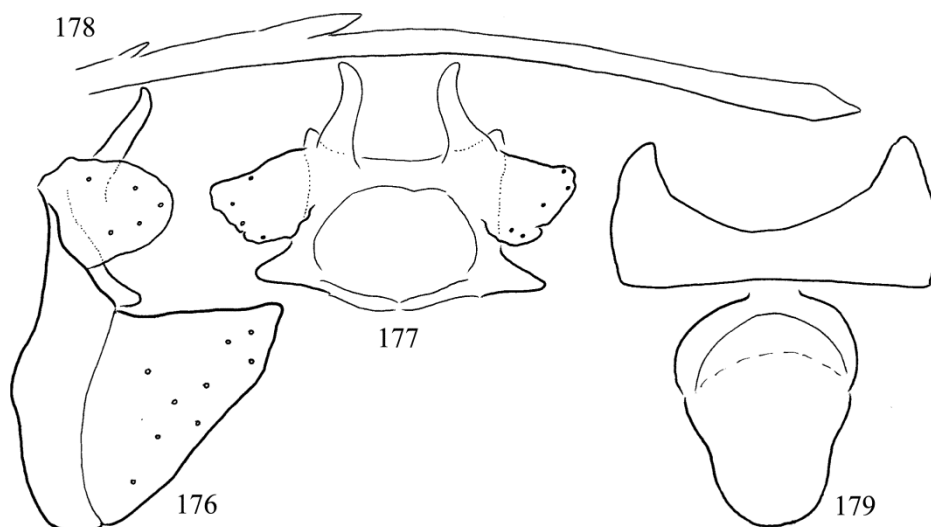
Figures 176−179. *Drusus fuesunae* Malicky, 1974. 176 = male genitalia in left lateral view, 177 = paraproct with cerci in caudal view, 178 = paramere in left lateral view, 179 = tergite IX and vaginal sclerite profile in dorsal view.

Drusus ketes Oláh & Mey, sp. nov.

(Figures 180–185)

Material examined. Holotype male. **Iran**, Hamadan Province, Hamedan, Moradbeyk Valley, 21−22. VI. 2004 (1 male ZMB). Paratypes: same as holotype (1 male, ZMB; 2 males, OPC).

Diagnosis and description. Light brown animal with forewing length of 12 mm. Most close to *Drusus bayburtii* sp. nov. but differs by having principal spine on paramere robust, not delicate; secondary paramere spines single, not 2−3; the outer arm of the bilobed fused structure, that is the setose cerci rounded broad, not slender spine-like tapering in caudal view. The pattern of the spinulose area on tergite VIII different.

Etymology. ketes, dubious or doubtful in Hungarian, refers to the delicate divergences in the structure of speciation traits of paraproct and paramere.

Drusus simplex species complex

The setaless dorsal arm of the paraproct is shifted dorsolaterad and produced into abbreviated or elongated variously shaped knobby structure. Paramere terminalia inflated and usually rather tomentose. With routine structure analysis all the specimens from the Caucasus and from Iran has been determined earlier as *Drusus simplex* (Schmid1956; Kumanski 1980b). Applying the fine structure analysis of speciation trait we have detected stable and consistent divergences in the structure of the paraproct and paramere directly involved in copulation processes and we have realised that there are multitude of undiscovered species in this complex in various isolated mountain ranges.

Until the discovery of the speciation traits there was no attention directed to *Drusus* paramere and no special care was paid to the fine structure of the paraproct. We relied entirely on gross morphology and the subtle deviations detected in fine structures were considered simply either as intrapopulational or interpopulational variations. Emerging currents in phenomics of the new taxonomy emphasize the potential of the so called subtle phenomic divergences in species delimitation. Delicate divergences in speciation traits proved to be very stable and consistent in several stenophylacini and chaetopterygini genera. It's getting more confirmed that these easily visible shape divergences are the result of adaptive mechanisms in early stages of speciation processes powered by sexual selection or integration and realised in reproductive isolation (Oláh *et al.* 2015). We have recorded simply empirically, without any model calculations of geometric morphometry, subtle, but stable diver-
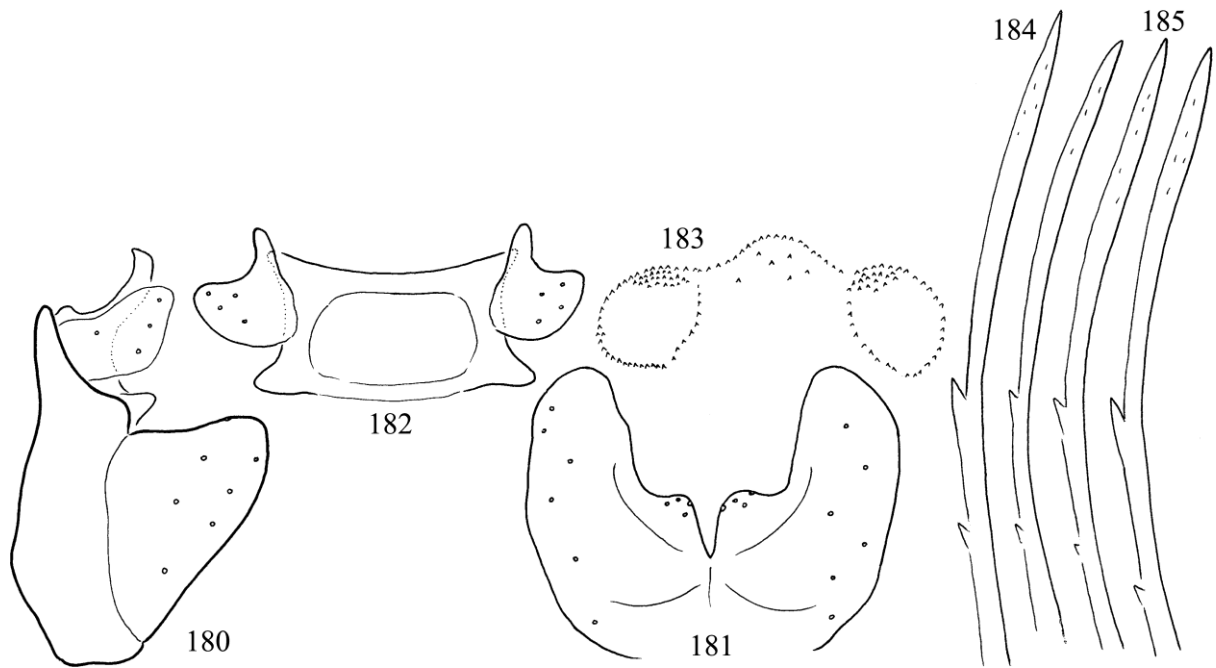
Figures 180−185. *Drusus ketes* Oláh & Mey, sp. nov. Holotype: 180 = male genitalia in left lateral view, 181 = gonopods in ventral view, 182 = paraproct with cerci in caudal view, 183 = pegged spinulose area on tergite VIII in dorsal view, 184 = paramere in left lateral view, 185 = parameres of paratypes in left lateral view.
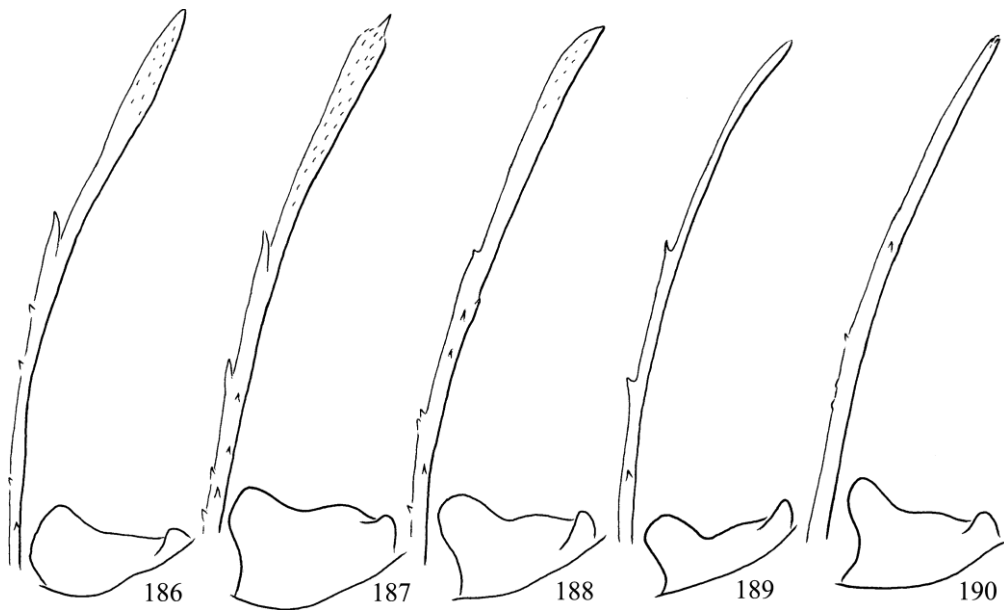
Figures 186−190. Comparative interspecific matrix indicates the subtle divergences in the lateral profile of the the paraproct and the paramere at Drusus species with abbreviated dorsal arm of the paraproct: 186 = *armeniacus*, 187 = *bolhos*, 188 = *polur*, 189 = *aranos*, 190 = *iranicus*.
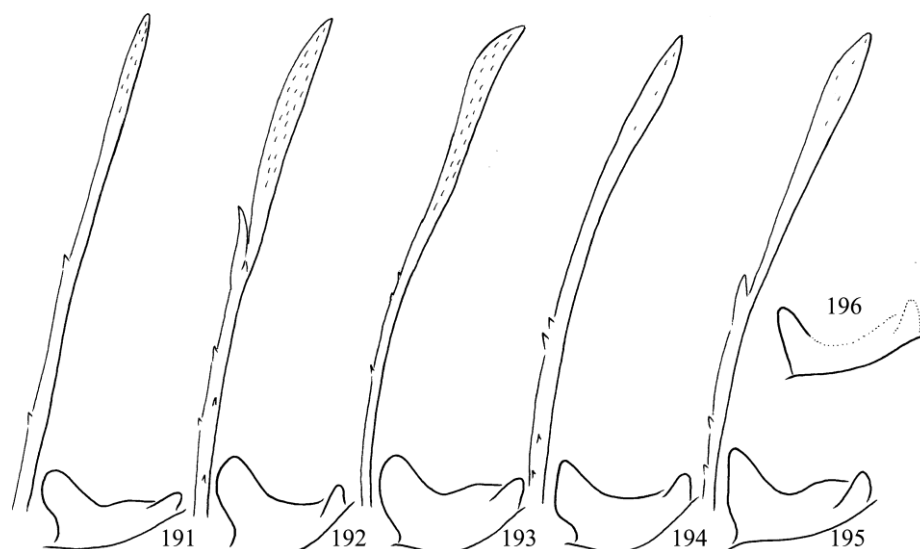
Figures 191−196. Comparative interspecific matrix indicates the subtle divergences in the lateral profile of the the paraproct and the paramere at *Drusus* species with elongated dorsal arm of the paraproct: 191 = *hassankif*, 192 = *quruk* 193 = *zanus*, 194 = *nultas*, 195 = *barajan*, 196 = *simplex*.

gences also in *Drusus discolor* species complex (Oláh *et al.* 2016). Even more subtle morphological divergences, which are not visible by empirical fine structure analysis, but detectable by tedious virtual procedures of geometric morphometry, have been documented with complex genetic architectures at various *Drosophila* species.

In the *Drusus simplex* species complex it has been confirmed again that the taxonomic application of speciation trait divergences which are tiny, delicate, subtle or visible only by geometric morphometry could be very powerful in delimiting taxa, especially in the early stages of divergences. In this complex the diverged trait intrapopulation matrices indicate stable fine structures in speciation trait of paraproct at the measurable species, those which have population sampling of at least 3 or 6 specimens. Similarly, as a rule, the fine architecture of paramere was stable, but accompanied with consistent individual variation ranges and characterized by frequent fluctuating asymmetry of developmental instabilities. The comparative interspecific matrices indicate the subtle divergences in the lateral profile of the the paraproct and the paramere both at species with abbreviated (Figs. 186–190) or with elongated (Figs.191–196) dorsal arm of the paraproct. There

is a discernible trend, but needs further studies, of a complementing effect in divergence distances between paraproct and paramere. Species having small paraproct divergence develop larger paramere divergences.

Every sampled mountain ranges has produced an endemic incipient sibling species of this complex. It seems that the number of species depends on how many isolated mountain ranges are we able to sample. Unfortunately in the present practice of the resource-deprived taxonomy and under the dominating pharisaic biodiversity scenario there is no resource for valid biodiversity population sampling. We had to follow our principle of „put together" what we have (Oláh *et al.* 2015) in order to substitute somehow the missing capacity of the proper population sampling. All the available historical specimens have been loaned from several museums. In spite of the limited historical collecting effort as well as the total lack of recent collections the high biodiversity potential of the region is demostrated by the fact that based on this small sample we could distinguish and describe here ten new species. We do belive that this is only a small fraction of the total diversity of this species complex in the Caucasian and Iranian mountain ranges. This is a conservative esti-

mate! With only a limited sampling effort and in a much smaller area around Albania there have been discovered and described eighteen *Drusus* species only in the single *Drusus bosnicus* species group. In Bosnia eight species were described in the *Drusus bosnicus* species complex.

Drusus simpex species complex is comprised of eleven species: *aranos* sp. nov., *armeniacus* sp. nov., *barajan* sp. nov., *bolhos* sp. nov., *hassankif* sp. nov., *iranicus* sp. nov., *nultas* sp. nov., *polur* sp. nov., *quruk* sp. nov., *simplex* Martynov, 1927, and *zanus* sp. nov.

Drusus aranos Oláh, sp. ov.

(Figures 197−206)

Material examined. Holotype: **Russia**,Teberda, Teberda stream, light, 22.VII.1954, leg. L. Zhiltzova (1 male, OPC). Allotype: Teberda, Teberda stream, light 2.VIII.1954, leg. L. Zhiltzova (1 female, OPC). Paratypes: Teberda, Teberda stream, light 2.VIII.1954, leg. L. Zhiltzova (2 females,OPC). Teberda, Muhu River, light, 18. VIII. 1954, leg. E. Tetsoeva (9 males, 16 females, OPC). Teberda, Muhu River, light, 21. VIII. 1954, leg. E. Tetsoeva (3 males, 2 females, OPC). Teberda, Muhu River, light, 22. VIII. 1954, leg. E. Tetsoeva (8 males, 28 females, OPC). Teberda,1300 m, 16. VIII. 1974 (1 female, OPC).

Diagnosis and description. Light brown animal with forewing length of 12 mm. Intermediate between species with abbreviated and elongated dorsal arm of the paraproct. Most close to *Drusus polur* sp. nov. but differs by having T-shaped spinulose pattern on tergite VIII, not invert U-shaped; paramere terminalia less inflated; principal spine on paramere small, but distinct; tercier spines lacking or few. Dorsal arm of the paraproct with more slender lateral, but more robust caudal profile. Tergite IX of female with a tendency of bipartite lateral lobe in dorsal view, as well represented on allotype. Dorsal profile of the vaginal sclerite complex less narrowing anterad.
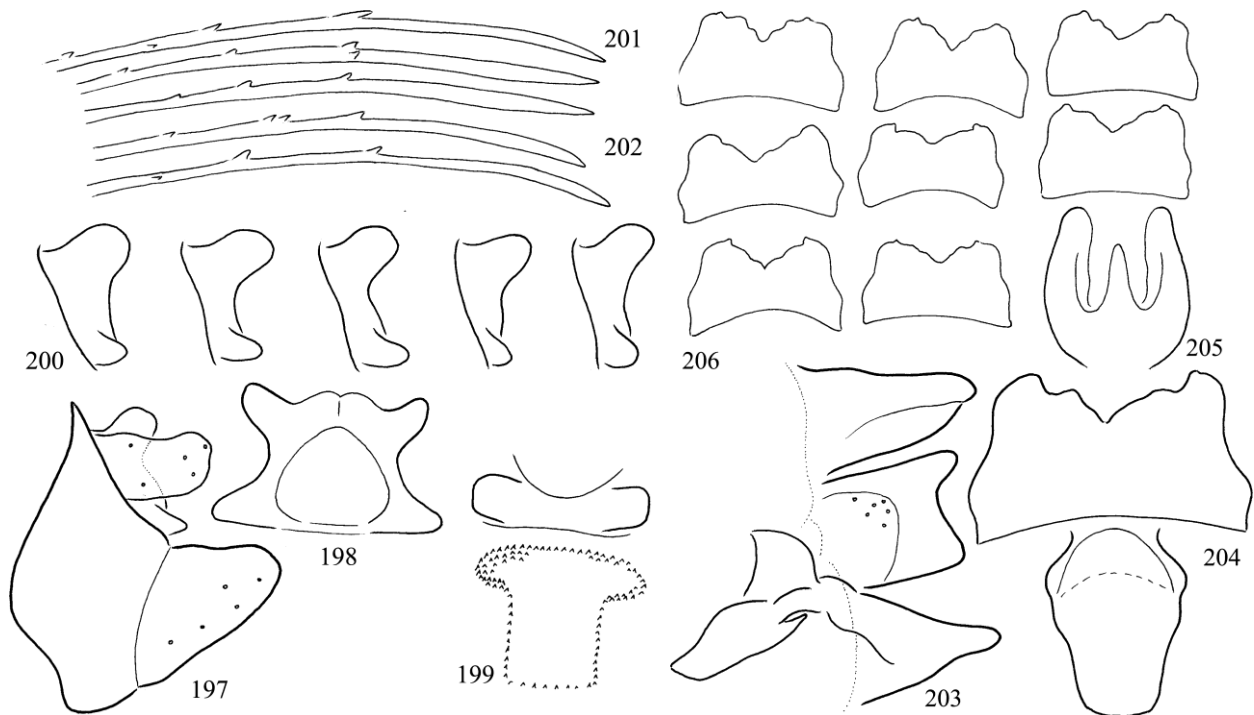
Figures 197−206. *Drusus aranos* Oláh sp. nov. Holotype: 197 = male genitalia in left lateral view, 198 = paraproct in caudal view, 199 = apical arms of the dorsal branches of paraproct and the pegged spinulose area on tergite VIII in dorsal view, 200 = paraproct of paratypes in lateral view, 201 = holotype paramere in left lateral view, 202 = parameres of paratypes in left lateral view. Allotype: 203 = female genitalia with vaginal sclerite complex in lateral view 204 = tergite IX and dorsal profile of vaginal sclerite complex from in dorsal view 205 = vulvar scale, 206 = tergite IX of paratypes in dorsal view.

Female genitalia. Tergite of segment IX forming short tube, open ventrally, with V-shaped mesal excision and bipartite apical margin on the lateral lobes in dorsal view; its apical tip on lateral lobes tiny or absent; the lateral setose lobe of sternite IX rounded elongate and continuing into setaless less pigmented downward section. Segment X membranous and embedded inside segment IX and encircling anus; supragenital plate of segment X well-developed and quadrangular in lateral view with concave apical margin. Median lobe of the vulvar scale (lower vaginal lip) present and long triangular, acute-angled. Dorsal profile of the vaginal sclerite complex slightly narrowing anterad.

Etymology.aranos, from "aranyos" gold-like in Hungarian, refers to the golden wing color.

Drusus armeniacus Oláh, sp. nov.

(Figures 207−210)

Material examined. Holotype male: **Armenia**, Idzevan, 1500 m, 23. IX. 1983, leg. Z. Varga, (1 male, OPC).

Diagnosis and description. Light brown animal with forewing length of 10 mm. With its
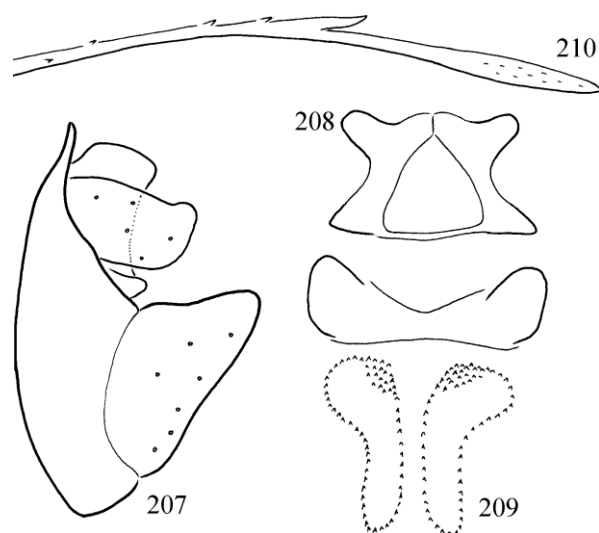
Figures 207–210. *Drusus armeniacus* Oláh sp. nov. Holotype: 207 = male genitalia in left lateral view, 208 = paraproct in caudal view, 209 = apical arms of the dorsal branches of paraproct and the pegged spinulose area on tergite VIII in dorsal view, 210 = paramere in left lateral view.

shortest arm belongs to species with abbreviated dorsal arm of the paraproct. Most close to *Drusus bolhos sp. nov.* but differs by having completely separated horizontal bands of spinulose area on tergite VIII; paramere terminalia inflated, very much tomentose and its top is modified into a pin-tipped apex; principal spine on paramere is similar to that of *D. bolhos*, the second large-sized spines more anterad lacking; tercier spines are few. Dorsal arm of the paraproct short and broad in lateral and robust, not slender in apical view.

Etymology. Named after country of collection.

Drusus barajan Oláh, sp. nov.

(Figures 211–217)

Material examined. Holotype male: **Iran** (Maz), Barajan, 15. IX. 1955, leg. F. Schmid, (1 male, CMZL). Allotype: (1 female, CMZL)

Diagnosis and description. Light brown animal with forewing length of 11 mm. Belongs to species with elongated dorsal arm of the paraproct. Most close to *Drusus nultas* sp. nov. but differs by having larger and more compact spinulose area on tergite VIII; paramere terminalia more inflated, tomentose; principal spine on paramere is more developed; tercier spines lacking. Dorsal arm of the paraproct obliquely truncated longer, but arms visible shorter in apical view.

Female genitalia. Tergite of segment IX forming short tube, open ventrally, with V-shaped mesal excision; lateral lobes rounded in dorsal view; its tiny apical tip shifted middle; the lateral setose lobe of sternite IX rounded. Segment X membranous and embedded inside segment IX and encircling anus; supragenital plate of segment X well-developed with more produced dorsal margin in lateral view. Median lobe of the vulvar scale (lower vaginal lip) present and long triangular. Dorsal profile of the vaginal sclerite complex narrowing anterad.

Etymology. named after the type locality.

Drusus bolhos Oláh, sp. nov.

(Figures 218–221)

Material examined. Holotype male. **Iran**, Golhak, 1400 m, b. Teheran, 18. VIII. 1961, leg. J. Klapperlich (1 male, OPC).

Diagnosis and description. Light brown animal with forewing length of 10 mm. Belongs to species with abbreviated dorsal arm of the paraproct. Most close to *Drusus armeniacus* sp. nov. but differs by having horizontal bands of spinulose area contiguous posterad, not completely separated on tergite VIII; paramere terminalia inflated, very much tomentose and its top is not modified into a pin-tipped apex; principal spine on paramere is similar to that of *D. bolhos*, a second large-sized spines more anterad present; tercier spines are numerous. Dorsal arm of the paraproct longer and narrowerd in lateral view and slender, not robust in apical view.

Etymology. bolhos, from "bolyhos" tomentose in Hungarian, refers to the very piliferous, pubescent surface of the inflated paramere terminalia.
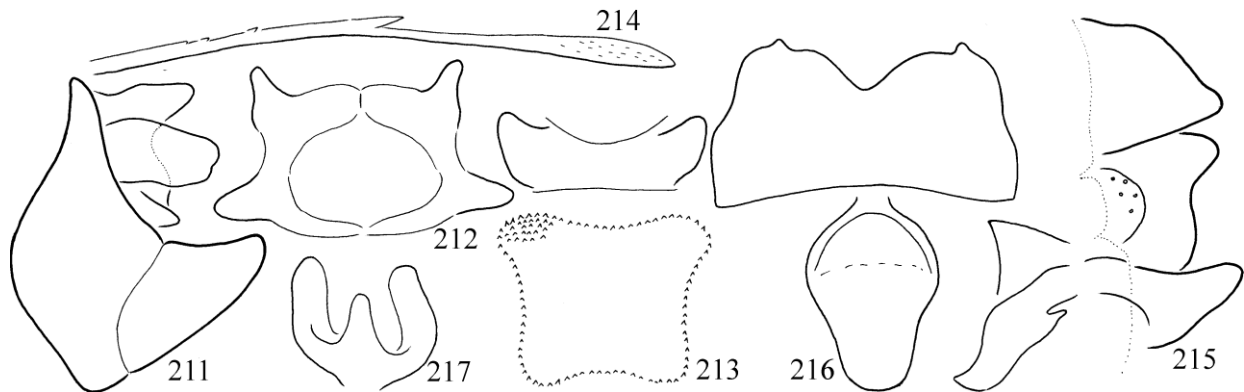
Figurers 211–217. *Drusus barajan* Oláh sp. nov. Holotype: 211 = male genitalia in left lateral view, 212 = paraproct in caudal view, 213 = apical arms of the dorsal branches of paraproct and the pegged spinulose area on tergite VIII in dorsal view, 214 = paramere in left lateral view. Allotype: 215 = female genitalia with vaginal sclerite complex in lateral view, 216 = tergite IX and dorsal profile of vaginal sclerite complex in dorsal view, 217 = vulvar scale in ventral view.
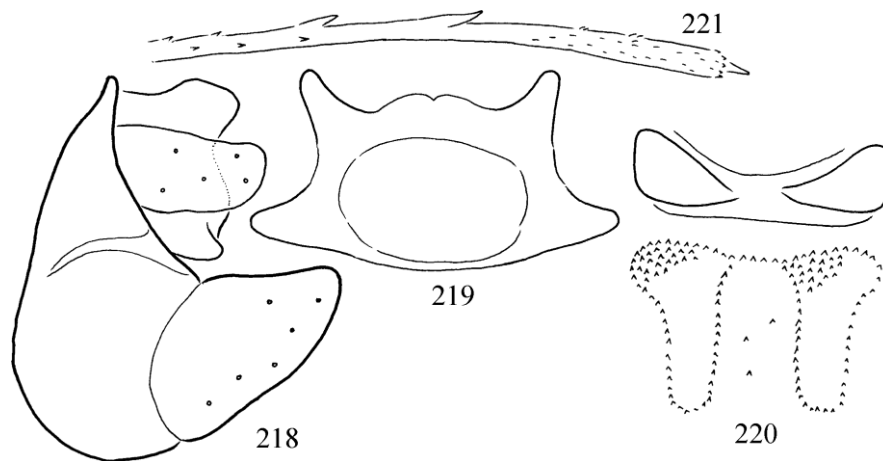
Figures 218–221. *Drusus bolhos* Oláh sp. nov. Holotype: 218 = male genitalia in left lateral view, 219 = paraproct in caudal view, 220 = apical arms of the dorsal branches of paraproct and the pegged spinulose area on tergite VIII in dorsal view, 221 = paramere in left lateral view.

Drusus hassankif Oláh, sp. nov.

(Figures 222–228)

Material examined. Holotype male: **Iran** (Maz), Hassankif, 15. IX. 1955, leg. F. Schmid, (1 male, CMZL). Allotype: same as holotype (1 female, CMZL). Paratypes: same as holotype (4 females, CMZL).

Diagnosis and description. Light brown animal with forewing length of 12 mm. Belongs to species with elongated dorsal arm of the paraproct. Most close to *Drusus iranicus* sp. nov. but differs by having shorter spinulose area on tergite VIII; paramere terminalia more inflated and tomentose; principal spine on paramere more developed; tercier spines lacking, top of the inlated paramere terminalia without any top modification. Dorsal arm of the paraproct longer.

Female genitalia. Tergite of segment IX forming short tube, open ventrally, with V-shaped mesal excision; lateral lobes triangular in dorsal view; its tiny apical tip shifted middle; the lateral setose lobe of sternite IX rounded. Segment X membranous and embedded inside segment IX and encircling anus; supragenital plate of segment X well-developed with more produced and upward dorsal margin in lateral view. Median lobe of the vulvar scale (lower vaginal lip) present and very slender. Dorsal profile of the vaginal sclerite complex short and narrowing anterad.

Etymology. named after the type locality.

Drusus iranicus Oláh & Chvojka, sp. nov.

(Figures 229–232)

Material examined. Holotype male. **Iran**, Central Elburz, Kuhha-ye Tu Chal, 3600–3900 m, Loc. No. 60, 18–19. VII. 1970, Exp. Nat. Mus. Praha (1 male, NMPC). Paratype: same as holotype (1 male, NMPC).

Diagnosis and description. Light brown animal with forewing length of 12 mm. Intermediate between species with abbreviated and elongated dorsal arm of the paraproct. Most close to *Drusus hassankif* sp. nov. but differs by having longer spinulose area on tergite VIII; paramere terminalia less inflated and tomentose; principal spine on paramere less developed; few tercier spines present, top of the inlated paramere terminalia with any top modification. Dorsal arm of the paraproct shorter.

Etymology. Named after country of collection.
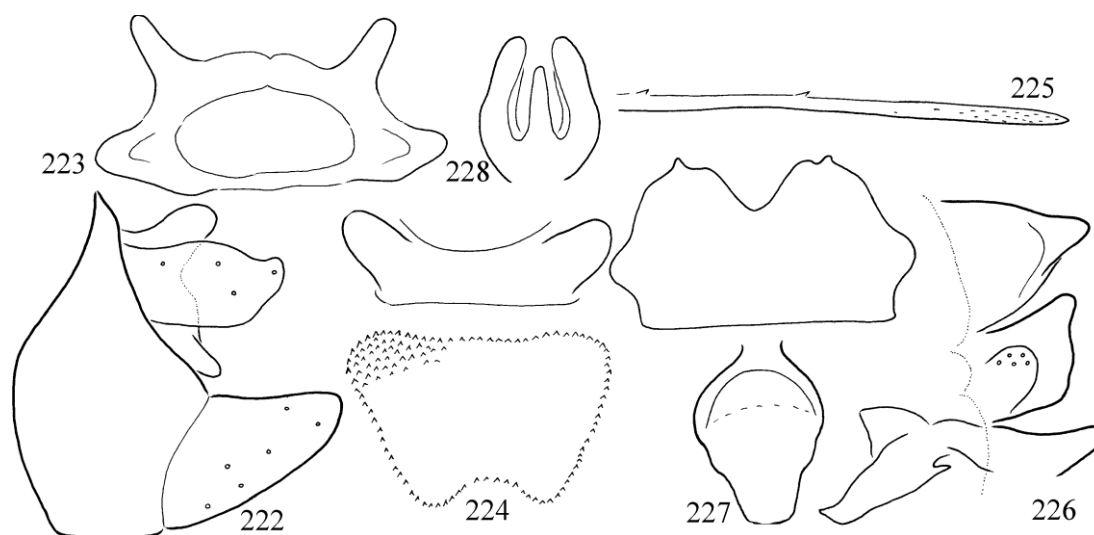
Figures 222–228. *Drusus hassankif* Oláh sp. nov. Holotype: 222 = male genitalia in left lateral view, 223 = paraproct in caudal view, 224=apical arms of the dorsal branches of paraproct and the pegged spinulose area on tergite VIII in dorsal view, 225 = paramere in left lateral view. Allotype: 226 = female genitalia with vaginal sclerite complex in lateral view, 227 = tergite IX and dorsal profile of vaginal sclerite complex in dorsal view, 228 = vulvar scale in ventral view.

Drusus nultas Oláh & Chvojka, sp. nov.

(Figures 233–236)

Material examined. Holotype male. **Iran**. Central Elburz, Kuhha-ye Tu Chal, 2000–2500 m, Loc. No. 59, 18–19. VII. 1970, Exp. Nat. Mus. Praha (1 male, NMPC).

Diagnosis and description. Light brown animal with forewing length of 12 mm. Belongs to species with elongated dorsal arm of the paraproct. Most close to *Drusus barajan* sp. nov. but differs by having smaller and less compact spinulose area on tergite VIII; paramere terminalia less inflated, tomentose; principal spine on paramere is less developed; tercier spines present. Dorsal arm of the paraproct obliquely truncated shorter, but arms visible longer in apical view.

Etymology. nultas, from nyúlt in hungaran fererring to elongated dorsal arm of paraproct in caudal view.
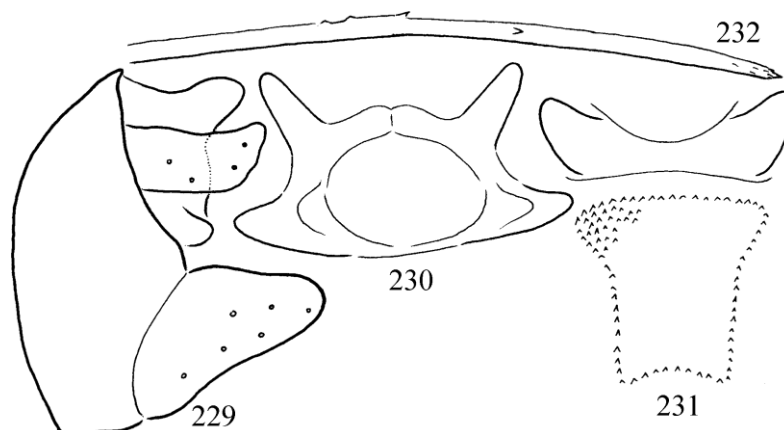
Figures 229–232. *Drusus iranicus* Oláh & Chvojka, sp. nov. Holotype: 229 = male genitalia in left lateral view, 230 = paraproct in caudal view, 231 = apical arms of the dorsal branches of paraproct and the pegged spinulose area on tergite VIII in dorsal view, 232 = paramere in left lateral view.
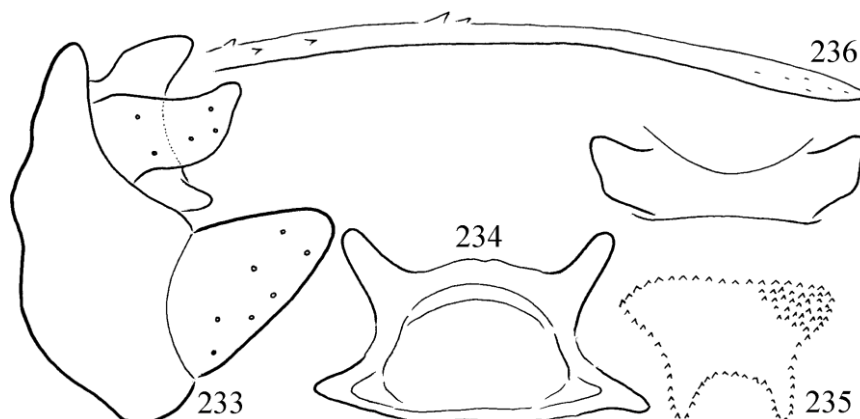
Figures 233–236. *Drusus nultas* Oláh & Chvojka, sp. nov. Holotype: 233 = male genitalia in left lateral view, 234 = paraproct in caudal view, 235 = apical arms of the dorsal branches of paraproct and the pegged spinulose area on tergite VIII in dorsal view, 236 = paramere in left lateral view.

Drusus polur Oláh, sp. nov.

(Figures 237–245)

Material examined. Holotype male: **Iran** (Ost 2), Polur, 17. VII. 1956, leg. F. Schmid, (1 male, CMZL). Allotype: same as holotype (1 female, CMZL). Paratypes: same as holotype (1 male, 1 female, CMZL; 1 male, 1 female, OPC)).

Diagnosis and description. Light brown animal with forewing length of 12 mm. Intermediate between species with abbreviated and elongated

dorsal arm of the paraproct. Most close to *Drusus aranos* sp. nov. but differs by having inverted U-shaped spinulose pattern on tergite VIII, not T-shaped; paramere terminalia inflated; principal spine on paramere modified into an eleveted step; tercier spines frequent. Dorsal arm of the paraproct with robust lateral, but more slender caudal profile. Tergite IX of female without a tendency of bipartite lateral lobe in dorsal view, as well represented on allotype. Dorsal profile of the vaginal sclerite complex more narrowing anterad.

Female genitalia. Tergite of segment IX forming short tube, open ventrally, with V-shaped mesal excision; lateral lobes rounded in dorsal view; its tiny apical tip shifted middle; the lateral setose lobe of sternite IX rounded elongate and continuing into setaless less pigmented downward section. Segment X membranous and embedded inside segment IX and encircling anus; supragenital plate of segment X well-developed and quadrangular in lateral view with straight apical margin. Median lobe of the vulvar scale (lower vaginal lip) present and long paralell-sided. Dorsal profile of the vaginal sclerite complex narrowing anterad.

Etymology. Named after the type locality.

Drusus quruk Oláh, sp. nov.

(Figures 246–249)

Material examined. Holotype male: **Iran** (Ost 1), Quruk Pass, 16. VIII. 1956, leg. F. Schmid, (1 male, CMZL). Paratype: **Iran** (Ost 1), Waliabad, 16. IX. 1956, leg. F. Schmid, (1 male, CMZL).

Diagnosis and description. Light brown animal with forewing length of 12 mm. Belongs to species with elongated dorsal arm of the paraproct. Most close to *Drusus zanus* sp. nov. but differs by having slightly shorter spinulose area on tergite VIII; paramere terminalia inflated, tomentose; principal spine on paramere present and large, not vestigial; tercier spines present. Dorsal arm of the paraproct with obliquely rounded apex; arms visible as elongated rounded process, not taperring long triangular in apical view.

Etymology. Named after the type locality.

Drusus simplex Martynov, 1927

(Figure 196)

Drusus simplex Martynov, 1927: 126–127. „**Russia**, Northern Osetia, Vladikavkas district, Verchnij Sadon, 6. VIII. 1925, leg. Kiritshenko, 1 male. Dzelal-ogly, 26. VIII. 1920, leg. Shelkovnikov, 3 males, 3 females."
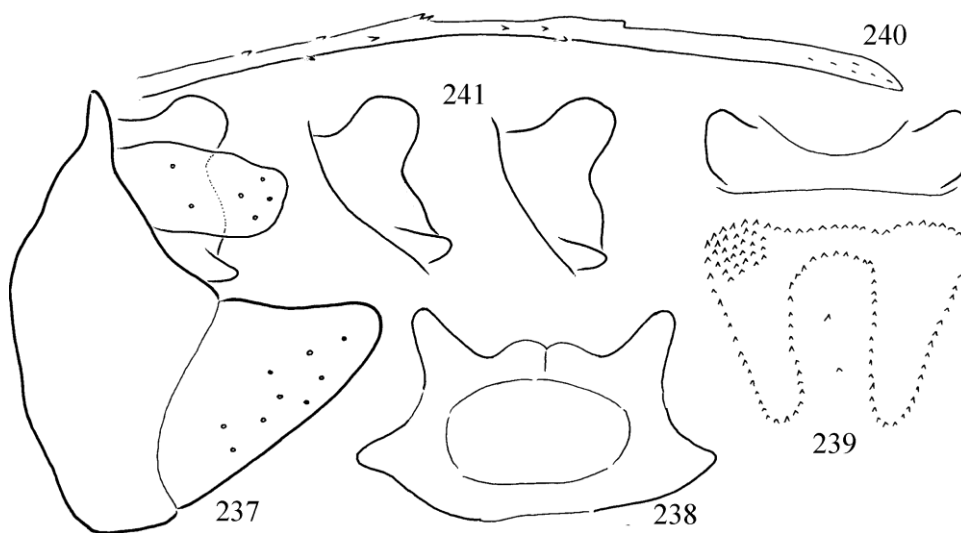
Figures 237–241. *Drusus polur* Oláh, sp. nov. Holotype: 237 = male genitalia in left lateral view, 238 = paraproct in caudal view, 239 = apical arms of the dorsal branches of paraproct and the pegged spinulose area on tergite VIII in dorsal view, 240 = paramere in left lateral view. 241 = paraproct of paratypes in lateral view.
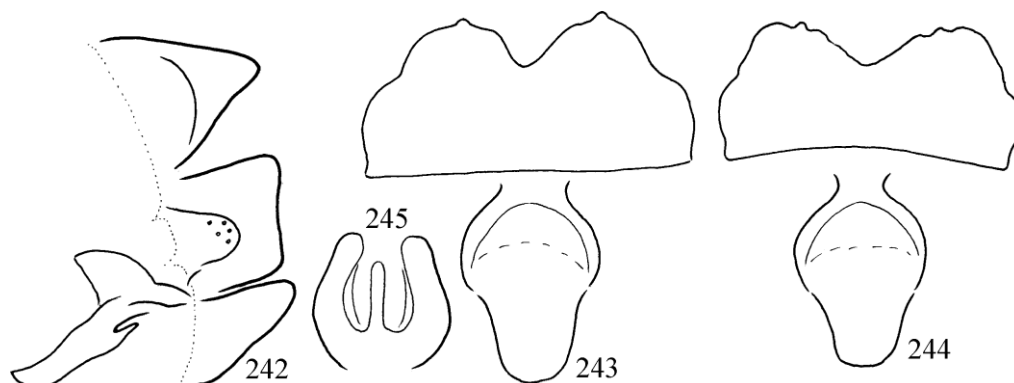
Figures 242–245. *Drusus polur* Oláh, sp. nov. Allotype: 242 = female genitalia with vaginal sclerite complex in lateral view, 243 = tergite IX and dorsal profile of vaginal sclerite complex in dorsal view, 244 = tergite IX and dorsal profile of vaginal sclerite complex of paratype in dorsal view, 245 = vulvar scale.
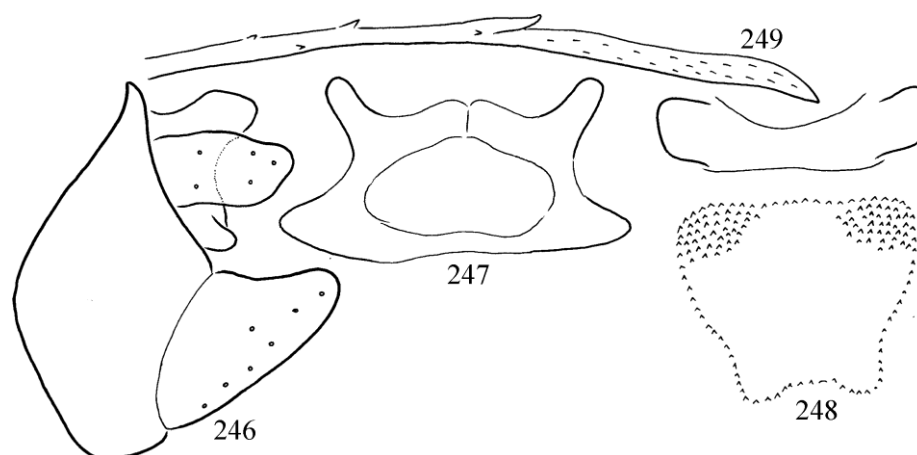
Figures 246–249. *Drusus quruk* Oláh, sp. nov. Holotype: 246 = male genitalia in left lateral view, 247 = paraproct in caudal view, 248 = apical arms of the dorsal branches of paraproct and the pegged spinulose area on tergite VIII in dorsal view, 249 = paramere in left lateral view.

Diagnosis. Species was described from the central North Caucasus as resembling *Drusus caucasicus* Ulmer, and related to the European group of *Drusus annulatus* (Martynov, 1927).

Additional diagnosis. Unfortunately the holotype and any specimens of *Drusus simplex*, the nominate species of the complex described from northern Osetia, has been lost. Fortunately the author, Martynov's drawings as usual are reliable and detailed enough to distinguish at least the most important structural item, the lateral profile of the paraproct. The dorsal arm of the paraproct seems very slender and long distinguishable from all the other species. The paramere was not drawn by Martynov.

Drusus zanus Oláh, sp. nov.

(Figures 250–256)

Diagnosis and description. Light brown animal with forewing length of 11 mm. Belongs to species with elongated dorsal arm of the paraproct. Most close to *Drusus quruk* sp. nov. but differs by having slightly longer spinulose area on tergite VIII; paramere terminalia inflated, tomentose; principal spine on paramere vestigial, not present and large; tercier spines lacking; the
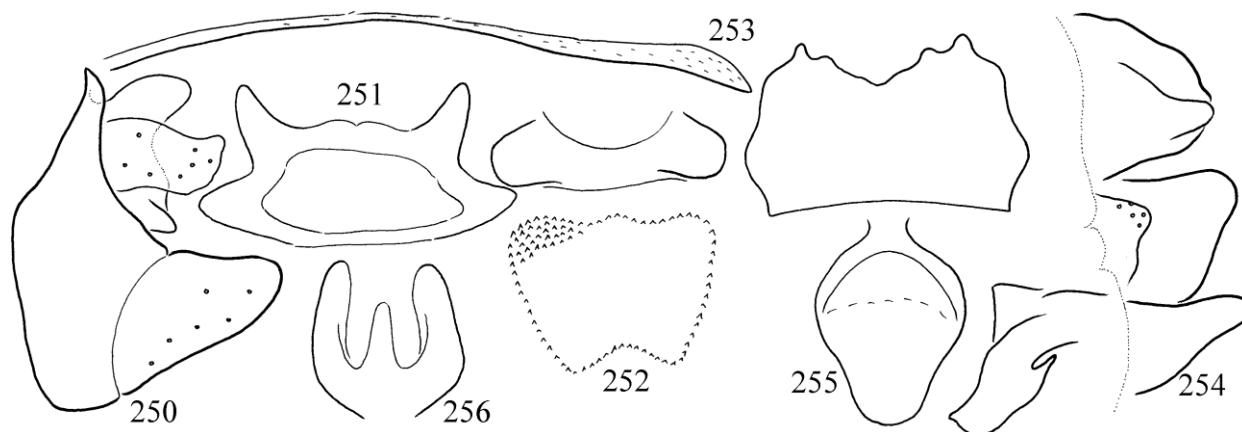
Figures 250–253. *Drusus zanus* Oláh, sp. nov. Holotype: 250 = male genitalia in left lateral view, 251 = paraproct in caudal view, 252 = apical arms of the dorsal branches of paraproct and the pegged spinulose area on tergite VIII in dorsal view, 253 = paramere in left lateral view. Allotype: 254 = female genitalia with vaginal sclerite complex in lateral view, 255 = tergite IX and dorsal profile of vaginal sclerite complex in dorsal view, 256 = vulvar scale in ventral view.

entire paramere is practically without any distinct discernible spine. Dorsal arm of the paraproct obliquely and roundly truncated; arms visible tapering long triangular in apical view.

Female genitalia. Tergite of segment IX forming short tube, open ventrally, with small and shallow V-shaped mesal excision; lateral lobes with 4 smaller or larger concavity in dorsal view; its tiny apical tip shifted middle; the lateral setose lobe of sternite IX rounded triangular continuing into setaless less pigmented downward section. Segment X membranous and embedded inside segment IX and encircling anus; supragenital plate of segment X well-developed subtriangular in lateral view. Median lobe of the vulvar scale (lower vaginal lip) present and long triangular. Dorsal profile of the vaginal sclerite complex narrowing anterad.

Etymology. Named after the type locality.

Drusus bosnicus species group

Drusus bosnicus species group is integrated through ancestral divergence by a single robust erected primary paramere spine accompanied by secondary or tertiary spines anterad. The entire group exhibits rather stable paramere pattern. Paramere divergences inside the species group are small and limited mostly to (1) size increase or decrease of the erected primary paramere spine; (2) increase or decrease of the number of secondary paramere spines; (3) absence, presence and distribution of tertiary paramere spines; (4) abbreviation or elongation of the terminal paramere shaft.

Larval mandible shape of all the examined members of the *Drusus bosnicus* species group from the Balkan Peninsula suggests a feeding habit of grazing on epilithic algae in the periphyton of stones, mosses, cobbles, pebbles and gravels (Kucinic *et al.* 2015). *Drusus bosnicus* species group is comprised of five species complexes and fourty two species.

Regarding phylogenetic ranking further lineage divergences have organised the five species complexes inside the species group by integration. These younger lineages are detectable by the significant modifications in paraproct shape either throught simplification or complexation. The more recent, younger contemporary divergences produced the incipient sibling species are distinguishable by subtle, but stable shape modifications mostly in the fine structures of the paraproct head. The delineation of all the species complexes in the species group is based on paraproct shape divergenses.

(1) *Drusus bosnicus* species complex has dorsal branch of the paraproct with variously patterned pair of apical arms in lateral view, not much enlarged laterad in caudal view;

(2) *Drusus discophorus* species complex has dorsal branch of the paraproct with variously patterned pair of apical arms in lateral view, much enlarged laterad, forming a pair of variously shaped lateral lobes in caudal view;

(3) *Drusus graecus* species complex has dorsal branch of the paraproct with fused blunt apical arms in lateral view, slightly enlarged laterad in caudal view;

(4) *Drusus improvisus* species complex has dorsal branch of the paraproct with horizontal digitiform fused apical arms with slightly upward directed tip in lateral view, digitiform with variously laterad diverging tips in caudal view;

(5) *Drusus muranyorum* species complex has dorsal branch of the paraproct with blunt apical arms in lateral view, enlarged laterad foming a pair of variously rounded lateral lobes in caudal view. In this species complex the robust erected primary paramere highly reduced in size, and subdivided.

Drusus bosnicus species complex

The dorsal branch of paraproct (internal, apical, horizontal branch) having plate-form in sagittal plane, mostly fused mesad; paraproct ventral branch (body of segment X or inferior branch of paraproct by Schmid, or basal, vertical branch) less developed. The group exhibits some tendency also to a reduced body of paraproctal dorsal branch as visible in caudal and dorsal view. The paraproct ventral branch is reduced, frequently open ventrad without any sclerotized transversal section.

This diverse species complex under integrative adaptation of allopatric speciation has been radiated along isolated mountain ranges of the Balkan Peninsule. It consists of eighteen incipient species and many more is waiting to be described from poorly sampled isolated habitats of high elevations: *arbanios*, *bosnicus*, *crenophylax*, *dacothracus*, *gombos*, *illyricus*, *klapaleki*, *kovacsi* sp. nov., *lepcos*, *medianus*, *ostot* sp. nov., *paros* sp. nov., *pelasgus*, *plicatus*, *radovanovici*, *ramae*, *septemtrionis*, *vespertinus*.

Drusus arbanios Oláh, 2010

(Figures 257–260)

Drusus arbanios Olah, 2010: 98–100, A species described from a single specimen collected in Albania, Ostrovice Mts. Etymology. Name was given to remind the old ancient city of Arbon and his people the Arbanios, nearby the type locality.

Material examined. Holotype male, HNHM. **Albania**: Skrapar district, Ostrovice Mts, Backe, stream under the pass between Mt. Frengu and Mt. Faqekuq, 1915 m, N40°31.614', E20°25.021' 4.VII.2005, leg. Z. Barina, D. Pifkó & D. Schmidt(1 male HNHM)

Diagnosis. Olah 2010: 100, "This dark species with almost ebony black sclerites belongs to the species complex with large upward arching triangular gonopods and triangular or bilobed cerci inhabiting the Balkan Mountains. Most close to *Drusus illyricus* sp. nov., but differs by having (1) small animal with forewing length of 8 mm, not large animal of 14 mm; (2) posterodorsal spinate area on VIIIth tergite four-lobed in dorsal view, not trilobed; (3) the longitudinal groove of IXth segment linear, not with ventral arm; (4) cerci with dorsal lobe quadratic, not tapering in lateral view; (5) inner branch of paraproct forming an almost regular quadratic plate in lateral view, not supplied with a dorsal pronounced subapical wart-shaped process."
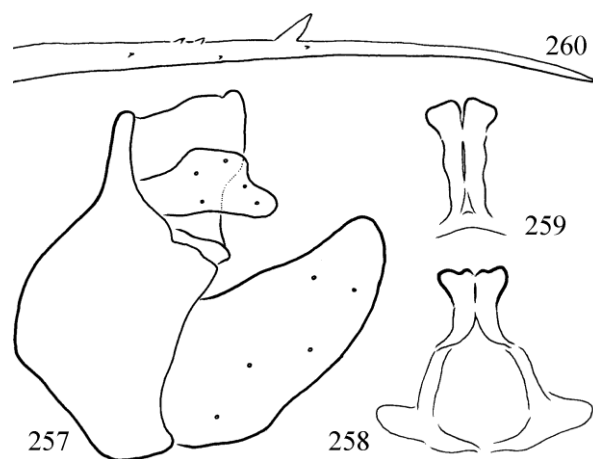
Figures 257–260. *Drusus arbanios* Oláh, 2010. 257 = male genitalia in left lateral view, 258 = paraproct in caudal view, 259 = apical arms of the dorsal branches of paraproct in dorsal view, 260 = paramere in left lateral view.

Drusus bosnicus **Klapálek, 1899**

(Figures 261–265)

Drusus bosnicus Klapalek, 1899: 327–329. „Ilice i Vrelo Bosne (Apfelb.), Pazaric, Dolina Krupe, 3. novembra 1898. (Apfelb.)."

Drusus bosnicus Klapalek 1900: 674–675. „Ilidze und Vrelo Bosna (Apfelb.), Pazaric, Krupathal, 3. November 1898 (Apfelb.).

Drusus bosnicus Klapálek ,1899: 327–329, Schmid,1956: 31–32, "Cette espèce a été décrite de Bosnie; M. Radovanovic l'a signalée de Sarajevo. J'ai étudié un assez grand nombre d'exemplaires que j'ai capturés à mi-juilett en Bosnie au massif de Treskavitza."

Material examined. **Bosnia & Herzegovina**, Federation of Bosnia and Herzegovina, Sarajevo, Ilidža, Bosna springs, 43°49'08.4", 18°16'09.4", 645 m, 2.X.2015, leg. P. Juhász, T. Kovács (26 males, 14 females; OPC).

Diagnosis. Klapálek 1900: 675, "Die Analanhänge dieser Art zeigen eine grosse Ähnlichkeit mit den homologen Theilen des *Dr. monticola*, und ich würde es nicht wägen sie als eine distincte Art zu beschreiben, ware nicht der Unterschid in der Farbung und in der Form der Discoidalzelle so auffalend; auch die Form der oberen Anhange ist etwa verschieden."

Schmid 1956: 32, "*Dr. bosnicus* est sans doute l'espèce la plus évoluée du groupe; ceci est visible à ses appendices de forme très spécialisée: IXe segment concave latéralement, appendices inférieurs très divergent, appendices intermédiaires formant une assez grande surface prolongeant la zone spinulifère."

Kucinic *et al.* 2015: Larval head shape relates *D. bosnicus* to *D. ramae*, although the present efforts in larval research focus rather on morphological separations than on phylogenetic relations. Surprisingly, recent moleclar study suggested two different species from the *Drusus bosnicus* species group coexisting in the spring area of Bosna River, but so far, there was no any records of adult of last instar larvae of this possible new species (Kucinic *et al.* 2015). The fine structure analysis carried out on the paraproct, paramere and vaginal sclerite complex of 26 males and 14 females, collected in the autumn of 2015 in the spring area of Bosna River, has demonstrated the presence of only a single species: *Drusus bosnicus*.
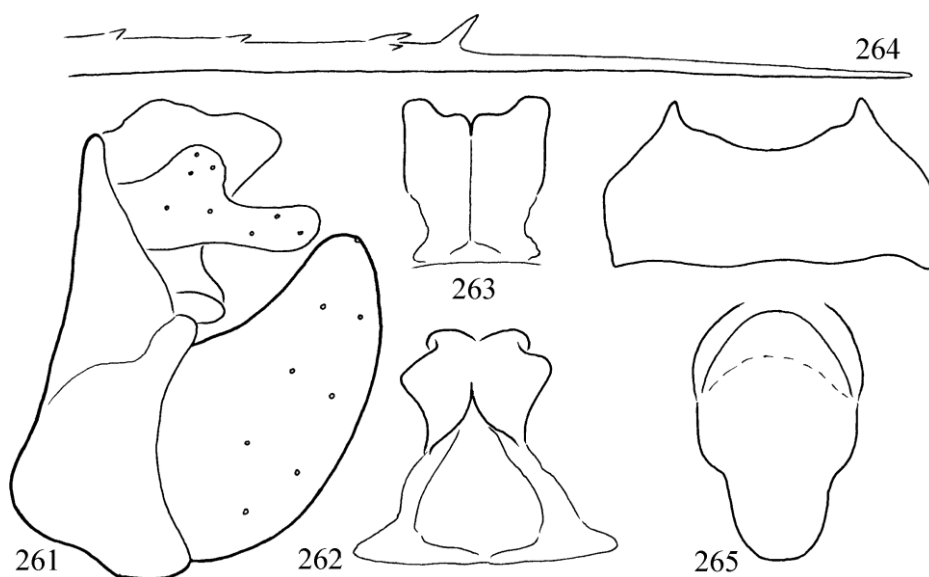
Figures 261–265. *Drusus bosnicus* Klapálek, 1899. 261 = male genitalia in left lateral view, 262 = paraproct in caudal view, 263 = apical arms of the dorsal branches of paraproct in dorsal view, 264 = paramere in left lateral view, 265 = tergite IX and dorsal profile of vaginal sclerite complex in dorsal view.

Drusus crenophylax **Graf & Vitecek, 2015**

(Figures 266–269)

Drusus crenophylax Graf & Vitecek, 2015, in Vitecek *et al.* 2015. "Material. Holotype. 1 male: Bosnia and Herzegovina, Cvrka river; 44°32.932'N 17°23.562'E; 393 m a.s.l.; 1. X. 2014; leg. Dejan Dmitrovic, Goran Sukalo, specimen identifier: fDsp4501M. Paratypes: 2 females: Bosnia and Herzegovina, Spring of Cvcka river, Vilenjska vrela; 44°33.003'N 17°23.580'E; 456 m a.s.l.; 12. IX. 20124; leg. Dejan Dmitrovic, specimen identifier: fDsp3401F. 4 males, 3 females, 19 larvae: Bosnia and Herzegovina, Cvrka river; 44°33.003'N 17°23.580'E; 456 m a.s.l.; 12. IX. 2012; leg. Dejan Dmitrovic, Goran Sukalo, Goran Sukalo; specimen identifier for 3 larvae: fDsp4502L, fDsp4503L, fDsp4504L. Holotype and paratypes currently in coll. W. Graf, will deposited in the Biologiezentrum des Oberösterreichischen Landesmuseums, Linz, Austria."

*Material examined.***Bosnia & Herzegovina**: Republika Srpska, Večići, Cvrcka river, 44°32'55.4", 17°23'33.7", 1.X.2015, leg. P. Juhász, T. Kovács (1 male, OPC).

Diagnosis. Vitecek *et al.* 2015: 88–89, "Males of the new species are most similar to *Drusus discophorus* Radovanovic and *D. vernonensis* Malicky, but exhibit (1) subtriangular superior appendages In lateral view, (2) subtriangular, low
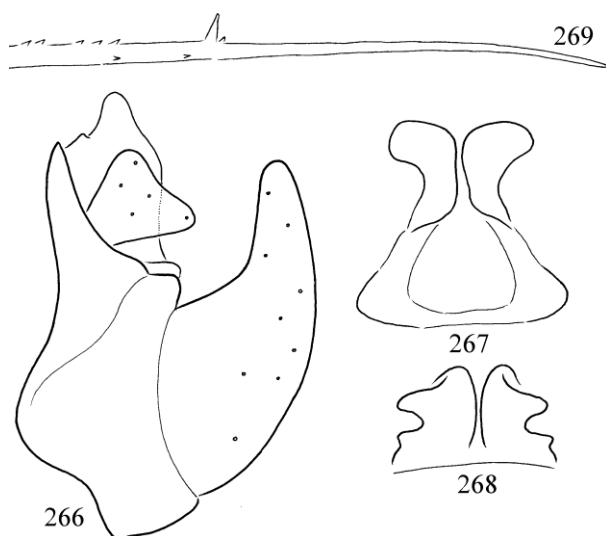
Figures 266–269. *Drusus crenophylax* Graf & Vitecek, 2015. 266 = male genitalia in left lateral view, 267 = paraproct in caudal view, 268 = apical arms of the dorsal branches of paraproct in dorsal view, 269 = paramere in left lateral view.

tip of the intermediate appendages in lateral view, and (3) simple, rounded tips of intermediate appendages in caudal view. *Drusus discophorus* males have suboval superior appendages and a high round tip of the intermediate appendage in lateral view; *D. vernonensis* males have round superior appendages in lateral view and trilobate tips of intermediate appendages in caudal view."

"Females of the new species show the reduced median lobe of the vaginal sclerite and gigh base of the lateral lobe of segment IX as typical for Balkan Drusinae and most similar to *Drusus vernonensis*."

"Larvae of the new species are most similar to *Drusus klapaleki* Marinkovic-Gospodnetic and *D. serbicus* Marinkovic-Gospodnetic."

Drusus dacothracus **Oláh, 2010**

(Figures 270–274)

Drusus dacothracus Oláh, 2010: 101, "Etymology. Name was given to remind Dacian-Thracian origin of the Albanian people inhabiting the type locality. Three theories exist: the Illyrian, Dacian-Thracian and Pelasgian origin of the Albanians."

Material examined. Holotype male. **Albania**: Periferi Dibrë, 3 km W of q. e Murrës, Shkëmb i Skanderbeut, gorge of Lumi i Varoshit [cave spring and its outlet, stream Varoshit, limestone walls], N41°38.792' E20°11.390', 975m, 11.X.2005, leg. T. Deli, Z. Erőss, Z. Fehér & D. Murányi (1 male HNHM). Paratypes. Albania: Periferi Dibrë, 3 km W of q. e Murrës, Shkëmb i Skanderbeut, gorge of Lumi i Varoshit, N41° 38.792' E20° 11.406', 975 m, 13.IV.2006, leg. Z. Erőss, Z. Fehér, A. Hunyadi & D. Murányi (1 male, HNHM). Periferi Dibrë, 3 km W of q. e Murrës, Shkëmb i Skanderbeut, gorge of Lumi i Varoshit [cave spring and its outlet, stream Varoshit, limestone walls], N41°38.792' E20°11.390', 975m, 11.X.2005, leg. T. Deli, Z. Erőss, Z. Fehér & D. Murányi(1 male, 3 associated females, HNHM). Periferi Dibrë, ca. 2 km W of Cidhnë along the footpath to Gurrë-Lurë, gorge of Pr. i Setës (730–750 m) [limestone rocks, in and around an aquaduct], 10.X.2005, leg. T. Deli, Z. Erőss, Z. Fehér & D. Murányi (1 male, HNHM).

Diagnosis. Oláh 2010: 102, "This dark species belongs to the species complex with large upward arching triangular gonopods and triangular or bilobed cerci inhabiting the Balkan Mountains. Most close to *Drusus illyricus* sp. nov., but differs by having (1) smaller size; (2) upper lobe of the
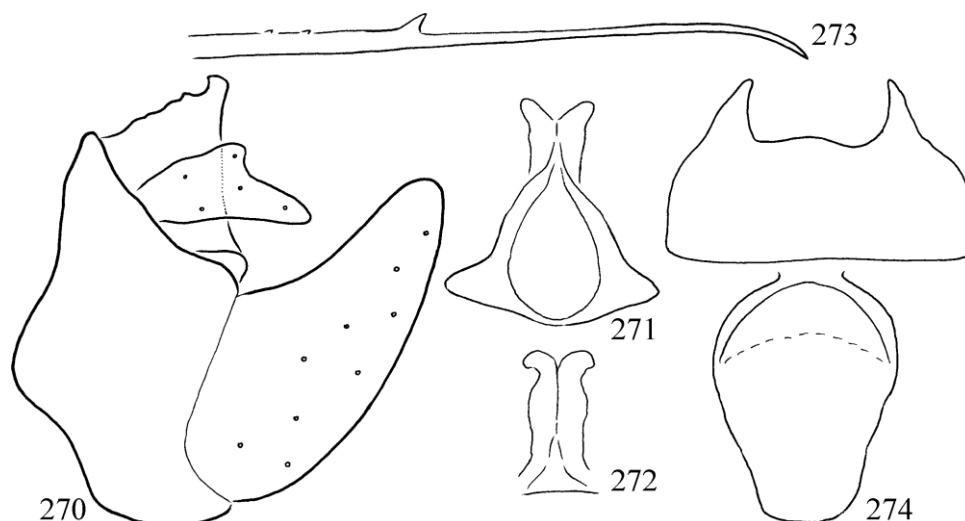
Figures 270–274. *Drusus dacothracus* Oláh, 2010. 270 = male genitalia in left lateral view, 271 = paraproct in caudal view, 272 = apical arms of the dorsal branches of paraproct in dorsal view, 273 = paramere in left lateral view, 274 = tergite IX and dorsal profile of vaginal sclerite complex in dorsal view.

trilobed spinate area on tergite VIII narrow and clearly monolobed, not broad bilobed with some mesal depression; (3) sternal lateral suture of the fused IXth segment without middle fork, not with well-developed middle ventral brach; (4) segment IX not very long ventrally; (4) cerci with dorsal lobe short triangular, not long and downward curving; (5) the ventral lobe of the cerci long triangular, not long digitiform; (6) inner branch of paraproct differently shaped both in lateral, dorsal and caudal view."

Drusus gombos Oláh, 2013

(Figures 275–278)

Drusus gombos Oláh, 2013: 112–114, "*Etymology – gombos*, from "gombos" buttum-like in Hungarian, refers to the rounded knob-shaped dorsoapical lateral processes of the paraproct."

Material examined. Holotype: **Montenegro**, Žabljak municipality, Sinjajevina Mts, Dobrilovina, forest stream at the monastery, N43°01.652', E19°24.086', 765 m, 25.V.2013, leg. P. JUHÁSZ, T. KOVÁCS, G. MAGOS, G. PUSKÁS, (1 male, OPC). Allotype: same as holotype (1 female, OPC). Paratypes: same as holotype (2 females, OPC).

Diagnosis. Oláh, 2013: 112–113. "This castanean brown species beongs to the species complex with large upward arching triangular gono-

pods inhabiting the Balkan Mountains. Most close to *Drusus klapaleki* Marinkovic-Gospodnetic, 1971 but differs by having cerci less slender with more bulky ventroapical corner; lateral profile of the paraproct different and female has trilobed apical margin on the anal tube in dorsal view, not bilobed; the median lobe on the vulvar scale present, not absent; the dorsal profile of the vaginal sclerite coplex different".
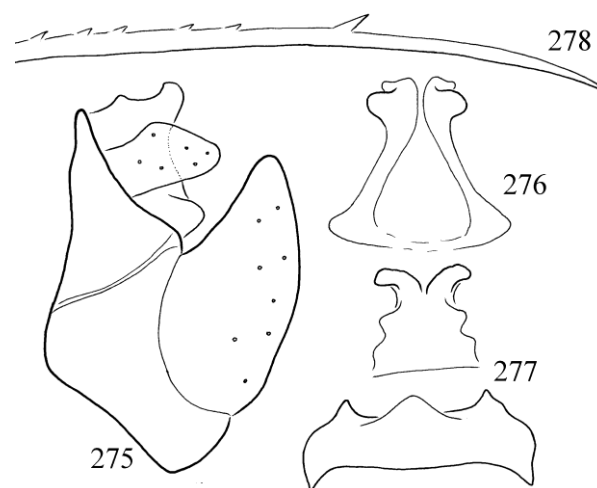
Figures 275–278. *Drusus gombos* Oláh, 2013. 275 = male genitalia in left lateral view, 276 = paraproct in caudal view, 277 = apical arms of the dorsal branches of paraproct in dorsal view, 278=paramere in left lateral view.

Drusus illyricus Oláh, 2010

(Figures 279–282)

Drusus illyricus Oláh, 2010: 102–104, *"Etymology*. Name was given to remind one possible origin of the Albanian people inhabiting the type locality. Three theories exist: the Illyrian, Dacian-Thracian and Pelasgian origin of the Albanians."

Material examined. Holotype male. **Albania**: Mat county, Kreshtes Mts, Vajkal, Fusha e Kaliut, brook on serpentine 3.5 km N of the village, 1730m, N41.541800º E20.206500º, 30.V.2008, leg. Z. Barina, D. Pifkó & B. Pintér (1 male HNHM).

Diagnosis. Oláh 2010: 104, "This dark species belongs to the species complex with large upward arching triangular gonopods and triangular or bilobed cerci inhabiting the Balkan Mountains. Most close to *Drusus pelasgus* sp. nov., but differs by having (1) larger size; (2) sternal lateral suture of the fused IXth segment with middle fork, not without; (3) segment IX very long ventrally, not medium long; (4) cerci with dorsal lobe slender, downward curving, not blunt rounded; (5) inner branch of paraproct with short and narrow dorsal apex as visible both in lateral, dorsal and caudal view, not long and broad."
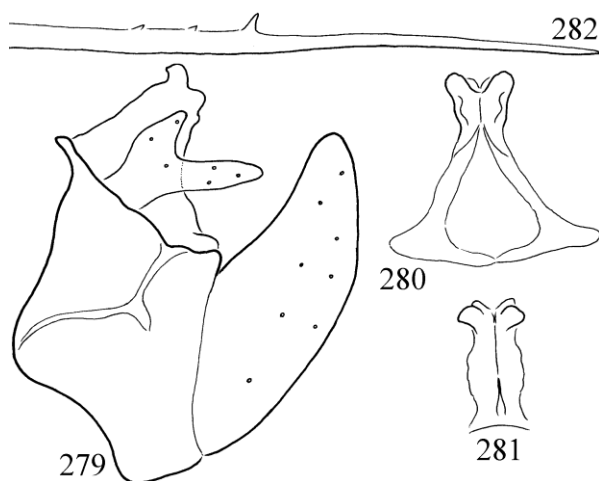
Figures 279–282. *Drusus illyricus* Oláh, 2010. 279 = male genitalia in left lateral view, 280 = paraproct in caudal view, 281 = apical arms of the dorsal branches of paraproct in dorsal view, 282 = paramere in left lateral view.

Drusus klapaleki Marinkovic-Gospodnetic, 1971

(Figures 283–287)

Drusus klapaleki Marinkovic-Gospodnetic, 1971a: 80. „Southeast Bosnia, mm and ff in small springs of tributary of the river Sutjeska, between Tjentiste and Curevo."
Drusus klapaleki Marinkovic-Gospodnetic, 1971b: 144. „Southeast Bosnia, ♂♂ ♀♀ in small springs of tributary of the river Sutjeska."
Drusus klapaleki Marinkovic-Gospodnetic, 1971: Oláh & Kovács 2013: 115–116, Female description together with new male drawings.

Material examined. **Bosnia & Herzegovina**, Jablanica, spring stream, 4.IX.1988, singled leg. J. Oláh (3 males, 1 female; OPC).

Diagnosis. Marinkovic-Gospodnetic 1971a: 80, "This species is closely related to *D. bosnicus* Klap. The greatest difference between these two species is in the shape of the superior appendages and of the intermediate appendages."

Oláh & Kovács 2013: 115–116, „The female of this species is unknown. We have collected a single female from a spring area together with three males. Here we describe the female and redraw the male in order to compare it with its close relative, with *Drusus gombos* sp. nov. Compared to male of *D. gombos*, *D. klapaleki* has more slender cerci, differently shaped paraproct having apicolateral lobes hook-shaped, and slightly different spine pattern of the paramere."

Drusus kovacsi Oláh sp. nov.

(Figures 288–294)

Drusus dacothracus Oláh, 2010: 101, "Albania, Skrapar district, Ostrovice Mts, Ceremica, brook W of the village, 1820m, N40°32.649' E20°26.573', 5. VII. 2005, leg. Z. Barina, D. Pifkó & D. Schmidt (1 male, HNHM)." Misidentification!
Drusus arbanios Oláh, 1910: Oláh & Kovács 2012: 90–91, Female description and drawings. "Allotype female. **Albania**: Skrapar district, Ostrovicë Mts, Backë, Krojmbret Spring and its outlet brook NE of the village, N40°31.753' E20°25.152', 1965 m, 12.10.2012, leg. P. Juhász, T. Kovács, D. Murányi, G. Puskás (1 female, OPC). Same as allotype (3 males, 6 females; OPC).
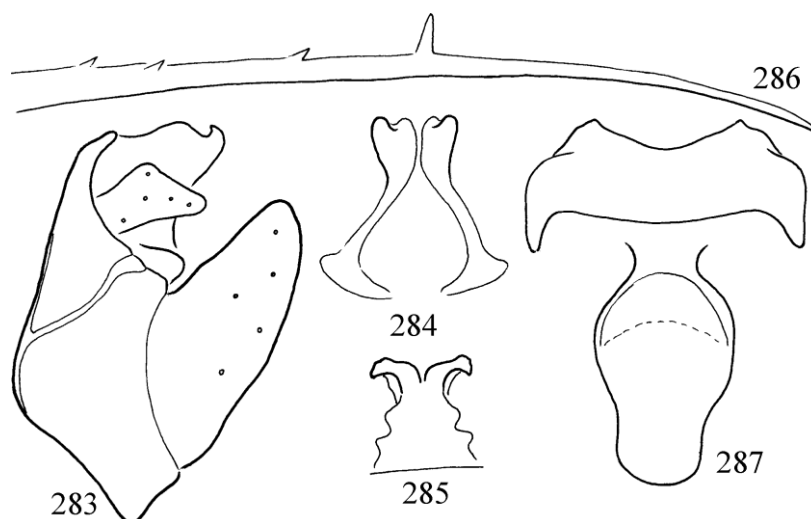
Figures 283–287. *Drusus klapaleki* Marinkovic-Gospodnetic, 1971. 283 = male genitalia in left lateral view, 284 = paraproct in caudal view, 285 = apical arms of the dorsal branches of paraproct in dorsal view, 286 = paramere in left lateral view, 287 = tergite IX and dorsal profile of vaginal sclerite complex in dorsal view.
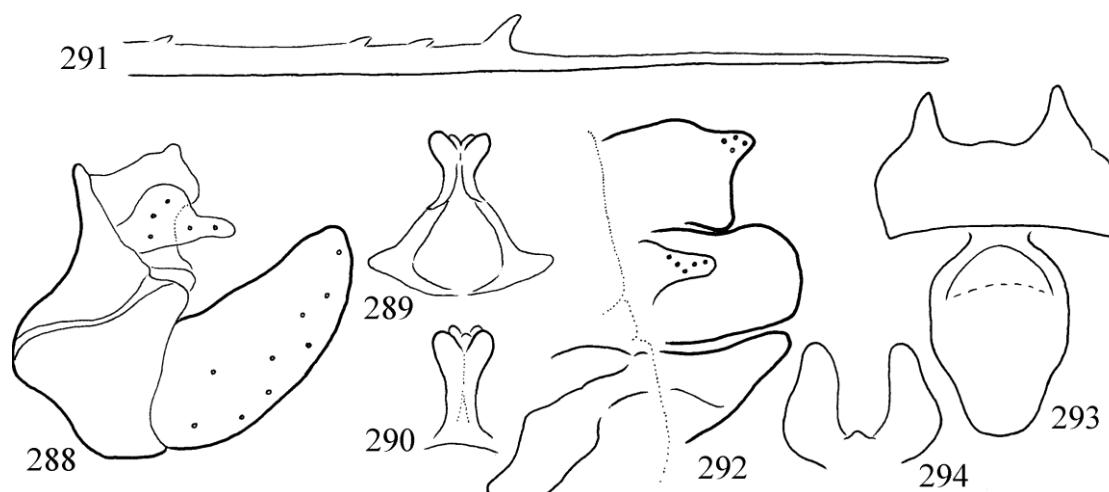
Figures 288–294. *Drusus kovacsi* Oláh, sp. nov. Holotype: 288 = male genitalia in left lateral view, 289 = paraproct in caudal view, 290 = apical arms of the dorsal branches of paraproct in dorsal view, 291 = paramere in left lateral view. Allotype: 292 = female genitalia with vaginal sclerite complex in left lateral view, 293 = tergite IX and dorsal profile of vaginal sclerite complex in dorsal view, 294 = vulvar scale in ventral view.

Skrapar district, Ostrovicë Mts, Backë, brook and spring NE of the village, N40°31.346' E20°25.096', 1650 m, 12.10.2012, leg. P. Juhász, T. Kovács, D. Murányi, G. Puskás (1 male, 4 females, OPC)." Misidentification!

Drusus arbanios Oláh, 1910: Oláh & Kovács 2013: 112, "Albania, Korçë district, Ostrovicë Mts, Çemerricë, open brook W (above) the village, N40°32'38.9", E20°26' 33.5", 1820 m, 28.V.2013, leg. P. Juhász, T. Kovács, G. Magos, G. Puskás, (2 males, 7 females; OPC). Albania, Skrapar district, Ostrovicë Mts, Backë, Krojmbret Spring and its outlet brook NE of the village, N40°31.753',

E20°25.152', 1965 m, 28.V.2013, leg. P. Juhász, T. Kovács, G. Magos, G. Puskás, (19 males, 7 females; OPC). Albania, Skrapar district, Ostrovicë Mts, Backë, brook and spring NE of the village, N40°31.346', E20°25.096', 1650 m, 29.V.2013, leg. P. Juhász, T. Kovács, G. Magos, G. Puskás, (10 males, 13 females; OPC). Albania, Skrapar district, Ostrovicë Mts, open stream 3 km S of village Faqekuq, N40°32'19.3, E20°24'22.0", 1730 m, 29.V.2013, leg. P. Juhász, T. Kovács, G. Magos, G. Puskás, (3 males, 9 females; OPC)." Misidentification!

Material examined. Holotype male. **Albania**: Skrapar district, Ostrovicë Mts, Backë, Krojmbret Spring and its outlet brook NE of the village, N40°31.753' E20°25.152', 1965 m, 12.10.2012, leg. P. Juhász, T. Kovács, D. Murányi, G. Puskás (3 males, 6 females; OPC). Allotype: same as holotype (1 female, OPC). Paratypes: same as holotype (2 males, 6 females; OPC). Albania, Skrapar district, Ostrovice Mts, Ceremica, brook W of the village, 1820m, N40°32.649' E20°26.573', 5. VII. 2005, leg. Z. Barina, D. Pifkó & D. Schmidt (1 male, HNHM). Skrapar district, Ostrovicë Mts, Backë, brook and spring NE of the village, N40°31.346' E20°25.096', 1650 m, 12.10.2012, leg. P. Juhász, T. Kovács, D. Murányi, G. Puskás (1 male, 4 females, OPC). Albania, Korçë district, Ostrovicë Mts, Çemerricë, open brook W (above) the village, N40°32'38.9", E20°26'33.5", 1820 m, 28.V.2013, leg. P. Juhász, T. Kovács, G. Magos, G. Puskás (2 males, 7 females; OPC). Albania, Skrapar district, Ostrovicë Mts, Backë, Krojmbret Spring and its outlet brook NE of the village, N40°31.753', E20°25.152', 1965 m, 28.V.2013, leg. P. Juhász, T. Kovács, G. Magos, G. Puskás (19 males, 7 females; OPC). Albania, Skrapar district, Ostrovicë Mts, Backë, brook and spring NE of the village, N40° 31.346', E20°25.096', 1650 m, 29.V.2013, leg. P. Juhász, T. Kovács, G. Magos, G. Puskás (10 males, 13 females; OPC). Albania, Skrapar district, Ostrovicë Mts, open stream 3 km S of village Faqekuq, N40°32'19.3, E20°24'22.0", 1730 m, 29.V.2013, leg. P. Juhász, T. Kovács, G. Magos, G. Puskás (3 males, 9 females; OPC).

Diagnosis and description. After the description of *D. arbanios* from the single male holotype, several male and female specimens were collected and identified as *D. arbanios* from nearby habitats in the Ostrovicë Mts. Even the female was described from these material as *D. arbanios* (Oláh & Kovács 2012). The reexamination of all these specimens and carefully compared as well with other species we have found that all these specimens represent a new species widely distributed in the Ostrovicë Mts. As a result *Drusus arbanios* has remained known only from the holotype.

Drusus kovacsi is most close to *D. arbanios*, but differs by having cerci with rounded dorsal lobe, not flat; lateral profile of paraproct with convex vertical dorsoapical margin, not straight vertical as well as dorsoapical tips, the diverging tips is rounded lobed, not truncate. The erected primary spine differently shaped, however it is not known how stable is this divergion having only the single holotype of *D. arbanios* available.

Etymology. We named this species after the collector Tibor Kovács, who has performed a systematic and specialised collecting program to sample target populations of Drusinae subfamily in the sky islands of high altitude crenon and hypocrenon habitats in the Balkan mountan ranges during the years of 2010 and 2017.
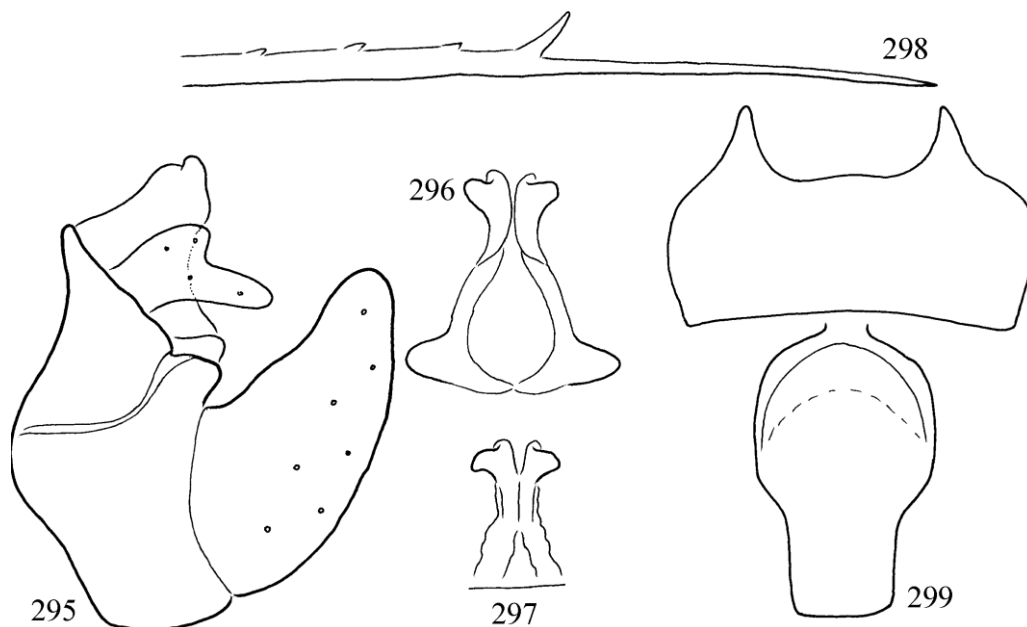
Figures 295–299. *Drusus lepcos* Oláh, 2011. 295 = male genitalia in left lateral view, 296 = paraproct in caudal view, 297 = apical arms of the dorsal branches of paraproct in dorsal view, 298 = paramere in left lateral view, 299 = tergite IX and dorsal profile of vaginal sclerite complex in dorsal view.

Drusus lepcos **Oláh, 2011**

(Figures 295–299)

Drusus lepcos Oláh, 2011: 116–117, "*Etymology – lepcos*, from „lépcsős", stepwise in Hungarian, refers to the shape of the dorsum of the paraproct in lateral view."

Material examined. Holotype male. **Albania**: Mirdite district, Shent Mts. Kurbnesh, Urake River and its sidespring NE of the city, 800 m, N41°47.711' E20°06.703' 20.V.2010, leg. Z. Fehér, D. Murányi & Zs Ujvari (1 male HNHM). Paratypes: same as holotype (1 male, 2 females, HNHM)

Diagnosis. Oláh 2011: 116, "This dark brown species belongs to the species complex with large upward arching triangular gonopods inhabiting the Balkan Mountains. Most close to *Drusus dacothracus* Oláh and *D. ilyiricus* Oláh, but differs from both by having dorsum of paraproct stepwise formed in lateral view. However, these species are very close, moreover the lateral shape of their cerci varying. Most easy to distinguish between the 3 species is to stretch out the paraproct of the cleared genitalia out under the dark spinose tergite VIII and compare the paraproctal dorsum in lateral view: flat sloping at *D. dacothracus*, towering at *D. illyricus* and stepwise in *D. lepros* sp. nov."

Drusus medianus **Marinkovic, 1976**

(Figures 300–304)

Drusus medianus Marinkovic-Gospodnetic, 1976: 80, „Localities in the springs of the left tributaries of the river Bosna are: Lasva (Plave vode), 30♂ 12♀, 5. VI. 1965; 8♂ 4♀, 4. V. 1973; Holotype ♂, allotype ♀, paratypes ♂♂♀♀ in author's collection. Lasva (Komar), 12♂ 4♀, 13. V. 1971; 6♂,4. V. 1972; 4♂ 3♀, 15. V.1973. Zujevina, 5♂ 2♀, 10. V. 1970. Zujevina (Ljubovcica potok), 26♂ 2♀, 14. V. 1957; 5♂ 1♀, 15. V. 1958; 2♂ 23. IV.1958; 12♂ 3♀, 15. V. 1960. –Zujevina (Krupa) 2♂ 28. VI. 1957. Fojnica (Pozarna) 22♂ 10♀, 31. V. 1967. Localities in the springs of the right tributaries of the river Vrbas are: Bistra (near Gornji Vakuf), 1♂, 15.VI.1973. Krusnica (tributary of the river Bistrica), 1♂, 18. VI. 1972."

Material examined. **Bosnia & Herzegovina**: Federation of Bosnia and Herzegovina**,** Travnik, Plava voda spring, 44°13'49.67" 17°40'17.24", 523 m, 3.X.2015, P. Juhász, T. Kovács(13 males, 14 females; OPC).

Diagnosis. Marinkovic-Gospodnetic 1976: 80, "Appendices intermediales differ from those of other Bosnian species of *Drusus* gr. *bosnicus* in being small. They bear two narrow tips on the dorsal part. In dorsal view, appendices intermediales are narrow and with a deep recess laterally. Appendices superiores are concave and similar to those of *D. radovanovici septemtrionis*. The surface beset with tubercules is also similar to that of *D. radovanovic septemtrionis*, but its darker semicircular zones are more separated by the light zone beset with few tubercules."

Drusus ostot **Oláh sp. nov.**

(Figures 305–307)

Material examined. Holotype female. **Albania**: Prokletije Mts. Creek above village, Sylbice, 2010 m, N42° 31.326' E20°05.919' 8. VII. 2011, leg. Z. Barina, A. Kovács, G. Puskás & B. Sárospataki (1 female OPC). Paratype. Same as holotype (1 female, OPC).

Diagnosis and description. This species is known only by the female holotype and by the female paratype. *Female genitalia*. The very specialised tergit IX makes it possible to distinguish this species from all the other known species. Tergite of segment IX clearly bipartite well visible from both dorsal and lateral view; on the middle of the tergite there is a traversal rim separating the basal and distal parts of the segment; the lateral setose lobe of sternite IX rounded. Segment X membranous and embedded inside segment IX and encircling anus; supragenital plate of segment X well-developed and rounded quadrangular in lateral view. Median lobe of the vulvar scale (lower vaginal lip) vestigial, very short triangular. Dorsal profile of the vaginal sclerite complex tripartite and narrowing anterad. The dorsal profile of the bipartite segment IX has some resemblence both to *D. klapaleki* and *D. medianus*, but the the mesal excision on the apical margin of segment IX is deeper than at *D. klapaleki* and wider than at *D. medianus*. Morover, the lateral profile of the segment IX differs very much from the other two species.

Etymology. ostot, from „osztott", divided in Hungarian, refers to the shape of segment IX divided by pronounced rim into basal and distal parts.
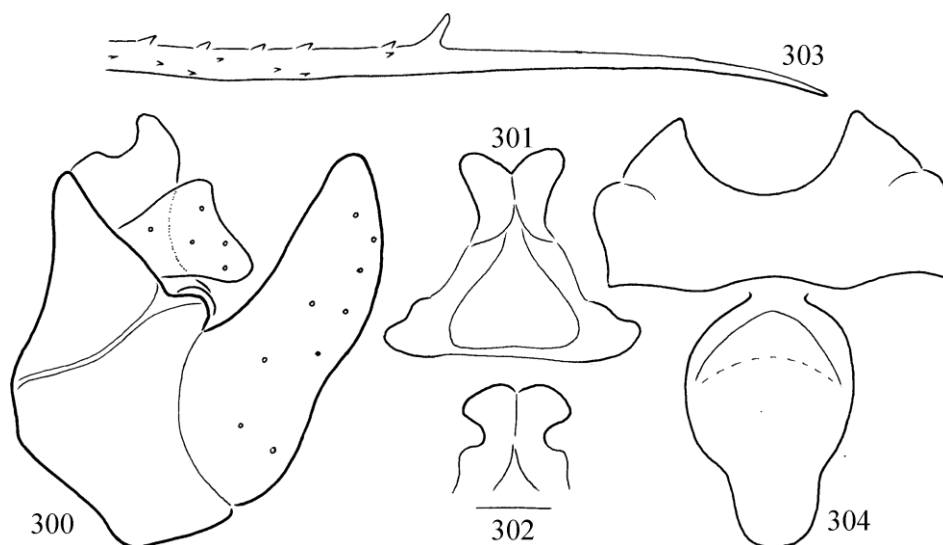
Figures 300–304. *Drusus medianus* Marinkovic, 1976. 300 = male genitalia in left lateral view, 301 = paraproct in caudal view, 302 = apical arms of the dorsal branches of p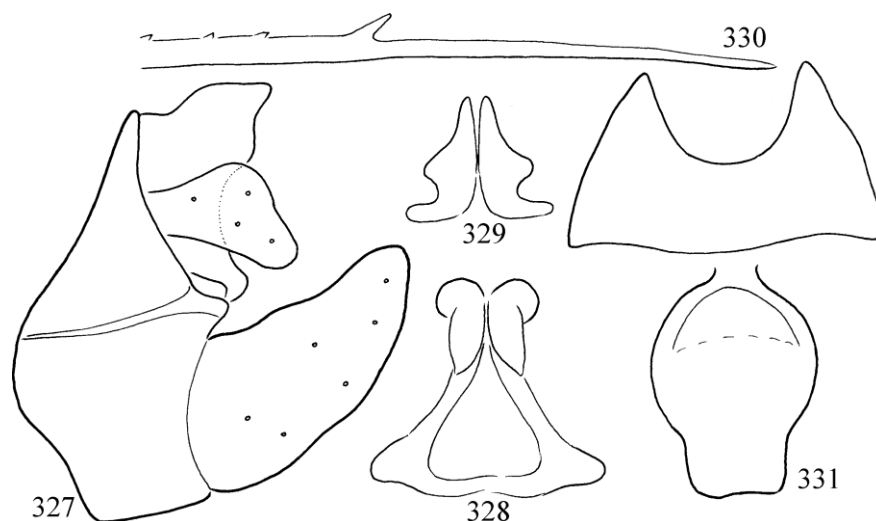araproct in dorsal view, 303 = paramere in left lateral view, 304 = tergite IX and dorsal profile of vaginal sclerite complex in dorsal view.
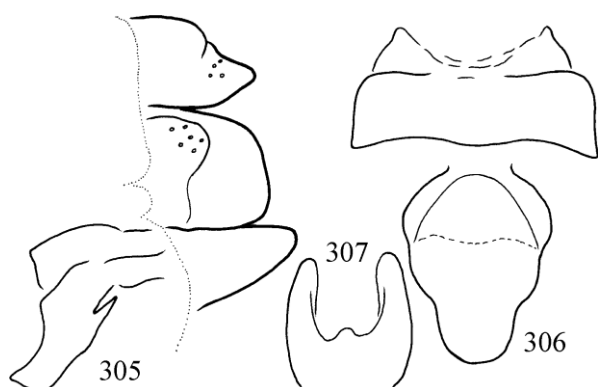
Figures 305–307. *Drusus ostot* Oláh, sp. nov. 305 = female genitalia with vaginal sclerite complex in left lateral view, 306 = tergite IX and dorsal profile of vaginal sclerite complex in dorsal view, 307 = vulvar scale in ventral view.

Drusus paros Oláh sp. nov.

(Figures 308–310)

Material examined. Holotype female. **Albania**: North Albanian Alps (Prokletije Mts.), Cerem, 42º29'48"N 19º56'55"E, 1225 m, 29. VII. 2016, light leg. Z. Varga (1 female, OPC).

Diagnosis and description. This species is known only by the female holotype. *Female genitalia.* The very specialised tergit IX makes it possible to distinguish this species from all the other known species. Tergite of segment IX clearly bipartite well visible from both dorsal and lateral view; lateral broadening of the basal part separating the basal and distal parts of the segment; apical margin of the segment IX is very specific, quadrifid; the lateral setose lobe of sternite IX rounded continuing ventrad by setaless slightly pigmented ventrum. Segment X membranous and embedded inside segment IX and encircling anus; supragenital plate of segment X well-developed with concave apical margin in lateral view. Median lobe of the vulvar scale (lower vaginal lip) very long digitiform; lateral lobes of the vulvar scales mesad directed rounded lobes. Dorsal profile of the vaginal sclerite complex tripartite and narrowing anterad.

The dorsal profile of the bipartite segment IX is very specific, especially the quadrifid apical margin is remarkable. Only *D. gombos* has mesal lobe on the apical margin of segment IX, but it is not bifid.

Etymology. paros, from „páros", paired in Hungarian, refers to the bifid "paired" shape of the mesal lobe on the apical margin of segment IX.

Drusus pelasgus Oláh, 2010

(Figures 311–317)

Drusus pelasgus Oláh, 2010: 106–108, "Etymology. Name was given to remind the origin of the Albanian people inhabiting the type locality. *Pelasgus* was the ancestor of the Pelasgians, the son of Zeus, the Ancient Greeks even used to believe that he was the first man. In a wider sense Albanians are Illyrians and Illyrians are Pelasgians, as a result the Albanian language explains the names of the ancient Greek gods, the Greek mythology originates from the Illyrian-Pelasgian."

Diagnosis. Oláh 2010: 108, "This dark species with almost ebony black sclerites belongs to the species complex with large upward arching triangular gonopods and triangular or bilobed cerci inhabiting the Balkan Mountains. Most close to *Drusus plicatus* Radovanovic, 1942, but differs by having (1) posterodorsal spinate area on VIIIth tergite guadrangular in dorsal view, not triangular; (2) rounded mesal lobe of the spinate area in lateral view, not rectangular; (3) cerci not deeply bilobed; (4) cerci with dorsal lobe broad and short, not slender and long; (5) inner branch of paraproct stepped in lateral view, not rounded triangular; (6) inner branch with quadrangular lateral lobe in dorsal view, not with triangular; (7) outer branch robust and straight vertical, not thin and arching; (8) outer branch met mesad forming a closed structure around anus, not open." The lateral profile of both cerci and paraprocts is similar to *D. plicatus*, but the dorsal branch of the paraproct is lower; the dorsal arm of cerci more robust; the semiperpendicular teeth of paramere much reduced, not robust.

Material examined. Holotype male. **Albania**, Dibre county, Korab Mts, torrent and wet meadow NE of the Mt Korab, 2300 m, N41 48.143° E20 33.285°, 27.VI.2007, leg. L. Dányi, Z. Erőss, Z. Fehér, A. Hunyadi & D. Murányi (1male, HNHM). Allotype: same as holotype (1 female). Paratypes.Same as holotype (1male, HNHM). *New material*. Albania, Diber district, Korab Mts., 4.5 km SE of Radomire, open brook, N41° 47'44.2" E20° 31'51.7", 2050 m, 11. X. 2014, leg. P. Juhász, T. Kovács & G. Puskás (1 female, OPC).

Description of female. In the original species description a single female was associated, but not described. Later we have collected another female nearby locus typicus. Here we describe female from the originally associated female, as allotype. Similarly to the male, the female is most similar to *Drusus plicatus* female. Tergite of segment IX forming even shorter tube, open ventrally, roundly excised dorsally; its apical lateral lobes setose, tapering almost pointed in dorsal view; the lateral setose lobe of sternite IX triangular and continuing into setaless less pigmented downward section. Segment X membranous and embedded inside segment IX and encircling anus; supragenital plate of segment X well-developed and quadrangular both in lateral and dorsal view; slightly concave middle in lateral view. Median lobe of the vulvar scale (lower vaginal lip) present and small in ventral view. Genital chamber, the vagina is medium sized reaching 2 thirds of sternite VIII. Vaginal sclerite pattern clearly visible.

Drusus plicatus Radovanovic, 1942

(Figures 318–322)

Drusus plicatus Radovanovic, 1942: 186–188, "Fundort: Labuniste, nordwestlich von Struga, am fusse des Jablanitza-Gebirges.

Material examined. **Albania**, Bulqizë district, Çermenikë Mts, brooks in open forest beneath Mt. Kaptinë, N41°23.199', E20°17.338', 1600 m, 27.V.2013, leg. P. Juhász, T. Kovács, G. Magos, G. Puskás, (3 males, OPC). Librazhd district, Çermenikë Mts, tributary of stream Zalli i Steblevës at forest edge 4 km SW of Steblevë, 31.V.2013, N41°18'29.8", E20°26'33.2", 1270 m, leg. P. Juhász, T. Kovács, G. Magos, G. Puskás, (2 males, 2 females; OPC). **Macedonia**, Southwestern region, Jablanica Mts, Vevčani, Vevčani Springs and outlet stream at the city, N41°14.371', E20°35.056', 935 m, 07.05.2014, leg. T. Kovács, D. Murányi (8 males, 14 females; OPC). Southwestern region, Jablanica Mts, Vevčani, Vevčani Springs and outlet stream at the city, N41°14.371', E20°35.056', 935 m, 26.06.2014, leg. P. Juhász, T. Kovács, D. Murányi (2 males, 2 females; OPC). Southwestern region, Jablanica Mts, Vevčani, Vevčani Springs and outlet stream at the city, N41°14.371', E20° 35.056', 935 m, 10.10.2014, leg. P. Juhász, T. Kovács, G. Puskás (13 males, 58 females; OPC).

Diagnosis. Radovanovic, 1942:186-190: Compared to *Drusus bosnicus* and *D. graecus* among the known species in the Balkan Peninsula. "Von dieser Art (*Drusus graecus*) sowie von *Drusus bosnicus* Klap. Unterscheiden
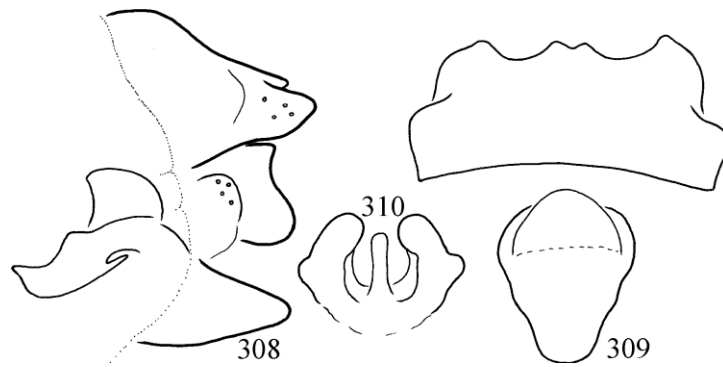
Figures 308–310. *Drusus paros* Oláh, sp. nov. 308 = female genitalia with vaginal sclerite complex in left lateral view 309 = tergite IX and dorsal profile of vaginal sclerite complex in dorsal view, 310 = vulvar scale in ventral view.
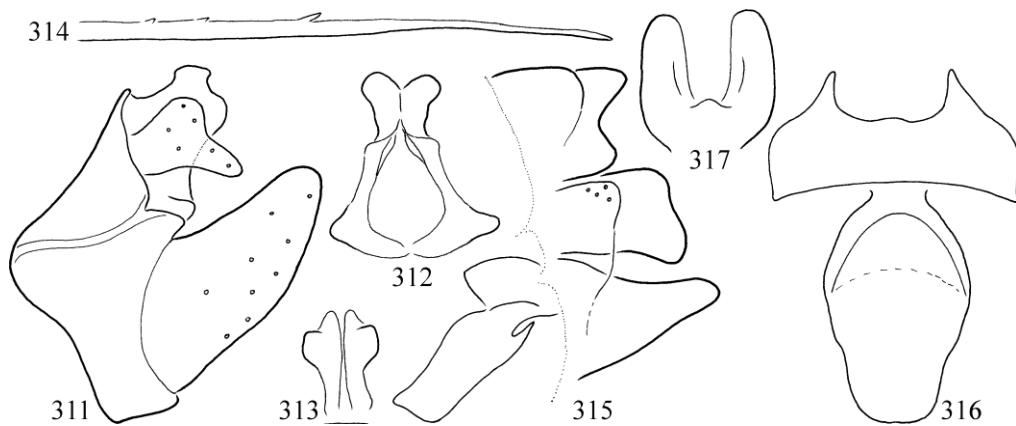
Figures 311–314. *Drusus pelasgus* Oláh, 2010. 311 = male genitalia in left lateral view, 312 = paraproct in caudal view, 313 = apical arms of the dorsal branches of paraproct in dorsal view, 314 = paramere in left lateral view, 315 = female genitalia with vaginal sclerite complex in left lateral view, 316 = tergite IX and dorsal profile of vaginal sclerite complex in dorsal view, 317=vulvar scalerite.
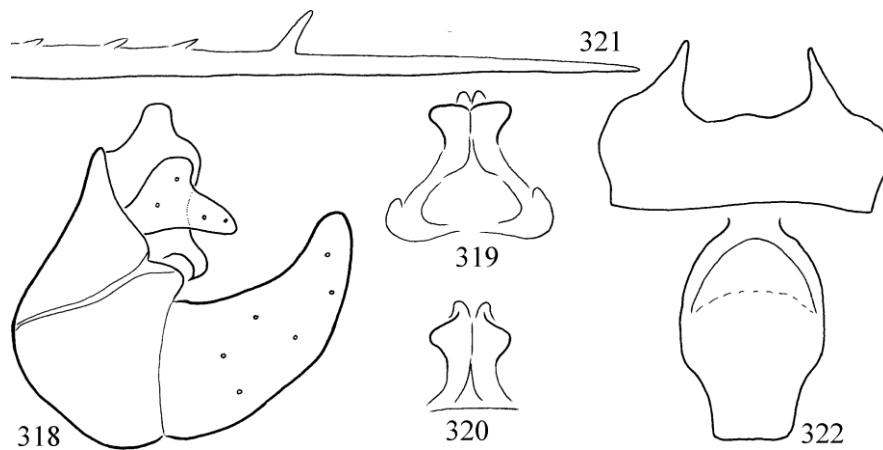
Figures 318–322. *Drusus plicatus* Radovanovic, 1942. 318 = male genitalia in left lateral view, 319 = paraproct in caudal view, 320 = apical arms of the dorsal branches of paraproct in dorsal view, 321 = paramere in left lateral view, 322 = tergite IX and dorsal profile of vaginal sclerite complex in dorsal view.

sich die Exemplare von der Jablanitza (*Drusus discophorus*) und von Labuniste (*Drusus plicatus*) nach einigen augenscheinlichen charakteristischen Merkmalen, vorwiegend nach der Form der Genitalanhange und nact der Gestalt des 8. Tergits.''

Drusus radovanovici Marinkovic-Gospodnetic, 1971

(Figures 323–326)

Drusus radovanovici Marinkovic-Gospodnetic, 1971a: 80, "Many males and females in samll springs of the tributaries of the river Sutjeska, on the mountain Zelengora, up to 1400 m."
Drusus radovanovici radovanovici Marinkovic-Gospodnetic 1976: 78, subspecies status indicated by the description of *Drusus radovanovici septentrionis* Marinkovic-Gospodnetic, 1976.
Drusus radovanovici Marinkovic-Gospodnetic, 1976: Kucinic *et al.* 2011: 150, Based on larval and adult morphology as well as by mtCOI gene sequences.

Material examined. **Bosnia & Herzegovina**: Zelengora, Suha, forest spring above the settlement, 43°15'53.5", 18°35'35.7", 1112m, 10.V.2006, leg. L. Dányi, J. Kontschán & D. Murányi (3 males, HNHM).

Diagnosis. Marinkovic-Gospodnetic, 1971a: 80, "This species belongs to the group *bosnicus* too, but it is mostly similar to *D. plicatus* Rad. The differences between *D. radovanovici* and *D. plicatus* is in the structure of the eighth tergit, in the shape of its front margin as well as in the shape of its zones with tubercula. These characters of *D. radovanovici* correspond to those of D. *bosnicus* and *D. klapaleki*."

Drusus ramae Marinkovic-Gospodnetic, 1971

(Figures 327–331)

Drusus ramae Marinkovic-Gospodnetic, 1971a: 80, "This species (mm and ff) is found only in the large karst springs of the river Rama."

Material examined. **Bosnia & Herzegovina**: Federation of Bosnia and Herzegovina, Široki Brijeg, Listica spring, 43°23'43.6", 17°35'45.5", 2.X.2015, leg. P. Juhász, T. Kovács (10 males, 18 females; OPC).
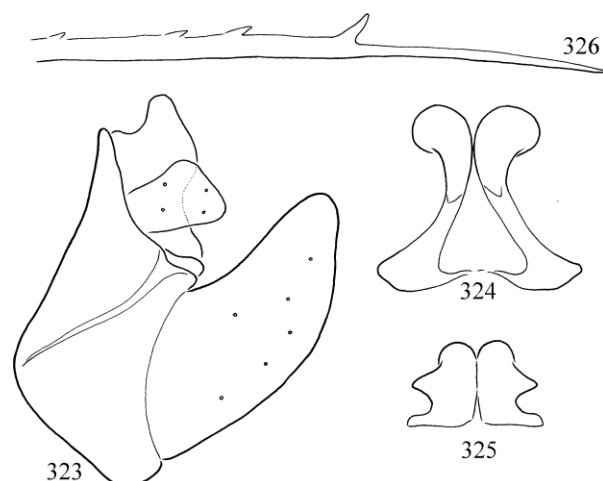
Figures 323–326. *Drusus radovanovici* Marinkovic-Gospodnetic, 1971. 323 = male genitalia in left lateral view, 324 = paraproct in caudal view, 325 = apical arms of the dorsal branches of paraproct in dorsal view, 326 = paramere in left lateral view.

Diagnosis. Marinkovic-Gospodnetic 1971a: 80, "*D. ramae* is closely related to *D. radovanovici*. It differs from it in the form of intermediate appendages. They are concave on the back side (lateral view). In dorsal view, they are narrower, more pointed than by *D. radovanovici*. The differences appear in the shape of superior appendages and inferior appendages, too."

Drusus septentrionis Marinkovic-Gospodnetic, 1976

(Figures 332–336)

Drusus radovanovici septentrionis Marinkovic-Gospodnetic, 1976: 78–80, "Inhabits the north-western part of Bosnia. The localities are: the source of the river Pliva, 13♂ 2♀, 8.VI.1972; 10♂ 4♀, 4.V.1973. (Holotype ♂, allotype ♀, paratypes ♂♂♀♀ are in the author's collection, the Faculty of Natural Science and Mathematics, Sarajevo.), the source of the rivers in Livanjsko polje: river Bistrica, 7♂ 2♀, 8.VI.1966; 9♂ 1♀, 19.X.1970; 1♂ 1♀, 16.VII.1971; Sturba, 2♂ 2♀, 8.VI.1966; 29♂ 19♀, 17.X.1970; 4♂ 5♀, 15.VII.1971, the source on the left bank of the river Vrbas near Bocac, 10♂ 2.VI.1966; 4♂ 4♀, 8.VI.1972."
Drusus septentrionis Marinkovic-Gospodnetic, 1976: Kucinic *et al.* 2011: 150, Based on larval and adult morpho-

Figures 327–331. *Drusus ramae* Marinkovic-Gospodnetic, 1971. 327 = male genitalia in left lateral view, 328 = paraproct in caudal view, 329 = apical arms of the dorsal branches of paraproct in dorsal view, 330 = paramere in left lateral view, 331 =t ergite IX and dorsal profile of vaginal sclerite complex in dorsal view.
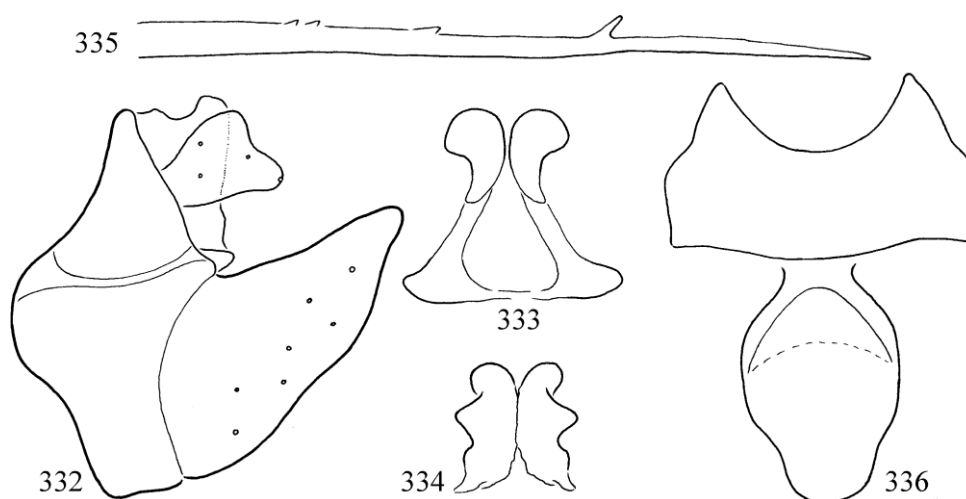
Figures 332–336. *Drusus septentrionis* Marinkovic-Gospodnetic, 1976. 332 = male genitalia in left lateral view, 333 = paraproct in caudal view, 334 = apical arms of the dorsal branches of paraproct in dorsal view, 335 = paramere in left lateral view 336 = tergite IX and dorsal profile of vaginal sclerite complex in dorsal view.

logy as well as by mtCOI gene sequences taxonomic status raised to species level.

Material examined. **Bosnia & Herzegovina**: Canton 10, Livno, Duman Spring, cave, limestone rocks and dry grassland in the Old Town, 755m, N43°49.893' E17°00.504' leg. L. Dányi, J. Kontschán, D. Murányi, 4.X.2007 (2 males, OPC). Federation of Bosnia and Herzegovina, Livno, Bistrica spring, 43°49'56.96", 17°00'30.25", 802m, 2.X.2015, leg. P. Juhász, T. Kovács (17 males, 21 females; OPC).

Diagnosis. Marinkovic-Gospodnetic, 1976: 78, "The difference between *D. radovanovici radovanovici* and *D. radovanovici septemtrionis* appears in the form of appendices intermediales and appendices superior as well as in the shape of tubercules zone of the 8th tergite."

Drusus vespertinus Marinkovic-Gospodnetic, 1976

(Figures 337–341)

Drusus vespertinus Marinkovic-Gospodnetic, 1976: 80, „Has been found only in a large karstic spring of the river Ribnik, a tributary of the river Sana: 68♂ 5♀, 26.III.1968 (Holotype ♂, allotype ♀, paratypes ♂♂♀♀ are in the author's collection);. 20♂ 11♀, 25.V.1968; 12♂ 1♀, 28.III.1975."

Material examined. **Bosnia & Herzegovina**: Republika Srpska, Gornji Ribnic, Ribnic spring, N44°24'07.9", E16°48' 05.0", 1.X.2015, leg. P. Juhász, T. Kovács (18 males, 27 females; OPC).

Diagnosis. Marinkovic-Gospodnetic, 1976: 80, "The structure of appendices intermediale is complex. The shape of the dark part of appendices intermediales is very similar to appendices intermediales of *D. radovanovici septemtrionis*. Appendices superiores are concave and similar to those of *D. radovanovici septemtrionis* and *D. medianus*."

Drusus discophorus species complex

The delineation of species complexes in the species group is based on paraproct shape divergenses. *Drusus discophorus* species complex has dorsal branch of the paraproct with variously patterned pair of apical arms in lateral view, much enlarged laterad forming a pair of variously shaped lateral lobes in caudal view. This medium sized species complex is comprised of eight species: *discophorus, juliae, kerek, komanus* sp. nov., *krusniki, popovi, sharensis, vernonensis*.

Drusus discophorus Radovanovic, 1942

(Figures 342–346)

Drusus discophorus Radovanovic, 1942: 184–186. „Fundstelle: An den Quellen und Bachen am 1. und 3. Gebirgssee auf dem Jablanitza-Gebirge." „Dieses Gebirge liegt etwa 16 km nordwestlich von Struga am Ochridsee und bildete damals das Grenzgebiet zwischen Albanien und Jugoslawien. In einer Höhe von etwa 1960 m befinden sich vier Gebirgsseen von vreschiedener Grösse. Diese liegen im Bereiche der am Fusse des Gebirges gelegenen Dörfer Labuniste, Podgoratz und
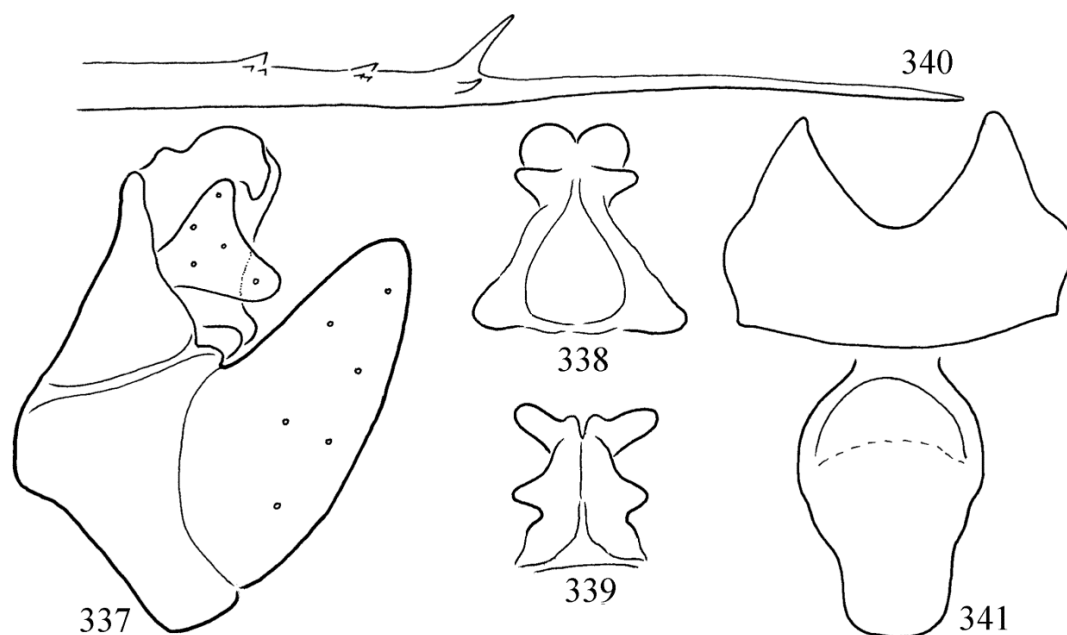
Figures 337–341. *Drusus vespertinus* Marinkovic-Gospodnetic, 1976. 337 = male genitalia in left lateral view, 338 = paraproct in caudal view, 339 = apical arms of the dorsal branches of paraproct in dorsal view, 340 = paramere in left lateral view, 341 = tergite IX and dorsal profile of vaginal sclerite complex in dorsal view.
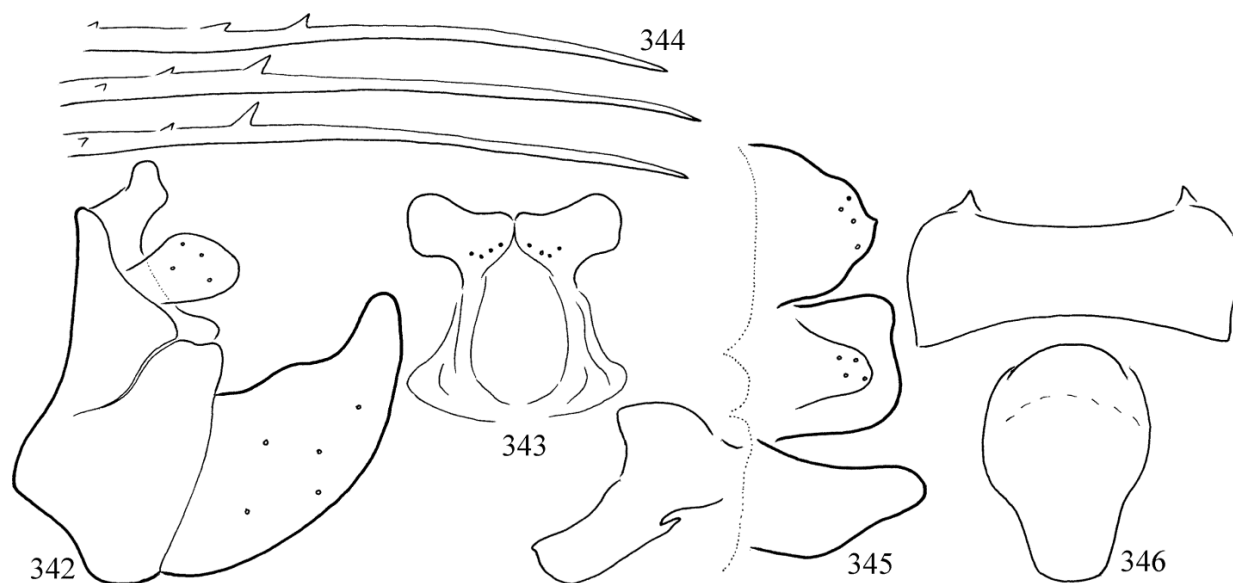
Figures 342–346. *Drusus discophorus* Radovanovic, 1942. 342 = male genitalia in left lateral view, 343 = paraproct in caudal view, 344 = parameres in left lateral view, 345 = female genitalia with vaginal sclerite complex in left lateral view, 346 = tergite IX and dorsal profile of vaginal sclerite complex in dorsal view.

Vevcane und werden auch nach diesen Dörfern als Labunisko (1. Und 2. See), Podgoracko (3. See) und Vevcansko Jezero (4. See; jezero=See) genannt. Die drei erstgenannten Seen konnte ich gelegentlich meines Besuches (13.-16.VII.1939) ziemlich eingehend trichopterologisch erforschen.","Der 1. Gebirgsee auf der Jablanitza („1. Labunisko Jezero") hat eine etwa trapezförmige Gestalt und geht mit seinem nordlichen Winkel in einen gegen Labuniste abfliesenden Bach über der bald danach unterirdisch verschwindet. Westlich von See, unter dem Gebirgsrücken, befinden sich einige kraftige Quellen, deren Wasser dem See zufliesst. Der 3 See (Podgoracko Jezero) liegt etwa 1300 m südlich von 1. See und ist bedeutend grösser als die zwei vorher geschilderten." „In dem Trichopteren-Material, das mir nachtraglich von Herrn Winneguth aus Sarajevo zum Bestimmen nachgesandt wurde, befanden sich etliche Exemplare, die ebenfalls zu dieser Art gehören. Von diesen waren zwei Stück am Limflusse bei Andrijewitza erbeutet, und die zwei anderen (samtlich ♂) an der Wrujaquelle bei Gusinje."

Material examined. **Macedonia**: Southwestern region, Jablanica Mts, Labuništa, open brook W of the city, N41° 16.069', E20°31.242', 1905 m, 26.06.2014, P. Juhász, T. Kovács, D. Murányi (7 males, 1 female; OPC).

Diagnosis. Radovanovic 1942: 186–190. Compared to *Drusus bosnicus* and *D. graecus* among the known species in the Balkan Peninsula. "Von dieser Art (*Drusus graecus*) sowie von *Drusus*

bosnicus Klap. Unterscheiden sich die Exemplare von der Jablanitza (*Drusus discophorus*) und von Labuniste (*Drusus plicatus*) nach einigen augenscheinlichen charakteristischen Merkmalen, vorwiegend nach der Form der Genitalanhange und nact der Gestalt des 8. Tergits."

Drusus juliae Oláh, 2011

(Figures 347–351)

Drusus juliae Oláh, 2011: 114, "Etymology – Patronym in honor of my wife Erzsébet Julia Tóth, who accompanies and supports my various activities in science."

Material examined. Holotype male. **Albania**: Mirdite district, Oroshi area, Nanshene, open stream in the village 1175 m, N41°51.848' E20°07.088' 21.V.2010, leg. D. Murányi (1 male HNHM). Paratypes: same as holotype (4 males, 2 females, HNHM).

Diagnosis. Oláh 2011: 113, "This castanean brown species belongs to the species complex with large upward arching triangular gonopods inhabiting the Balkan Mountains. Most close to *Drusus radovanovici* Marinkovic, but differs by having sternal lateral suture of the fused IXth segment curving, not straight; cerci subquadratic,

108

not subtriangular in lateral view; inner branch of paraproct with rounded lateral lobes, not with triangular in dorsal view."

Drusus kerek Oláh, 2011

(Figures 352–356)

Drusus kerek Oláh, 2011: 114–116. Described from North Albania, Prokletije Mts. as most close to *Drusus juliae*.

Drusus krusniki Malicky, 1981: Oláh, 2010: 104, "**Albania**: Tropoje district, Tropoje, Prokletije Mts, open stream on Mt. Callumit above the town, 1970 m, N42.498620º E20.124430º, 7.VII.2009, leg. D. Pifkó, Z. Barina, D. Schmidt & G. Runk (3 males, HNHM)." Misidentification! One male is *Drusus kerek*.

Material examined. Holotype male. **Albania**: Prokletije Mts. Creek above village, Sylbice, 2010 m, N42º31.326´ E20º05.919´ 8. VII. 2011, leg. Z. Barina, A. Kovács, G. Puskás & B. Sárospataki (1 male HNHM). Paratypes: Prokletije Mts. S slope of Mt maja e Shpatit above village Doberdol, rocky creek covered with tall herbs, 1940 m, N42º33.040´ E20º05.919´ 9. VII. 2011, leg. Z. Barina, A. Kovács, G. Puskás & B. Sárospataki (1 male, 1 female, HNHM). Albania: Tropoje district, Tropoje, Prokletije Mts, open stream on Mt. Callumit above the town, 1970 m, N42.498620º E20.124430º, 7.VII.2009, leg. D. Pifkó, Z. Barina, D. Schmidt & G. Runk (1 male, HNHM).

Diagnosis. Oláh 2011: 114–115, "This dark brown species belongs to the species complex with large upward arching triangular gonopods inhabiting the Balkan Mountains. Most close to *Drusus juliae* sp. nov. but differs by having sternal lateral suture of the fused IXth segment curving, not so deep; cerci rounded, not subquadratic in lateral view; inner branch of paraproct more robust; apical third of gonopods more tapering. *Female*: segment IX triangular in lateral view, not subquadrangular, lateral setose lobe double long than high, not similar; supragenital plate not regular quadrangular in lateral view; median lobe of the vulvar scale (lower vaginal lip) enterily lacking; lateral lobes of the vulvar scale differently shaped."

Notes. On Callumit Mountain we have detected a contact zone where *D. kerek* lives together with *D. krusniki*. The single *D. kerek* male is larger without any modifications in the genital structure.
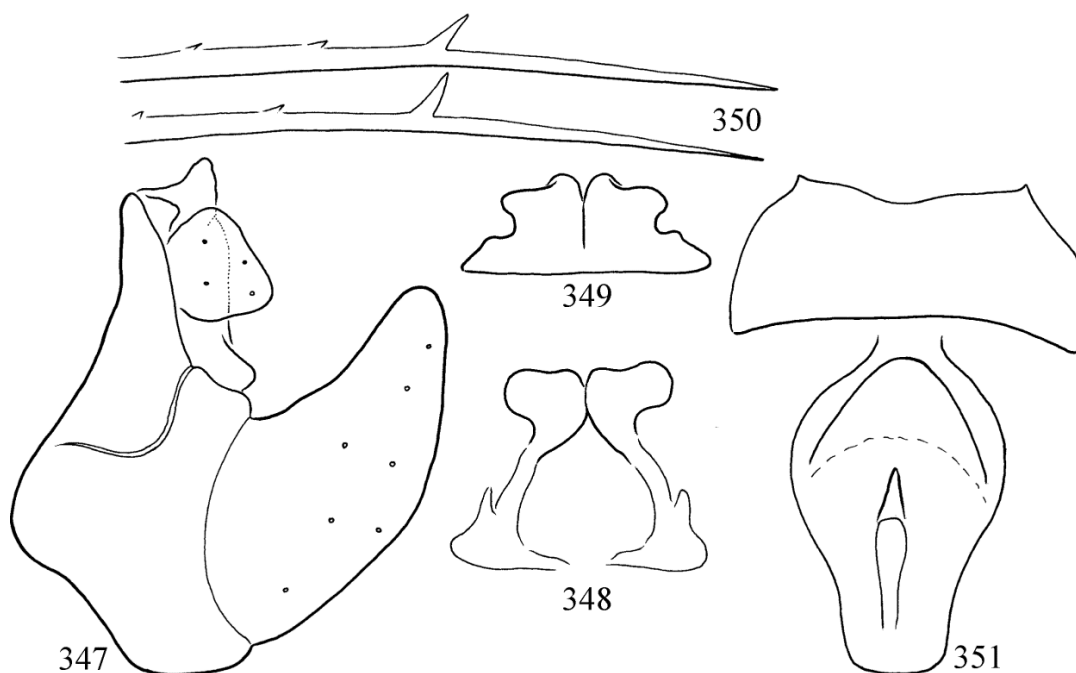
Figures 347–351. *Drusus juliae* Oláh, 2011. 347 = male genitalia in left lateral view, 348 = paraproct in caudal view, 349 = apical arms of the dorsal branches of paraproct in dorsal view, 350 = paramere in left lateral view, 351 = tergite IX and dorsal profile of vaginal sclerite complex in dorsal view.
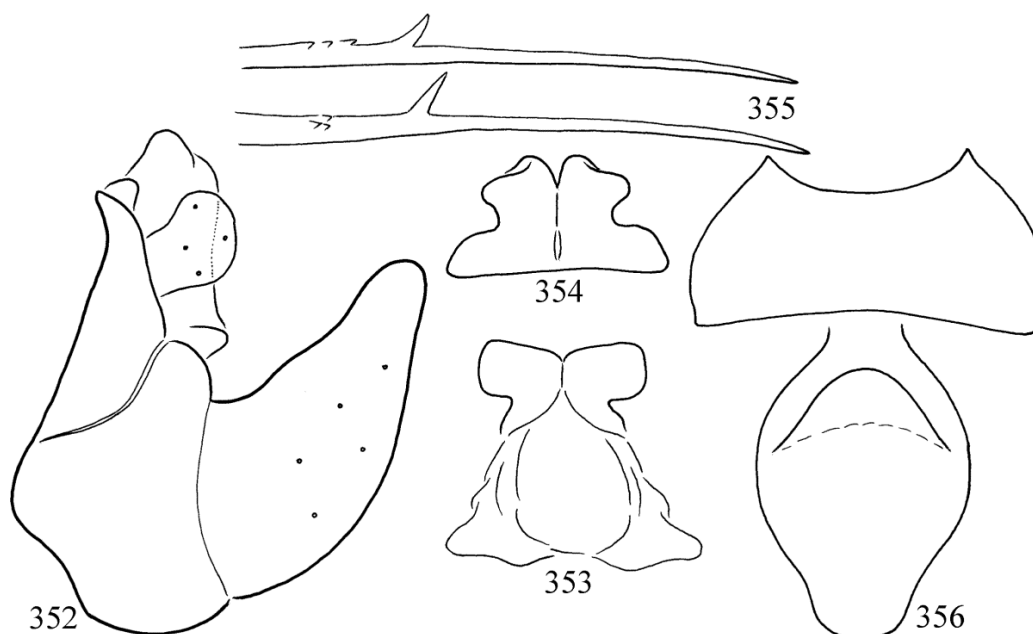
Figures 352–356. *Drusus kerek* Oláh, 2011. 352 = male genitalia in left lateral view, 353 = paraproct in caudal view, 354 = apical arms of the dorsal branches of paraproct in dorsal view, 355 = paramere in left lateral view, 356 = tergite IX and dorsal profile of vaginal sclerite complex in dorsal view.

Drusus komanus Oláh, sp. nov.

(Figures 357–360)

Drusus krusniki Malicky, 1981: Oláh & Kovács 2015: 109. Misidentification!

Material examined. Holotype: **Albania**, Shkodër district, Prokletije Mts, Mollë, Maljag Stream on the right bank of Koman Lake, N42°11.673', E19°49.063', 185 m, 18.06. 2012, leg. Z. Fehér, T. Kovács, D. Murányi(1 male, OPC).

Diagnosis and description. Before recognising the paramount importance of the contemporary diverging speciation traits expressed in the *Drusus* genus by the subtle shape divergences in the head of the apical arms of the dorsal branch of para-proct we have determined this single specimen as *D. krusniki*. The *D. komanus* is closest to *D. krusniki* and *D. kerek*, but differs from both by having the dorsal branches of the paraproct, that is the speciation trait, differently shaped. In lateral view both *D. krusniki* and *D. kerek* characterized by having a hump subdorsad on the apical margin of the paraproct. At *D. komanus* this hump structure is modiofied into a triangular process

well visible both in lateral and dorsal view. In caudal view the dorsal margin of paraproct clearly V-shaped at the new species, not straigh as at *D. krusniki* or shallow V-shaped as at *D. kerek*. The transversally plate forming measally touching pair of the dorsal branches of the paramere, that is the transversal plate characteristic for the species complex is differently formed at all the three species. This plate configuration of the speciation trait visible in caudal view is very stable. Stability is the result of selective, non-random, non-neutral processes.

Etymology. named after the locus typicus.

Drusus krusniki Malicky, 1981

(Figures 361–365)

Drusus krusniki Malicky, 1981: 342–343, "Holotypus ♂: Crna Gora, Snjili Potok, Andrijevica, 25. V. 1979, leg. Sivec, coll. Malicky."

Drusus kerek Oláh, 2011: 116. Albania, Prokletije Mts. Creek above village, Sylbice, 2010 m, N42°31.326' E20° 05.919' 8.VII.2011, leg. Z. Barina, A. Kovács, G. Puskás & B. Sárospataki (2 females, HNHM). Prokletije Mts. Valley of stream Topoje below village Sylbice, tall herb
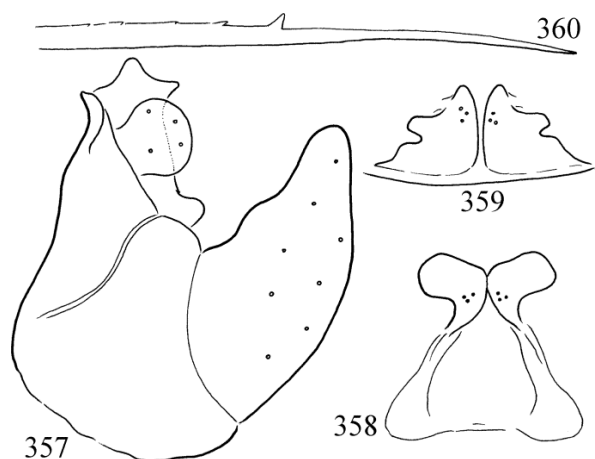
Figures 357–360. *Drusus komanus* Oláh, sp. nov. Holotype: 357 = male genitalia in left lateral view, 358 = paraproct in caudal view, 359 = apical arms of the dorsal branches of paraproct in dorsal view, 360 = paramere in left lateral view.

community of the creek 1460 m, N42°30.283ʹ E20°08.917ʹ 8. VII. 2011, leg. Z. Barina, A. Kovács, G. Puskás & B. Sárospataki (3 males, 2 females, HNHM). Prokletije Mts. Valley of stream Topoje, small side creek in village Sylbice 1580 m, N42°30.557ʹ E20°08.054ʹ 8. VII. 2011, leg. Z. Barina, A. Kovács, G. Puskás & B. Sárospataki (1 female, HNHM). Misidentification!

Material examined. **Albania**: Tropoje district, Tropoje, Prokletije Mts, open stream on Mt. Callumit above the town, 1970 m, N42.498620° E20.124430°, 7.VII.2009, leg. D. Pifkó, Z. Barina, D. Schmid& G. Runk(2 males, HNHM). Albania, Prokletije Mts. Creek above village, Sylbice, 2010 m, N42°31.326ʹ E20°05.919ʹ 8. VII. 2011, leg. Z. Barina, A. Kovács, G. Puskás & B. Sárospataki (2 females, HNHM). Prokletije Mts. Valley of stream Topoje below village Sylbice, tall herb community of the creek 1460 m, N42°30.283ʹ E20°08.917ʹ 8. VII. 2011, leg. Z. Barina, A. Kovács, G. Puskás & B. Sárospataki (3 males, 2 females, HNHM). Prokletije Mts. Valley of stream Topoje, small side creek in village Sylbice 1580 m, N42°30.557ʹ E20°08.054ʹ 8. VII. 2011, leg. Z. Barina, A. Kovács, G. Puskás & B. Sárospataki (1 female, HNHM). **Kosovo**, Novoselo (Novosellë), Beli Drim spring (Burimi i Drinit te Bardhë) (580 m) [in and around the spring and the outlet stream, limestone rocks, caves and karstic forest], N42° 44.239' E20°18.408', 12.X.2005, leg. T. Deli, V. Erőss, V. Fehér& D. Murányi (2 males, 1 female, HNHM). **Montenegro**: Gushinje S 2 km, Alipašini Izvori (935 m) [springs and their outlets, limestone rocks], N42° 33.014' E19° 49.486', 4.X.2005, leg. T. Deli, V. Erőss, V. Fehér& D. Murányi (5 males, HNHM). Sinjajevina Mts. Gornji Lipovo NW 7km, alpine grassland, 1643m, N42° 54.181' E19° 22.933', 11.X.2009, leg. L. Dányi, Z. Fehér, J. Kontschán & D. Murányi (1 male, HNHM). Prokletije Mts, Gusinje, Alipašini Izvori, N42°33'01.2", E19°49'30.5", 930

m, 08.11.2011, leg. Kovács, T.-Magos, G. (2 males, 2 females; OPC).

Diagnosis. Malicky 1981: 343, "Diese Art gehört in die Gruppe der miteiander nahverwandten und durchwegs allopatrischen Arten um *Drusus bosnicus* Klapálek, 1899, über die Marinkovic-Gospodnetic (1976) ausführlich berichtet hat. Die Unterschide zwischen diesen Arten sind relativ gering und liegen hauptsachlich in der Form der mittleren Anhange."

Described as an allopatric species of the *Drusus bosnicus* species group, and most close to *Drusus klapaleki* Marinkovic-Gospodnetic, 1971.

Notes. On Callumit Mountain we have detected a contact zone where *D. krusniki* lives together with *D. kerek*. The two *D. krusniki* males are smaller with significant modifications in the paramere spine pattern. The subterminal perpendicular enlarged spine less perpendicular, almost horizontal in one male.

Drusus popovi Kumanski, 1980

(Figures 366–370)

Drusus popovi Kumanski, 1980: 203–204. „Holotype ♂ and 2♀♀ Paratypes: Western Stara Planina Mts., Petrohan pass, stream Burzija (ca. 1000 m a.s.l.), 25.V.1979, (leg. Popov), in the National Natural History Museum, Sofia."

Material examined. Holotype and Allotype: **Bulgaria**, Western Stara Planina Mts. Petrohan Pass, stream Burzija (ca. 1000 m a.s.l.), 25. V. 1979, leg A. Popov (male, female; NMNHS). Bulgaria, Montana region, Stara Planina, Petrohan Pass, Burzija stream, N43°07'27.7", E23°07'31.5", 30. VI. 2016, leg. K. Harmos, T. Kovács & G. Magos (1 male, OPC). Bulgaria, Montana region, Stara Planina, Petrohan Pass, right side stream Burzija stream, N43°07'34.8", E23°08'23.7", 1. VII. 2016, leg. K. Harmos, T. Kovács & G. Magos (1 female, OPC).

Diagnosis. Kumanski 1980: 203–204, "This is another member of the *discophorus*-group, related closely to *Dr. bureschi* Kum. It can be recognised from the latter by the different shape of the intermediate appendages and by the long, bearing a series of thorns, parameres of the male, as well as by the dorsal shape of female genitalia and the longer central pice of the subgenital plate. These features also complete the differential diagnosis of *Dr. popovi* n. sp."
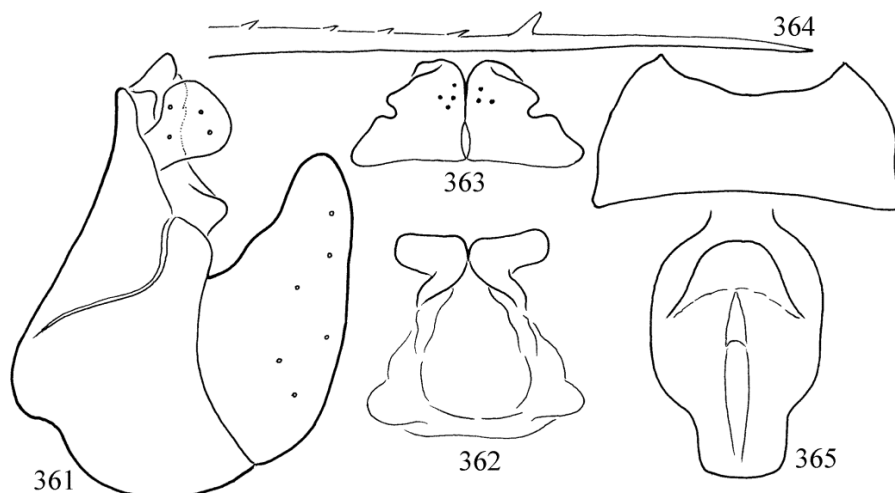
Figures 361–365. *Drusus krusniki* Malicky, 1981. 361 = male genitalia in left lateral view, 362 = paraproct in caudal view, 363 = apical arms of the dorsal branches of paraproct in dorsal view, 364 = paramere in left lateral view, 365 = tergite IX and dorsal profile of vaginal sclerite complex in dorsal view.
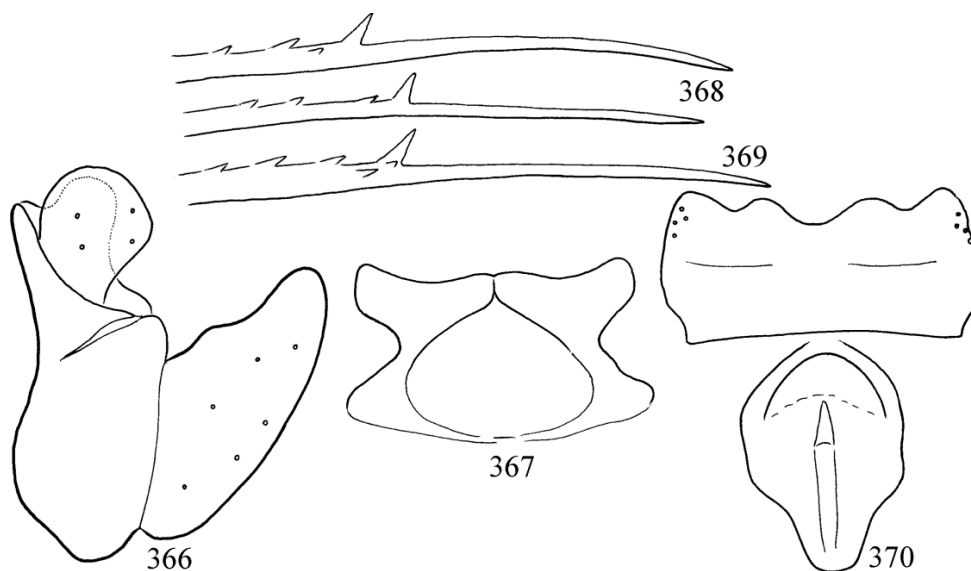
Figures 366–370. *Drusus popovi* Kumanski, 1980. Holotype: 366 = male genitalia in left lateral view, 367 = paraproct in caudal view, 368 = paramere in left lateral view, 369 = paratype paramere in left lateral view. Allotype: 370 = tergite IX and dorsal profile of vaginal sclerite complex in dorsal view.

Drusus sharrensis Ibrahimi, Vitecek & Previšić, 2016

(Figurers 371–375)

Drusus sharrensis Ibrahimi, Vitecek & Previšić, 2016 in Ibrahimi *et al.* 2016: 111–119, "Holotype. 1 male: Republic of **Kosovo**, Shterpce Municipality, Sharr Mountains, tributary of the Lepenc River, 2 km above the main road Prizren-Shterpce, 1558 m, 42.17228°N, 20.98823°E, 21. V. 2014, leg. Halil Ibrahimi (DBFMNUP)."

Material examined. Republic of **Kosovo**, Shterpce Municipality, Sharr Mountains, tributary of the Lepenc River, 2 km above the main road Prizren-Shterpce, 1558 m, 42.17228°N, 20.98823°E, 21. V. 2014, leg. Halil Ibrahimi (3 males, 1 female; OPC).

Diagnosis. Ibrahimi *et al.* 2016: 111, 114. "Males of the new species are most similar to *Drusus krusniki*, *D. kerek* and *D. juliae* but differ in exhibiting (1) a dorsally distinctly indented tergite VIII; (2) a narrow, laterally suboval, caudally protruding spinose area of tergite VIII that is medially indented; (3) anteriorly curved intermediate appendages with broad tips; (4) inferior appendages with a distinct dorsal protrusion in the proximal half; (5) parameres with 3 distinct medial spines. *Drusus krusniki* males have (1) a flat, caudally depressed tergite VIII lacking a distinct indentation; (2) a laterally broad, subtriangular, almost straight spinose area of tergite VIII lacking an indentation; (3) intermediate appendages straight, with narrow tips, in lateral view protruding somewhat dorsocaudad; (4) inferior appendages with a slight dorsal protrusion in the proximal half; (5) parameres with a single, dorsal spine in the posterior half and several medial small spines. *Drusus kerek* males have (1) a flat tergite VIII lacking a distinct indentation; (2) a laterally narrow, suboval, almost straight spinose area of tergite VIII lacking an indentation; (3)

straight intermediate appendages, with narrow tips; (4) inferior appendages subconical, curved dorsad; (5) parameres with 3 distinct medial spines. *Drusus juliae* males have (1) a rounded tergite VIII lacking a distinct indentation; (2) broad, subtriangular, spinose area of tergite VIII lacking an indentation, lateral parts of spinose area protrude caudad; (3) straight intermediate appendages, tips in dorsal view narrow, in lateral view somewhat pointed posteriad; (4) inferior appendages subconical, curved dorsad; (5) parameres with a single, dorsal spine in the posterior third and several medial small recumbent spines.

Females of the new species are most similar to *D. krusniki*, *D. kerek*, *D. juliae*, and *D. plicatus* but differ in exhibiting (1) segment X longer than the supragenital plate with distinctly pointed tips, distally tall in lateral view, caudal margin shallowly concave in dorsal view; (2) a quadrangular supragenital plate with a distinct round dorsal protrusion; (3) a vulvar scale with a small median lobe. *Drusus krusniki* females have a more slender segment X that is shorter than the supragenital
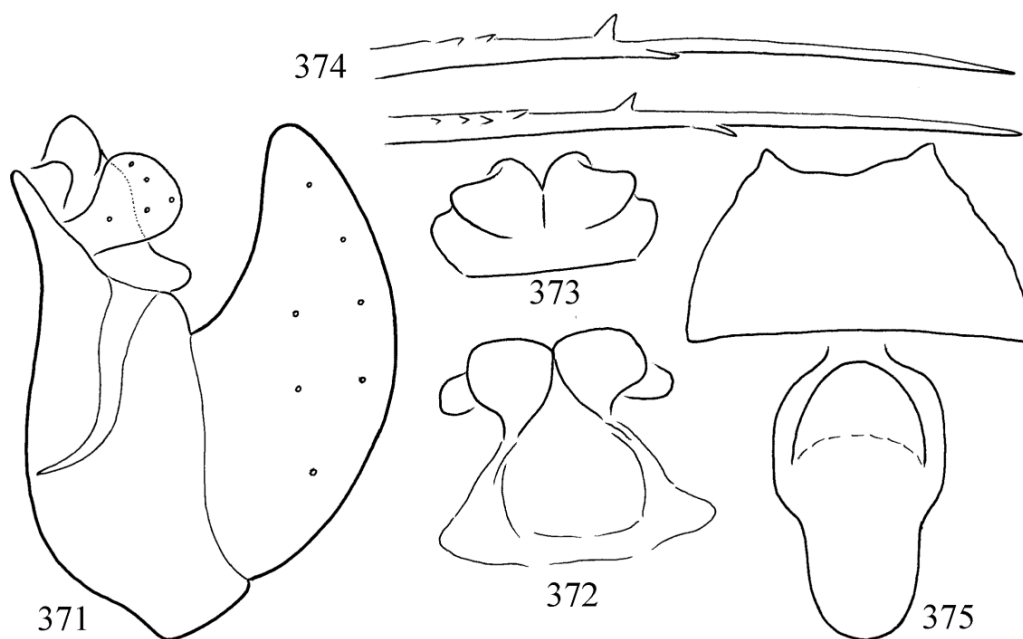
Figures 371–375. *Drusus sharensis* Ibrahimi, Vitecek & Previsic, 2016. 371 = male genitalia in left lateral view, 372 = paraproct in caudal view, 373 = apical arms of the dorsal branches of paraproct in dorsal view, 374 = parameres in left lateral view 375 = tergite IX and dorsal profile of vaginal sclerite complex in dorsal view.

plate in dorsal view and has round tips and a deeply concave caudal margin. *Drusus kerek* females have a ventrally curved segment X shorter than the supragenital plate, a dorsally irregularly rounded supragenital plate, and a vulvar scale lacking the median lobe. *Drusus juliae* females have round tips of segment X and lack a distinct dorsal protrusion of the supragenital plate. *Drusus plicatus* females have a more-slender segment X that is shorter than the supragenital plate in dorsal view and has round tips and a deeply concave caudal margin, and a rounded supragenital plate in ventral view that lacks a distinct dorsal protrusion in lateral and caudal views."

Drusus vernonensis **Malicky, 1989**

(Figures 376–380)

Drusus vernonensis, Malicky, 1989: 303−304, "Holotypus ♂ und Paratypen (1♂, 1♀): Griechenland, Vernon-Gebirge bei Bitsi, ca. 1700 m, 11.VI.1989, in meiner Sammlung."

Material examined. **Greece**, GR416, Vernon-Gebirge, E. Bitsi, 1700 m, 40°38'N, 21°24'E, 15. VII. 1991, leg. H. Malicky (1 male, 1 female; OPC).

Diagnosis. Malicky 1989: 303, "Kopulationsarmaturen ♂ ahnlich wie bei *Drusus krusniki* Malicky. *Drusus krusniki* aus Crna Gora ist etwas grösser, im habitus und in der Farbung gleich, das hyaline Dorsalfeld des 8. Tergits ist breiter, der Endteil der unteren Anhange in Ventralansicht viel plumper, und die Form der freien Dorsalteile der mittleren Anhange ist anders."

Drusus graecus **species complex**

Drusus graecus species complex has dorsal branches of the paraproct fused forming simple, rounded hump-like, blunt apical arm in lateral view, with laterad slightly enlarged shape in caudal view. The species group is represented by two sibling groups:

(1) *Drusus greacus* siblings having fused apical arms without basolateral lobes distributed in the Eastern Balkan;
(2) *Drusus lepidopterus* siblings having fused apical arms with basolateral lobes distributed in the South-Western Alps and in the Northern Apennine Mountains.

Schmid (1956) has already suggested certain relationship between *D. graecus* and *Monocentra lepidoptera*. His conclusion was based on paraproct similarity: it is small and fused at both species. Here we confirm the realationship between the two sibling groups based on the ancestral divergences of their paramere pattern as well.

Drusus graecus **siblings**

These siblings has dorsal branches of the paraproct fused forming simple, rounded hump-like, blunt apical arm in lateral view, with laterad slightly enlarged shape without basolateral lobes in caudal view. Eastern Balkan is populated by the *Drusus graecus* siblings with two species: *D. graecus* inhabits the Parnass Mts. and *D. lakmos* sp. nov. inhabits the Lakmos Mts.

Drusus graecus **(McLachlan, 1876)**

(Figures 381–384)

Peltostomis graeca McLachlan, 1876: 180–181, "One pair (♂ ♀) from Geece (Parnassus, Krüper), forwarded to me by Dr. Rogenhofer from Vienna Museum."

Material examined. Holotype and allotype: **Greece**, Parnass, 1869, Krüper, 20. VII. 1866 in other label (1 male, 1 female, WM)
.

Diagnosis. McLachlan 1876: 180–181, "I can discover no trace of spur on the anterior tibiae of the ♂; the insect therefore falls into the genus *Peltostomis*. The short discoidal cell is a somewhat remarkable feature."

Additional diagnosis. See the comparative trait values evaluated at its sibling *D. lakmos* sp. nov.

Drusus lakmos **Oláh, sp. nov.**

(Figures 385–397)

Drusus graecus McLachlan, 1876: Malicky 2005b: 107. All specimens collected by Sivec in Pindos and Lakmos Mts. Misidentification!
Drusus graecus McLachlan, 1876: Oláh & Kovács 2015: 109. Misidentification!

Material examined. Holotype: **Greece**, Thessaly, Trikala peripheral unit, Lakmos Mts, Chaliki, springs on Verliga Plateau, N39°40.825', E21°07.551', 2020 m, 09.05.2014, T.
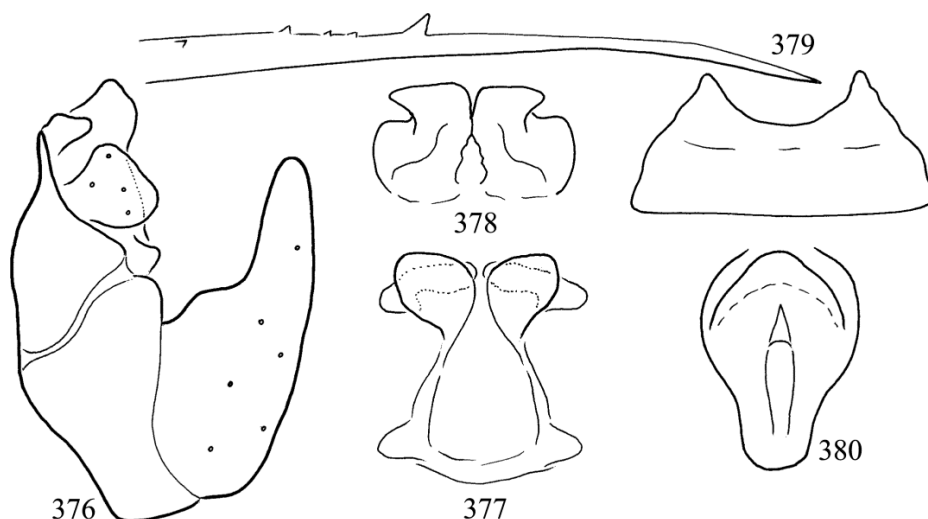
Figures 376−380. *Drusus vernonensis* Malicky, 1989. 376 = male genitalia in left lateral view, 377 = paraproct in caudal view, 378 = apical arms of the dorsal branches of paraproct in dorsal view, 379 = parameres in left lateral view 380 = tergite IX and dorsal profile of vaginal sclerite complex in dorsal view.
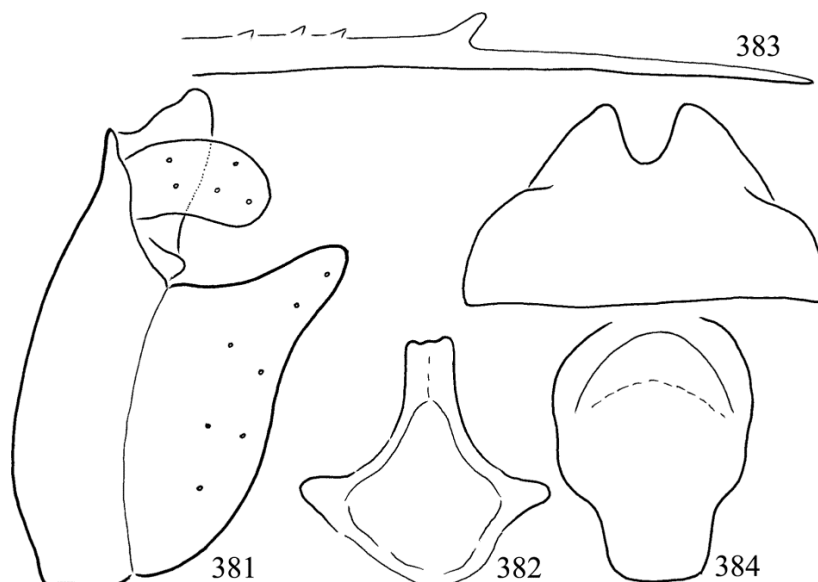
Figures 381−384. *Drusus graecus* (McLachlan, 1876). Holotype: 381 = male genitalia in left lateral view, 382 = paraproct in caudal view, 383 = parameres in left lateral view. Allotype: 384 = tergite IX and dorsal profile of vaginal sclerite complex in dorsal view.

Kovács, D. Murányi (1 male, OPC). Allotype: same as holotype (1 female, OPC). Paratypes: same as holotype (2 males, 1 female, OPC). Greece, Thessaly, Trikala peripheral unit, Lakmos Mts, Chaliki, open brook W of the village, N39°40.895', E21°08.261', 1840 m, 09.05.2014, T. Kovács, D. Murányi (1 male, 1 female; OPC). Thessaly, Trikala peripheral unit, Lakmos Mts, Chaliki, open stream SW of the village, N39°40.267', E21°09.176', 1430 m, 09.05.2014, T. Kovács, D. Murányi (1 male, 2 females; OPC).

Diagnosis and description. The dorsal branches of the paraproct fused forming simple, rounded hump-like, blunt apical arm in lateral view at all the examined five specimens; not hump, more pointed at *D. graecus*. The paraproct caudal profile is low, high at *D. graecus*; the apex of the fused dorsal branches rounded with small pointed mesal structure, apex is straigt or rather concave

without any mesal structure at *D. graecus*. Cerci are rounded at all the five specimens; elongated at *D. graecus*. The primary erect spine on the paramere is highly reduced, almost vestigial at all the five males; this erect spine an ancestral character of the *Drusus bosnicus* species group is retained, almost fully developed at *D. graecus*.

Female description. Female has similar genital architecture as the examined female allotype of *D. graecus*, except the dorsal profile of the segment IX differs, it is short at all the examined five specimens.

Etymology. Named after the locus typicus.

Drusus lepidopterus siblings

Drusus lepidopterus siblings has dorsal branches of the paraproct fused and forming a simple, rounded hump-like, blunt apical arm in lateral view. In caudal view the fused dorsal branches of paraproct slightly enlarged laterally with basolateral lobes.

Delineation by higher resolution. This simple monotonous structure of the paraproct, both in lateral and dorsal view, with fine shape divergences is just visible to distinguish between siblings, even with the highest magnification of stereomicroscopy. At the same time at higher resolution of compound microscopy we have
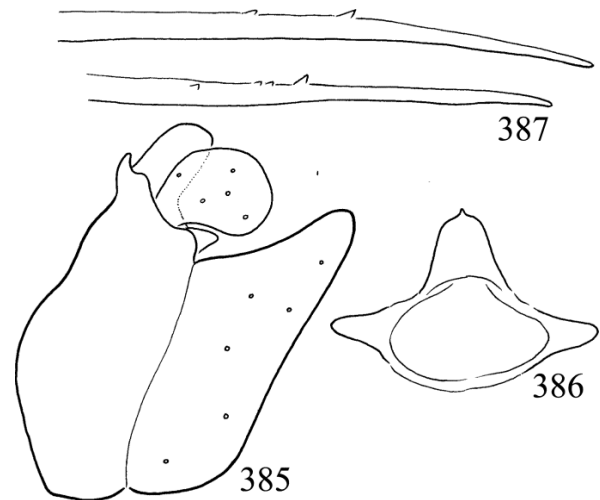
Figures 385−387. *Drusus lakmos* Oláh, sp. nov. Holotype: 385 = male genitalia in left lateral view, 386 = paraproct in caudal view, 387 = parameres in left lateral view.

recognised divergent and very stable dorsal shape profiles at the different sibling species integrated in the isolated mountain ranges. Besides the definite divergences in dorsal shape profiles we have found very diverse surface pattern on these selective shape divergences. The additional taxonomic tool of setal/surface pattern further enlarge our capacity to delineate closely related incipient sibling species. This finding realise again the immense taxonomic potential of sophisticated fine phenomics of the selective, non-random, non-
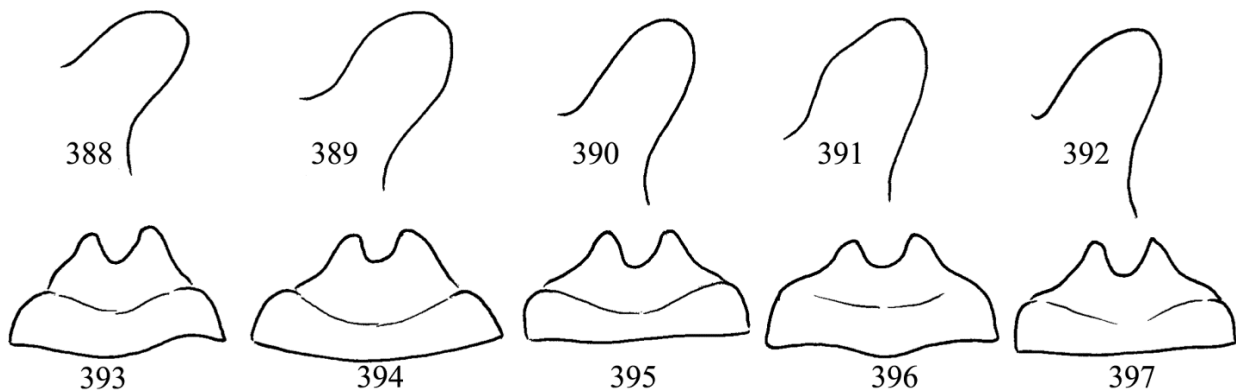
Figures 388−397. *Drusus lakmos* Oláh, sp. nov. 388−392 = lateral profile of the apical arm on the dorsal branches of paratype paraprocts. Allotype: 393 = tergite IX in dorsal view. 394−397 = tergite IX of paratypes in dorsal view.

neutral speciation traits as compared to the blind DNA genomics.

Organisation of fine surface structure. The development of sensory setal structures and possibly also other cuticular surface processes of spines, spinules, pits, ridges, plates or any noncellular processes or outgrowths is organised by a pre-pattern of field centres of morphogenes and substrate concentration (Maynard Smith & Sondhi 1961, Simpson & Marcellini 2006). Sensory setal structures, like macrochaetes of *Drosophila* on mesonotum are species specific, usually constant in number and distributed with stereotyped pattern for a species. Bristles of frequent mechanoreceptor macrochaetes, or primary setae of macrochaetes usually arranged in a constant and bilaterally symmetrical pattern peculiar to a species and applicable as constant taxonomic characters. Microchaetes are more numerous, but show no fixed number, but show some regularity in spacing. Noncellular processes of cuticular structures, minute scobinate points, nodules or small irritant spicules, spines, thorns, irregularly shaped knobs, microplates of various shapes, spatulates fixed and confluent with exosceleton may exhibit organised spacing offering another taxonomic alternative for fine phenomics. The patterns of small groups of cells in proneural cluster responsible for structure spacing are regulated by the genes of *achaete-scute* complex and mediated by lateral inhibition and Notch-signalling pathway (Simpson & Marcellini 2006).

Fine surface structural elements. In the *D. lepidopterus* siblings we have recorded the number and position of macrochaetes in definite sta-

bility ranges on the dorsal surface of the fused dorsoapical surface of the paraproct examined in dorsal view. All of the different sibling species have species specific taxonomic surface pattern. In this sibling taxa the taxonomic surface pattern is comprised of and characterised by (1) the number and distribution pattern of the primary setae of macrochaetes; (2) number and distribution pattern of microchaetes; (3) number and distribution pattern of microspines; (4) microplates of various forms, with or without superimposed microspines; (5) probable suture lines. On our schematic and diagrammatic drawings the surface patterns are not intended copies of realities, we have drawn macrochaetes, microchaetes, microspines, plates and lines just to symbolise the apparent locations and extension of the these structures. The drawn numbers of macrochaetes are more close to reality. On our drawings (1) the long bristles are symbols of macrochaetes; (2) pointed inverted small "v" are symbols of microchaetes; (3) pointed inverted larger, frequently curved "V" are symbols of microspines; (4) small irregular circles, compact, partially pointed or lined are symbols of microplates; (5) dotted lines are symbols of probable suture lines (Figures 398−400, 401−403).

Application, limits and further research. Our first trial to specify surface pattern to distinguish between incipient sibling species is just a symbolic presentation. This is not a detaliled anatomical study of sensory development on the surface of the speciation traits functioning in sexual selection processes and establishing reproductive isolation between species.
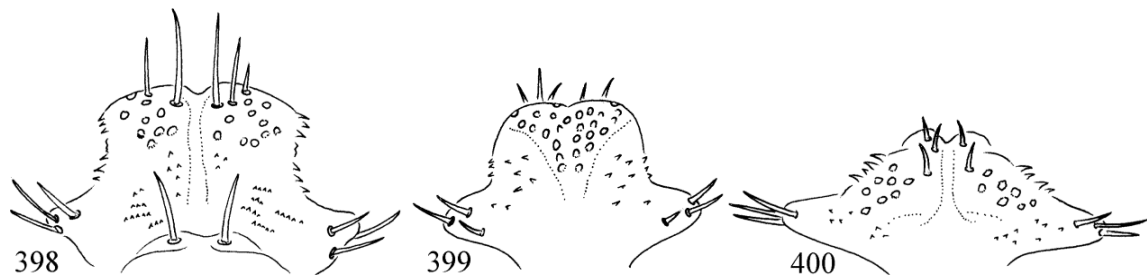
Figures 398–400. Fine dorsal profile and surface structure of paraproct at the southern clade in dorsal view: 398 = *lepidopterus*, 399 = *liguriensis*, 400 = *apuanensis*.

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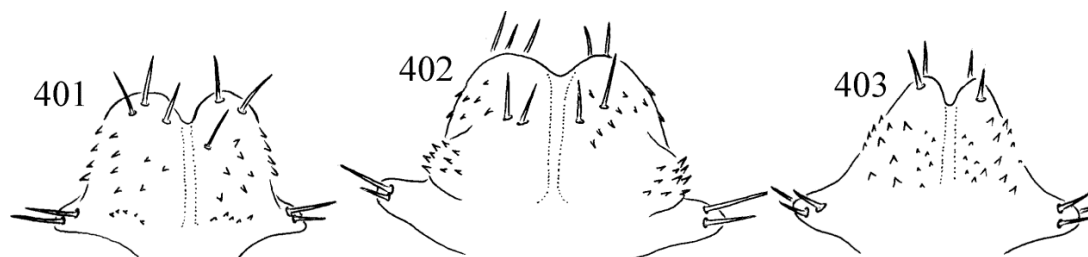
Figures 401–403. Fine dorsal profile and surface structure of paraproct at the northern clade in dorsal view:
401 = *piemontensis*, 402 = *dudor*, 403 = *savoiensis*.

Here we introduce this new taxonomic tool to provoke further studies in order to recognise specific divergences in the future among the *D. lepidopterus* populations still not sampled and waiting to be studied in various isolated mountain ranges both in the northern and southern distributional area of these taxa. The details of the individual components of the surface pattern structures and their variability ranges need more careful studies to distinguish between incipient species and their hybrids in contact zones and along contact clines under potential reinforcement processes. Here we describe the new incipient sibling species of the *D. lepidopterus* siblings by applying the dorsal profile and the dorsal surface of the fused arms of the dorsal arms of the paraproct together with the setal pattern of the paramere as we see these structure under high magnification of the compound microscope. However, we have also drawn the lateral profile of the entire male genitalia, the dorsal and caudal view of the paraproct, as well as the lateral profile of the female genitalia, the dorsal profiles of the female segment IX and the vaginal sclerite complex, as we see them under the higherst resolution of the stereomicroscopy. Based on the basic information of dorsal profiles and surface patterns gained by compound microscopy that is in the aquired knowledge of reality at higher resolution we are more prepared to distinguish the incipient sibling species by traditional drawings of stereomicroscopy. Here, for comparison, we have prepared drawings by applying both compound and stereo microscopy.

Based on the surface pattern on the dorsum of the fused dorsal branches of paraproct we can recognised two clades of siblings: (1) northern clades distributed in Savoie and Piemonte having no pronounced, distinguished microplates in the surface pattern on the dorsum of paraproct: *dudor*, *piemontensis*, *savoiensi*s; (2) southern clades distributed in Alpes Maritimes, Liguria and Toscana having pronounced microplates in various arrangements in the surface pattern on the dorsum of paraproct: *apuanensis*, *lepidopterus*, *liguriensis*.

Drusus apuanensis Oláh, sp. nov.

(Figures 400, 404–410)

Material examined. Holotype: **Italy**, Alpi Apuane, staz. N. 28, 17-21. VI. 1970, leg. G. P Moretti (1 male, MC). Allotype: same as holotype (1 female, MC).

Diagnosis and description. This species belongs to the southern group of *D. lepidopterus* siblings having pronounced microplate structures in the surface pattern on the dorsal surface of the fused dorsal branches of the paraproct. The architectural shape of the dorsal profile of the fused dorsal arm of the paraproct is characterized by longitudinal shortening and transversal elongation. The transversal elongation is the result of the elongetad basolateral lobes. The mesal body of the fused arms of the paraproct is short and broad triangular with small V-shaped apicomesal excision. The microplate field are located basolaterad on the fused subtriangular mesal body. The suture lines running mesad with some basal lateral diversion. The paramere setal pattern of the holotype asymmetrical, the erect primary spine is accompanied by a few secondary or tertiary spines located both dorsad and ventrad, left paramere is supplied by an additional less pigmented large ventral structure.
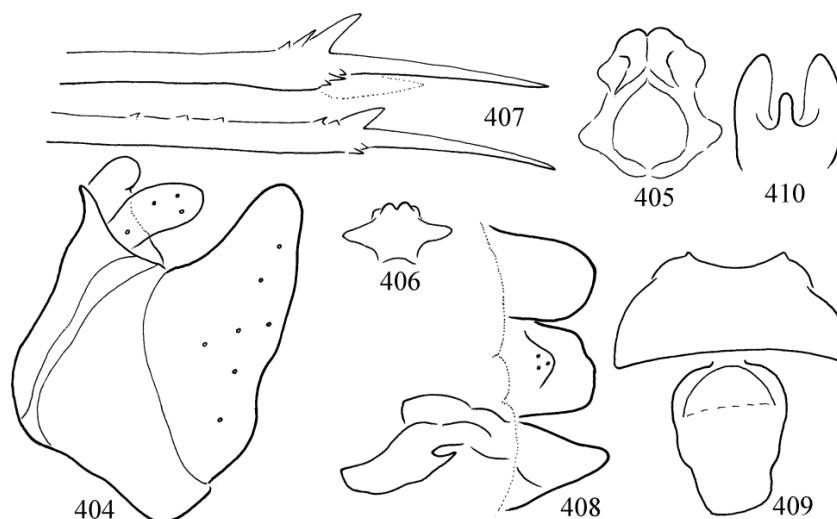
Figures 404–410. *Drusus apuanensis* Oláh, sp. nov. Holotype: 404 = male genitalia in left lateral view, 405 = paraproct in caudal view, 406 = apical arms of the dorsal branches of paraproct in dorsal view, 407 = parameres in left lateral view. Allotype: 408 = female genitalia with vaginal sclerite complex in left lateral view, 409 = tergite IX and dorsal profile of vaginal sclerite complex in dorsal view, 410 = vulvar scale in ventral view.

Female description. Tergite of segment IX forming short tube, open ventrally, with shallow rounded mesal excision; lateral lobes rounded with tiny pointed triangular ending in dorsal view; the lateral setose lobe of sternite IX rounded triangular. Segment X membranous and embedded inside segment IX and encircling anus; supragenital plate of segment X well-developed and subquadrangular in lateral view. Median lobe of the vulvar scale (lower vaginal lip) present, digitiform and half as long as the lateral lobes. Dorsal profile of the vaginal sclerite complex narrowing anterad.

Etymology. Named after the locus typicus.

Drusus dudor Oláh, sp. nov.

(Figures 402, 411–419)

Material examined. Holotype: **Italy**, Piemonte, Valchiusella, Fondo, 1700 m, 12.VII.2012, leg. G. Vincon (1 male, MCSNBG). Allotype: Piemonte, Ceresole Reale (TO), 2060 m, torr. Orco sopra Chiapili, 45.463°N 7.142°E, 21. VIII. 1965, leg. A. Viganò (1 female, MCSNBG). Paratypes: same as allotype (1 male, MCSNBG). Piemonte, Quittengo (BI), 1390 m, Artignaga ruscello, 45.6815°N 8.0300°E, light trap, 28. VI. 2001, leg. O. Lodovici, P. Pantini & M. Valle (1 male, 1 female; OPC).

Diagnosis and description. This species belongs to the northern group of *D. lepidopterus* siblings without pronounced microplates str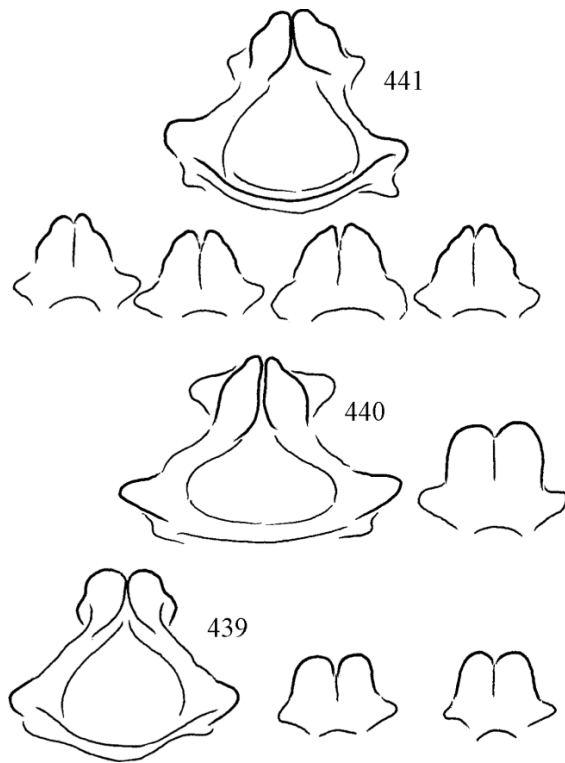uctures in the surface pattern on the dorsal surface of the fused dorsal branches of the paraproct. The architectural shape of the dorsal profile of the fused dorsal arm of the paraproct is rounded quadrangular, but broader than at *D. piemontensis*, and supplied with a basolateral humps. Area with microspine structures well developed. The paramere setal pattern is without pronounced asymmetry, the erect primary spine is broad triangular.

Female description. Tergite of segment IX forming a medium long tube, open ventrally, with deep rounded mesal excision; lateral lobes ending in rounded pointed apex in dorsal view; the lateral setose lobe of sternite IX subquadrangular. Segment X membranous and embedded inside segment IX and encircling anus; supragenital plate of segment X well-developed and quadrangular in lateral view. Median lobe of the vulvar scale (lower vaginal lip) present, triangular and half as long as the lateral lobes. Dorsal profile of the vaginal sclerite complex narrow quadrangular anterad.

Etymology. dudor, from „dudor", hump in Hungarian, refers to the pair of basolateral humps present on the paraproct.
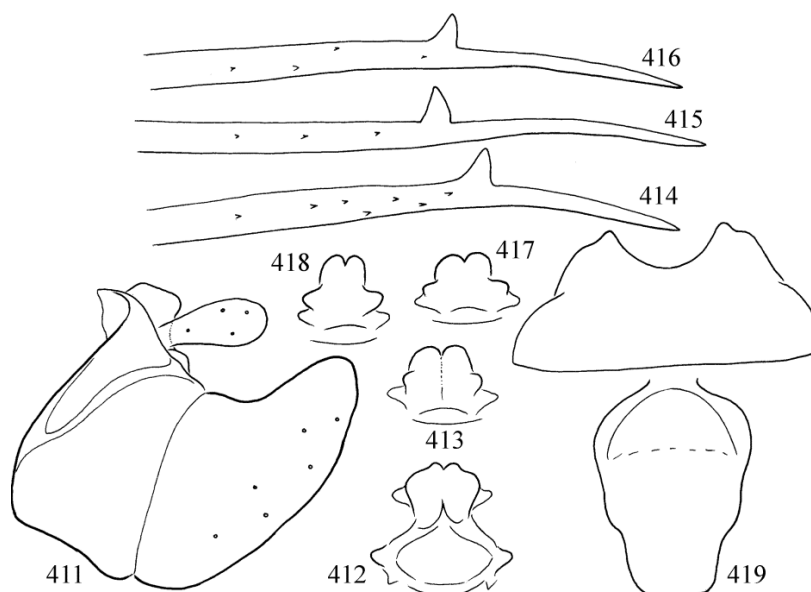
Figures 411–419. *Drusus dudor* Oláh sp. nov. Holotype: 411 = male genitalia in left lateral view, 412 = paraproct in caudal view, 413 = apical arms of the dorsal branches of paraproct in dorsal view, 414 = parameres in left lateral view. 415 = paratype paramere from Ceresole Reale in left lateral view, 416 = paratype paramere from Quittengo in left lateral view, 417 = paratype apical arms of the dorsal branches of paraproct from Ceresole Reale in dorsal view, 418 = paratype apical arms of the dorsal branches of paraproct from Quittengo in dorsal view, 419 = tergite IX and dorsal profile of vaginal sclerite complex in dorsal view.

Drusus lepidopterus (**Rambur, 1842**) **comb. nov.**

(Figures 398, 420–429)

Monocentra lepidoptera Rambur, 1842: 489, "Cette curieuse espèce m'a été communiquée par M. Géné, qui la découverte dans l'ile de Sardaigne."

Monocentra lepidoptera Rambur, 1842: McLachlan 1876: 178–179, "I owe the whole of my information and materials for this interesting insect to the kindness of Cav. Victor Ghiliani, of Turin. In 1868 he lent me the specimen which served Rambur for type, and which there is every reason to believe was (as stated by the author) taken in the island of Sardinia (not in the old kingdom of Sardinia on the mainland) by Géné. Furthermore, I received from him several males and females of the typical form taken in the Valley of Monsivo, eastern Alpes Maritimes, in June (where it was common), and a female labelled Turin. Also ♂♀ of the form indicated as a variety, from a locality in the western Alpes Maritimes. These latter are evidently a good local variety, but I see no structural differences entitling them to rank as a species: the less dense scales of the anterior-wings may be accidental, but even if constant, the character is scarcely specific, not being strengthened by any differences in neuration and anal structure."

Monocendra lepidoptera Rambur , 1842: Schmid 1956: 72, "*Mon. lepidoptera* est localisée dans le Nord de l'Italie. Elle semble assez commune dans Nord des Appenins et

remonte les vallées alpines. Peut-être a-t-elle deux générations annuelles, car elle a été signalée en mars et avril et en août et septembre. J'ai étudié 7 exemplaires capturés à Gênes, en Ligurie et dans le Piemont; ils montrent une coloration très variable."

Examined material. **France**, Department Alpes-Maritime, La Brique, Notre-Dame-des-Fontaines, 4.VII.2013, leg. G. Coppa (3 males, 3 females; OPC). Department Alpes-Maritime, Saorge, Source parking du Cairos, 2.VII.2016, leg. G. Coppa (1 male, OPC). Department Alpes-Maritime, Saorge, Cairos Sainte Claire, 1000 m, 22.IX.20083, leg. G. Coppa (1 male, OPC).

Diagnosis. Rambur 1842: 489. "Ailes d'un brun fuligineux ou noirâtre, ayant la membrane rugueuse couverte sur les quatre, de petites é-cailles noires entremêlées de poils."

Schmid 1956: 72. "Les parentés de *Mon. lepidoptera* sont difficiles a établir; il est probable que son plus proche voisin soit *D. graecus*. Les deux espèces ont en commun une coloration brun foncé uniforme, des spinules du VIIIe tergite grandes, clairsemées et déterminant une zone à fort relief, des appendices intermédiaires petits et entière-
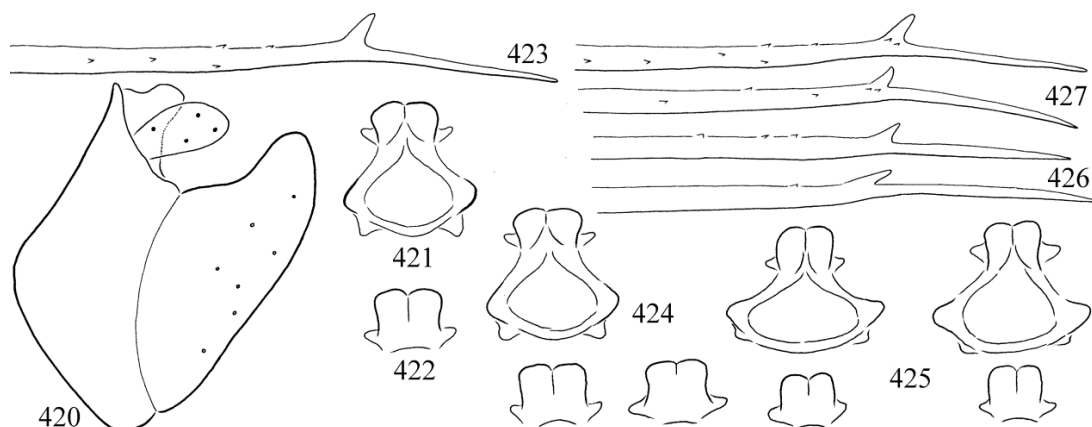
Figures 420–427. *Drusus lepidopterus* (Rambur, 1842). From La Brigue: 420 = male genitalia in left lateral view, 421 = paraproct in caudal view, 422 = apical arms of the dorsal branches of paraproct in dorsal view, 423 = parameres in left lateral view, 424 = paraproct in caudal view and apical arms of the dorsal branches of paraproct in dorsal view from La Brigue, 425 = paraproct in caudal view and apical arms of the dorsal branches of paraproct in dorsal view from Saorge, 426 = parameres from Saorge in left lateral view, 427 = parameres from La Brigue in left lateral view.
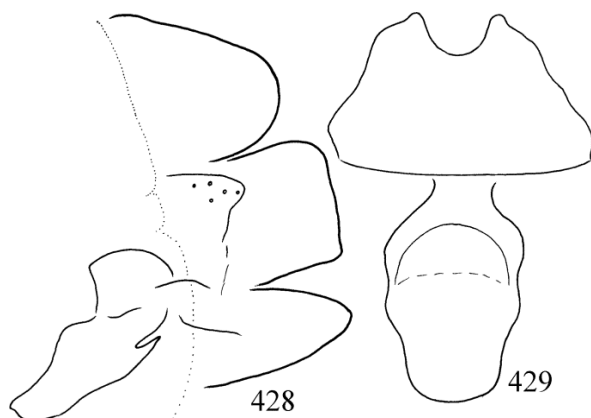
Figures 428–429. *Drusus lepidopterus* (Rambur, 1842). 428 = female genitalia with vaginal sclerite complex in left lateral view, 429 = tergite IX and dorsal profile of vaginal sclerite complex in dorsal view.

ment fusionnés, des appendices inférieurs très largement soudés au IXe segment et portant des spinules à l'apex. Toutefois, les dissemblances entre les deux formes sont importantes et ce voisinage reste lointain."

Additional diagnosis. Until now our trials have failed to receive from the Turin Museum the holotype collected by M. Géné in Sardinia Island. This particular specimen served for Rambour's description of *D. lepidopterus* (Rambur, 1842) and later was also examined by McLachlan (McLachlan 1876). McLachlan examined more speci-

mens from Alpes Maritimes in more details and actually these specimens from Alpes Maritimes served for his drawings and for the re-description of *D. lepidopterus*. Having experienced already the unreliability of some old collecting data of insect dealers (Oláh *et al.* 2016) and relying upon our recent collecting effort we presume that representatives of *D. lepidopterus* siblings do not live in Sardinia, but they are present and common in Alpes Maritimes and in many other mountain ranges. We suppose that the holotype was collected in the old kingdom of Sardinia on the mainland, probaly in Alpes Maritimes based on McLachlan. However, Schmid (1956) has drawn *D. lepidopterus* form Ligurian specimens (*D. liguriensis* sp. nov.) and Malicky (1988) has drawn *D. lepidopterus* from Lombardian specimen (*Drusus* sp.) when comparing it with *D. concolor*.

At this time we do not know what species is really *D. lepidopterus* among the here described six sibling species. Still there is some hope to locate and to receive for study the original holotype and after a detailed fine structure analysis, applying the potential resolution sensitivity of the sophisticad phenomics we can easily determine the exact locality of the original holotype. At this stage we follow McLachlan and treat specimens as *D. lepidopterus* collected from Alpes Maritimes and the other five siblings

distinguished with fine structure analysis from various mountain ranges as new species.

The nominate species belongs to the southern group of *D. lepidopterus* siblings having pronounced microplate structures in the surface pattern on the dorsal surface of the fused dorsal branches of the paraproct. The architectural shape of the dorsal profile of the fused dorsal arm of the paraproct is characterized by short basolateral lobes and medium long quadrangular mesal body. The microplate field are located apicolaterad on the mesal body. The suture lines running mesad. There is a pair of large macrochaete bristles on the dorsum of basal humps. The paramere setal pattern of the examined specimens is without pronounced asymmetry, the erect primary spine with narrowing, but blunt apex.

Female description. Tergite of segment IX forming short tube, open ventrally, with deep and narrow rounded mesal excision; lateral lobes rounded with tiny roundeded triangular ending in dorsal view; the lateral setose lobe of sternite IX triangular. Segment X membranous and embedded inside segment IX and encircling anus; supragenital plate of segment X well-developed and quadrangular in lateral view. Dorsal profile of the vaginal sclerite complex narrowing anterad.

Drusus liguriensis Oláh, sp. nov.

(Figures 399, 430–438)

Monocendra lepidoptera Rambur, 1842: Schmid 1956: 71–72. According to the drawings the species redescription was based on 7 specimens from Genes, Liguria and from Piemont. Misidentification!

Material examined. Holotype: **Italy**, Liguria, Calizzano (SV), 920 m, torrente Frassino, light trap, 28.V.2001, leg. Museo Caffi BG (1 male, MCSNBG). Allotype: same as holotype (1 female, MCSNBG). Paratypes: same as holotype (2 males, 2 females, MCSNBG; 2 males, 1 female; OPC). Liguria, Vittoria, III. 1916, leg. G. Mantero, det. Navas like *D. trifidus* (1 male, MCSNG)

Diagnosis and description. This species belongs to the southern group of *D. lepidopterus* siblings having pronounced microplates structures in the surface pattern on the dorsal surface of the

fused dorsal branches of the paraproct. The architectural shape of the dorsal profile of the fused dorsal arm of the paraproct is basically quadrangular, but more rounded compared to *D. lepidopterus*. The microplate field are located apicad in a mesal V-shaped area on the fused mesal body delineated by the V-shaped suture lines well visible also with stereomicroscopy. The paramere setal pattern of the holotype is without pronounced asymmetry, the erect primary spine is blunt dilated without secondary spines.

Female description. Tergite of segment IX forming short tube, open ventrally, with shallow and narrow rounded mesal excision; lateral lobes with tiny rounded pointed triangular ending in dorsal view; the lateral setose lobe of sternite IX rounded triangular. Segment X membranous and embedded inside segment IX and encircling anus; supragenital plate of segment X well-developed and quadrangular in lateral view. Median lobe of the vulvar scale (lower vaginal lip) present, broad lobe and half as long as the lateral lobes. Dorsal profile of the vaginal sclerite complex narrowing anterad.

Etymology. Named after the locus typicus.
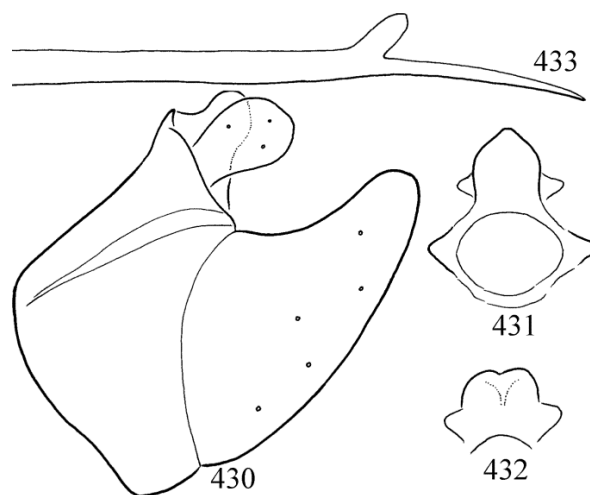
Figures 430–433. *Drusus liguriensis* Oláh, sp. nov. Holotype: 430 = male genitalia in left lateral view, 431 = paraproct in caudal view, 432 = apical arms of the dorsal branches of paraproct in dorsal view, 433 = parameres in left lateral view.
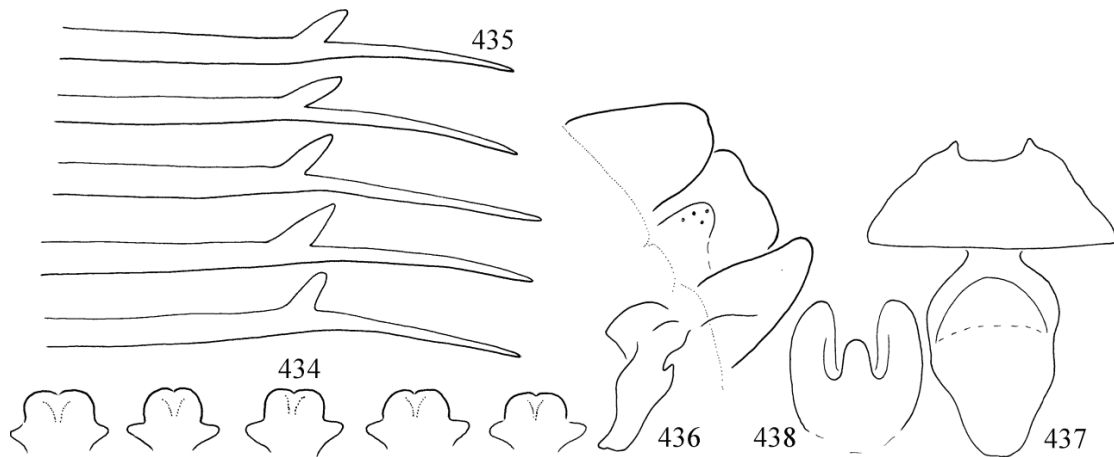
Figures 434–438. *Drusus liguriensis* Oláh, sp. nov. Paratypes: 434 = apical arms of the dorsal branches of paraproct in dorsal view, 435 = parameres in left lateral view. Allotype: 436 = female genitalia with vaginal sclerite complex in left lateral view, 437 = tergite IX and dorsal profile of vaginal sclerite complex in dorsal view, 438 = vulvar scale in ventral view.

Figures 439–441. *Drusus piemontensis* Oláh, sp. nov. Holotype: 439 = paraproct in caudal view and apical arms of the dorsal branches of paraproct in dorsal view. Paratypes: 440 = paraproct in caudal view and apical arms of the dorsal branches of paraproct from Alpes de Hautes-Provence in dorsal view, 441 = paraproct in caudal view and apical arms of the dorsal branches of paraproct from Crissolo in dorsal view.

Drusus piemontensis **Oláh, sp. nov.**

(Figures 401, 439–441)

Material examined. Holotype: **France**, Department Hautes-Alpes, Molines-en-Queyras, torrent de l'Eychassier, 2650 m, 18.VII.2012, leg. G. Coppa (1 male, MCSNBG). Allotype: Department Hautes-Alpes, Abries, source Val Fourane, 2480 m, 4.IX.2010, leg. G. Coppa (1 female; OPC). Paratypes: same as allotype (1 male, OPC). Department Alpes-de-Hautes-Provence, Saint-Paul-sur-Ubaye, source Sainfoin, 1700 m, 20. VIII. 2012, leg. G. Coppa (2 males, OPC). **Italy**, Piemonte, Crissolo (CN), 1700 m, Pian della Regina fiume Po, light trap, 2. IX. 1997, leg. M. Valle (2 male, 1 female, MCSNBG; 2 males, 1 female, OPC). Piemonte, Piemasura, Passo Forris, Val Sesia, 1300-1850 m, 9. VIII. 1936, leg. Sala (3 males, MJC). Piemonte, Alagna Valsesia, 1900 m, 12. IX. 1936, leg. Sala (3 males, MJC).

Diagnosis and description. This species belongs to the northern group of *D. lepidopterus* siblings without pronounced microplates structures in the surface pattern on the dorsal surface of the fused dorsal branches of the paraproct. The architectural shape of the dorsal profile of the fused dorsal arm of the paraproct is rounded quadrangular, but less broad than at *D. dudor*, and without a basolateral humps. Area with microspine structures well developed. The paramere setal pattern is without pronounced asymmetry, the erect primary spine is triangular. This sibling species is distributed both Hautes-Alpes, Alpes-de Hautes-Provence and in Piemonte and may

require a more detailed population study. The dorsal profile of the fused arm of the dorsal branches of the paraproct appears subtriangular in stereomicroscopy in the France populations and regular quadrangular in the Italian Crissolo population. On compound microscopy the difference was not so pronounced.

Etymology. Named after the locus typicus.

Drusus savoiensis Coppa & Oláh, sp. nov.

(Figures 403, 442–450,)

Material examined. Holotype: **France**, Department Savoie, Bramans, Ru d'Etache zone d'Eboulis, 1745 m, 13. VIII.2009 leg. G. Coppa (1 male, CPC). Allotype: same as holotype (1 female, CPC). Paratypes: same as holotype (1 male, CPC; 1 males, OPC). Department Savoie, Lanslebourg-Mont-Cenis, torrent Savalin versant adriatique, 2100 m, 8. VII. 2007 leg. G. Coppa (2 males, MCSNBG; 2 males, OPC).

Diagnosis and description. This species belongs to the northern group of *D. lepidopterus* siblings without pronounced microplates structures in the surface pattern on the dorsal surface of the fused dorsal branches of the paraproct. The architectural shape of the dorsal profile of the fused dorsal arm of the paraproct is basically triangular, but longer than *D. apuanensis*. Area with microspine structures less developed. The paramere setal pattern is without pronounced asymmetry, the erect primary spine is frequently accompanied by additional smaller spines.

Female description. Tergite of segment IX forming a medium long tube, open ventrally, with deep and narrow rounded mesal excision; lateral lobes triangular with ending in tiny pointed apex in dorsal view; the lateral setose lobe of sternite IX subquadrangular. Segment X membranous and embedded inside segment IX and encircling anus; supragenital plate of segment X well-developed and quadrangular in lateral view. Median lobe of the vulvar scale (lower vaginal lip) present, triangular and half as long as the lateral lobes. Dorsal profile of the vaginal sclerite complex quadrangular anterad.

Etymology. Named after the locus typicus.
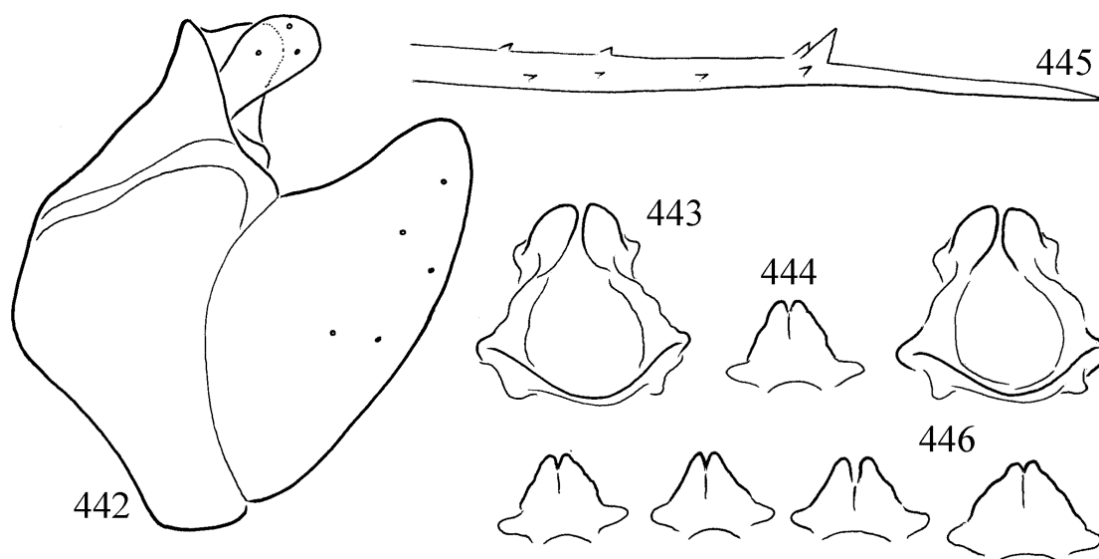
Figures 442–446. *Drusus savoiensis* Coppa & Oláh, sp. nov. Holotype: 442 = male genitalia in left lateral view, 443 = paraproct in caudal view, 444 = apical arms of the dorsal branches of paraproct in dorsal view, 445 = paramere in left lateral view. Paratypes: 446 = paraproct in caudal view and apical arms of the dorsal branches of paraproct.

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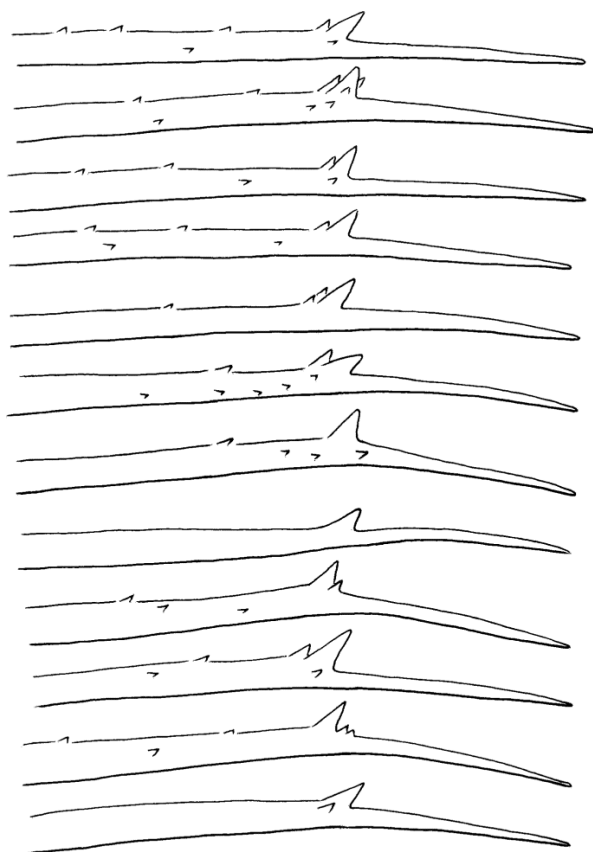
Figures 447. *Drusus savoiensis* Coppa & Oláh, sp. nov. Paratypes: paramere in left lateral view.
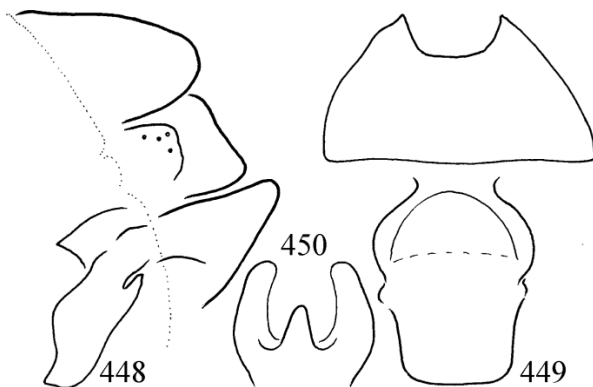
Figures 448–450. *Drusus savoiensis* Coppa & Oláh, sp. nov. Allotype: 448 = female genitalia with vaginal sclerite complex in left lateral view, 449 = tergite IX and dorsal profile of vaginal sclerite complex in dorsal view, 450 = vulvar scale in ventral view.

Drusus sp.

Monocentra lepidoptera (Rambur, 1842): Malicky 1988: 67, "Lombardei, Staffano bei Casanóva, 11.V.1980, leg. Zwick."

Notes. This specimen may represent an unknown species, having relation to *Drusus liguriensis*. The published collecting details of this single specimen was verified to us by Dr. Zwick on 29.XI. 2016 "the locality is Stáffora river, in the extreme S of Lombardia, projecting between Piemonte and Emilia". Upon our request Malicky was unable to give us information about the present availability of the single specimen of his drawings. New population sampling is required along the indicated section of Stáffora river to establish the species status of this specimen.

Drusus improvisus species complex

Drusus improvisus species complex has dorsal branch of the paraproct with horizontal digitiform fused apical arms with slightly upward directed tip in lateral view; digitiform with variously laterad directed tips in dorsal view. This poorly known species complex is distributed in the Northern and Central Apennine. Further intensive samplings are required in isolated mountain ranges to survey its biodiversity and to understand more comprehensively the diverging pattern of paraproct with variability ranges in various taxa and in the contact populations. To recognise properly the subtle shape divergences we need to apply the higher magnifying capacity of compound microscope with higher resolution also for the paraproct, not only for paramere, similarly to the *Drusus lepidopterus* species complex. At *D. lepidopterus* complex the dorsal view contained more and stable information to recognise species delineation, at *D. improvisus* complex the lateral view gives us more and stable information. *D. improvisus* species complex comprised of four species: *camerinus*, *improvisus*, *konok* sp. nov., *cianficconiae* sp. nov.

Drusus camerinus Moretti, 1981

(Figures 451–457)

Drusus camerinus Moretti, 1981: 181–182, "Holotype ♂, allotype ♀: Marche, Fonti di Selvazzano, 655 m, Camerino, Macerata, 10.V.1954, leg. Verdarelli; Paratypes ♂♂ ♀♀ collected between 1954 and 1976: Umbria 22♂,

Martche (several springs) 361♂ 92♀. In Moretti's collection. Marche 1♂ 1♀ in Malicky's collection."

Material examined. **Italy**: Marche, Macerata Province, Camerino, Fonti di Brescia, Sorgente fiume Potenza, 680 m, 4.I.1967, leg. F. Cianficconi (1 male, 1 female; OPC). Umbria, Sigillo, Monte Cucco, Rio Freddo, 1000 m, 19.V.1971, leg. P. Camici (1 male, CC n°106). Lazio, M. Terminillo, Rio Fuggio, 15. V. 1985, leg. Chiappafreddo & Piottoli (24 males, 1 female, MC; 8 males, OPC). Lazio, M. Terminillo, Rio Fuggio, 15.V.1985, leg. Moretti, Cianficconi & Chiappafreddo (3 males, 1 female, MC). Marche, M. Sibillini, sorgente, 1280 m, 27.VII.1955, leg. Tomasi (14 males, MC; 3 males, OPC).

Diagnosis. Moretti 1981: 181, "The 8th tergite is trilobed as in *D. aprutiensis*." "♀ genitalia are similar to those of *D. improvisus*, for this reason *D. camerinus* has been assigned to the *improvisus* groupe."

Additional diagnosis. D. camerinus has the fused dorsal brances of the paraproct without upward directed apices in lateral view and laterad directed apices in dorsal view. The only known species in the complex having such a character combination of scepiacition traits.

Moretti (1981) has related his species near to *D. improvisus* based on the female genitalia and compared the male to *D. aprutiensis*. Based on our ranking system *D. aprutiensis* belongs to *D. annulatus* species group far from the *D. improvisus* species group. But Moretti's species group selection based on female structure is confirmed by our male ranking system.

Drusus improvisus (**McLachlan, 1884**)

(Figures 458–459)

Monocentra improvisa McLachlan, 1884: 15, "Apenino Pistjese, Central Italy (Near Boscolungo, 3760 ft., 31st July, Slopes of Serra Fariola, 5600 ft., 1st August, and Valle Sestajone, over 4000 ft., 2nd August, Eaton, 4 ♂, 5♀."
Drusus improvisus McLachlan, 1884: Schmid 1956: 46–47, "*Dr. improvisus* habite les montagnes du Nord et le centre de l'Italie péninsulaire. J'ai étudié 1 ♂ toscan."

Material examined. **Italy**, Toscana, Pistoia, dintorni Collina, 44,3°N 10,94°E, 19. VI. 1961, leg. A. Viganò (2 males, MCSNBG). Toscana, Arezzo, torrente Singerna, 1030 m, 25. V. 1986, leg. Baviera (2 males, MC; 2 males, 1 female, OPC).
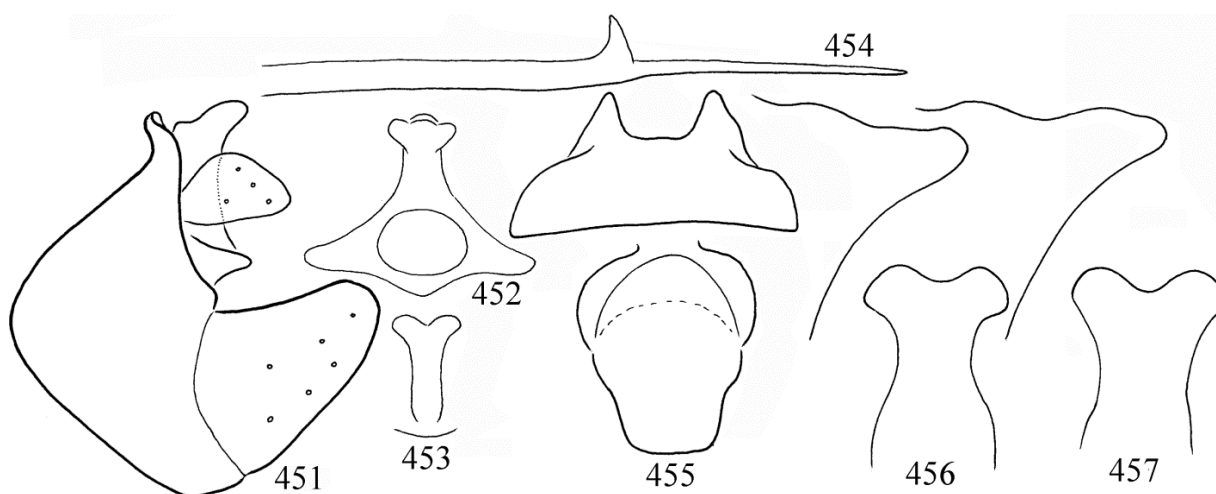
Figures 451–455. *Drusus camerinus* Moretti, 1981. 451 = male genitalia in left lateral view, 452 = paraproct in caudal view, 453 = apical arms of the dorsal branches of paraproct in dorsal view, 454 = parameres in left lateral view, 455 = tergite IX and dorsal profile of vaginal sclerite complex in dorsal view, 456 = fused apical arms of the dorsal branches of paraproct from Marche at higher magnification in lateral and dorsal view, 457 = fused apical arms of the dorsal branches of paraproct from Lazio at higher magnification in lateral and dorsal view.

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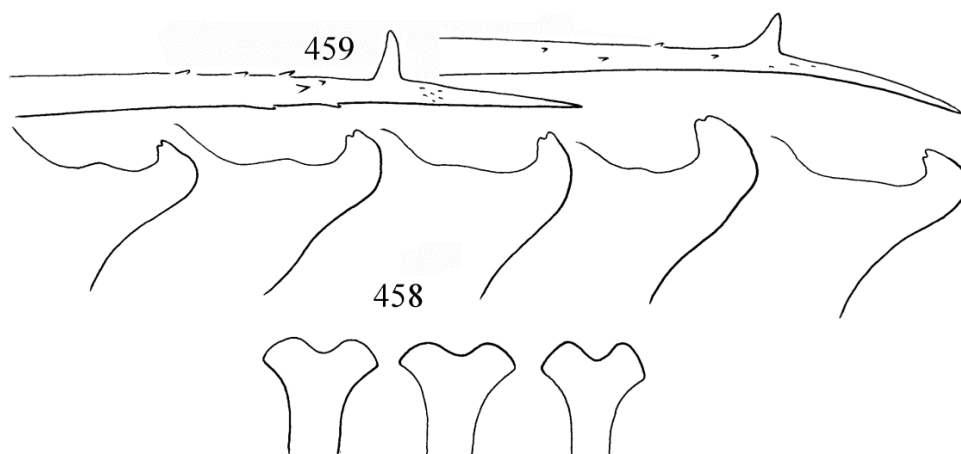
Figures 458–459. *Drusus improvisus* (McLachlan, 1884). 458 = fused apical arms of the dorsal branches of paraproct from Tuscany at higher magnification in lateral and dorsal view, 459 = parameres from Tuscany in left lateral view.

Diagnosis. McLachlan 1884: 15, Posterior "wings in the ♂ have a very deep pouch, ending considerably before the margin, in which are whitish waxy-looking scales, arranged in several series on either side, and directed outward." "It is a *Monocentra* to the extent that the pouch of the posterior-wing of the male is furnished with scales (of the same nature as in *M. lepidoptera*, but shorter, and the pouch does not extend so far towards the margin), but the membrane in both pairs of wings has only the ordinary pubescence. From the presence of "scales" on any portion of the wings I consider it a *Monocentra*; the anal parts are quite analogous to those of *M. lepidoptera* and also to those of *Drusus annulatus* and *Peltostomis sudetica* and *graeca*."

Schmid 1956: 47, "Dans le cadre subfamilial, cette espèce ne possède aucune parenté avec *Monocentra lepidoptera* Rambur. Par la forme de ses appendices intermédiaires, elle se place dans le groupe de *mixtus*, tout près de *spelaeus*. La présence d'écailles dans le repli est un simple caractère spécifique, qui n'a rien de commun avec la particularité de *M. lepidoptera*."

Additional diagnosis. *D. improvisus* has the fused dorsal brances of the paraproct with upward and slightly anterad directed apices in lateral view; the apical margin of the upturning is rounded in lateral view; apices are laterad directed in dorsal view, however the shape of the laterad directed apices differs from the shape of *D. camerinus*.

The presence of whitish scales, this secondary sexual trait inside the pencil pouches on the hindwing, inspired McLachlan to place this species into the *Monocentra* genus. According to Schmid (1956) the paraproct shape relates this species to *D. spelaeus* of the *D. mixtus* group. However the ancestral divergence of the paramere spine pattern clearly relate this species into the *D. bosnicus* species group, that is far from the *D. mixtus* species group.

Drusus konok Oláh, sp. nov.

(Figures 460–464)

Material examined. Holotype: **Italy**, Lazio – Cittareale (RI), Sorg. Velino loc. Cupello, 980 m, 42.619°N, 13.153°E, 22. VI. 1992 leg. P. Capoccia (1 male, CC n°503). Allotype: Italy, Lazio – Cittareale (RI), Sorg. Velino loc. Cupello, 980 m, 42.619°N, 13.153°E, 17.X.1991 leg. P. Capoccia (1 female, CC n°929). Paratypes: Lazio – Cittareale (RI), Sorg. Velino loc. Cupello, 980 m, 42.619°N, 13.153°E, 22. VI. 1992 leg. P. Capoccia (1 male, 2 females, OPC). Italy, Lazio – Cittareale (RI), Sorg. Velino loc. Cupello, 980 m, 42.619°N, 13.153°E, 17.X.1991 leg. P. Capoccia (2 females, CC n°929).

Diagnosis and description. *D. konok* sp. nov. has the fused dorsal brances of the paraproct with upward and slightly anterad directed apices in lateral view; the apical margin of the upturning is angled, elbow-shaped in lateral view; apex bilobed in dorsal view, spear-shaped, anterad directed apices long and laterad directed. Most

similar to *D. canficconiae* sp. nov., but differ by having longer anterad directed apices of paraproct and these anterad turning apices are clearly laterad directed in dorsal view.

The female has segment IX longer and the mesal excision broad based as compared to the females of the *D. canficconiae* sp. nov. The dorsal profile of the vaginal sclerite complex is differently shaped as at *D. canficconiae* sp. nov. However, shape variability of female genitalia of this new species is not studied on population samples.

Etymology. konok, from „könyök", elbow in Hungarian, refers to the shape of the apical margin of the upcurving apex of the paraproct. But "*konok*", the simplified, euphonic version of "könyök", has a peculiar meaning, thanks to the fractal nature of the Hungarian language. This meaning is "stubborn, refractory or self-willed" similarly as we are when we distinguish species by such a subtle, but stable slective, non-neutral and non-random divergences.

Drusus cianficconiae Olah sp. nov.

(Figures 465–473)

Material examined. Holotype: **Italy**, Marche, Mti. Sibil-lini, Oberlauf Tenna, Gola dell' Infernaccio 24.V.1977, leg. Zwick (1 male, MCSNBG). Allotype: same as holotype (1 female, OPC). Paratypes, Marche: fiume Tenna, 1100 m, M. Sibillini, Gola dell'Infernaccio, Montefortino, 16. V. 1969, leg. Venturi & Moretti (3 males, MC). Marche, fiume Tenna, M. Sibillini, Gola dell'Infernaccio, 22. IX. 1977, leg. Speziale & Moretti (1 male, MC). Marche, sorgente F. Tenna, 1178 m, 16. IV. 1971, leg. Lagana & Moretti (1 male, MC). Marche, fiume Tenna, 900 m, 4. IX. 1977, leg. D'Alessandro, Romagnoli & Moretti (1 male, MC). Marche, M. Sibillini, sorgente F. Tenna, 1180 m, 11. VIII. 1955, leg. Tomasi (4 males, MC; 3 females, OPC). Marche, M. Sibillini, sorgente F. Tenna, 1180 m, 11. VIII. 1955, leg. Tomasi (3 females, MC). Marche, Montemonaco (AP), Sorg. Fiume Aso, 950 m, 42.874° N, 13.269° E, 27.X.1972, leg. Boria (3 male, CC).

Diagnosis and description. D. canficconiae sp. nov. has the fused dorsal brances of the paraproct with upward and slightly anterad directed apices in lateral view; the apical margin of the upturning is less angled, rather rounded in lateral view; apex bilobed in dorsal view, parallel-sided, anterad directed apices short and not directed laterad. Most similar to *D. konok* sp. nov., but differ by having shorter anterad directed apices of paraproct and these anterad turning apices are clearly parallel-sided, not directed laterad in dorsal view.
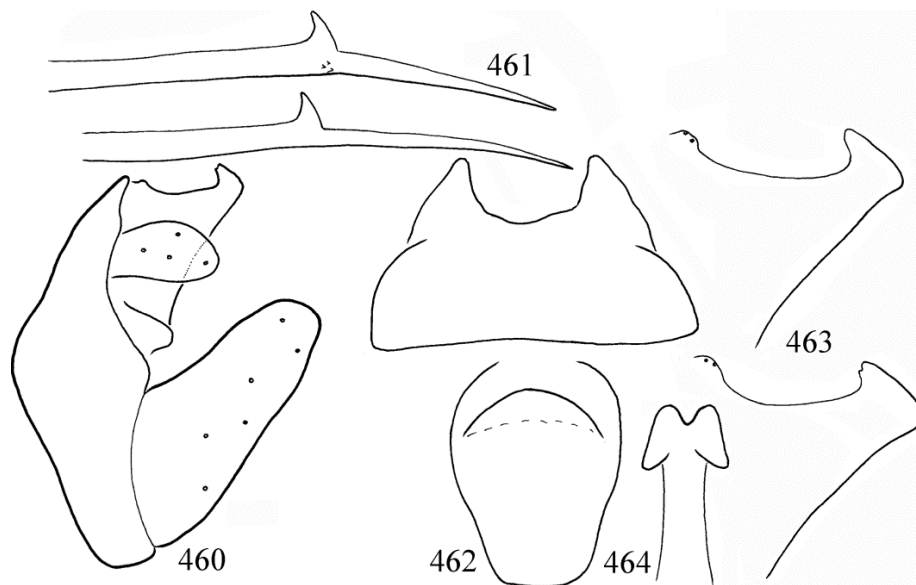
Figures 460–462. *Drusus konok* Oláh, sp. nov. Holotype: 460 = male genitalia in left lateral view, 461 = parameres in left lateral view. Allotype: 462 = tergite IX and dorsal profile of vaginal sclerite complex in dorsal view. Holotype and paratype: 463 = fused apical arms of the dorsal branches of holotype (left) and paratype (right) at higher magnification in lateral view, 464 = fused apical arms of the dorsal branches of holotype at higher magnification in dorsal view.
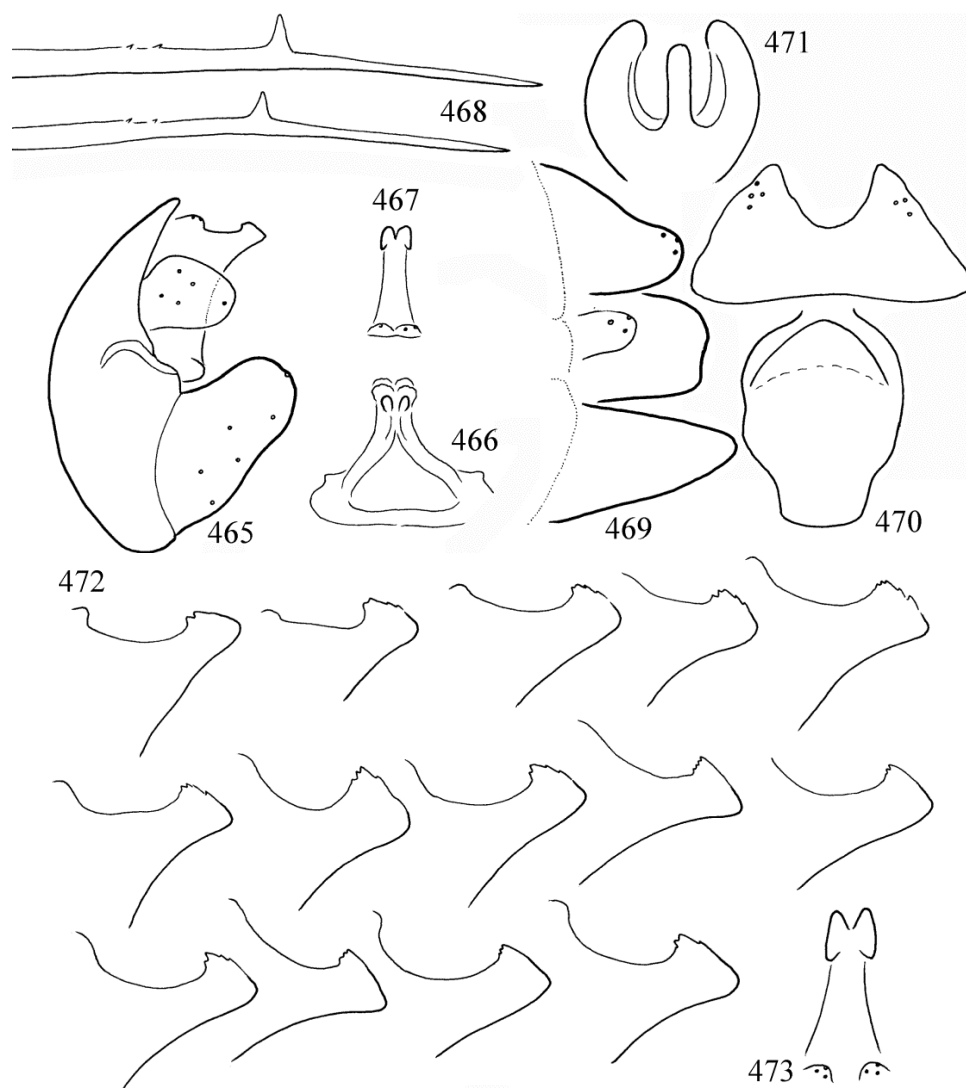
Figures 465–468. *Drusus cianficconiae* Olá, sp. nov. Holotype: 465 = male genitalia in left lateral view, 466 = paraproct in caudal view, 467 = apical arms of the dorsal branches of paraproct in dorsal view, 468 = parameres in left lateral view. Allotype: 469 = female genitalia with vaginal sclerite complex in left lateral view, 470 = tergite IX and dorsal profile of vaginal sclerite complex in dorsal view, 471 = vulvar scale in ventral view. 472 = fused apical arms of the dorsal branches of holotype (upper left) and paratypes at higher magnification in lateral view, 473 = fused apical arms of the dorsal branches of holotype at higher magnification in dorsal view.

Female description. Tergite of segment IX forming short tube, open ventrally, with shallow broad triangled mesal excision; lateral lobes rounded triangular in dorsal view; the lateral setose lobe of sternite IX elongated with rounded ending. Segment X membranous and embedded inside segment IX and encircling anus; supragenital plate of segment X well-developed and quadrangular in lateral view. Median lobe of the vulvar scale (lower vaginal lip) present, digitiform and long. Dorsal profile of the vaginal sclerite complex narrowing anterad.

The female has segment IX shorter and the mesal excision less broad based as compared to the females of the *D. konok* sp. nov. The dorsal profile of the vaginal sclerite complex is differently shaped as at *D. konok* sp. nov. However,

shape variability of female genitalia of this new species is not studied on population samples.

Etymology. We dedicate this new species to Professor Fernanda Cianficconi, the renowned Italian Trichopterologist for her kind support during our studies.

Drusus sp.

(Figures 474–476)

Material examined. **Italy**, Marche, M. Sibillini-Gola dell''Infernaccio, sorgente, 1000 m, 27.IX.1980, leg. D'Alessandro, Romagnoli (1 male, MC).

Notes. This specimen represents an unknown species, but the entire genitalia of this old specimen is in bad condition, deformed and overcleared. The reconstrcuted drawings suggest an interesting new species. Not a single specimen in the *D. improvisus* species complex has such a bristle megasetae of macrochaete on the very top of the paraproct apices!

Drusus muranyorum species complex

This species complex has dorsal branch of the paraproct with blunt apical arms in lateral view; enlarged laterad and forming a pair of variously
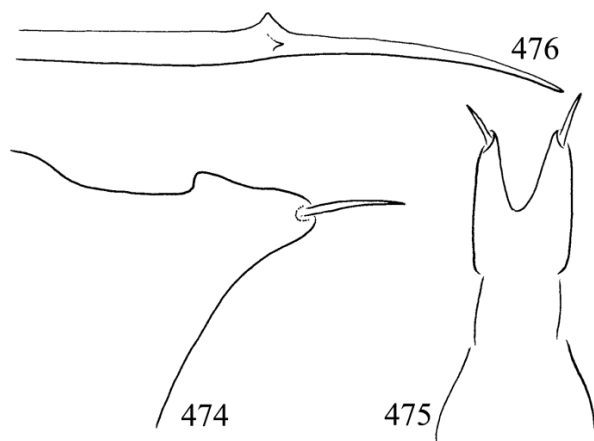
Figure 474–476. *Drusus* sp. 474 = fused apical arms of the dorsal branches ofparaproct at higher magnification in lateral view, 475 = fused apical arms of the dorsal branches of paraproct at higher magnification in dorsal view, 476 = paramere in left lateral view.

rounded lateral lobes in caudal view. In this species complex the robust erected primary spine on paramere is highly reduced in size, and subdivided. Unfortunately we had access and examined only two species in this complex. Three other species, after repeated trial for cooperation with the author of the species, were not available for study. If all the species becomes available for detailed study, the status of the entire *Drusus muranyorum* species complex, depending on the paramere fine structure, may need a reevaluation. This species complex is comprised of five species: *goembensis*, *ilgazensis*, *kazdagensis*, *muchei*, *muranyorum*.

Drusus goembensis Sipahiler, 1991

(Figures 477)

Drusus goembensis Sipahiler, 1991: 179–181, "Holotype ♂, allotype ♀ and paratypes (20♂♂, 18♀♀): Turkey, Antalya, Elmah, Gömbe 29°38' N, 36°36' E, 2700 m, 25.VI.1988, from the lake; same place, from stream, 1200–2800 m, 22–23.VI.1988 14♂♂, 13♀♀; Fethiye, Kemer, Dereköy, 26.VI.1988 10♂♂, 2♀♀, leg. and coll. Cakin."

Material examined. No specimen has been examined. Established taxonomic position is based on species description and drawings. Several personal or team trials to borrow type material or any specimens from the author remained unanswered. Further study is required on paramere fine structure to confirm the taxonomic postion.

Diagnosis. Sipahiler, 1991: 181, "This species is closely related to *Drusus muchei* Malicky (Sipahiler and Malicky, 1987) from west Anatola and can be easily distinguished from the related species by the following features: The spinulose zone of tergite 8 is larger than in *D. muchei* and possesses small projections on each side of the apical margin; in *D. muchei* the sides of the apical margin are rounded. The intermediate appendages of *D. goembensis* sp. nov. are small and rounded; in *D. muchei* they are very large and straight ventrally."

Drusus ilgazensis Sipahiler, 1996, stat. nov.

(Figures 479)

Drusus muchei ilgazensis Sipahiler, 1996:30-31: „Holotype ♂, allotype ♀ and paratypes 3♂♂: Turkey, Kastamonu,

Ilgaz Dagi, Kücük Hacet Tepesi, 2 km N of Geyik Gecidi, 1950 m, 14.VII.1994 leg. and coll. Sipahiler."

Material examined. No specimen has been examined. Established taxonomic position is based on species description and drawings. Several personal or team trials to borrow type material or any specimens from the author remained unanswered. Further study is required on paramere fine structure to confirm the taxonomic postion.

Diagnosis. Sipahiler 1996: 30–31, „*Drusus muchei* Malicky (Sipahiler & Malicky 1987) described from Turkey, is found in Bozdag in western Anatolia. *D. m. kazdagensis* ssp. nov. found in north western Anatolia, in Kaz Dagi, near the Aegian See, 170 km from the nominate species. The second subspecies *D. m. ilgazensis* ssp. nov. is found in northern Anatolia, 500 km from *D. muchei*. The differences are seen in the male genitalia especially in the shape of the spinulose zone, which is narrow in *D. m. muchei*, broad in *D. m. kazdagenzis* ssp. nov. and broad with side excisions in *D. m. ilgazensis* ssp. nov.; the intermediate appendages of *D. m. muchei* are rounded on the apical margin and narrow on the side in caudal view, while they are broad and rounded in *D. m. ilgazensis* ssp. nov., narrow and dilated on the sides in *D. m. kazdagensis* ssp. nov. *D. m. muchei* differs from the new subspecies, having strong dilatation on the anterior margin of segment 9. The inferior appendages of *D. m. ilgazensis* ssp. nov. differs from the related subspecies, having a small dilatation on the dorsal edge of the inferior appendages. The differences in female genitalia are also evident."

Re-diagnosed. Based on published description and drawings this taxa is an incipient species in the *Drusus muranyorum* species complex, stat. nov.

Drusus kazdagensis Sipahiler, 1996 stat. nov.

(Figures 478)

Drusus muchei kazdagensis Sipahiler, 1996: 30. Holotype ♂, allotype ♀ and paratype 1♂: Turkey, Balikesir, Evciler, Kazdagi Milli Parki, Ayazma, 6.VIII.1994 (at light), 500 m, leg and coll. Sipahiler."

Material examined. No specimen has been examined. Established taxonomic position is based on the species de-
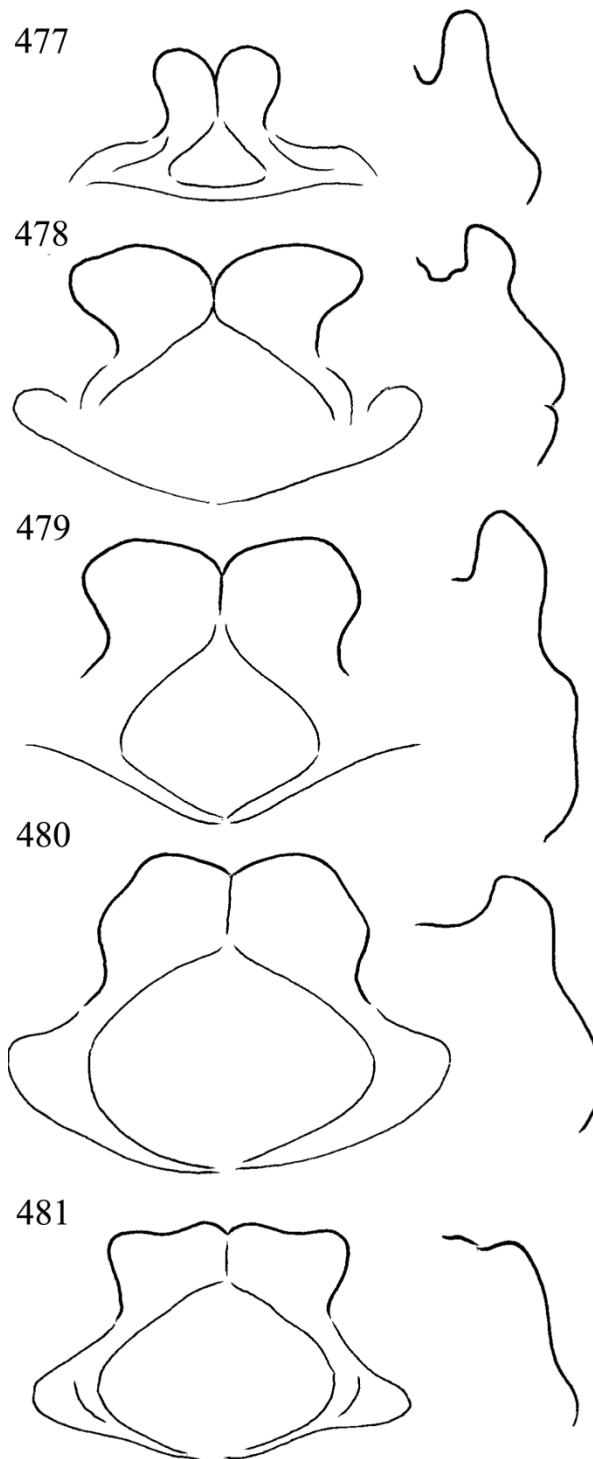
Figures 477–481. Comparative table of paraproct caudal and lateral profiles in the *Drusus muranyorum* species complex: 477 = *goembensis*, 478 = *kazdagensis*, 479 = *ilgazensis*, 480 = *muchei*, 481 = *muranyorum*.

scription and drawings. Several personal or team trials to borrow type material or any specimens from the author remained unanswered. Further study is required on paramere fine structure to confirm the taxonomic postion.

Diagnosis. Sipahiler, 1996: 30, „The dorsal portion of the intermediate appendages are large and close to each other; in dorsal view, the sclerotized parts appear an narrow long lobes, bearing densely black spinules; the ventral portions are hood-shaped curved on the sides and possess stout bands below the dorsal portion; in caudal view; in caudal view, the dorsal parts are narrow oval."

Re-diagnosed. Based on published description and drawings this taxa is an incipient species in the *Drusus muranyorum* species complex, stat. nov.

Drusus muchei Malicky, 1987

(Figures 480, 482–484)

Drusus muchei Malicky, 1987: 91–93. „Holotypus ♂ und zwei Paratypen ♀♀: Türkei, vil. Izmir, 3 km N Bozdag (Birgi – Salihli), 900 m, 38°22'N, 27°58'E, 19. V. 1983, leg. Aspöck, Rausch & Ressl, coll. Malicky."

Material examined. Holotype on loan from Malicky Private Collection.

Diagnosis. Malicky, 1987: 91–93, „Ähnlich wie bei einigen Arten von der Balkanhalbinsel (*D. bureschi* Kumanski, 1973; *D. balcanicus* Kumanski, 1973; *D. discophorus* Radovanovic, 1942; *D. discophoroides* Kumanski, 1979), aber gut characterisiert."
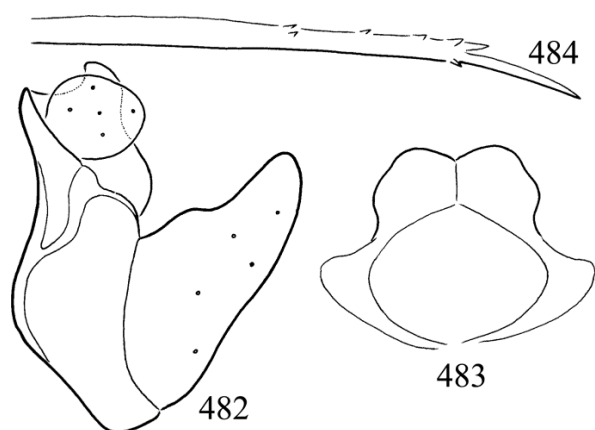
Figures 482–484. *Drusus muchei* Malicky, 1987. Holotype: 482 = male genitalia in left lateral view, 483 = paraproct in caudal view, 484 = parameres in left lateral view.

Drusus muranyorum Oláh, 2010

(Figures 481, 485–489)

Drusus muranyorum Oláh, 2010: 104–106. "Etymology. Name was given for the collectors Dávid Murányi and his wife Szilvia Czigány, who have made together extensive collection activity along alpine springs and streams on the Balkan."

Material examined . Holotype male. **Greece**: Rhodopi county, Sapka Mts, torrent in an oak forest, 14 km E of Nea Sanda, 651m, 41°07.672' N, 25°53.223' E, 4.IV.2007, leg. L. Dányi, Z. Erőss Z. Fehér, J. Kontschán & D. Murányi (1 male, HNHM). Paratypes. Greece: Rhodopi county, Sapka Mts, torrent in an oak forest, 14 km E of Nea Sanda, 651m, 41°07.672' N, 25°53.223' E, 4.IV.2007, leg. L. Dányi, Z. Erőss Z. Fehér, J. Kontschán & D. Murányi (5 females, HNHM).

Diagnosis. Oláh, 2010: 104–106, "This autumn collected dark fuscous species belongs to the species complex of *D. discophorus* described from the Balkan. Most close to *Drusus bureschi* Kumanski, 1973, but differs by having (1) almost black body color, not light brownish yellow; (2) IXth segment long, not short in lateral view; (3) lateral lobe on paraproctal complex in dorsal and caudal view narrow, not broad; (4) cerci subrectangular, not rounded; (5) gonopods S-shaped, not upward arching triangular; (6) parameres single filament, not bifid."

Drusus discolor species group

Drusus discolor species group is integrated through ancestral divergence by the reduction of setal pattern to a single large subapical spine without any secondary or tertiary spines. This "subapical spine" is probably the terminal portion of the paramere shaft and the apical elongation is a modified seta with various length and thickness. According to our ranking system elaborated for Drusinae subfamily the species complexes are distinguished by paraproct architecture. But inside this species group there are some complexes distingushable additionally by the periphallic organ of cerci or gonoponds or by contemporary divergence of the single subapical spine. This species group is comprised of seven species complexes and 28 species.

132
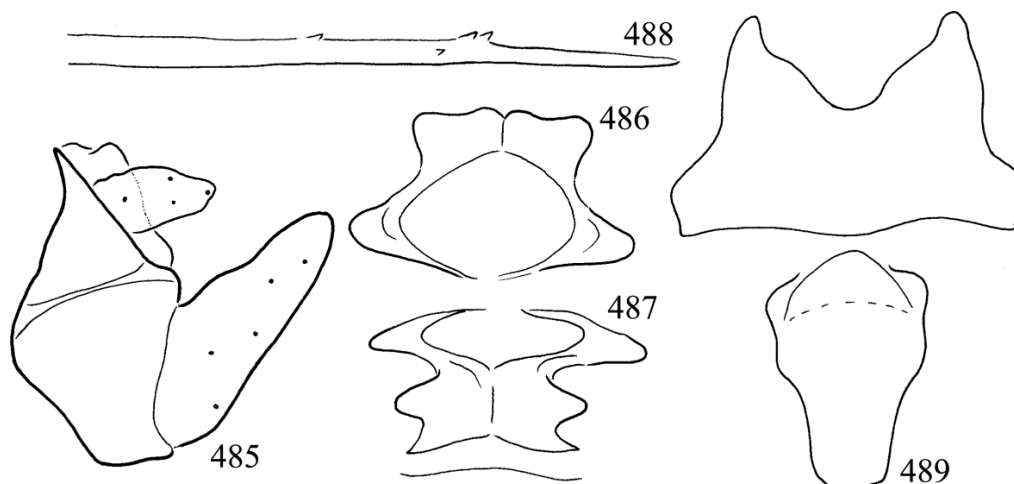
Figures 485–489. *Drusus muranyorum* Oláh, 2010. 485 = male genitalia in left lateral view, 486 = paraproct in caudal view, 487 = apical arms of the dorsal branches of paraproct with some discernibility of the downward curving ventral brances of the paraproct in dorsal view, 488 = parameres in left lateral view, 489 = tergite IX and dorsal profile of vaginal sclerite complex in dorsal view.

(1) *Drusus chapmani* species complex has the fused dorsal branches of paraproct rather robust with stair-like apical margin in lateral view, accompanied by elongated cerci and highly elongated subapical spine on the paramere.

(2) *Drusus chrysotus* species complex has the fused dorsal branches of paraproct rather robust with straith vertical apical margin in lateral view, accompanied by short cerci and short subapical spine on the paramere.

(3) *Drusus discolor* species complex is almost indistingishable from the *D. romanicus* species complex by the architecture of the paraproct except *D. discolor* has no decisive hump on the apical margin of the paraproct in lateral view. The two complex is clearly distinguishable by the shape of the periphallic organs. *D. discolor* complex has cerci and gonopods short compared to the long cerci and gonopods of *D. romanicus* complex.

(4) *Drusus macedonicus* species complex has the dorsoapical fused dorsal branches of paraproct produced into a short digitiform process, slightly broadened transversally as visible in caudal view and accompanied by medium sized cerci and apically elongated gonopods.

(5) *Drusus muelleri* species complex has the fused dorsal branches of paraproct rather robust with straith vertical apical margin in lateral view, accompanied by very long cerci and short subapical spine on the paramere.

(6) *Drusus romanicus* species complex is almost indistingishable from the *D. discolor* species complex by the architecture of the paraproct except *D. romanicus* has decisive hump on the apical margin of the paraproct in lateral view. The two complex is clearly distinguishable by the shape of the periphallic organs. *D. romanicus* complex has cerci and gonopods long compared to the short cerci and gonopods of *D. discolor* complex.

(7) *Drusus siveci* species complex has the dorsoapical fused dorsal branches of paraproct produced into an elongated digitiform slender process accompanied by medium sized periphallic organ of cerci and gonopods.

Drusus chapmani species complex

Drusus chapmani species complex has rather robust fused dorsal branches of paraproct with stairs-like apical margin in lateral view, accompanied by elongated periphallic organs of cerci and gonopods with highly elongated subapical spine on the paramere. Species of this complex seem rather rare, difficult to collect or simply indicates insufficient sampling effort due to the

overall deprived state of the western taxonomy. The whole species complex is represented only by a few specimens and comprised only of two species: *chapmani* and *letras* sp. nov.

Drusus chapmani McLachlan, 1901 stat. restit.

(Figures 490–493)

Drusus chapmani McLachlan, 1901: 162–163. "Hab.: Switzerland (Locarno), April 6th, 1899, one ♂ (Dr. T. A. Chapman) in my collection."
Drusus chapmani McLachlan, 1901: Schmid 1956: 28–29. "Je ne connais pas personnellement cette espèce; les dessins que je reproduis ci-dessous ont été aimablement effectués a mon intention par M. D. E. Kimmins." "Cette espèce n'est connue que par un ♂ capturé à Locarno (Suisse), le 6. IV. 1899 et deposé dans la collection de R. McLachlan."
Drusus chapmani McLachlan, 1901: Malicky 2005a: 567. "Ich vermute, dass *chapmani* und *muelleri* die selbe Art sind. Der dorsale Dörnchenfleck des 8. Tergits variiert etwas, und die beiden Arten haben das gleiche endemische Verbreitungsgebiet in den Südalpen."

Material examined. Holotype: deposited in The Natural History Museum, London, England. **Italy**, Bergamo, Averara, Alpe Cul versante sud, 1990 m, 23.V.2003, leg. Bertuetti (1 male, MCSNBG).
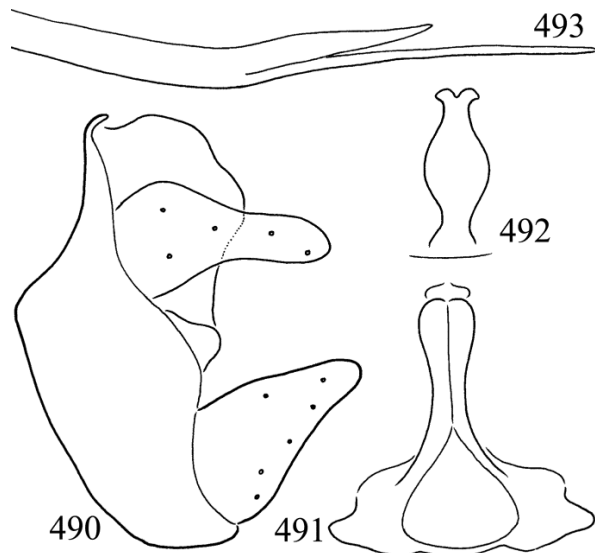
Figures 490–493. *Drusus chapmani* McLachlan, 1901. 490 = male genitalia in left lateral view, 491 = paraproct in caudal view, 492 = apical arms of the dorsal branches of paraproct in dorsal view, 493 = paramere in left lateral view.

Diagnosis. McLachlan, 1901: 162, "Belongs to the group of black species represented by *D. Muelleri*, McLachlan, *D. nigrescens* Meyer-Dür, and *D. melanchaetes* McLachlan; most allied to *D. Muelleri*." "It would be useless to draw a comparision with other black species (*nigrescens* and *melanchaetes*), because these differ widely in their anal structure, whereas with *Muelleri* there is apparently real affinity and at the same time quite sufficient specific differences. Among other species there is slight analogy with *D. alpinus*."

Schmid 1956: 28–29, "*Dr.chapmani* est très voisin de *transylvanicus* et de *romanicus*, il s'en distingue surtout par la grandeur de l'aire spinulifere du VIIIe segment et par la forme des appendices intermédiaires."

Malicky 2005a: 567, *Drusus chapmani* is a synonym of *D. muelleri*.

Additional diagnosis. According to the ancestral divergences of the paramere pattern *Drusus chapmani* represents a separate species complex with two known species, clearly differing from the *Drusus muelleri* species complex that comprised of four known species. The members of *D. chapmani* species complex have very elongated and enlarged subapical spine on the paramere. The same structure is very short, reduced at all members of the *D. muelleri* species complex. Already McLachlan (1901) has emphasized its real affinity to *D. muelleri*, but at the same time he has mentioned also quite sufficient specific differences between the two species. Malicky (2005) has found no real differences between the two species, but he has not examined the two holotypes and particularly not examined the fine structure of their parameres. Based on the ancestral divergence of the paramere pattern *D. chapmani* cannot be a synonym of *D. muelleri*, here we reinstate its species status.

Drusus letras Oláh, sp. nov.

(Figures 494–497)

Material examined. Holotype: **Italy**, Piemonte, Province Biella, 1000 m, Ruscelli tributary Torr, Viona, 20.IV.1979, leg. Ravizza (1 male, CC n°121).

Diagnosis and description. This is the second known sibling species in the *D. chapmani* species complex. The nominate species of the complex was described and known long only form a single male specimen (Schmid 1956). Here we describe the second member of the species complex also from a single male.

The rather robust fused dorsal branches of paraproct has stairs-like apical margin in lateral view; the stairs are more pronounced, angled, not rounded like at *D. chapmani*; this lateral profile of the diverged stair structure is confirmed by the different shapes of the fused dorsal branches in the dorsal and caudal profile. The shape divergence of the speciation trait is accompanied by differences in the lateral profiles of the periphallic organs of cerci and gonopods being more elongated at *D. letras* sp. nov. However these traits are mostly neutral and exposed to the stochastic processes of the gene flow and genetic drift. The paramere structure is also diverged at the two species; the highly elongated subapical spine are regular spine shaped at *D. chapmani*, but irregularly formatted at *D. letras* sp. nov.
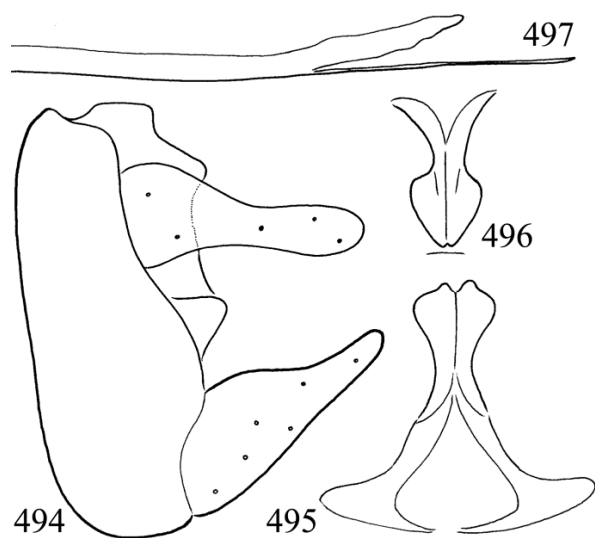
Figures 494–497. *Drusus letras* Oláh, sp. nov. 494 = male genitalia in left lateral view, 495 = paraproct in caudal view, 496 = apical arms of the dorsal branches of paraproct in dorsal view, 497 = paramere in left lateral view.

Etymology. „*letras*",from „létrás", ladder in Hungarian, refers to the very pronounced and angled stair-like apical margin of the paraproct in lateral view.

Drusus chrysotus species complex

Drusus chrysotus species complex has the fused dorsal branches of paraproct rather robust with almost straith and vertical apical margin in lateral view, accompanied by short periphallic organsd of cerci and gonopods with short sub-apical spine on the paramere. Species in this complex are also very rare, never common or abundant. This species complex comprised of five species: *chrysotus*, *lapos*, *noricus*, *sarkos*, *slovenicus*

Drusus chrysotus (Rambur, 1842)

(Figures 498–500)

Limnephila chrysota Rambur, 1842: 480. "Habite la vallée de Chamonuix. Je n'ai vu que le male".
Drusus chrysotus (Rambur, 1842): McLachlan 1876: 169–170. "Savoy (Chamounix, Barberine). Switzerland (Bergün, Steinalp, Pontresina, Dischmathal) Carinthia (Stelzing), Noric Alps (Mallnitz, Gross Glockner). Partly misidentification!
Drusus chrysotus (Rambur,1842): Schmid 1956: 24. "*Dr. chrysotus* a été signalé des Alpes centrales et orientales, de Thuringe, de Bavière et des Vosges; il ne pénètre pas dans le Jura. En Suisse il est assez nettement localisé le long des petits cours d'eau à courant faible et n'est jamais abondant."

Material examined. **France**, Department Savoie, Seez, torrent affluent du Reclus, 12.VII.2015, leg. G. Coppa (1 male, OPC). Department Vosges, Le Valtin, La Meurthe en amont du ruisseau central, 21.V.2008 leg G. Coppa (1 male, OPC). France, Department Vosges, Le Valtin, Col de la Schlucht, source. 21.V.2008 leg G. Coppa (1 female, OPC). France, Department Haut-Rhin, Oderen, Le Steinlerunz au pont de la route D25, 30.IV.2011 leg G. Coppa (1 male, OPC). **Switzerland**, Graubünden Canton, Quelle Flüela N (1), Davos, 2280 m, 9.VII.2010, leg. Lubini & Knispel (1 male, CMZL; 1 male, OPC). Switzerland, Graubünden Canton, Il Fuorn, Zernez, 1794 m, 15.VI.1952, leg. Aubert (1 male, CMZL). Switzerland, Graubünden Canton, Quelle Flüela S, Susch, 2280 m, 9.VII.2010, leg. Lubini & Knispel (1 male, CMZL). Switzerland, Vaud Canton, Gryonne, Taveannaz, Gryon, 1650 m, 28. VII. 1979, leg. C. Siegenthaler (1 male, CMZL).
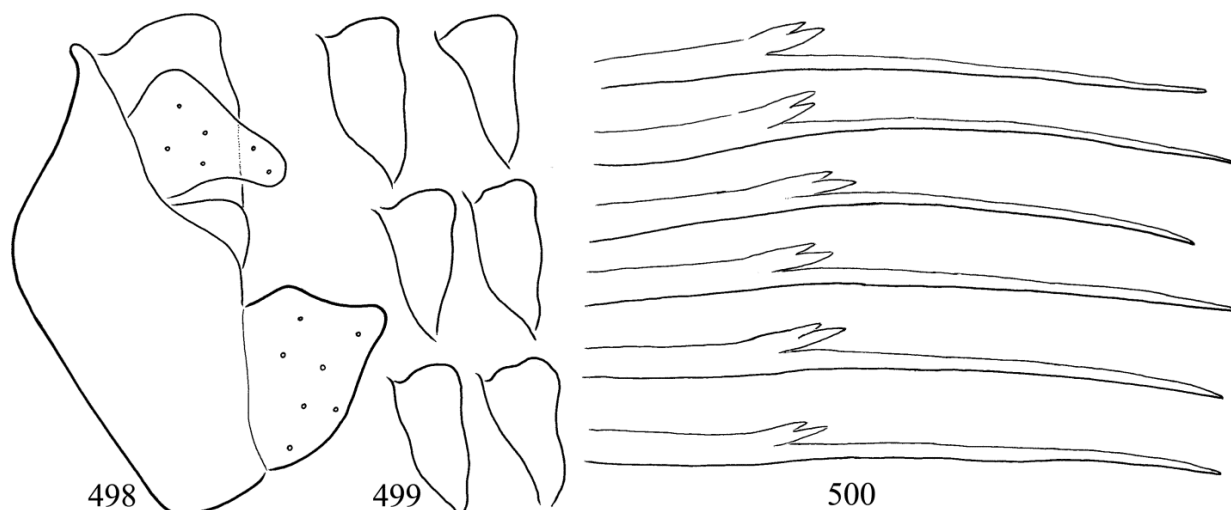
Figures 498–500. *Drusus chrysotus* (Rambur, 1842). 498 = male genitalia in left lateral view, 499 = dorsal branch of paraprocts from various localities in France and Switzerland in caudal view. 500 = parameres form various localities in France and Switzerland in left lateral view.

Diagnosis. Rambur, 1842: 480, "Presque complétement semblable a la *Discolora* dont elle diffère par les ailes plus jaunes."

Schmid 1956: 23, "Cette espèce est très voisine de *discolor* par les grandes lignes de l'armature génitale; mais elle est très remarquable par sa grande taille, sa stature lourde et trapue, sa coloration brillante, son repli très développé et la grandeur de ses segments génitaux. J'en ai examiné une série d'exemplaires capturés en Suisse romande."

Additional diagnosis. The fused dorsal branches of paraproct rather robust with almost straith and vertical apical margin in lateral view; the dorsum of the fused dorsal branches are sloping anterad in lateral view, not flat horizontal. Periphallic organs of cerci and gonopods are short. Subapical spine on the paramere short and subdivided into a shorter and a little longer spines. We have examined specimens from near the locus typicus in Savoie departments of France as well as from Vosges departments of France and from particular regions of Switzerland.

Drusus lapos Oláh, sp. nov.

(Figures 501–503)

Material examined. Holotype: **Italy**, Trentino Alto Adige, Trento, Telve, torr. Maso T.L. c/o Malga Cagnon di Sotto, 1670 m, 8.VIII.2001, leg. O. Lodovici (1 male, MCSNBG). Allotype: Trentino Alto Adige, Bolzano, Moso in Passiria, Ponte segheria, 1600 m, 19.VI.1993, leg M. Valle (1 female, MCSNBG). Paratypes: **Austria**, Weinebene, 46° 50.52 15° 00.33, 28.VII.2007. leg. W. Graf (1 male, OPC). Pinned specimen:1. label: Admont. 19.VIII.02; 2. Label: *chrysotus* Klapálek; 3. label: *chrysotus* det Kempny; 4. Label: *Drusus chrysotus* ♂ det. Malicky 1983 (1 male, WM). Pinned specimen:1. label: Carinthia, Glockner, 7.VIII 20; 2. label: *Drusus chrysotus* ♂ det. Dr. Döhler 1931; 3. label: *Drusus chrysotus* ♂ det. Malicky 1983 (1 male, WM). Pinned specimen:1. label: Admont, 19.VIII.02; 2. label: *chrysotus* det. Kempny; 3. label: *Drusus chrysotus* ♂ det. Malicky 1983 (1 male, WM). Pinned specimen: 1. label: Stelzing, Jul.01; 2. label: Coll Brauer, 3. label: *discolor* ♀ det. Brauer; 4. label: *H. flavipennis*; 5. label: *Drusus chrysotus* ♂ det. Malicky 1983 (1 male, WM). Pinned specimen: 1. label: Gesaues, subalpin H. Franz; 2. label: Coll. H. Franz; 3. label: *Drusus chrysotus* Ramb. ♂ det. Dr. Döhler 1948; *Drusus chrysotus* ♂ det. Malicky 1983 (1 male, WM). Pinned specimen: 1. label: Strechengraben, Nied. Tauern, leg. H. Franz; 2. label: coll. Franz; 3. label: *Drusus chrysotus* Ramb, ♂ det. Dr. Döhler 1952; 4. label: *Drusus chrysotus* ♂ det. Malicky 1983 (1 male, WM). Pinned specimen: 1. label: Manu? Glockn. Carin, M 856; 2. label: Flavipennis det Brauer; 3. label: *Drusus chrysotus* ♂ det. Malicky 1983 (1 male, WM). Pinned specimen: 1. label: Twong 12-1400 m; 2. label: Salzburg, Radstadter Tauern, 3-10. VIII. '40, Zerny; 3. label: *Drusus chrysotus* Ramb. ♀ det. Dr. Döhler 1941; 4. label: *Drusus chrysotus* det. Malicky 1983 (1 female, WM). Pinned specimen: 1. label: Austria Alp; 2. label: Ullr.; 3. label: *flavipennis* det Brauer; 4. label: *Drusus chrysotus* ♂det. Malicky 1984 (1 male, WM). Pinned specimen: 1. label: Manu, Glohner, carin 856; 2. label: *flavipennis* det
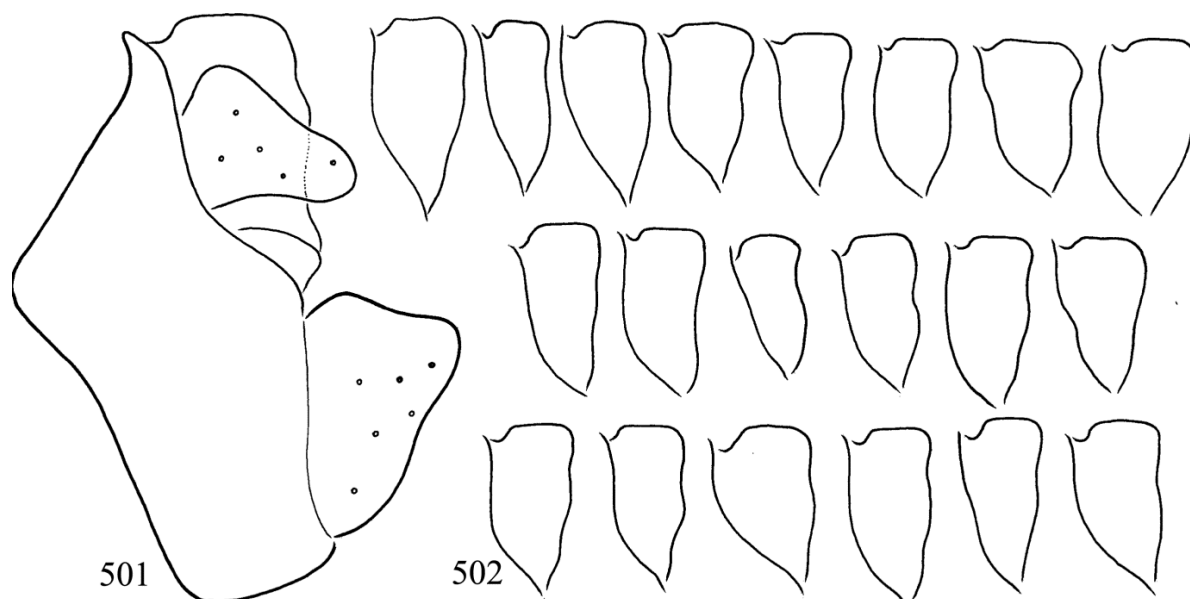
Figures 501–502. *Drusus lapos* Oláh, sp. nov. Holotype 501 = male genitalia in left lateral view. Paratypes: 502 = dorsal branch of paraprocts from various localities in Italy, Austria, Czech Republic and Switzerland in caudal view.

Brauer; 3. label: *Drusus chrysotus* ♂ det. Malicky 1984 (1 male, WM). Pinned specimen: 1. label: Austria Alp. 2. label: *flavipennis* det Brauer; 3. label: *Drusus chrysotus* ♂ det. Malicky 1984 (1 male, WM). Pinned specimen: 1. label: Gug 57. 2. label: *Drusus chrysotus* Rbr. (1); 3. label: *Drusus chrysotus* ♂ det. Malicky 1986 (1 male, WM). Pinned specimen: 1. label: Austria Alp; 2. label: *flavipennis* det Brauer; 3. label: *Drusus chrysotus* ♂ det. Malicky 1984 (1 male, WM). Pinned specimen: 1. label: Manu, Glocker 1861; 2. label: *flavipennis* det Brauer; 3. label: *Drusus chrysotus* ♂ det. Malicky 1984 (1 male, WM). Pinned specimen: 1. label: Triafoi, Handlirsch; 2. label: *Drusus chrysotus* Ramb, ♂ det. Dr. Döhler 1931; 3. label: *Drusus chrysotus* ♂ det. Malicky 1983 (1 male, WM). Pinned specimen: 1. label: Giglach-seegeb. Schlaum Tauern, leg. H. C. Franz; 2. label: *Drusus chrysotus* Ramb, ♂ det. Dr. Döhler 1958; 3. label: *Drusus chrysotus* ♂ det. Malicky 1983 (1 male, WM). Salzburg, Weiss See, 2300 m, 4.VIII.1970, leg. H. Malicky (1 male, OPC). **Czech Republic**, S. Bohemia, Sumava Mts. tributary of Cerne jezero lake, 15.V.2007 leg. P. Chvojka (1male, 2 females; NMPC). **Italy**, Friuli Venezia Giulia, Tarvisio (UD), 870 m, Rio del Lago, light trap, 21.VII.1996, leg Pantini & Valle, (1 male, OPC). **Switzerland**, Valais Canton, Gd St Bernard, 2472 m, 7.VIII.1981, leg. C. Siegenthaler (1 male, CMZL). Switzerland, Valais Canton, Gd St Bernard, Maringo, 1950 m, 14. VII. 2004, leg. P. Stucki (1 male, CMZL).

Diagnosis and description. The fused dorsal branches of paraproct robust with almost straith and vertical apical margin in lateral view. Similar to *D. chrysotus*, but the dorsum of the fused dorsal branches are flat horizontal in lateral view, not sloping anterad. Periphallic organs of cerci and gonopods are short. Subapical spine on the paramere short and intact, not subdivided like at *D. chrysotus*. All the old historical specimens collected from Austria and deposited in the Wien Museum have been mistakenly determined as *D. chrysotus*. Presentation of the examined specimens from the Wien Museum includes listing the original labels, sometimes with badly discernible hand writings difficult to read. Besides these historical specimens we have collected the holotype in Trento, allotype in Bolzano and paratypes in Tarvisio, Italy as well as paratypes in Valais Canton, Switzerland and in Czech Republic. There are no sufficient population sampling yet to speculate about the possible distributional area, about the possible allopatry, secondary sympatry or contact zones or clines with active reinforcement processes.

Etymology. „lapos",from „lapos", flat in Hungarian, refers to flat and horisontal dorsum of the fused dorsal branches of the paraproct in lateral view.
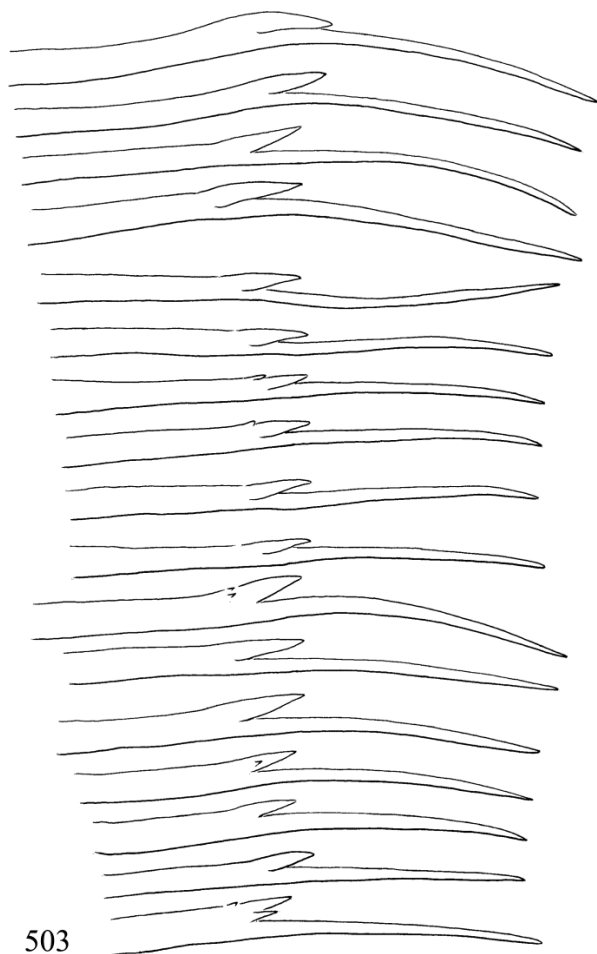
Figure 503. *Drusus lapos* Oláh, sp. nov. Paratypes: parameres from various localities in Italy, Austria, Czech Republic and Switzerland in left lateral view.

Drusus noricus **Malicky, 1981**

(Figures 504–506)

Drusus noricus Malicky, 1981: 44. "Holotype male: **Austria**, Carinthia, Saualpe 1900 m, Ladinger Alm, 12. VIII. 1980, leg et coll Malicky."

Material examined. The species was described from a single male. It is on loan at the W. Graf's laboratory from the Malicky Privat Collection, not available for our study. In spite of several sampling trial at the locus typicus there was no specimen collected.

Diagnosis. Malicky 1981: 44, "General appearance similar to *Drusus chrysotus* Rambur, but
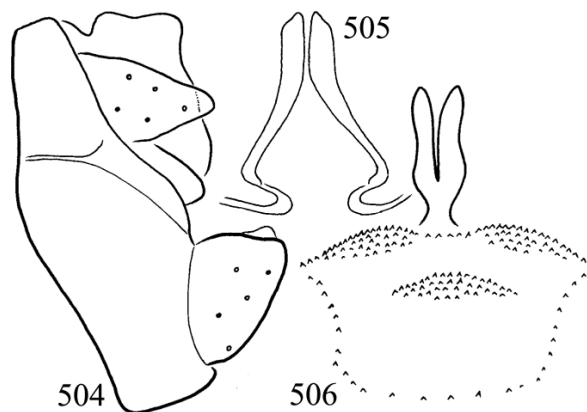
Figures 504–506. *Drusus noricus* Malicky, 1981. 504 = male genitalia in left lateral view, 505 = paraproct in caudal view, 506 = apical arms of the dorsal branches of paraproct and the pegged spinulose area on tergit VIII in dorsal view.

smaller and paler coloration." "The intermediate appendages are fused on their base only, but in *chrysotus* over their whole inner surface. The upper edge of the intermediate appendages decreases caudally in *D. noricus*, but increases in *D. chrysotus*."

Additional diagnosis. Based on the published drawings similar to *D. chrysotus*, but the dorsum of the partially fused dorsal branches of the paraproct gradually sloping posterad, not anterad.

Drusus sarkos **Olah, sp. nov.**

(Figures 507–510)

Material examined. Holotype: **Italy**, Friuli Venezia Giulia, Uccea (UD), 550 m, Uccea Rio Uccea, light trap, 24. V. 1996 leg. P. Pantini & M. Valle (1 male, MCSNBG).

Diagnosis and description. The partially fused dorsal branches of paraproct robust with straith apical margin in lateral view. Similar to *D. slovenicus*, but the dorsum of the fused dorsal branches has different profile in lateral view; the dorsoapical corner or angle is more produced upward. The divergences in the shape of the fused dorsal branches is more pronounced in the two species in the dorsal and caudal profile. Periphallic organs of cerci and gonopods are short. The paramere has short subapical spine accompanied by two small secondary spines anterad. The most pronounced
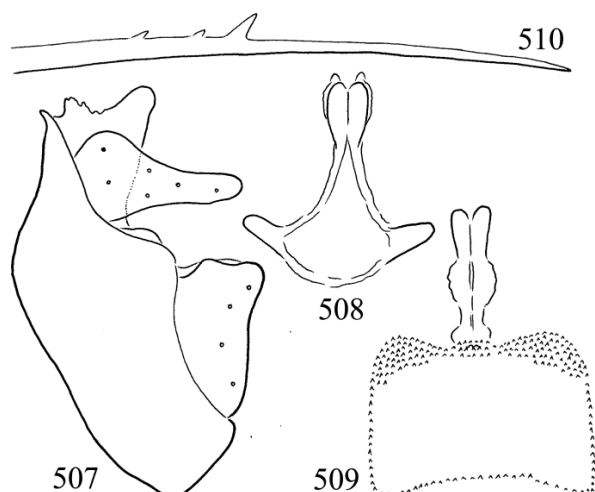
Figures 507–510. *Drusus sarkos* Oláh, sp. nov. Holotype: 507 = male genitalia in left lateral view, 508 = paraproct in caudal view, 509 = apical arms of the dorsal branches of paraproct and the pegged spinulose area on tergit VIII in dorsal view, 510 = paramere in left lateral view.

divergence between *D. sarkos* sp. nov. and *D. slovenicus* is well visible in the shape of the spinulose area on the VIII tergit. The shape is rounded oviform at *D. slovenicus* and regular quadrangular at *D. sarkos* sp. nov.

Etymology. „sarkos",from „sarkos", corner in Hungarian, refers to the more produced dorsoapical corner of the dorsal branches of the paraproct as well as the to the quadrangular shape of the spinulose area on tergite VIII.

Drusus slovenicus Urbanic, Krusnik & Malicky 2002

(Figures 511–513)

Drusus slovenicus Urbanic, Krusnik & Malicky, 2002: 35. „Holotype ♂: **Slovenia**, Triglav National Park, Bohinj, Studorski preval, 1740 m, 46°18' N, 13°54' E, 19.VII. 1983, leg. Sivec, in the collection of the first author."

Material examined. No new specimen available in spite of several collection trials in the locus typicus and around the time of collection of the single holotype, the only specimen of the species.

Diagnosis. Urbanic, Krusnik & Malicky 2002: 35, "It may be related with some endemic species of the Balkan peninsula such as *D. croaticus*

Marinkovic, 1971 or *D. siveci* Malicky, 1981. It is also somewhat similar to *Drusus noricus* Malicky, 1981."

Additional diagnosis. Relying on the published drawings the species is characterised by the completely separated dorsal branches of the paraproct and by the oviform spinulose area on the tergite VIII.

Drusus discolor species complex

Drusus discolor species complex is almost indistingishable from the *D. romanicus* species complex by the architecture of the paraproct except *D. discolor* has no decisive hump on the apical margin of the paraproct in lateral view. However, the two complex is clearly distinguishable by the shape of the periphallic organs. *D. discolor* complex has cerci and gonopods short compared to the long cerci and gonopods of *D. romanicus* complex. This species complex comprised of five species: *discolor*, *ferdes*, *kupos*, *leker*, *visas*

Drusus discolor (**Rambur, 1842**)

(Figure 514)

Limnephila discolora Rambur, 1842: 480. "Habite la vallée de Chamounix."

Material examined. **Albania**, Skrapar district, Ostrovicë Mts, Backë, brook and spring NE of the village, N 40°31.346', E 20°25.096', 1650 m, 29.V.2013, leg. P. Juhász, T. Kovács, G. Magos, G. Puskás, (4 males, 11 females; OPC). **Bulgaria**, Blagoevgrad region, Belassica Mts, Petrič, sping of Leshniska Stream SW of the city, 1025m, N 41°21.021', E 23°10.767', 27.X.2013 leg. J. Kontschán, D. Murányi, T. Szederjesi, (1 female, HNHM). **Czech Republic**, S Bohemia, Šumava Mts, Hamerský potok stream below Horská Kvilda, 49°03'25" N, 13°32'06" E, *ca.* 1000 m, 27.VII.1991, leg. P. Chvojka (1 male, NMPC). S Bohemia, Šumava Mts, Hamerský potok stream below Horská Kvilda, 49°03'25" N, 13°32'06" E, *ca.* 1000 m, 12.VI.1992, leg. P. Chvojka (1 male, NMPC). W Bohemia, Krušné hory Mts, Rájecký potok stream above Stříbrná, 50°22'38" N, 12°32'21" E, 640 m, 5.VI.1993, leg. P. Chvojka (3 males, 1 female, NMPC; 3 males, 1 female, OPC). N Bohemia, Jizerské hory Mts, Jedlová stream above Josefův Důl, 50°47'17" N, 15°14'32" E, 650 m, 5.VI.2002, leg. F. Krampl (6 males, 4 females; OPC). N Moravia, Králický Sněžník Mt., Morava River, 50°11'59" N, 16°50'36" E, 1100 m, 16.VII.2001, leg. P. Chvojka (2 females, OPC). N

Moravia, Králický Sněžník Mt., Morava River, 50°11'59" N, 16°50'36" E, 1100 m, 9.VII.2003, leg. P. Chvojka (12 males, OPC). **France**, Department Vosges, Le Valtin, la Meurthe, 2.VII.2008, leg G. Coppa (2 males, OPC). Department Alpes-Maritimes, Guila affluent Macruera ancien sentier, 8.VII.2008, leg G. Coppa (4 males, 1 female; OPC). Department Savoie, Bramans, Granges de Savine, 16.VIII.2009, leg G. Coppa (1 male, 1 female; OPC). **Italy**: Lombardia: Valbondione (BG), 1862 m, Lago Barbellino, 46.0630° N, 10,0482° E, light trap, 16.VII.2003, leg. R. Calandrina (5 males, 2 females, MCSNBG). Madesimo (SO), Montespluga, torrente, light trap, 1917 m, 46.4852° N, 9.3538° E, 23.VII.2004, leg. M. Valle (8 males, 2 females, MCSNBG; 5 males, 1 female, OPC). Valgoglio (BG), 1910 m, Val Sanguigno, torrente vicino al lago Prespontino, 45.9789° N 9.8457°E, 7.VIII.2009, light trap, leg. S. Cerea (24 males, 10 females, MCSNBG; 10 males, 7 females, OPC). Roncobello (BG), 1600 m, Baite di Mezzeno, 45.9652° N, 9.8084° E, light trap, 8.VII.1995, leg. Bertuetti (22 males, 12 females, MCSNBG). Roncobello (BG), 1600 m, Baite di Mezzeno, 45.9652° N, 9.8084° E, light trap, 8.VII.1995, leg. Bertuetti (22 males, 12 females, MCSNBG). S. Rocco al Porto (LO), Fiume Po, 45.0611° N 9.7042° E, 50 m, light trap, 29.VII. 1997, leg. F. Carrara & O. Lodovici (1 male, MCSNBG). Valbondione (BG), 1940 m, Baite di Sasna, 46.0177° N 10.0446° E, light trap, 24.VII.1995, leg. Albrici (16 males, 4 females, MCSNBG). Piemonte: Crissolo (CN), 1700 m, Pian della Regina fiume Po, 44.7000° N, 7.1163° E, light trap, 2.IX.1997, leg. M. Valle (74 males, 37 females, MCSNBG; 10 males, 8 females; OPC). Briga Alta (CN) 1600 m, affluente torrente Negrone, 44.1109° N 7.7252° E, light trap, 18.VII.2001, leg Museo Caffi BG (7 males, 19 females, MCSNBG). Ceresole (TO), 1800 m, Torrente Orco sopra Chiapili, 45.458° N, 7.1630° E, 21.VIII.1965, leg. A. Viganò (3 males, 1 female, MCSNBG). Torino, Balme, Cornettio, Rio Paschiet, 1550 m, 18. VIIII. 2004 leg. F. Vaccarino (4 females, MCSNBG). Liguria: Mendatica (IM), 1230 m, affluente torrente Tanarello c/o Valcona Sottana, 44.0977° N, 7.7509° E, 18.V.2001, light trap, leg. Museo Caffi BG (1 male, MCSNBG). Mendatica (IM), 1300 m, rio delle Salse, 44.1105° N, 7.7367° E, light trap, 18.VII.2001, leg. Museo Caffi BG (1 female, MCSNBG). Trentino Alto-Adige: Telve (TN), 1370 m, torrente Maso, 46.1497° N, 11.4496° E, light trap, 8.VIII.2001, leg. L. Bianchi & O. Lodovici (16 males, 18 females; OPC). Marebbe (BZ), 1600 m San Vigilio Marebbe Val de Rit, 46.6740° N, 11.9444° E, light trap, 27.VII.1994, leg. Becci & Pisoni (7 males, 4 females, MCSNBG). Valle d'Aosta: Courmayeur (AO), 1650 m, torr. Ferret – la Vachey, 45.850° N, 7.024° E, 11.VII.1964, leg. A. Viganò (4 males, MCSNBG). Cogne (AO), Pra Suppiaz – torr. Valnontey, 1700 m, 45.575° N, 7.145° E, 13–24.VIII. 1970, leg. A. Viganò (13 males, 1 female, CNSMB; 10 males, OPC). Veneto: Sappada, (BL), 1400 m, fiume Piave, 46.5847° N, 12.7269° E, 8.VIII.2002, leg. Museo BG (7 males, 1 female; MCSNBG). Friuli Venezia Giulia: Claut (PN), 950 m, torrente Cellina M.ga Casavento, 46.2689° N, 12.5991° E, light trap, 16.IX.1996, leg. P. Pantini & M. Valle (7 males, 5 females; MCSNBG). Resia (UD), 550 m, Uccea Rio Uccea, 46.3056° N, 13.4168° E, light trap, 20.IX.1996, leg. P. Pantini & M. Valle (5 males, 2 females; MCSNBG). **Kosovo**: Lepenc, 21.VI.2012 leg. H. Ibrahimi (1 male, 1 female; OPC). Prevall, 21.VI.2012 leg. H. Ibrahimi (1 male, OPC). **Macedonia**, Pelister Mts, Planinarski Dom "Shiroka", 1955m, N 41°00'17", E 021°10'07", 6.VIII.2016, leg. S. Beshkov & A. Nahirnic (3 males, OPC). Macedonia, Pelister Mt., on the road to Shiroka, 1493 m, N 41°01'52", E 21°11'43" 2.VII.2016, leg. S. Beshkov & A. Nahirnic (6 males, 1 female; OPC). **Poland**: Gorce Mts., Kamienice stream, 26. VI. 1985, light leg J. Oláh (3 males, OPC). **Romania**: Lacul Roşu, Valea Cupas, 19.VI.1981, light leg. L. Peregovits & L. Ronkay (1 male, OPC). Lacul Roşu, Valea Cupas, 9.VII.1981, light leg. L. Peregovits & L. Ronkay (1 male, OPC). Lacul Roşu, Valea Cupas, 17.VII.1981, light leg. L. Peregovits & L. Ronkay (1 male, OPC). Caraş-Severin county, Ţarcu Mts. Poina Mărului, upper section of Sucu Stream, S of the village, 955m, 45°20.907' N, 22°31.073', E 08.VI.2011, leg. T. Kovács, D. Murányi & G. Puskás, (2 males, HNHM). Bucegi Mts. Coteanu Padina, 45°22'35.33" N, 25°26'07.96" E, 1485 m, 29.VI.2007, leg. C. Ciubuc (2 males, CCPC). Bucegi Mts. Coteanu Padina, 45°22'35.33" N, 25°26'07.96" E, 1485 m, 6.VII.2007, leg. C. Ciubuc (1 male, CCPC). Bucegi Mts. Coteanu Padina, 45°22'35.33" N, 25°26'07.96" E, 1485 m, 13.VII.2007, leg. C. Ciubuc (1 male, CCPC). Bucegi Mts. Coteanu Padina, 45°22'35.33" N, 25°26'07.96" E, 1485 m, 3.VIII.2007, leg. C. Ciubuc (1 male, CCPC). Cindrel Mts. Râul Mic afl. stg. am Cabana Forestrieră, 45°40'26" N, 23°49'15" E, 22–23.VI.2009, leg. C. Ciubuc (4 males,1 female; CCPC). Cindrel Mts. Râul Mic afl. stg. am Cabana Forestrieră, 45°40'26" N, 23°49'15" E, 24–25.VI.2009, leg. C. Ciubuc (6 males, CCPC). Cindrel Mts. Crăciuneasa, Râul Mare, 45°40'22" N, 23°51'53" E, 28–29.VII.2009, leg. C. Ciubuc (1 male, CCPC). Cibin Mts. Crăciuneasa, Râul Mare, 45°40'22" N, 23°51'53" E, 29–30.VII.2009, leg. C. Ciubuc (2 males, CCPC). Cindrel Mts. Crăciuneasa, Râul Mare, 45°40'22" N, 23°51'53" E 7–8.VI.2010, leg. C. Ciubuc (4 males, CCPC). Cibin Mts. Crăciuneasa, Râul Mare, 45°40' 22" N, 23°51'53" E, 8–9.VI.2010, leg. C. Ciubuc (107 males, CCPC). Cibin Mts. Crăciuneasa, Râul Mare, 45°40' 22" N, 23°51'53" E, 9–10.VI.2010, leg. C. Ciubuc (226 males, 21 females, CCPC; 3 males, 2 females CCPC). Făgăraş Mts. Sâmbăta de Sus, 45°40'06.5" N 24°47'32.5" E 12–13.VII.2011, leg. C. Ciubuc (10 males, CCPC; 2 males, CCPC). Făgăraş Mts. Sâmbăta de Sus, 45°40'06.5" N, 24°47'32.5" E, 13–14.VII.2011, leg. C. Ciubuc (2 males, CCPC). Făgăraş Mts. Sâmbăta de Sus, 45°40'06.5" N 24°47'32.5" E, 14–15.VII.2011, leg. C. Ciubuc (2 males, CCPC). Bucegi Mts. Ialomiţa stream, 45.416957° N, 25.416958° E, 1837 m, 15.VII.2015, leg. Z. Baczó & J. Kecskés (4 males, 7 females; OPC). Bucegi Mts. Ialomiţa stream, 45.402125° N, 25.443147° E, 1680 m, 16.VII.2015, leg. Z. Baczó & J. Kecskés (3 males, 12 females; OPC). Romania, Damboviţa county, Southern Carpathians, Bucegi Mountains, Brătei stream valley, Negru stream, 45.383283° N, 25.350528° E, 14.VII.2016 leg. Z. Baczo & J. Kecskés (1 male, 1 female; OPC). Romania, Damboviţa county, South-

ern Carpathians, Bucegi Mountains, Brătei stream valley, Brătei stream, 45.383102° N, 25.385147° E, 13.VII.2016 leg. Z. Baczo & J. Kecskés (1 male, 2 females; OPC). Complex Semenic, 30.VI.1963, leg. B. Kiss (2 females, registration number TRH136/0023,). **Slovakia**: High Tatra Mts., Mlynica stream, 21.VII.1966, leg J. Oláh (1 male, OPC). Pleso nad Skokom, 21.VII.1966, leg J. Oláh (1 male, OPC). Biela voda, 22.VII.1966, leg J. Oláh (1 male, OPC). West Tatra Mts., Jamnicky stream, 12.VII.1978, light trap leg. Nagy (4 males, OPC). **Slovenia**: Julian Alp, Vrsic Pass, Soca spring, 22. VI. 1988 (4 females, OPC). Julian Alp, Radovna stream, 23. VI. 1988 (15 males, 2 females, OPC).

Diagnosis. Rambur 1842: 480, "D'une grandeur moyenne, rousse; tête en dessus dans les deux tiers externes brunâtre."

Schmid 1956: 21, "*Dr. discolor* est caractéristique par la coloration double, rousse et brune, de son corps et par ses ailes roux-gris; il est très voisin de *chrysotus* par son armature génitale."

Oláh *et al*. 2015: 111, "The ancestral shape of the paraproct in *Drusus discolor* (Rambur) is characterized by a lateral profile of flat convex serrated head, horizontal and rounded quadrangular relative to the vertically positioned apical margin. The serrated head is rounded truncated.

This shape is very stable in all the populations inhabiting huge distributional area from France to Albania through Italy, Slovenia, Czech Republic, Slovakia, Poland, Romania, Bulgaria, and Kosovo. The serrated head of the paraproct is composed of the two free, not fused dorsal branches of the paraproct. The branches are flat in sagittal plane and positioned oblique from anterolaterad to posteromesad. As a result a very tiny alteration in observation view from exact lateral may change dramatically the length (not the height!) of the head on the images what we see under microscope and consequently the drawings what we prepare. The spur formation, the actual terminal ending of the paramere is developed into a slightly upward curving and narrowing pointed structure with a variously produced dorsosubapical uprising or more frequently without any such outgrowth. The variation within or between populations is almost the same, due to dominating stochastic processes including fluctuating asymmetry, as it was discussed in the theoretical part."

In the year of 2016 we have sampled two populations in Macedonia and recorded the same shape stability of of the speciation traits.
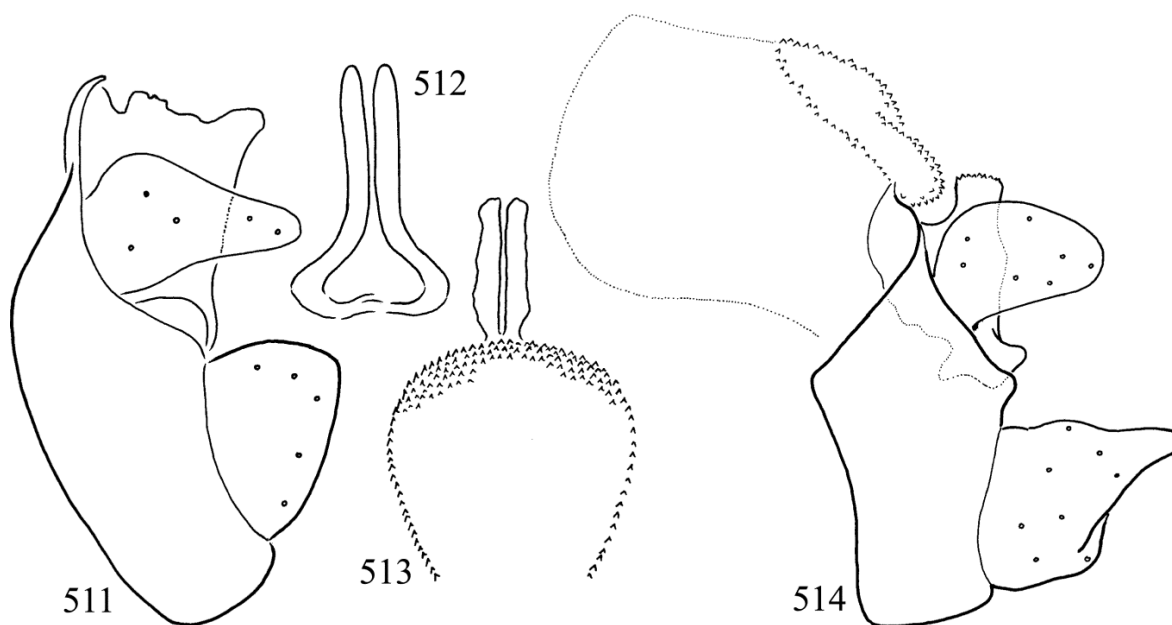
Figures 511–513. *Drusus slovenicus* Urbanic, Krusnik & Malicky, 2002. 511 = male genitalia in left lateral view, 512 = paraproct in caudal view, 513 = apical arms of the dorsal branches of paraproct and the pegged spinulose area on tergit VIII in dorsal view.
Figure 514. *Drusus discolor* Rambur, 1842. 514 = male genitalia in left lateral view.

Drusus ferdes **Oláh & Coppa,** 2016

(Figure 515)

Drusus ferdes Oláh & Coppa, 2016, in Oláh *et al.* 2016:120–123: "*Etymology – ferdes*, from "*ferde*" oblique or slant in Hungarian, refers to the direction, to the deviation from horizontal of the serrated dorsal margin of the paraproctal head."

Material examined. Holotype: **France**, Department Puy-de-Dôme, Chambon-sur-Lac, Ru Derriere la Dent de la Rancune Ru Granit, 23.VI.2012, leg G. Coppa (1 male, CPC). Paratypes: same as holotype (3 males, CPC; 3 males, OPC). Department Puy-de-Dôme, Chambon-sur-Lac, ru principal en aval du pont de Sainte-Anne, 21.VII.2012, leg G. Coppa (1 female, OPC). Department Puy-de-Dôme, Chambon-sur-Lac, Couze de Chaudefour Cascade Aval Reserve, 25.V.2009, leg G. Coppa (8 males, OPC). Department Puy-de-Dôme, Chastreix, Ru du Neve Zone de Source, 22.VIII.2015, leg G. Coppa (4 females, OPC). Department Puy-de-Dôme, Chastreix, ru du Névé, zone de source, 24.IX.2015, leg G. Coppa (3 males, 1 female; OPC). Department Cantal, Brezons, Sur le Brezons, Saut-de-la-Truite, 27.VI.2010, leg G. Coppa (2 males, OPC). Department Lozère, Meyrueis, Combe de Else, 22.VI.2014, leg G. Coppa (2 males, 1 female; OPC). Department Alpes-de-Haute-Provence, Uvernet-Fours, Torrent Braissette, Sentier, 25.VIII.2009, leg G. Coppa (2 males, 5 females; OPC). Department Alpes-de-Haute-Provence, Larche, Torrent Ornaye Source à 2380 m, 27.VII.2008, leg G. Coppa (2 males, 1 female; OPC).
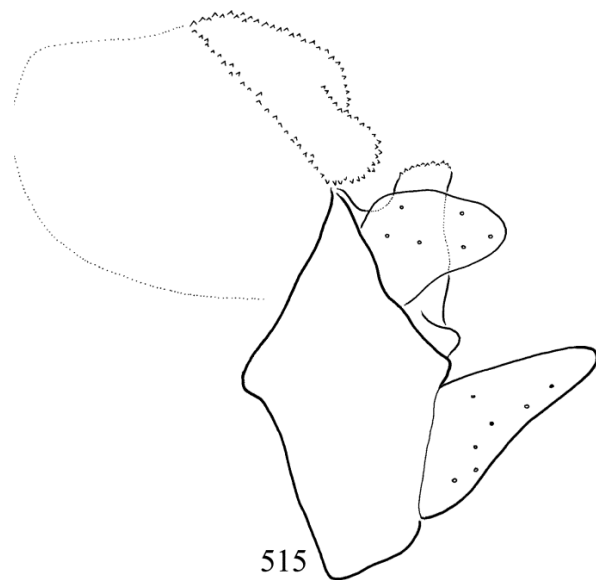
Figure 515. *Drusus ferdes* Oláh & Coppa, 2016. Holotype: 515 = male genitalia in left lateral view.

Diagnosis. Oláh *et al.* 2016: 120–123, "The divergence of this new incipient sibling species is realized in the speciation trait of the modified paraproct. The lateral profile of the paraproctal head is characterized by the slant serrated dorso-apical margin that is sloping downward obliquely from posterad to anterad. This divergence is stable in all of the examined population from Massif Central and from Alpes-de-Haute-Provence. It seems that the function of this modification on the serrated head of the paraproct works effectively alone or in combination with other premating barriers in mate recognition or in postmating pre-zygotic barriers of cryptic female choice or others, like gametic isolation. We have found no contact zone populations with hybrid effect."

Drusus kupos **Oláh & Coppa,** 2016

(Figure 516)

Drusus kupos Oláh & Coppa, in Oláh *et al.* 2016: 123–124. "*Etymology – kupos*, from "*kúpos*" conical in Hungarian, refers to narrowing conical shape of the serrated dorsal margin of the paraproctal head."

Material examined. Holotype: **France**, Department Pyrénées-Orientales, Err, Ru d'Err Aiguanein, 24.VIII.2011, leg G. Coppa (1 male, CPC). Paratypes: same as holotype (2 males, CPC; 2 males, OPC).

Diagnosis. Oláh *et al.* 2016: 123–124, "The divergence of this new incipient sibling species is realized in the speciation trait of the modified paraproct. The lateral profile of the paraproctal head is characterized by narrowing conical dorso-apical margin. This divergence is stable in the single population examined. The spur formation, the actual terminal ending of the paramere is developed into a slightly upward curving and narrowing pointed structure. Some sign of dorso-subapically produced uprising present in a single paratype."

Drusus leker **Oláh,** 2016

(Figure 517)

Drusus leker Oláh, in Oláh *et al.* 2016: 124–125. "*Etymology – leker*, from "*lekerekített*" rounded in Hungarian, refers to rounded shape of the serrated dorsal margin of the paraproctal head."
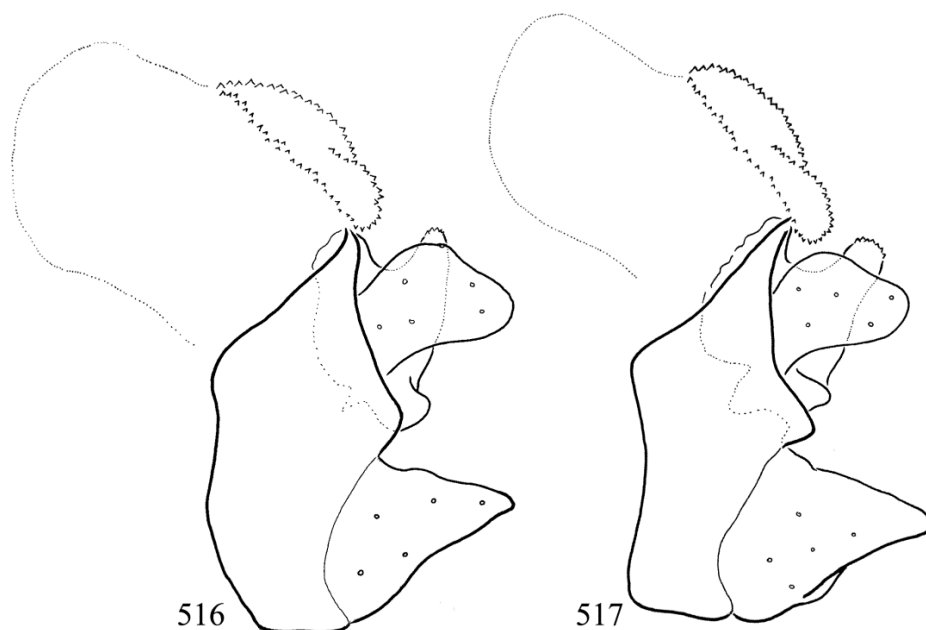
Figure 516. *Drusus kupos* Oláh & Coppa, 2016. Holotype: 516 = male genitalia in left lateral view.
Figure 517. *Drusus leker* Oláh, 2016. Holoptype: 517 = male genitalia in left lateral view.

Material examined. Holotype: **Italy**: Piemonte, Vinadio (CN), 2250 m, Col de la Lombarda lago, 44.20° N, 7.140° E, 18.VIII.1964, leg. A. Viganò (1 male, MCSNBG). Paratypes: same as holotype (2 males, 2 females, MCSNBG; 3 males, 2 females, OPC).Piemonte, Vinadio (CN), Santuario di S. Anna, 1880 m, N 44.238°, E 7.106°, 19.VII.2012, leg. G. Pezzi & I. Bendazzi (3 males, 1 female; MCSNBG; 2 males, OPC). **France**: Department Alpes-de-Haute-Provence, Saint Paul Sur Ubaye, Affluent Ubaye Sentier 2000 m, 27.VI.2008, leg G. Coppa (1 male, 3 females; OPC). Department Alpes-de-Haute-Provence, Uvernet Fours, Sanguinerette Amont, 25.VIII.2009, leg G. Coppa (4 males, 2 females; OPC, contact population with *D. discolor*).

Diagnosis. Oláh *et al.* 2016: 124, "The divergence of this new incipient sibling species is realized in the speciation trait of the modified paraproct. The lateral profile of the paraproctal head is characterized by the rounded serrated dorsoapical margin. This divergence is stable. It seems that the function of this modification on the serrated head of the paraproct works effectively alone or in combination with other premating barriers in mate recognition or in postmating prezygotic barriers of cryptic female choice or in others, like in gametic isolation. We have found sign of contact zone populations with possible hybrid effect."

Drusus visas Oláh & Coppa, 2016

(Figure 518)

Drusus visas Oláh, in Oláh *et al.* 2016: 127–129. "*Etymology – visas*, from "*vissza*" back in Hungarian, refers backward, anterad directed anterior corner of the serrated dorsal margin of the paraproctal head."

Material examined. Holotype: **France**, Department Pyré-nées-Orientales, Porte Puymorens, Ru de l'Orris, 21.VIII. 2011, leg G. Coppa (1 male, OPC). Paratypes: same as holotype (3 males, 4 females; OPC). Department Hautes-Pyrénées, Cauterets, Gave Cambasque, 16.VII.2010, leg G. Coppa (5 males, OPC). Department Hautes-Pyrénées, Gèdre, Pont Sauge Gave et suintement pres du pont, 27.VII.2010, leg G. Coppa (6 males, OPC).

Diagnosis. Oláh *et al.* 2016: 127, "The divergence of this new incipient sibling species is realized in the speciation trait of the modified paraproct. The lateral profile of the paraproctal head is characterized by backward, anterad directed anterior corner of the serrated head of the paraproct. This divergence is stable in the examined populations. It seems that the function of this modification on the serrated head of the

143
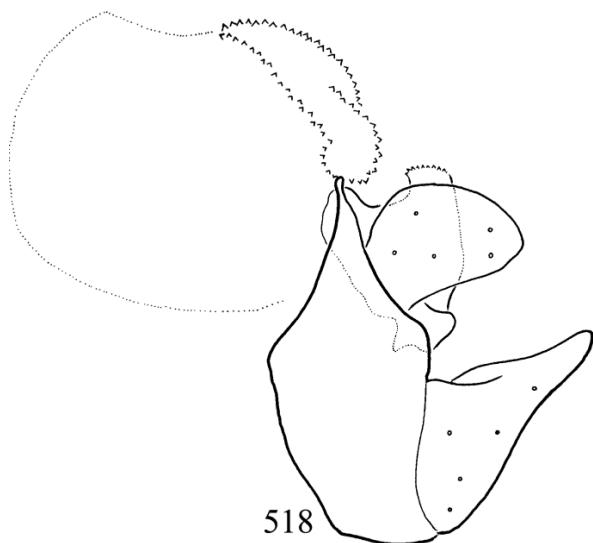
Figure 518. *Drusus visas* Oláh & Coppa, 2016. Holotype: 518 = male genitalia in left lateral view.

paraproct works effectively alone or in combnation with other premating barriers in mate recognition or in postmating prezygotic barriers of cryptic female choice or others, like gametic isolation. We have found no contact zone populations with hybrid effect."

Drusus macedonicus species complex

Drusus macedonicus species complex has the dorsoapical fused dorsal branches of paraproct produced into a short digitiform process, slightly broadened transversally in caudal view and accompanied by medium sized cerci and apically elongated gonopods. This species complex comprised of three species: *krpachi*, *macedonicus*, *malickyorum*

Drusus krpachi Kucinic, Graf & Vitecek, 2015 in Vitecek *et al.* 2015

(Figures 519–521)

Drusus krpachi Kucinic, Graf & Vitecek, 2015 in Vitecek *et al.* 2015: 81–83. „Holotype. 1 male. Macedonia, Mavrovo National Park, Korab Mountains, cesma Elem; N 41.857°, E 20.625°; leg. Kucinic, Krpac, Mihoci; 15. VIII.2011. Currently deposited in coll. WG, will be deposited in the Croatian Natural History Museum,

Zagreb, Croatia. Paratypes. 3 males: Macedonia, Mavrovo National Park, Korab Mountains, Rec; leg. Krpac, Mihoci, Kucinic; 1.VIII.2011. Currently deposited in coll. MK, two paratypes will be deposited in the Macedonian Museum of Natural History, Skopje, Republic of Macedonia, one paratype will be deposited in coll. WG."

Material examined. After several trials we have not got on loan the holotype or any male specimens for examination. We have been visited one time the locus typicus and collected only a single female. Macedonia, Polog region, Sar Planina, right side brook of right side brook of Radika Reka 41°51'12.7" N, 20°37'01.1" E, 1570 m, 15.09.2016, leg. P. Juhász, T. Kovács, G. Szilágyi (1 female, OPC).

Diagnosis. Vitecek *et al.* 2015: 82, „Males of the new species are most similar to *D. macedonicus.*"

Female description. Female genitalia. Tergite of segment IX forming medium long tube, open ventrally, with V-shaped deep mesal excision; lateral lobes acute triangular in dorsal view; its tiny apical tip shifted middle; the lateral setose lobe of sternite IX vertical. Segment X membranous and embedded inside segment IX and encircling anus; supragenital plate of segment X well-developed quadrangular with concave apical margin in lateral view. Median lobe of the vulvar scale (lower vaginal lip) present, long and slender. Dorsal profile of the vaginal sclerite complex rounded and less narrowing anterad.
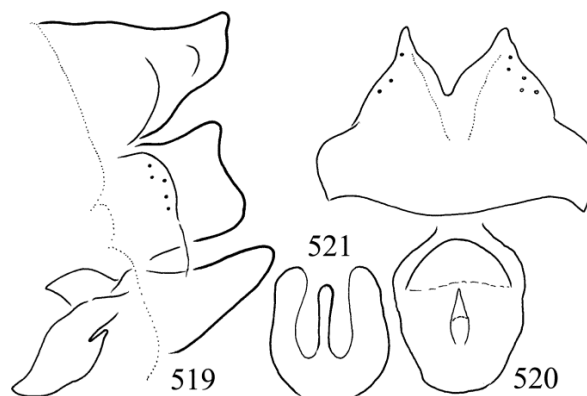
Figures 519–521. *Drusus krpachi* Kucinic, Graf & Vitecek, 2015. 519 = female genitalia with vaginal sclerite complex in left lateral view, 520 = tergite IX and dorsal profile of vaginal sclerite complex in dorsal view, 521 = vulvar scale in ventral view.

Drusus macedonicus Schmid, 1956

(Figures 522–524)

Drusus macedonicus Schmid, 1956: 90–91. "Holotype ♂, allotype ♀ et paratypes ♂♂♀♀: Massif du Périster (Macédoine yougoslave), 10–12.VIII.1955. L'espèce était assez commune le long des petits torrents d'alpage entre 1.500 et 2.000 m d'altitude."

Material examined. Macedonia, Pelagonia region, Pelister Mts, Capari, springs area of Caparska Reka, 41°00'14.0" N, 21°10'4.6" E, 1952 m, 13.09.2016, leg. P. Juhász, T. Kovács, G. Szilágyi (1 male, OPC).

Diagnosis. Schmid 1956: 90–91, "Le *Drusus* de Macédoine est très voisin de *discolor* comme en témoignent la coloration et les génitalia. Il s'en distingue par sa coloration moins grise, par les appendices supérieurs du ♂ plus grand, plus proéminents et rappelant ceux de *transylvanicus* et par les appendices inférieurs plus élancés. Il est toujours bien distinct de *discolor* avec qui il cohabite."
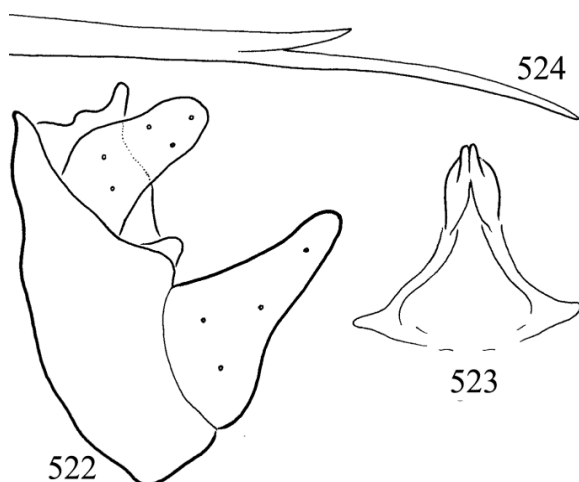
Figures 522–524. *Drusus macedonicus* Schmid, 1956. 522 = male genitalia in left lateral view, 523 = paraproct in caudal view, 524=paramere in left lateral view.

Drusus malickyorum Oláh, nom. nov.

(Figures 525–527)

Drusus malickyi Oláh & Vitecek, 2015 in Vitecek *et al*. 2015: 83–85. „Material examined. Holotype. 1 male: Albania, Shkoder County, Shkoder District, Prokletije Mts, beech forest with brook above Okol; N 42.42258°, E1 9.76127°; leg. Puskás 05.IX.2013. Currently deposited in coll. WG, will be deposited in János Oláh Private Collection under national protection of the Hungarian Natural History Museum, Budapest, Hungary (JO)."

Drusus malickyorum Oláh **nom. nov**. We have synonymised the genus *Metanoea* with genus *Drusus*, therefore by preoccupation *Drusus malickyi* Oláh & Vitecek became a junior homonym of *Drusus malickyi* (Sipahiler, 1992) comb. nov. of *Metanoea malickyi* Sipahiler, 1992. We dedicate the new name to H. Malicky, to his wife and their son.

Material examined. We have presented our single male specimen, collected in the Prokletije Mts. Albania, to W. Graf's laboratory, but we have not succeded to receive back for our routine detailed fine structure analysis of the holotype's paramere.

Diagnosis. Vitecek *et al*. 2015: 83, „The holotype of the new species is most similar to *D. macedonicus*, but exhibits (1) a sharp mediocaudal protrusion of segment IX; (2) a dorsally straight and rough tip of the intermediate appendage distinctly separated by a proximal intendation; (3) a distinctly slender and constricted distal half of the inferior appendage in lateral view. *Drusus macedonicus* males have a mediocaudal and a ventrocaudal protrusion of segment IX, intermediate appendages with two rough rounded dorsal protrusions but lacking a distinct proximal indentation, and to a lesser degree constricted inferior appendages."
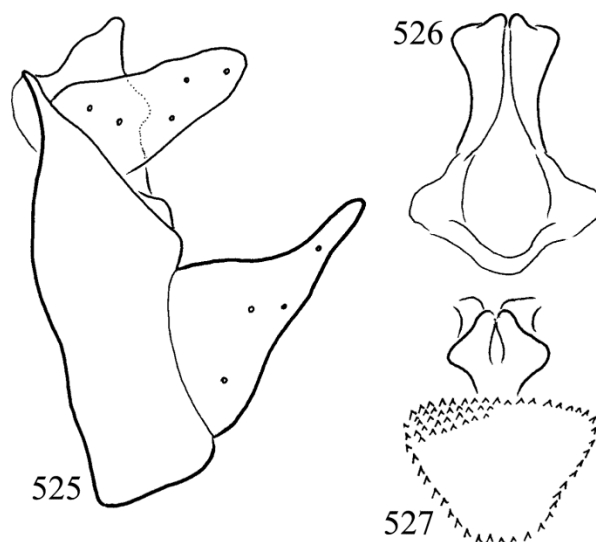
Figures 525–527. *Drusus malickyorum* Oláh, nom. nov. 25 = male genitalia in left lateral view, 526 = paraproct in caudal view, 527 = apical arms of the dorsal branches of paraproct and the pegged spinulose area on tergit VIII in dorsal view.

Drusus muelleri species complex

Drusus muelleri species complex has the fused dorsal branches of paraproct rather robust with straith vertical apical margin in lateral view, accompanied by very long cerci and short subapical spine on the paramere. This species complex comprised of four species: *arkos* sp. nov., *horgos* sp. nov., *magas* sp. nov., *muelleri*.

Drusus arkos Oláh, sp. nov.

(Figures 528–532)

Material examined. Holotype: **Italy**, Piemonte, Cuneo-Crissolo, Pian della Regina, fiume Po, 1700 m, 19.VII.1998, light trap leg. O. Lodovici (1 male, MCSNBG). Allotype: same as holotype (1 female, MCSNBG). Paratypes: Piemonte, Ceresole Reale (TO), 2300 m, verso Passo Nivolet, 6. VII. 1990, leg. Ravizza, (1 female, CC n°249; 1 male, 1 female; OPC).

Diagnosis and description. This new species has the fused dorsal branches of paraproct rather robust with straith vertical apical margin in lateral view; the dorsum of the fused dorsal branches of the paraproct is flat sinking anterad into a deep very characteristic ditch. Periphallic organ of cerci and gonopods are long. The subapical spine on the paramere is accompanied by two small secondary spines in variable position at the holotype and paratype.

Female description. Female genitalia. Tergite of segment IX forming a long tube, open ventrally, with U-shaped deep mesal excision; the basal half of the tergite is almost double wide than its apical part. Dorsal profile of the vaginal sclerite complex rounded quadrangular, not narrowing anterad.

Etymology. „*arkos*",from „árkos", bearing ditch in Hungarian, refers to the deep ditch present anterad on dorsum of the fused dorsal branches of the paraproct in lateral view.
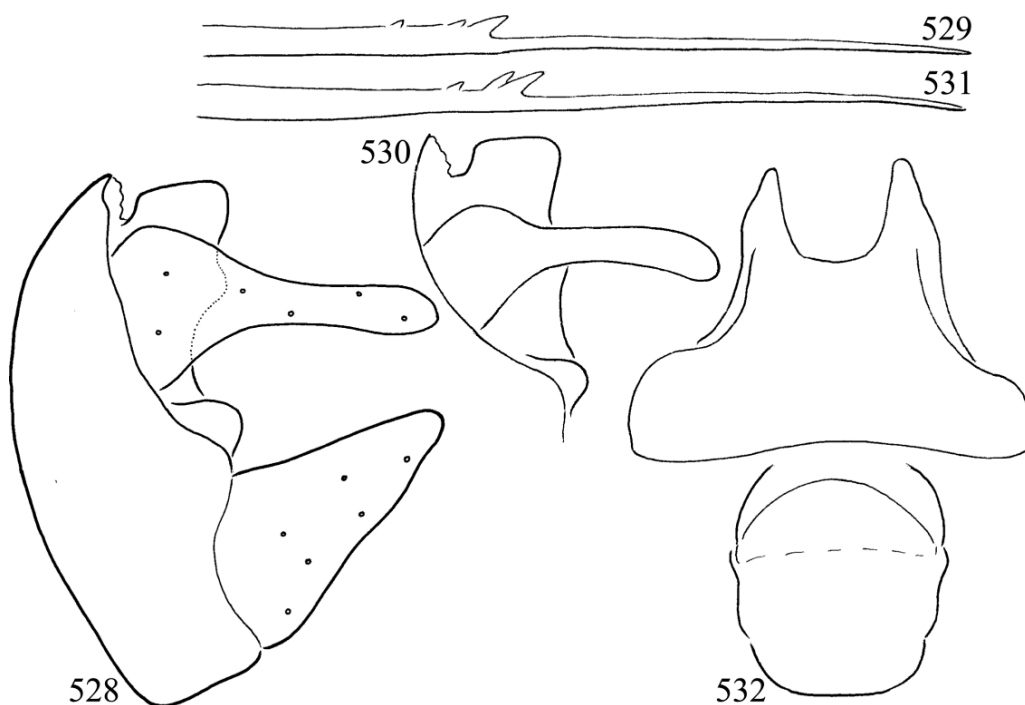
Figures 528–532. *Drusus arkos* Oláh, sp. nov. Holotype: 528 = male genitalia in left lateral view, 529 = paramere in left lateral view. Paratype: 530 = cerci and paraproct in lateral view, 531 = paramere in left lateral view.
Allotype: 532= tergite IX and dorsal profile of vaginal sclerite complex in dorsal view.

Drusus horgos Oláh, sp. nov.

(Figures 533–538)

Material examined. Holotype: **Italy**, Lombardia, Bergamo, Valbondione, Lago Malgina, 2339 m, 15.VII.2003, light trap leg. R. Calandrina (1 male, MCSNBG). Paratypes: same as holotype (1 male, OPC). Lombardia, Valbondione (BG), 2000 m, Val Cerviera, 2. VII. 2003, leg. Calandrina (1 male, MCSNBG). Lombardia, Valbondione (BG), 2000 m, Val Cerviera, 3. VII. 2003, leg. Calandrina (1 male, OPC). Lombardia, Valbondione (BG), 2120 m, Lago Corni Neri, 1. VII. 2003, leg Calandrina (1 male, MCSNBG).

Diagnosis and description. Similarly to the species complex this new species has the fused dorsal branches of paraproct rather robust with straith vertical apical margin in lateral view; the dorsum of the fused dorsal branches of the paraproct is rounded with posterad directed dorsoapical tip. The speciation trait of the paraproct dorsal branches, that is the posterad directed dorsoapical tip is very stable at all the paratypes. Cerci is medium long, gonopods with slender apical portion. The subapical spine on the paramere is small with a very small tertiary spine anterad on the holotype; this tertiary spine is lacking at three paratypes and soubled at one paratypes. As a rule in the Drusinae subfamily the speciation trait of the paraproct is more stable than the parameres liable to fluctuating symmetry.

Etymology. „horgos",from „horgos", armed wit hook in Hungarian, refers to the posterad directed tip on dorsum of the fused dorsal branches of the paraproct in lateral view.

Drusus magas Oláh sp. nov.

(Figures 539–545)

Drusus muelleri Mclachlan, 1868: Schmid 1956: 25–27. "J'en ai étudié un nombre important de spéciments capturés dans les Alpes suisses. *Dr. muelleri* n'a été signalé que dans les Alpes centrales. En Suisse, il est commun de 1.600 a 2.600 m d'altitude en VI et VII, en compagnie de *Dr. melanchaetes* et *monticola*, au moment de la fonte des neiges." Misidentification!

Material examined. Holotype: **Switzerland**, Furkapass, N46° 35.314', E8° 25.814', 2348 m, 21.VII.2006, leg W. Graf (1 male, OPC). Allotype: same as holotype (1 female, OPC). Paratypes: **Italy**, Valle d'Aosta, Valpelline (AO), 1850 m, Torrente affl. Dora di Valpelline, 8. VIII. 1969, Ravizza, (1 male, MCSNBG; 1 male CM; 1 male, OPC).

Diagnosis and description. Schmid's drawing prepared for *D.muelleri* is not identical with the holotype of *D. muelleri*, it represents a new species diverging in the shape of the speciation trait of the paraproct. Similarly to the species complex this new species has the fused dorsal branches of
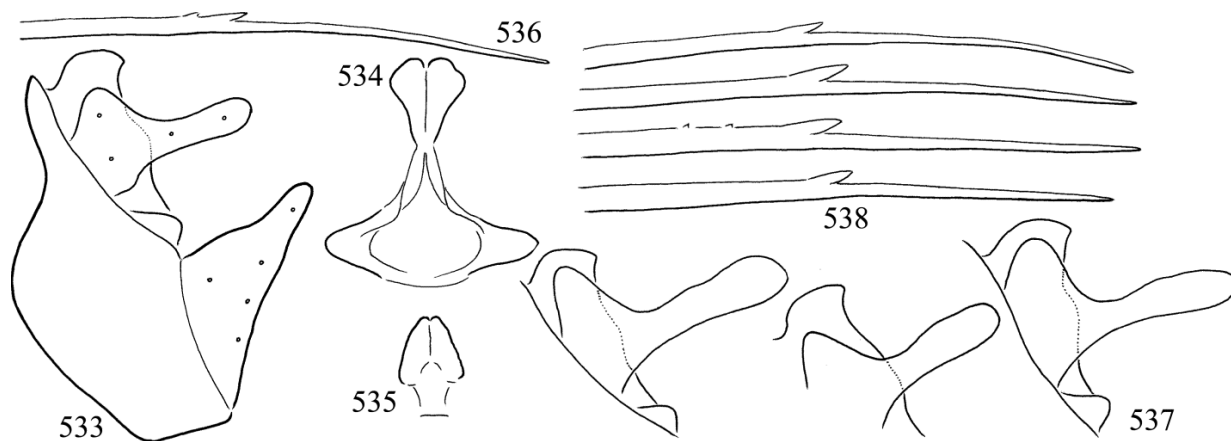
Figures 533–538. *Drusus horgos* Oláh, sp. nov. Holotype: 533 = male genitalia in left lateral view, 534 = paraproct in caudal view, 535 = apical arms of the dorsal branches of paraproct in dorsal view, 536 = paramere in left lateral view. Paratypes: 537 = cerci and paraproct in left lateral view, 538 = parameres in left lateral view.
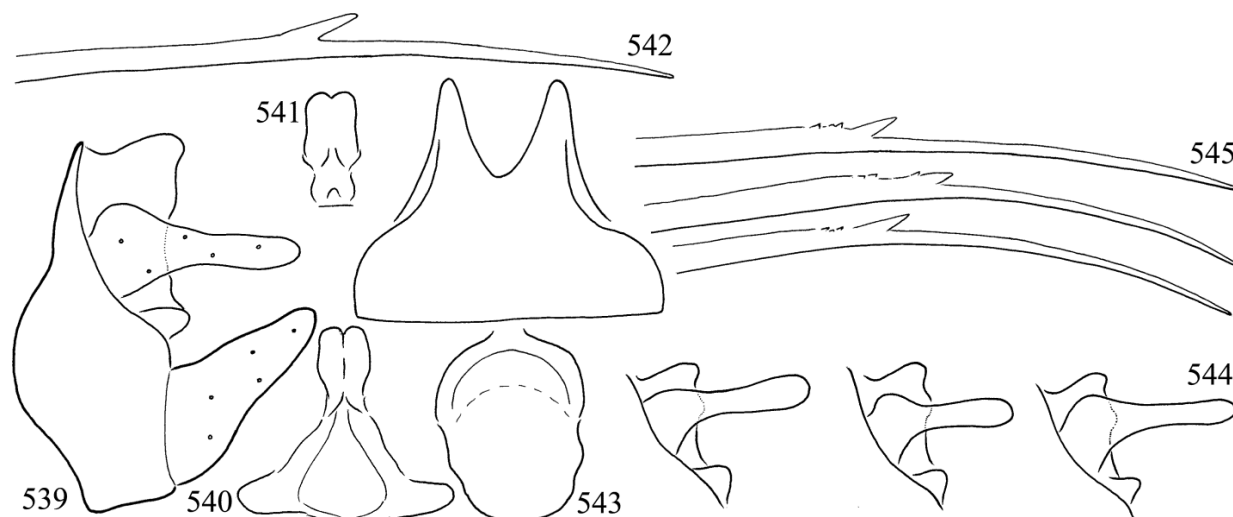
Figures 539–543. *Drusus magas* Oláh, sp. nov. Holotype: 539 = male genitalia in left lateral view, 540 = paraproct in caudal view, 541 = apical arms of the dorsal branches of paraproct in dorsal view, 542 = paramere in left lateral view. Allotype: 543 = tergite IX and dorsal profile of vaginal sclerite complex in dorsal view. Paratypes: 544 = cerci and paraproct in left lateral view, 545 = parameres in left lateral view.

paraproct rather robust with straith vertical apical margin in lateral view; the dorsum of the fused dorsal branches of the paraproct is ascending dorsoapicad into a produced corner, not simply rounded like at the holotype of *D. muelleri*. The speciation trait of the paraproct dorsal branches, that is the ascending dorsoapical tip is very stable at all paratypes. Cerci and gonopods are medium long. The subapical spine on the paramere is medium sized without any accompanying tertiary spine anterad on the holotype; some very small tertiary spine are present at the three paratypes. Again as a rule in the Drusinae subfamily the speciation trait of the paraproct is more stable than the parameres liable to fluctuating symmetry.

Etymology. „magas",from „magas", high in Hungarian, refers to fused dorsal branches of the paraproct ascending high dorsoapicad into a produced corner tip in lateral view.

Drusus muelleri (McLachlan, 1868)

(Figures 546–549)

Halesus (Drusus) muelleri McLachlan, 1868: 292–294. "Hospenthal, Switzerland (Albert Müller), 1♂."

Material examined. Holotype: deposited in The Natural History Museum, London, England. **France**, Department Savoie, Seez, torrent affluent du Reclus, 12.VII.2015, leg. G. Coppa (1 male, OPC). **Switzerland**, Valais Canton, Binntal, Balme, Binn, 2180 m, 22. VII.2004, leg. P. Stucki (1 male, CMZL). Switzerland, Valais Canton, Gd. St-Bernard, Maringo, Bourg-St-Pier, 1950 m, 14.VII.2004, leg. P. Stucki (3 males, CMZL). Switzerland, Bern Canton, Grimselpass, Zufluss Grimselsee, Diemtigen, 1992 m, 18.VII.2004, leg. V. Lubini (3 males, 1 female; CMZL). Switzerland, Valais Canton, Muttbach 3, Oberwald, 2450 m, 3-11.VIII.1997, leg. B. Lods-Grozet (1 male, CMZL). Switzerland, Valais Canton, Quellbach, Muttbach Oberalpen, 2200 m, 17.VII.2004, leg. V. Lubini (8 males, 4 females; CMZL; 2 males, 1 female; OPC). Switzerland, Bern Canton, Sustenpass Obertal, Bach, Gadmen, 2220 m, 3. VIII.2004, leg. H. Vicentini (1 female, CMZL). Switzerland, Uri Canton, Sustenpass Chli Sustli, Bach, Wassen, 1965 m, 3. VIII.2004, leg. H. Vicentini (1 female, CMZL). Switzerland, Uri Canton, Sustenpass, Obersusten, Bach, Wassen, 2177 m, 3.VIII.2004, leg. H. Vicentini (1 male, 1 female; CMZL). Switzerland, Valais Canton, Binn Pierrien, 5.VIII.1980, leg. C. Ruedi (1 male, CMZL).

Diagnosis. McLachlan 1868: 293–294, "app. intermed. intensely black, broad, and triangular, lying so close together as to appear as one piece, their basis extending downwards, and diverging, forming carinate projections on the part whence they arise, at the beginning of each of which is a rounded reddish tubercle." "Remarkable for the great length of the app. sup."

148
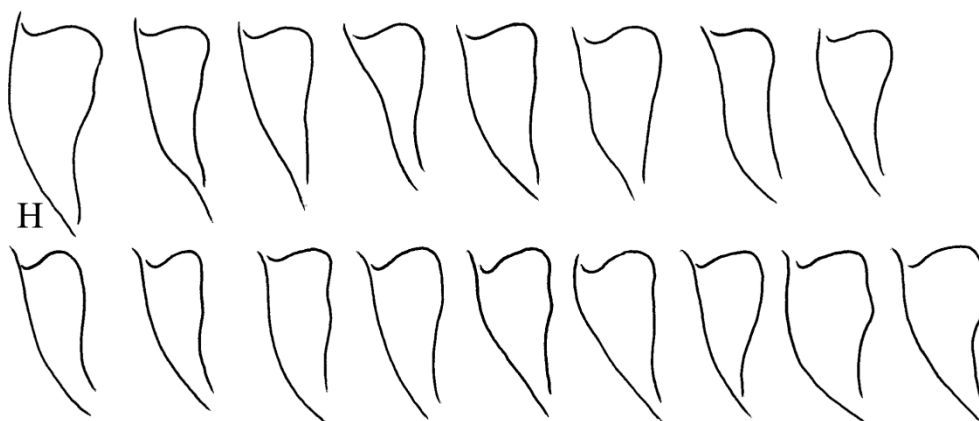
Figure 549. *Drusus muelleri* (McLachlan, 1868). 549 = dorsal branches of paraproct of holotype (H, upper left) and paratypes in lateral view.
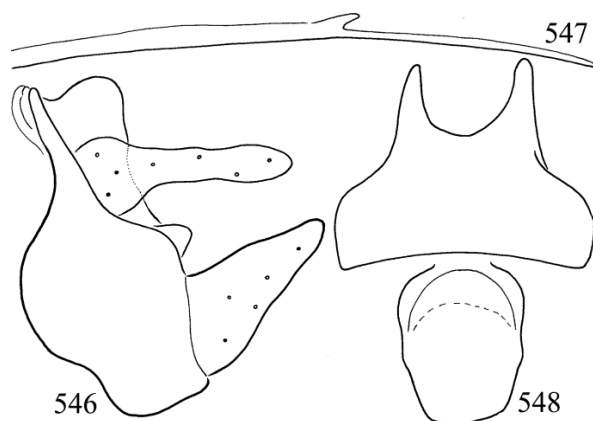
Figures 546–548. *Drusus muelleri* (McLachlan, 1868). Holotype: 546 = male genitalia in left lateral view, 547 = paramere in left lateral view. 548 = tergite IX and dorsal profile of vaginal sclerite complex in dorsal view.

McLachlan 1876: 176, The ♂ is readily distinguish from any of the black, or blackish, species, and, in fact, from any species of the genus, by the extremely long slender superior appendages."

Additional diagnosis. The fused dorsal branches of the gonopods has a rounded profile in lateral view at the holotype and at all the examined specimens from France and Switzerland.

Drusus romanicus species complex

Members of the *Drusus romanicus* species complex is almost indistingishable from the *D. discolor* species complex by the architecture of the paraproct, at least in routine examination procedures. The only recognised difference is that *D. romanicus* complex has a decisive hump on the apical margin of the paraproct in lateral view. However, the two complex is clearly distinguishable by the shape of the periphallic organs. *D. romanicus* complex has cerci and gonopods long slender with different shape configuration compared to the short cerci and gonopods of *D. discolor* complex.

Paraproct homoplasy. It was remarkable to discover distinct homoplasy in the lateral profile of the fused dorsal branches of paraproct in three species pairs of the *D. discolor* and *D. romanicus* species complexes. Homoplasy (1) of the flat horizontal top at *D. discolor* and *D. romanicus*, (2) of the rounded top at *D. leker* and *D. meridionalis* and (3) and of the anterad sloping and posterad produced top at *D. ferdes* and *D. ekes*.

In the Darwin industry the term homology, often results from divergent evolution, referring to structures on two species diverged from a common recent ancestor. In contrary homoplasy, often results from convergent or parallel evolution, refers to similar characteristic of two species not inherited from their recent ancestor. Homoplasy evolves independently usually due to natural selection in similar environments or filling the same type of niche as the other species with that trait. The wings of insects, birds and bats are homopla-

sious. However this mechanistic simplification of the reductionist approach does not explain the detected homoplastic speciation traits in the two *Drusus* complexes. The similar shape divergences in the two diverged clades are not homologous, they are homoplastic because they have different recent ancestors. Most recent ancestor of *D. romanicus* species complex has hump on the paraproct and elongated periphallic organs of cerci and gonopods while the ancestor of *D. discolor* species complex has no decisive hump and has short periphallic organs. The homoplasious divergence is an adaptive product of the integrative organisation by sexual selection in isolated allopatry and based on genomic stochastic constraints of active and sleeping agents under the permanent flux of environmental perturbations.

This species complex is comprised of four species: *ekes* sp. nov., *meridionalis*, *pirinensis* sp. nov., *romanicus*.

Drusus ekes Oláh, sp. nov.

(Figures 550–558)

Material examined. Holotype: **Romania**, Apuseni Mts., Vlădeasa Mt., Stâna de Vale, upper section of Ciripa stream, N46°40.546', E22°38.515', 1360 m, 6.VI.2015, leg. M. Kiss, J. Oláh & L. Szél (1 male, OPC). Allotype: same as holotype (1 female, OPC). Paratypes: same as holotype (12 males, OPC). Apuseni Mts., Vlădeasa Mt., Stâna de Vale, Galbenele stream, N46°40.809', E22°37.147', 1180 m, 7.VI.2015, leg. M. Kiss, J. Oláh & L. Szél (2 males, OPC). Apuseni Mts., Mt. Bihor, Gârda de Sus, tributary of Arieşul Mare, N46°270.493', E22°47.895', 788 m, 29.V.2013, singled leg. J. Oláh, E. Bajka, Cs. Balogh, & G. Borics(1 male, OPC). Apuseni Mts. Munţii Gilăului, Staţiunea Muntele Băişorii, Lupinus stream, 18.VI.2013, singled leg. J. Oláh, Cs. Balogh, & S. Fekete (1 male, OPC). Apuseni Mts. Munţii Gilăului, Staţiunea Muntele Băişorii, La Mocirle, spring streams, N46°30.241', E23°15.550', 1552 m, 19–20.VI.2015, singled leg. J. Oláh, Cs. Balogh, & P. Juhász(1 male, OPC). Apuseni Mts., Vlădeasa Mt., Stâna de Vale, upper section of Ciripa stream, N46°40.546', E22°38.515', 1360 m, 6.VII.2016, leg. J. Kecskés (3 females, OPC). Stana de Vale, 3. VI. 1956, leg V. Cirligat (1 male, registration number TRH136/013, CCPC).

Diagnosis and description. The hump on the apical margin of the paraproct, that is the only recognised paraproct divergence between *D. chrysotus* and *D. romaicus* complexes, is very
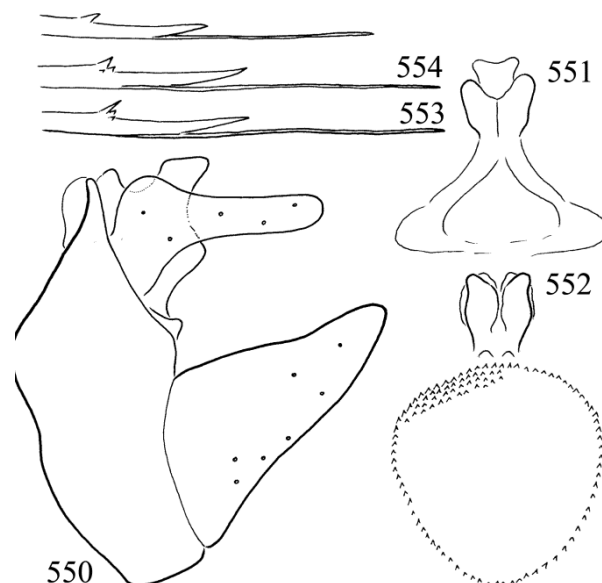
Figures 550–554. *Drusus ekes* Oláh, sp. nov.Holotype: 550 = male genitalia in left lateral view, 551 = paraproct in caudal view, 552 = apical arms of the dorsal branches of paraproct and the pegged spinulose area on tergite VIII in dorsal view, 553 = paramere in left lateral view. Paratypes: 554 = parameres in left lateral view.
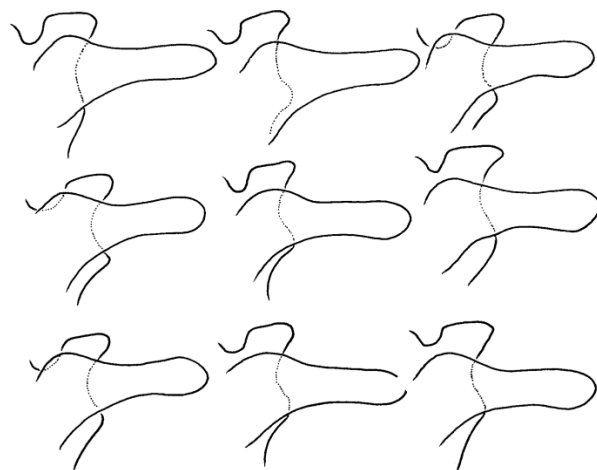
Figure 555. *Drusus ekes* Oláh, sp. nov. Paratype: 555 = cerci and paraprocts in lateral view.

decisive and pronounced at *D. ekes* sp. nov. The lateral profile of the fused dorsal branches of paraproct has the flat top sloping anterad and produced posterad, similar to *D. ferdes*, differing from the lateral configuration of the other three species. The top configuration of the speciation trait of paraproct is rather stable in the sampled

populations of the three main montain ranges of the Apuseni Mts.: Vlădeasa Mt., Bihor Mt., and Gilăului Mt. The subapical spines, that is the true terminal of the paramere shaft long and armed basad with a few small tertiary spine like structures; the apparent terminalia of modified setal origin is very long and thin. This paramere pattern differs from the paramere patterns of the other three species.

Female description. *Female genitalia.* Tergite of segment IX forming long tube, open ventrally, with deep V-shaped mesal excision; lateral lobes the most elongated triangular in dorsal view compared to the females of the other species in the complex; the lateral setose lobe of sternite IX rounded. Segment X membranous and embedded inside segment IX and encircling anus; supragenital plate of segment X well-developed elongated quadrangular with somehow bipartite apical margin in lateral view. Median lobe of the vulvar scale (lower vaginal lip) present, little more than half as long as the lateral lobes. Dorsal profile of the vaginal sclerite complex rounded.

Etymology. „ekes", from „ékes", supplied with wedge in Hungarian, refers to the flat top of the paraproct sloping anterad and produced posterad into a wedge shape. But "*ékes*", has the peculiar meaning of glory, an outstanding beauty, more than beautiful, thanks to the fractal nature of the Hungarian language. The given name refers to both characters, this animal is really elegant and beautiful.
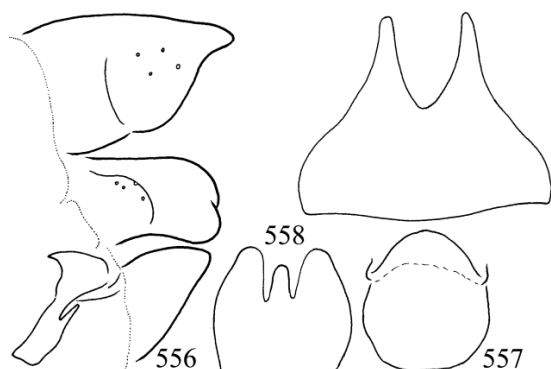
Figures 556–558. *Drusus ekes* Oláh, sp. nov. Allotype: 556 = female genitalia with vaginal sclerite complex in left lateral view, 557 = tergite IX and dorsal profile of vaginal sclerite complex in dorsal view, 558 = vulvar scale in ventral view.

Drusus meridionalis Kumanski, 1973

(Figures 559–564)

Drusus romanicus Murgoci & Botosaneanu, 1954. Szczesny 1970: 775. Rila Mts. Malovitsa stream, 9.VIII.1969, 2 males; 12.VIII.1969, 4 females. Noted numerous differences in genital structure between the Rila and the Romanian specimens. Misidentification!

Drusus romanicus meridionalis Kumanski, 1973: 108–110. „Die Material der neuen Unterart is aus Pirin-Gebirge, Banderischki-Zirkus, Bergbach unterhalb der Muratowi-Seen (2200 m Höhe), 21.IX.1967, 1 ♂ und 3♀ und aus der Umgebung der Berghütte „Demjanitza" (1900 m Höhe), 1.VIII.1970, 1♂, wie auch aus dem Rila-Gebirge, Bergbach in dem Malöwitza-Zirkus, 9–12.VIII.1969, 2♂ (leg. M. Kownacka) und oberhalb der Hütte „Sawratschitza" (etwa 2200 m Höhe), 10.VIII.1968, 2♂ (leg. Dr. I. Buresh)." Partly misidentification! Specimens from the the Pirin Mts. are *Drusus pirinensis* Oláh & Chvojka 2017 in Oláh *et al.* 2017)

Drusus romanicus meridionalis Kumanski, 1973. Kumanski & Malicky 1976: 105. Rila Mts. Nebenbach des Beli Iskar ob Borowez, 2300 m, 23-24.VIII.1971, 1 male, 2 females. Rila Mts. Nebenbach des Beli Iskar ob Borowez, 1200-1800 m, 24.VIII.1971, 1 female. Rila Mts. Nebenbach des Beli Iskar ob Borowez, 2200-2300 m, 18-21.VII.1968, 3 males.

Drusus romanicus meridionalis Kumanski 1988: 42–44. Rila Mts. and Pirin Mts. are given for distribution. No exact collecting data is given, however the lateral profile of the paraproct as well as the paramere pattern on the drawings are identical with specimens from the Rila Mts.

Drusus meridionalis Kumanski, 1973. Vitecek *et al.* 2015a: 258. Raised to species level by performance of morphological data in phylogenetic reconstruction of Drusinae.

Drusus meridionalis Kumanski, 1973. Vitecek *et al.* 2015b: 90–93. Redrawn and redescribed from specimens collected in Pirin Mts. Misidentification!

Material examined. **Bulgaria**, Rila, Mesta basin, Džanka, sidetorrent of the Stream Grănčarica, N42°07'57.4", E23°35'51.4" 2287m 07.IX.2005, leg. D. Murányi (1 male, HNHM). Rila Mts., Kirilova Poljana env. NE Rilski Monastir, 42 09 13N 23 23 53E, 1500 m, 11.VII.1998, leg. Jiri Hájek (1 male, NMPC).

Diagnosis. Kumanski 1973: 108: "App. superiores bei den ♂ bemerkenwert kürzer als bei der Nominatform (*Drusus romanicus romanicus*). App intermediales im Profil mit schwacher individualisiertem oberen (feien) Teil; derselbe erhebt sich bei romanicus romanicus in seinem Vorderende unter einem geraden Winkel."

Additional diagnosis. The hump on the apical margin of the paraproct, that is the only recog-
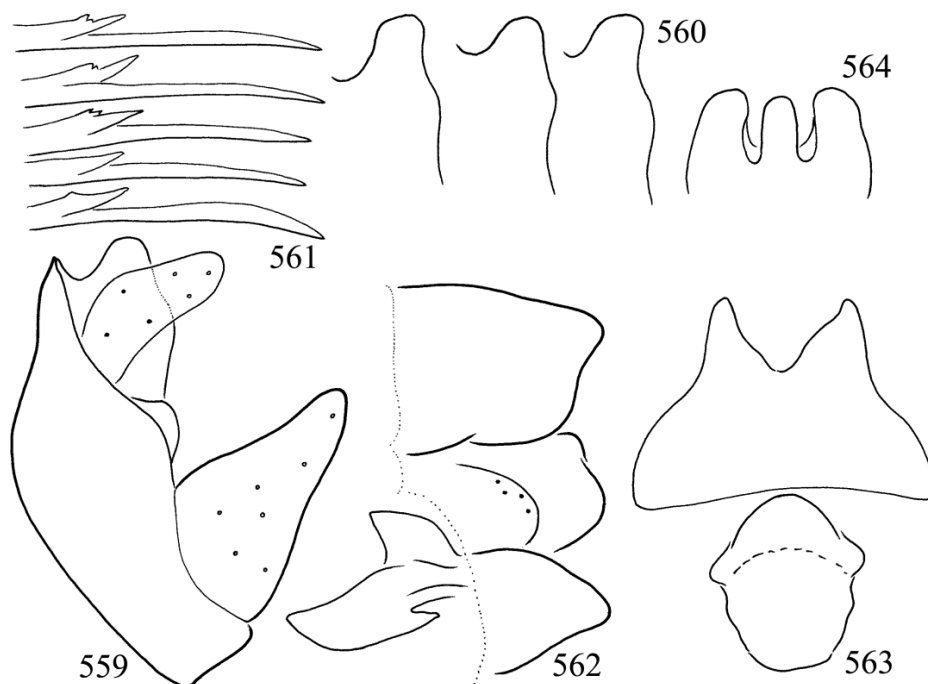
Figures 559–564. *Drusus meridionalis* Kumanski, 1973. 559 = male genitalia in left lateral view, 560 = dorsal branches of paraprocts in lateral view, 561 = parameres in left lateral view, 562 = female genitalia with vaginal sclerite complex in left lateral view, 563 = tergite IX and dorsal profile of vaginal sclerite complex in dorsal view, 564 = vulvar scale in ventral view.

nised paraproct divergence between *D. chrysotus* and *D. romanicus* complexes, is less pronounced. The lateral profile of the fused dorsal branches of paraproct has the flat top high and rounded, similar to *D. leker*, differing from the lateral configuration of the other three species. The subapical spines, that is the true terminal of the paramere shaft short and armed basad with not so distinct structures; the apparent terminalia of modified setal origin is long and thick. This paramere pattern differs from the paramere patterns of the other three species.

Female description. Female genitalia. Tergite of segment IX forming long tube, open ventrally, with V-shaped mesal excision; lateral lobes the triangular in dorsal view; the lateral setose lobe of sternite IX rounded. Segment X membranous and embedded inside segment IX and encircling anus; supragenital plate of segment X well-developed elongated quadrangular with somehow bipartite concave apical margin in lateral view. Median lobe of the vulvar scale (lower vaginal lip) pre-sent, robust and almost as long as the lateral lobes. Dorsal profile of the vaginal sclerite complex rounded.

Drusus pirinensis Oláh & Chvojka, sp. nov.

(Figures 565–569)

Drusus romanicus Murgoci & Botosaneanu, 1954. Kumanski 1969: 177. Identification of specimens from Bulgaria, Pirin Mts. (Banderiski Circus. Ottokana Muratovi Ozera), collected on 21.IX.1967 was confirmed by L. Botosaneanu. At the same time the authors have recorded difference in the structure of paraproct (intermediate appendage) between the Romanian specimens and specimens from the Pirin Mts. Misidentification!

Drusus romanicus meridionalis Kumanski, 1973: 108–110. "Pirin Gebirge, Banderischki-Zirkus, Bergbach unterhalb der Muratowi-Seen (2200 m Höhe), 21.IX.1967, 1♂ und 3♀ und aus der Umgebung der Berghütte Dem, janitza (1900 m Höhe), 1.VIII.1970, 1♂. Misidentification!

Drusus romanicus meridionalis Kumanski, 1973: 108–110. „Die Material der neuen Unterart is aus Pirin-Gebirge, Banderischki-Zirkus, Bergbach unterhalb der Muratowi-Seen (2200 m Höhe), 21.IX.1967, 1♂ und 3♀ und aus der Umgebung der Berghütte „Demjanitza" (1900 m Höhe), 1.VIII.1970, 1♂, wie auch aus dem Rila-Gebirge,
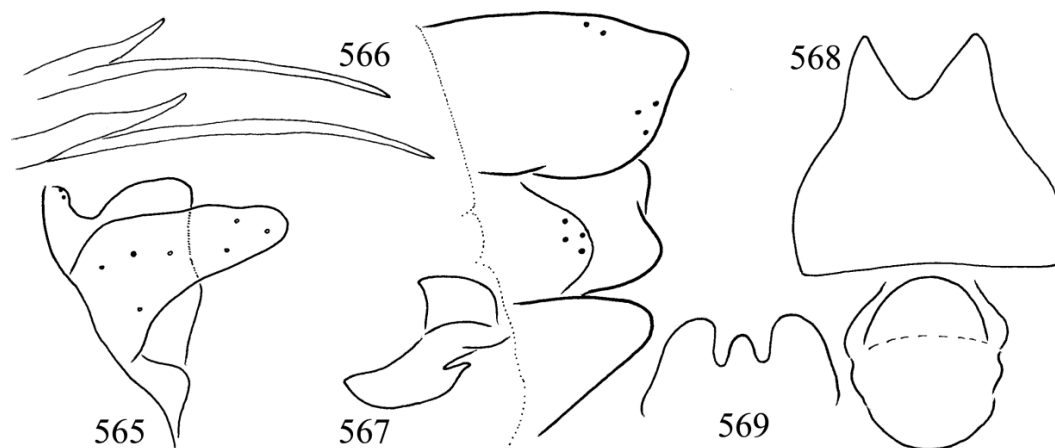
Figures 565–569. *Drusus pirinensis* Oláh & Chvojka, sp. nov. Holotype: 565 = cerci and paraproct in lateral view, 566 = left and right parameres in lateral view, 567 = female genitalia with vaginal sclerite complex in left lateral view, 568 = tergite IX and dorsal profile of vaginal sclerite complex in dorsal view, 569 = vulvar scale in ventral view.

Bergbach in dem Malöwitza-Zirkus, 9–12.VIII.1969, 2♂ (leg. M. Kownacka) und oberhalb der Hütte „Sawratschitza" (etwa 2200 m Höhe), 10.VIII.1968, 2♂ (leg. Dr. I. Buresh)." Partly misidentification! Specimens from the the Rila Mts. are *Drusus meridionalis*)

Drusus romanicus meridionalis Kumanski, 1973. Kumanski & Malicky 1976: 105. Pirin Mts. Banderiza-Einzugsgebiet mit Nebenbachen, 1000–2000 m, 24.VII.1968, 1 male. Pirin Mts. Banderiza-Einzugsgebiet mit Nebenbachen, 2000–2300 m, 26.VII.1971, 1 male, 3 females. Misidentification!

Drusus meridionalis: Vitecek *et al.* 2015: 91–93. "Bulgaria, Vihren, Pirin Mountains, Okotovo-Banserishka, marshy spring; N41.7389°, E23.4462°; 23.VIII.2013 leg. Keresztes, Török, Kolcsár; 10 males: in coll WG." Misidentification!

Material examined. Holotype: **Bulgaria**, Pirin Mts. 2100 m, above Vichren challet, 27.VIII.1979, leg. Beron (1 male, NMPC). Allotype. Same as holotype (1 female, NMPC). Paratypes: Bulgaria, Blagoevgrad region, Pirin Mts, between Ribno Ezero and Gorno Ezero, left side brook of Vasilashki Potok, 41°44'26.3"N, 23°26'51.7"E, 2191 m, 12.IX.2016, leg. P. Juhász, T. Kovács, G. Szilágyi (2 females, OPC).

Diagnosis and description. The hump on the apical margin of the paraproct, that is the only recognised paraproct divergence between *D. chrysotus* and *D. romaicus* complexes, is less pronounced. The lateral profile of the fused dorsal branches of paraproct has the rounded flat top low, sloping anterad, differing from the lateral configuration of the other three species. The subapical spines, that is the true terminal of the paramere shaft long and without any basal structures;

the apparent terminalia of modified setal origin is long and thick. This paramere pattern differs from the paramere patterns of the other three species.

Female description. Female genitalia. Tergite of segment IX forming long tube, open ventrally, with short V-shaped mesal excision; lateral lobes triangular in dorsal view; the lateral setose lobe of sternite IX rounded. Segment X membranous and embedded inside segment IX and encircling anus; supragenital plate of segment X well-developed elongated quadrangular with somehow bipartite concave apical margin in lateral view. Lobes of vulvar scale short, median lobe of the vulvar scale (lower vaginal lip) present, robust and half as long as the lateral lobes. Dorsal profile of the vaginal sclerite complex rounded.

Etymology. Named after the locus typicus.

Drusus romanicus **Murgoci & Botosaneanu, 1954**

(Figures 570–588)

Drusus romanicus Murgoci & Botosaneanu, 1954: 967–972. „Masivul Retezat: circa 30 de exemplare (♂♂ et ♀♀) in regiunea izvoarelor lacurilor Bucura, Galesul, Stinisoara, Pietrela (Peste 2000 m altitudine) (leg. Botosaneanu, 1950–1952. Masivul Bucegi: 1 exemplar ♂ si 1 exemplar ♀ in Valea Casariei, in iunie 1951, la circa 900 m altitude."

Drusus transylvanicus Schmid,1956: 27–28. "Holotype ♂: Retyezat (Transylvanie), déposé au musée de Budapest.
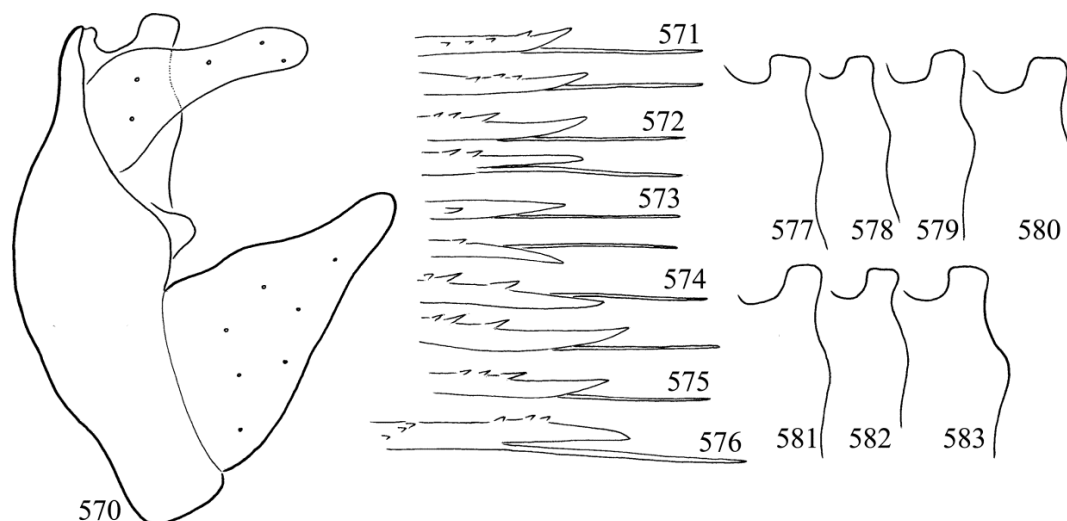
Figures 570–583. *Drusus romanicus* Murgoci & Botosaneanu ,1954. 570 = male genitalia in left lateral view. Parameres in left lateral view from various mountain ranges in the Southern Carpathians: 571 = Retezat, 572 = Fagaras, 573 = Lotru, 574 = Pareng, 575 = Cibin, 576 = Bucegi. Dorsal branches of paraproct in lateral view from various mountain ranges in the Southern Carpathians: 577 = Bucegi, 578 = Fagaras, 579 = Pareng, 580 = Lotru, 581 = Cibin, 582 = Retezat, 583 = Banat.
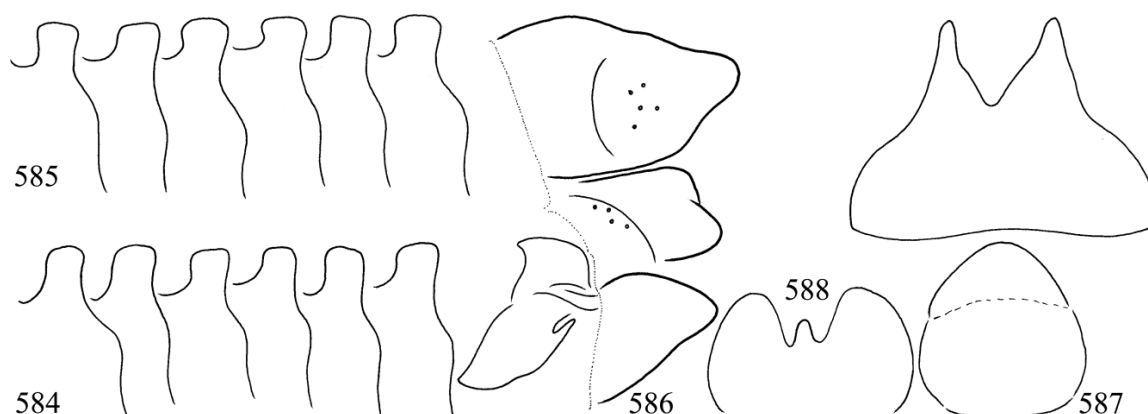
Figures 584–588. *Drusus romanicus* Murgoci & Botosaneanu, 1954. 584 = infrapopulation variability of the dorsal branches of paraproct in a population from the Pareng Mts. 585 = infrapopulation variability of the dorsal branches of paraproct in a population from the Lotru Mts. 586 = female genitalia with vaginal sclerite complex in left lateral view, 587 = tergite IX and dorsal profile of vaginal sclerite complex in dorsal view, 588 = vulvar scale in ventral view.

Dr. transylvanicus est très voisin de *romanicus* et surtout de *chapmani*; il s'en distingue principalement par la forme de ses appendices intermédiaires et supérieurs."

Drusus romanicus Murgoci & Botosaneanu, 1954: Botosaneanu 1967: 300, *Drusus transylvanicus* has been synonymized with *Drusus romanicus*.

Material examined. The original description was based on specimens collected in the Retezat and Bucegi Mts. We have devoted rather significant field effort to recollect specimens from the Bucegi Mts. with very meager result (Table 1.). **Romania**, Muntii Banatului, Poiana Mărului, L. Botosaneanu (1 male, OPC). Retezat Mts., Bucura stream, 150m below Bucura lake, 2015m, N45°21'25.43" E22°52'31.09" 10.VII.2013, light trap, leg. E. Bajka, Cs. Balogh, G. Borics, P. Borics, (4 males, 1 female; OPC). Retezat Mts., Bucura stream, below Bucura lake, 2070 m, N45°21'27.872", E22°52'28.695" 8.VIII.2015, light leg. J. Kecskés, & Zs. Pap (1 female, OPC). Retezat Mts., Bucura stream, below Bucura lake, 2070 m, N45°21'27.872", E22°52'28,695" 8.VIII.2015, singled leg. J. Kecskés, & Zs. Pap (2 males, 2 females; OPC). Cibin Mts. Crăciuneasa, Râul Mare, N45°40'22", E23°51'53" 9–10.VI.2010, leg. C. Ciubuc (1 male, CPC). Lotru Mts, Obârşia Lotrului, 1578 m, N45.463°, E23.620°, 4.VII.2007, leg. N. K. Nagy & M. Bálint(1 male, OPC). Romania, Lotru Mts, Obârşia Lotrului,

1578 m, N45.463°, E23.620°, 29.VI.2016, singled leg. J. Oláh & J. Oláh jr. (2 males, OPC). Romania, Lotru Mts, Obârşia Lotrului, 1578 m, N45.463°, E23.620°, 30.VI.2016, swarming after rain, singled leg. J. Oláh & J. Oláh jr. (19 males, 2 females; OPC). Parâng Mts, Gâlcescu Lake, 1935 m, N45.35°, E23.61°, 4.VII.2007, M. Bálint (1 male, OPC). Romania, Vâlcea county, Parâng Mts, Obrâşia Lotrului, open spring area, 500 m along Transalpina (67C) road, downstream from N45°22'27.7", E23°39'4.0", 1915 m, 30.VI.2016, leg. J. Oláh & J. Oláh jr. (13 males, 1 female; OPC). Argeş county, Făgăraş Mts, Căpăţânenii Ungureni, sidebrook of Capra Stream along road No.7C, N45°35.185', E24°37.691' 1705 m, 29.VIII.2012 leg. T. Kovács, D. Murányi, J. Oláh (1 male, OPC). Romania, Dambovița county, Southern Carpathians, Bucegi Mountains, Brătei stream valley, Negru stream, N45.383283°, E25.350528° 14.VII.2016 leg. Z. Baczo & J. Kecskés (1 male, 1 female; OPC).

Diagnosis. Murgoci & Botosaneanu 1954: 971, "In conclusie, cele mai importante caractere permitind diferentierea speciei *D. romanicus* n. sp., de toate celelalte descrise, sint urmatoarele: ♂ - forma trapezoidala a ariei spinigere pe tergitul abdominal VIII (observate dorsal); - aspectul apendicelor preanale (privite lateral), - structura picioarelor genitale si mai ales a regiunii lor mediana si ventrale; - forma titilatorilor."

Additional diagnosis. The hump on the apical margin of the paraproct, that is the only recognised paraproct divergence between *D. chrysotus* and *D. romanicus* complexes, is less pronounced. The lateral profile of the fused dorsal branches of paraproct has the flat top, similar to *D. discolor*, differing from the lateral configuration of the other three species. This flat or convex flat head profile of the speciation trait is rather stable in interpopulations of the sampled mountain ranges and stable also in infrapopulations of the Lotru and Paring Mts. The subapical spines, that is the true terminal of the paramere shaft long and with several small tertiary spines scattered randomly; the apparent terminalia of modified setal origin is short and thin. This paramere pattern differs from the paramere patterns of the other three species.

Female description. Female genitalia. Tergite of segment IX forming long tube, open ventrally, with deep V-shaped mesal excision; lateral lobes long triangular in dorsal view; the lateral setose lobe of sternite IX rounded. Segment X membranous and embedded inside segment IX and encircling anus; supragenital plate of segment X well-developed elongated quadrangular with

somehow bipartite concave apical margin in lateral view. Lobes of vulvar scale short, median lobe of the vulvar scale (lower vaginal lip) present, small and less than half as long as the lateral lobes. Dorsal profile of the vaginal sclerite complex rounded.

Drusus siveci species complex

The *Drusus siveci* species complex has the dorsoapical fused dorsal branches of paraproct produced into an elongated digitiform slender process in lateral view, accompanied by medium sized periphallic organs of cerci and gonopods. Here we describe this new incipient species complex with four new sibling species distributed in mountain ranges of the Dinara Mountains and in the northern Apennines. The divergences of the species is realised and recognised in the subtle configurations in the shape of the speciation trait of the paraproct. That is the fused dorsal branches of paraproct modified into various dorsoapical digitiform processes best visible in lateral view (Figs. 589–593).

Most of these mountain ranges are not surveyed with adequate and targeted collecting effort. There are possibly many more uncollected and undetected new species in isolated mountain ranges belonging to this complex. It was not surprising to us that the *Drusus siveci* complex evolved similarly rapidly, subtly and stably by speciation trait of paraproct and diverged in allopatry under sexual selection and integrated into local adaptations. However, we have sampled almost exclusively mixed populations of *D. fortos* sp. nov. and *D. vekon* sp. nov. probably in secondary sympatry and with hybrids of reinforcement in the contact zones and clines. These crenon area in Kosovo offer an excellent ground for in vivo studies of the speciation processes with reinforcement. This species complex is comprised of five species: *fortos* sp. nov., *puskasi* sp. nov., *siveci*, *fabbrii* sp. nov., *vekon* sp. nov.

Drusus fortos Ibrahimi & Oláh, sp. nov.

(Figures 594–599)

Material examined. Holotype: **Kosovo**: Çakor, streamlet along the border line between Kosovo and Montenegro. 42.685542°N, 20.053636°E, 1289 m, 25.VIII.2015 leg. E.
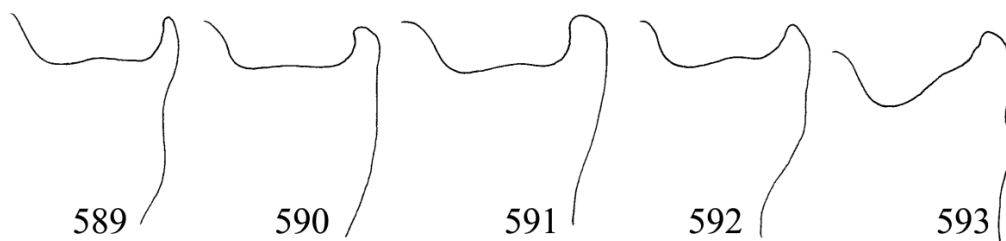
Figures 589–593. Comparative table of paraprocts of sibling species in *Drusus siveci* species complex at higher magnification in lateral view: 589 = *vekon*, 590 = *siveci*, 591 = *fabbrii*, 592 = *fortos*, 593 = *puskasi*.
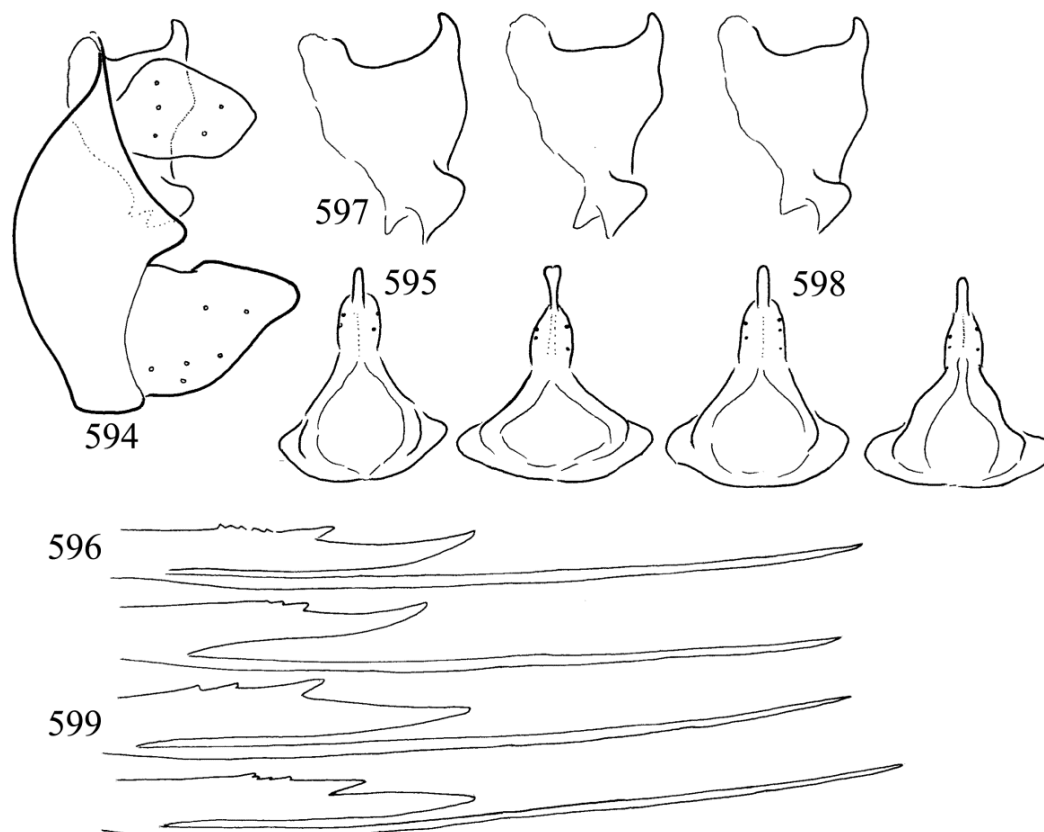
Figures 594–599. *Drusus fortos* Ibrahimi & Oláh, sp. nov. Holotype: 594 = male genitalia in left lateral view, 595 = paraproct in caudal view, 596 = paramere in left lateral view. Paratypes: 597 = paraproct in lateral view, 598 = paraproct in caudal view 599 = paramere in left lateral view.

Dimitrou & V. Dragobia (1 male, DBFMNSUP). Allotype: Lloqan, Krojet e Gucise, 42.55143°N, 20.1335°E, 2110 m, 3. VIII.2016, leg. H. Ibrahimi (1 female, DBFMNSUP). Paratypes: same as holotype (1 male hybrid, OPC). Haxhaj, spring area of a tributary of Lumbardhii Pejës River, 42°42'30N, 20°2'32E, 1278 m, 25.VIII.2015 leg. E. Dimitrou & V. Dragobia (1 male, OPC). Lloqan, Gurrat e Hasan Agës springs, Bjeshkët e Nemuna. 42.557155°N, 20.152696°E 1991 m, 18.VIII.2015 leg. H. Ibrahimi (1 male, DBFMNSUP). Lloqan, Gurrat e Hasan Agës springs, Bjeshkët e Nemuna. 42.557155°N, 20.152696°E, 1991 m, 3.

VIII.2016, leg. H. Ibrahimi (3 males DBFMNSUP). Lloqan, Krojet e Gucise, 42.55143°N, 20.1335°E, 2110 m, 3.VIII.2016, leg. H. Ibrahimi (2 males OPC).

Diagnosis and description. The lateral profile of the fused dorsal branches of paraproct has short dorsoapical digitiform process with medium thickness, most similar to name bearing species *D. siveci*, but differs by having variously produced hump on the apical margin of the paraproct,

completely lacking at *D. siveci*; by the slightly anterad turning and tapering apex of the fused digitiform dorsoapical process, vertical and not tapering at *D. siveci*; and the very tip of the fused dorsal branches of the paraproct is entirely fused into a narrow and straight pencil-like black process without any mesal suture, that is the vestigium of the fusion surface completely disappeared as visible in caudal view, the tip is bilobed and the mesal suture is discernible both at *D.siveci* and at *D. vekon* sp. nov. The subapical spine of the paramere is robust bearing small dorsal spine or corrugations. In the sampled habitats *D. fortos* sp. nov. lives together with *D. vekon* sp. nov. with hybrid forms.

Etymology. „fortos", from „összeforrt", fused in Hungarian, refers to the completely fused state of the dorsoapical digitiform process of the paraproct.

Drusus puskasi Oláh & Ibrahimi, sp. nov.

(Figures 600–604)

Material examined. Holotype: **Bosnia & Herzegovina**: Republika Srpska, Foča, Sutjeska NP, Zelengora Mts, S of village Govza, brooks and outlets of Bijelo jezero, 1420 m, N43.380°, E18.584°, netting, leg. G. Puskás & G. Szövényi 8.VIII.2014 (1 male, OPC). Paratypes: same as holotype (1 male DBFMNSUP; 3 males, OPC).

Diagnosis and description. The lateral profile of the fused dorsal branches of paraproct has short, stout and slightly anterad turning dorsoapical digitiform process, most similar to the name bearing species *D. siveci*, but differs by having small hump on the apical margin of the paraproct; by the anterad turning and tapering apex of the fused digitiform dorsoapical process; by the very tip that is hardly bilobed just the mesal suture is discernible. The subapical spine of the paramere is short robust, not long and bearing additional variously shaped small spine-like formation on middle dorsum. The periphallic organ of gonopod is elongated compared to *D. siveci*.

Etymology. We have dedicated this species to the collector Gellért Puskás, who collects adult and juvenile Orthoptera on dry highlands, but devoted to visit crenon area to collect caddisflies.
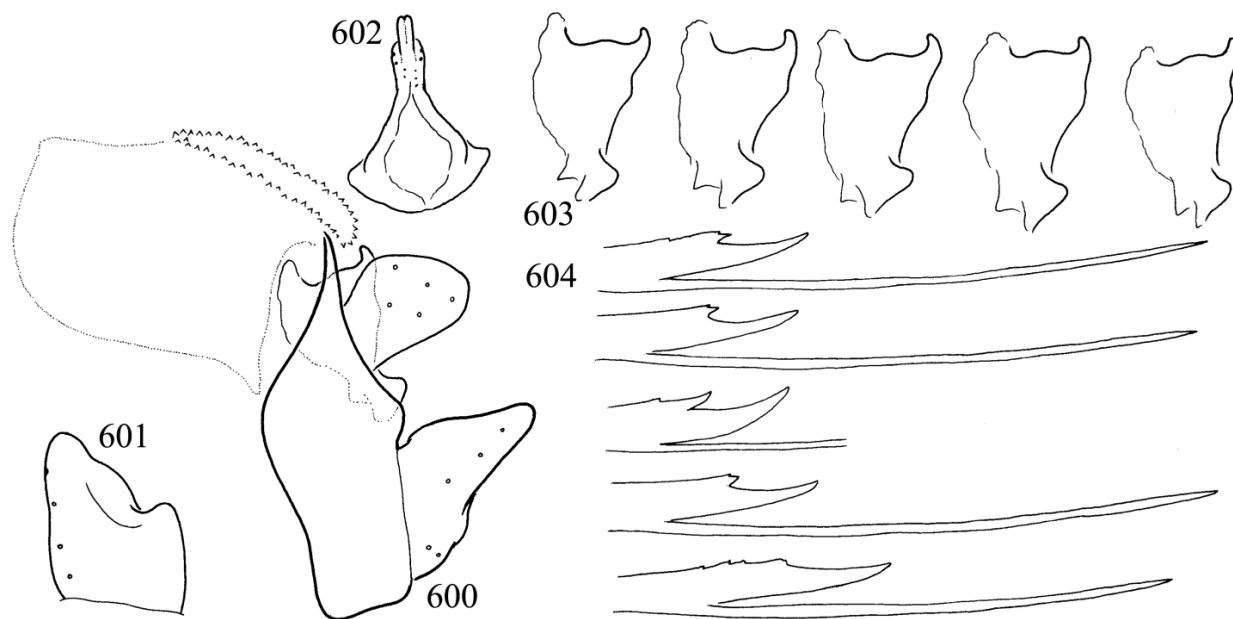
Figures 600–604. *Drusus puskasi* Oláh & Ibrahimi, sp. nov. Holotype: 600 = male genitalia in left lateral view, 601 = left gonopod in ventral view, 602 = paraproct in caudal view. Paratypes: 603 = paraproct in lateral view, 604 = paramere (holotype upper) in left lateral view.

Drusus siveci **Malicky, 1981**

(Figures 605–607)

Drusus siveci Malicky, 1981: 343–344. "Holotypus ♂: Crna Gora, Snjili Potok stream, Andrijevica, 25.V.1979, leg. Sivec, coll. Malicky."

Material examined. Holotype: Crna Gora (**Montenegro**), Snjili Potok stream, Andrijevica, 25.V. 979, leg. Sivec, coll. Malicky. Received on loan from the Malicky's collection.

Diagnosis. Malicky 1981: 343–344, "Diese Art gehört in die Verwandtschaft von *Drusus croaticus*, Marinkovic, 1971, *Drusus macedonicus* Schmid, 1956, *Drusus improvisus* McLachlan, 1884, *Drusus biguttatus* Pictet, 1834, und anderen."

Additional diagnosis. The lateral profile of the fused dorsal branches of paraproct has short and stout dorsoapical digitiform process with medium thickness, most similar to *D. fortos*, but differs by having no produced hump on the apical margin of the paraproct, the apical margin is straigh vertical; by the upward turning and not tapering apex of the fused digitiform dorsoapical process; by the very tip that is bilobed and the mesal suture is discernible. The subapical spine of the paramere is robust bearing only some small corrugations
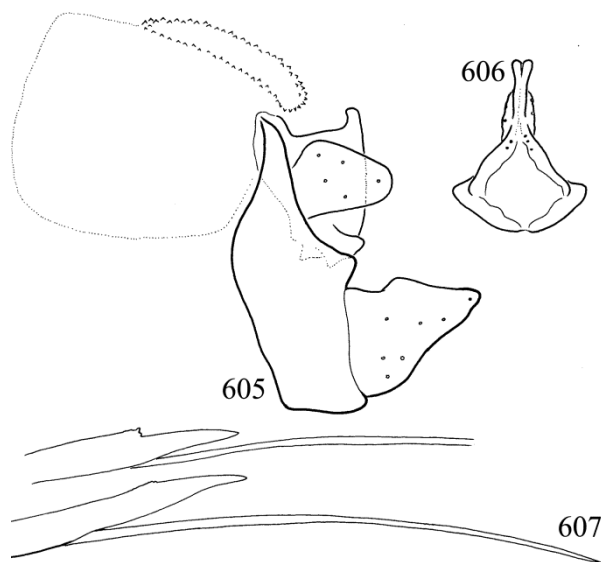
Figures 605–607. *Drusus siveci* Malicky, 1981. Holotype: 605 = male genitalia in left lateral view, 606 = paraproct in caudal view, 607 = parameres in left lateral view.

dorsad. There is slight asymmetry between the parameres. This name bearing species is described and known only from the single male of the holotype.

Drusus fabbrii **Oláh, sp. nov.**

(Figures 608–612)

Material examined. Holotype: Italy, Emilia Romagna, Corniglio (PR) Bosco Lagdei, torrente Parma di Francia; 15.VII.1999 leg. R. Fabbri (1 male, MCSNBG). Paratypes: same as holotype (35 males, MCSNBG; 1 male, OPC).

Diagnosis and description. The lateral profile of the fused dorsal branches of paraproct has dorsoapical digitiform process enlarged, robust, stout and anterad turning, resembling to *D. puskasi* sp. nov., but differs by having no any hump on the apical margin of the paraproct; by the robust anterad turning apex of the fused digitiform dorsoapical process. The subapical spine of the paramere is long and low, armed with a few very tiny tertiary spines nested in small groups subbasad, not robust, not short and bearing no additional variously shaped spine-like formation on middle dorsum. The periphallic organ of gonopod is elongated similar to *D. puskasi* sp. nov.

Etymology. Dedicated to Roberto Fabbri, the renowned Italian entomologist, who has collected all the specimens of this new species.

Drusus vekon **Ibrahimi & Oláh, sp. nov.**

(Figures 613–618)

Material examined. Holotype: **Kosovo**: Çakor, streamlet along the border line between Kosovo and Montenegro. 42.685542°N, 20.053636°E, 1289 m, 25.VIII.2015 leg. E. Dimitrou & V. Dragobia (1 male, DBFMNSUP). Allotype: Lloqan, Gurrat e Hasan Agës springs, Bjeshkët e Nemuna. 42.557155°N, 20.152696°E, 1991 m, 3.VIII.2016, leg. H. Ibrahimi (1 female, DBFMNSUP). Paratypes: same as holotype (1 male, 1 female; DBFMNSUP; 1 male hybrid, OPC). Haxhaj, spring area of a tributary of Lumbardhii Pejës River, 42°42'30N, 20°2'32E, 1278 m, 25.VIII.2015 leg. E. Dimitrou & V. Dragobia (1 male, OPC). Lloqan, Gurrat e Hasan Agës springs, Bjeshkët e Nemuna. 42.557155°N, 20.152696°E, 1991 m, 18.VIII.2015 leg. H. Ibrahimi (2 males, DBFMNSUP, 1 male, OPC). Lloqan, Gurrat e Hasan Agës springs, Bjeshkët e Nemuna. 42.557155°N, 20.152696°E, 1991 m, 3.VIII.2016, leg. H. Ibrahimi (3 males OPC). Lloqan, Krojet e Gucise, 42.55143°N, 20.1335°E,

2110 m, 3. VIII.2016, leg. H. Ibrahimi (3 DBFMNSUP). Lloqan, Gurrat e Hasan Agës springs, Bjeshkët e Nemuna. 42.557155°N, 20.152696°E, 1991 m, 3.VIII.2016, leg. H. Ibrahimi (1 female, OPC). Lloqan, Krojet e Gucise, 42.55143°N, 20.1335°E, 2110 m, 3. VIII.2016, leg. H. Ibrahimi (1 female, DBFMNSUP).

Diagnosis and description. The lateral profile of the fused dorsal branches of paraproct has long and slender dorsoapical digitiform process, most similar to *D. fortos* sp. nov., but differs by the anterad turning slender, long and tapering apex of the fused digitiform dorsoapical process, and the very tip of the fused dorsal branches of the paraproct is not completely fused, the tip is bilobed and the mesal suture is discernible that is the vestigium of the fusion surface present and visible in caudal view, The subapical spine of the paramere long and robust and frequently more complex, than the subapical spine of *D. fortos*. In the sampled habitats *D. vekon* sp. nov. lives together with *D. fortos* sp. nov. with hybrid forms.

Etymology. „vekon",from „vékony", thin in Hungarian, refers to the slender dorsoapical digitiform process of the paraproct.

Drusus monticola species group

The *Drusus monticola* species group is integrated through ancestral divergence by multidivision of the single subapical spine into a single spine bunch composed of various numbers and various shapes of smaller spines. The species group comprised of three species groups and seventeen species. The delineation of the species complexes in the species group is based on paraproct shape divergenses.

(1) *Drusus balcanicus* species complex has dorsal branch of the paraproct with vertical hump shaped apical arms of slightly diverging forms in lateral view; laterad enlarged plates of diverged forms in caudal view;

(2) *Drusus destitutus* species complex has dorsal branch of the paraproct with apicad directed long rod shaped apical arms in lateral view; fused or diverged apex in caudal view;

(3) *Drusus monticola* species complex has dorsal branch of paraproct with enlarged round apical arms in lateral view; mesally touching broad plates in caudal view.
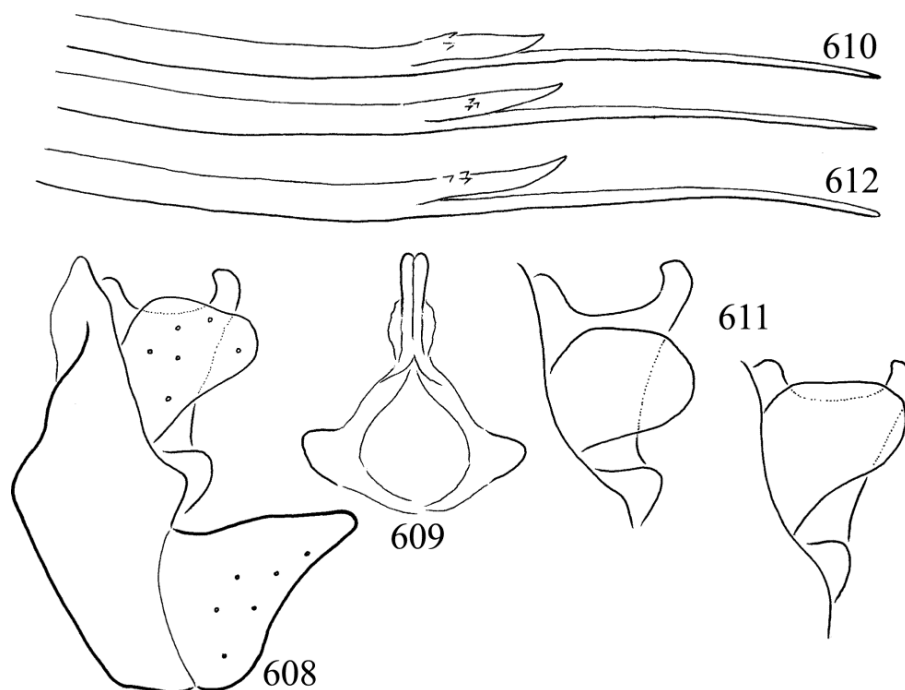
Figures 608–612. *Drusus fabbrii* Oláh, sp. nov. Holotype: 608 = male genitalia in left lateral view, 609 = paraproct in caudal view, 610 = parameres in left lateral view. Paratypes: 611 = cerci and paraproct in left lateral view, 612 = parameres in left lateral view.
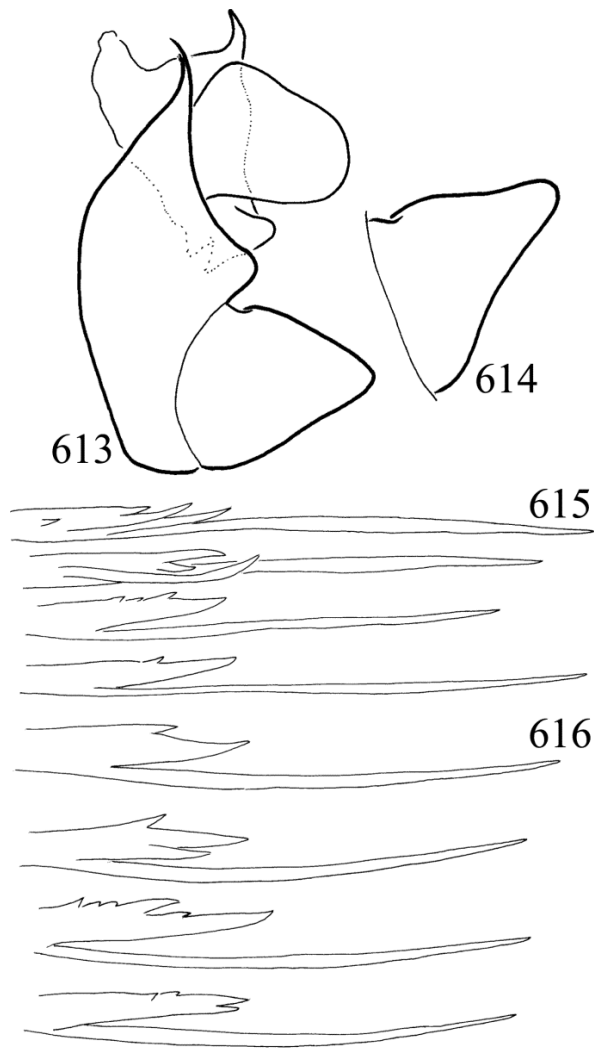
Figures 613–616. *Drusus vekon* Ibrahimi & Oláh, sp. nov. Holotype: 613 = male genitalia in left lateral view, 614 = paratype gonopod in left lateral view, 615 = parameres in left lateral view. Paratypes: 616 = parameres in left lateral view.

Drusus balcanicus species complex

Drusus balcanicus species complex has dorsal branch of the paraproct with variously formatted vertical hump shaped apical arms of slightly diverging forms in lateral view, laterad enlarged plates of diverged forms in caudal view. This species complex comprised of ten species: *balcanicus, bureschi, concolor, dardanicus, discophoroides, osogovicus, pallidus, rhodopeus, tovises* sp. nov., *Drusus* sp.

Drusus balcanicus Kumanski, 1973

(Figures 619–622)

Drusus discophorus Radovanovic, 1942: Kumanski 1971: 102. "Stara Planina, below "Tdza" (1500 m), 17.V. 1968, leg. P. Beron (3♂, 1♀)." Misidentification!
Drusus discophorus balcanicus Kumanski, 1973: 113–114. „Die Fundorte der neuen subspecies befinden in dem Zentral-Balkangebirge: Berghütte „Taza" (1500 m Höhe), 17.V.1968, 3♂ und 1♀; Bach bei der Berghütte „Raj", 1♀ und subalpiner Bach (1900-2000 m Höhe), rechter Zufluss des Baches Taza, 10.VI.1971, massenhaft anzutreffen (insgesamt 43♂ und 10♀ gesammelt."
Drusus discophorus balcanicus Kumanski, 1973: Kumanski & Malicky 1976: 104. Stara Planina, Teteven, Beli Vit, Ribariza und Nebenbache, 600 m, 15–18.V.1969, 1 male. Stara Planina, Trojan Pass, Einzugsgebiet des Tscherni Osam, 1400–1600 m, 20.V.1969, 2 females.
Drusus balcanicus Kumanski, 1973. Kumanski 1981: 142. Raised to species rank.

Material examined. Holotype and allotype: **Bulgaria**, Zentral Balkangebirge, subalpiner Bach (1900–2000 m Höhe), rechter Zufluss des Baches Tazha, 10.VI.1971. (1 male, 1 female; NNHM).

Diagnosis. Kumanski 1973: 113–114: "In allgemeinen Linien nach dem Bau von *D. discophorus discophorus* konstruiert."

Additional diagnosis. Based upon the ancestral divergence of the paramere pattern *D. balcanicus* has no close relation to *D. discophorus* of the *D. bosnicus* group.

Drusus bureschi Kumanski, 1973

(Figures 623–626)

Drusus bureschi Kumanski, 1973: 114–117. „Material und Fundorte: Östliche Balkangebirge, a) Eleno-Twardischki-Pass (1000 m Höhe), 25.V. 969, 1♂ (leg. Al. Popov); b) Langs eines kleinen Berbaches, 4 km östlich vom Pass und c) Bei einem ungestümen Bergbach, am Beginn des Twardischka-Baches (eines Zuflusses der Tundza), ungefähr 10 km östlich von Pass, 12.VI.1971, ingesamt 3♂ und 4♀; d) Balkangebirge bei der Stadt Sliwen, Örtlichkeit Karandilja, 21.V.1969, 1♂ (leg. Al. Popov). Als Typusexemplar bezeichnete ich ein ♂ von Fundort c). Dasselbe sowie auch die übrigen Exemplare sin din Alkohol in der Sammlung des Zoologischen Instituts mit Museum bei der Bulgarischen Akademie der Wissenschaften aufbewahrt."
Drusus bureschi Kumanski, 1973: Kumanski 1975: 63. Stara Planina, Sliven, 4.VII.1911, 1 male. Below Raj, Basmandra, 1800 m, 22.VIII.1970, 32 female.
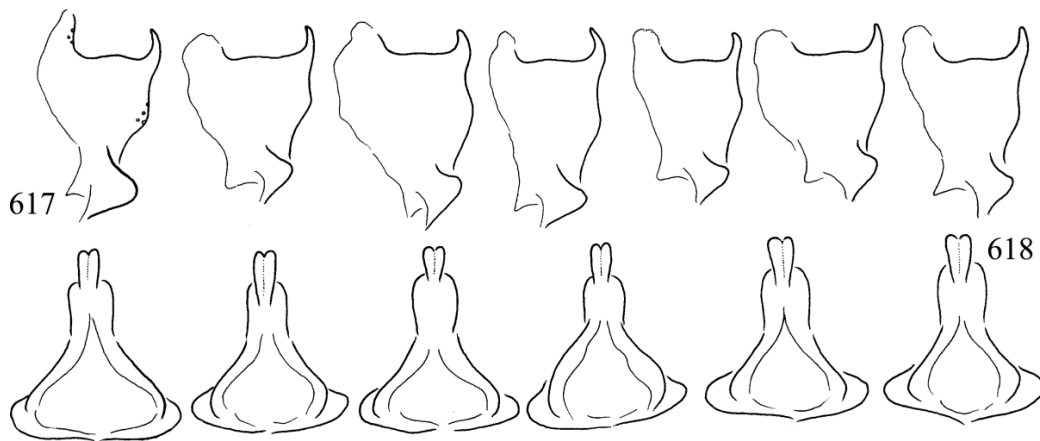
Figures 617–618. *Drusus vekon* Ibrahimi & Oláh, sp. nov. Paratypes: 617 = paraprocts in left lateral view, 618 = paraprocts in caudal view.
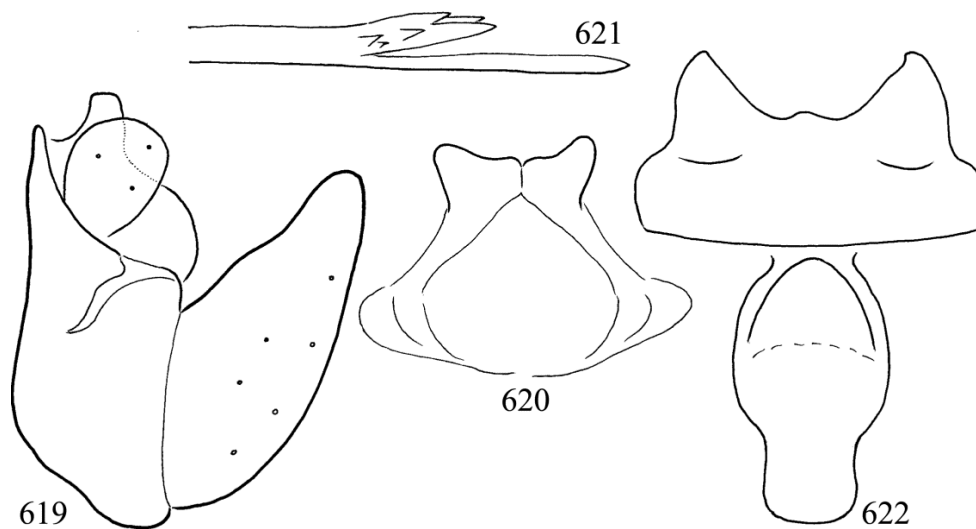
Figures 619–622. *Drusus balcanicus* Kumanski, 1973. 619 = male genitalia in left lateral view, 620 = paraproct in caudal view, 621 = paramere in left lateral view, 622 = tergite IX and dorsal profile of vaginal sclerite complex in dorsal view.

Drusus bureschi Kumanski, 1973: Kumanski & Malicky 1976: 105. Stara Planina, Sliven, Oberlauf der Stara Reka, 500–800 m, 22.V.1969, 1 male. Stara Planina, Sliven, Tundscha-Einzugsgebiet mit Nebenbachen, 300–600 m, 23.V.1969, 1 male.

Material examined. Holotype and Allotype: **Bulgaria**, Bei einem ungestümen Bergbach, am Beginn des Twardischka-Baches (eines Zuflusses der Tundza), ungefahr 10 km östlich von Pass, 12.VI.1971, leg. Al. Popov (male, female; NNHM)

Diagnosis. Kumanski, 1973: 114–117, "Nach vielen ihrer Merkmale steht die neue Art *D. discophorus* ziemlich nahe; letztere galt als eine in dem Rahmen der Gattung isolierte Art (Schmid 1956). Die Auffindung ihrer Unterart *balcanicus* in den Balkangebirgen sowie auch das Antreffen von *D. bureschi* erlaubt die Vereinigung der drei Taxa in eine neue Gruppe – die Gruppe von *discophorus*."

Additional diagnosis. Based upon the ancestral divergence of the paramere pattern *D. bureschi* has no close relation to *D. discophorus* of the *D. bosnicus* group.
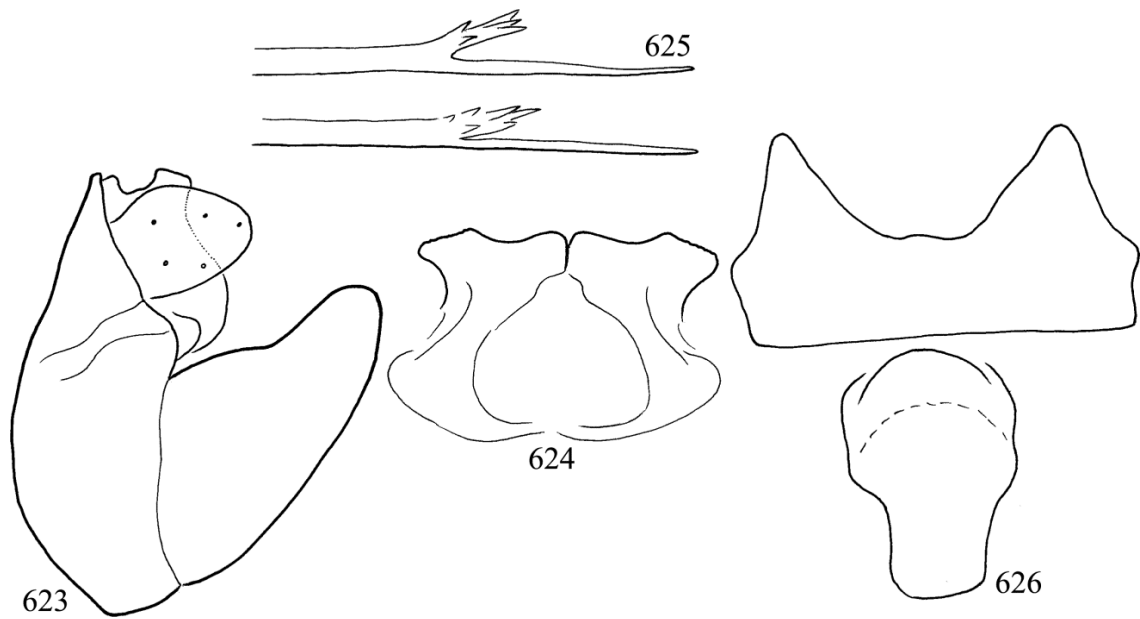
Figures 623–626. *Drusus bureschi* Kumanski, 1973. 623 = male genitalia in left lateral view, 624 = paraproct in caudal view, 625 = paramere in left lateral view, 626 = tergite IX and dorsal profile of vaginal sclerite complex in dorsal view.
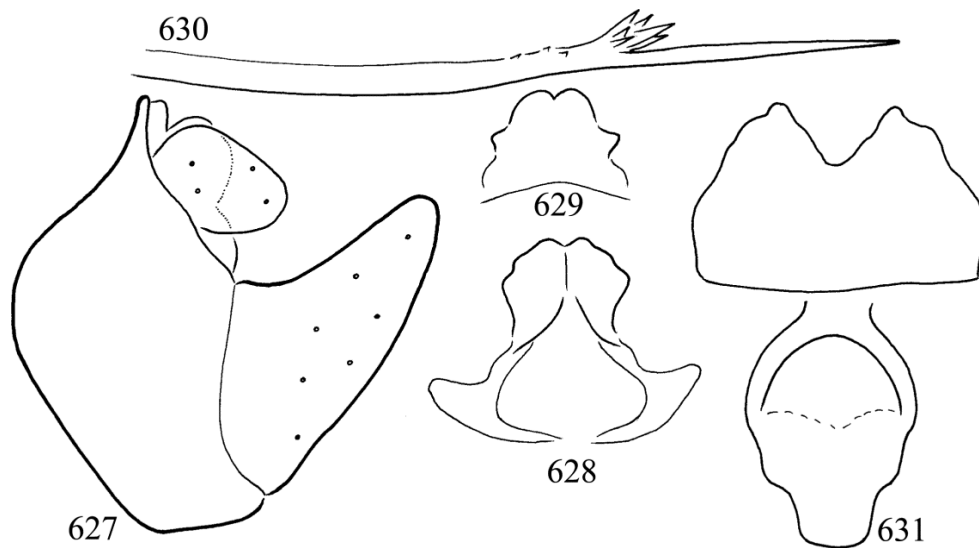
Figures 627–631. *Drusus concolor* Kempny, 1908. 627 = male genitalia in left lateral view, 628 = paraproct in caudal view, 629 = apical arms of the dorsal branches of paraproct in dorsal view, 630 = paramere in left lateral view, 631 = tergite IX and dorsal profile of vaginal sclerite complex in dorsal view.

Drusus concolor Kempny, 1908

(Figures 627–631)

Drusus concolor Kempny, 1908: 268–270. "Kleinasien, Keschisch Dagh, 2.000 m."

Drusus concolor Kempny, 1908: Schmid 1959: 799.: " J'ai étudié le type de cette espèce, actuellement déposé au Musée de Vienne. Cet exemplaire n'est autre qu'un *Monocentra lepidoptera* Ramb. Fortement décoloré et dont les ailes posterieures ont perdu leurs écailles. Il y a quelques différences dans les génitalia entre cet insecte et

les individus italiens que j'ai examinés, mais elles ne sauraient servir de base à une distinction spécifique."

Drusus concolor Kempny, 1908: Malicky 1988: 65–68. "According to the holotype, *Drusus concolor* Kempny, 1908 is not a synonym of *Monocentra lepidoptera* Rambur, 1842 as stated by Schmid (1959) but a good species of *Drusus*."

Material examined. **Turkey**, Uludag TR39, 7 km NW Sogukpinar, 40°03'N, 29°11'E, 4.VI.1992. leg. H. Malicky (1 male, 1 female; OPC).

Diagnosis. Kempny 1908: 268–270, "Diese neue Art gehört zur Gruppe des *Dr. monticola* McLachlan und steht dem *Dr. bosnicus* Klapálek am naschsten."

Additional diagnosis. Schmid (1956) has synonymised with *Monocentra lepidoptera*, but Malicky reconfirmed its species status. Based upon the ancestral divergence of the paramere pattern *D. concolor* has no close relation to *D. lepidopterus* of the *D. bosnicus* group.

Drusus dardanicus Ibrahimi, Kucinic & Vitecek, 2015

(Figures 632–634)

Drusus dardanicus Ibrahimi, Kucinic & Vitecek, 2015, in Ibrahimi *et al.* 2015: 558–561. "Type material. Holotype (1 male) and paratypes (2 males): Kosovo: Podujeve Municipality, Shatorice Mountains, stream above Bollosice Village, 1330 m a.s.l., 43.118169°N, 20.99330°E, 11.V. 2014, leg Halil Ibrahimi. Holotype deposited in the department of Biology, Faculty of Mathematics and Natural Sciences, University of Prishtina "Hasan Prishtina", Prishtine, Republic of Kosovo. Paratype (3 males): Same collection and locality data, deposited in the Croatian Natural History Museum, Zagreb (coll. Kucinic-Trichoptera), Croatia. Paratypes (3 males): Same collection and locality data, deposited in the Biologiezentrum des Oberösterreichischen Landesmuseum, Linz, Austria; specimen identifiers for 2 males: fDsp4301M, fDsp4302M."

Material examined. **Kosovo**: Podujeve Municipality, Shatorice Mountain, stream above Bollosice Village, 43.118169°N, 20.8271°E, 850 m, 13.VII.2016, leg. H. Ibrahimi (1 male, OPC).

Diagnosis. Ibrahimi *et al.* 2015: 558, "Males of the new species are most similar to *Drusus discophorus*, *D. bureschi*, and *D. balcanicus*."

Additional diagnosis. Based upon the ancestral divergence of the paramere pattern *D. dardanicus* has no close relation to *D. discophorus* of the *D. bosnicus* group.
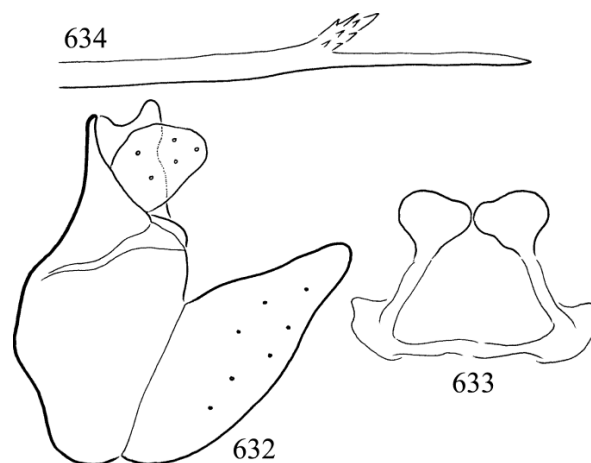
Figures 632–634. *Drusus dardanicus* Ibrahimi, Kucinic & Vitecek, 2015. 632 = male genitalia in left lateral view, 633 = paraproct in caudal view, 634 = paramere in left lateral view.

Drusus discophoroides Kumanski, 1979

(Figures 635–640)

Drusus discophoroides Kumanski, 1979: 67–69. "Material and locality. Belassitza Mt. (South-Western Bulgaria), brooklet 1.5 km western from the mountain hostel "Belassitza" (750 m a.s.l.), 10.VI.1975, 2♂♂ (leg. Kumanski). Holotype ♂ and 1♂ paratype in the author's collection in the National Natural Histoty Museum Sofia."

Material examined. Holotype and paratype: **Bulgaria**, Belassitza Mt. (South-Western Bulgária), brooklet 1.5 km western from the mountain hostel "Belassitza" (750 m a.s.l.), 10. VI. 1975, leg. K. Kumanski (2 males, NNHM). Bulgaria, Blagoevgrad region, Belassica Mts, Petrič, sping of Lesniska Stream SW of the city, N41°21.021', E23°10.767', 1025 m, 5.V.2014, T. Kovács, D. Murányi (20 males, 7 females; OPC).

Diagnosis. Kumanski 1979: 67–69. "*D. discophoroides* n. sp. is near to *D. discophorus* Rad. Both species have common plan of ♂ genitalia. This notwithstanding they can easily be distinguished both after the darker general colour of the new species and several details of the male genitalia: the upper appendages of *D. discopho-*
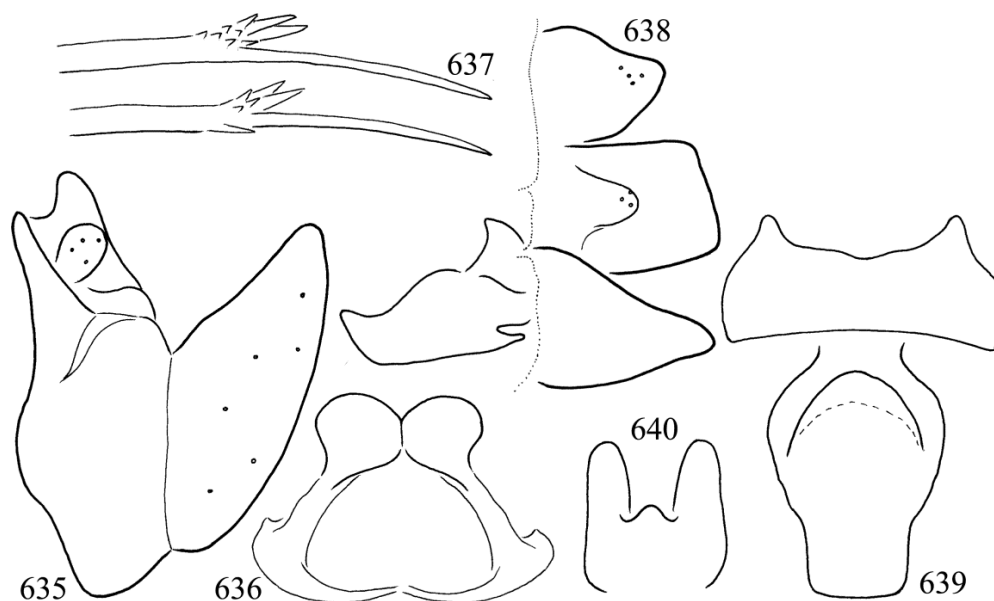
Figures 635–637. *Drusus discophoroides* Kumanski, 1979. 635 = male genitalia in left lateral view, 636 = paraproct in caudal view, 637 = paramere in left lateral view, 638 = female genitalia with vaginal sclerite complex in left lateral view, 639 = tergite IX and dorsal profile of vaginal sclerite complex in dorsal view, 640 = vulvar scale in ventral view.

roides n. sp. are so small that the intermediate appendages remain wholly visible from the side; in *D. discophorus* the latter almost invisible; the upper margin of the intermediate appendages rounded in the new species and formed as an undulate horizontal line in discophorus; the perianal region oval rounded (*discophorpides* n. sp.) or with nearly straight side borders (*discophorus*).″

Additional diagnosis. Based upon the ancestral divergence of the paramere pattern *D. discophoroides* has no close relation to *D. discophorus* of the *D. bosnicus* group.

Drusus osogovicus Kumanski, 1980

(Figures 641–644)

Drusus osogovicus Kumanski, 1980: 204–205. „Holotype ♂ and 4 Paratypes (2♂♂ and 2♀♀): Osogovska Mt. (SW Bulgaria), hostel „Osogovo", 1640 m a.s.l., 18–19.VI. 1979, (leg. J. Ganev, at light), in the National Natural History Museum, Sofia."

Material examined. Holotype ♂ and 4 Paratypes (2♂♂ and 2♀♀): **Bulgaria**, Ossogovska Mt. (SW Bulgaria), hostel „Osogovo", 1640 m a.s.l., 18-19.VI.1979, (leg. J. Ganev, at light), in the National Museum of Natural History, Sofia. Bulgaria, Kyustendil province, Ossogovska planina, spruce forest brook below Trite buki hut, 42°10'27.78"N, 22°38'3.96"E, 5.VII.2016, leg. K. Harmos, T. Kovács & G. Magos (2 females, OPC).

Diagnosis. Kumanski 1980: 204–205, "*Dr. osogovicus* n. sp. belongs to the group of *discophorus*, being in general one of the dark coloured species there. The contrast between the yellow thoracic sclerites scutum and scutellum on one hand and the darker rest of the insect on the other is one of its characteristics; thus, the darkest species in the group, *Dr. discophoroides* Kum., as well as the dark coloured population of *Dr. discophorus* Rad. found in the Rhodops are monotonous. The extremely narrow spinulate zone of 8th tergite and the turned inwards position of the superior appendages are the main diagnostic features of the male. As to the female, its genitalia are very similar to those of *Dr. balcanicus* Kum. and the coloration remains its most distinctive feature."

Additional diagnosis. Based upon the ancestral divergence of the paramere pattern *D. osogovicus* has no close relation to *D. discophorus* of the *D. bosnicus* group.
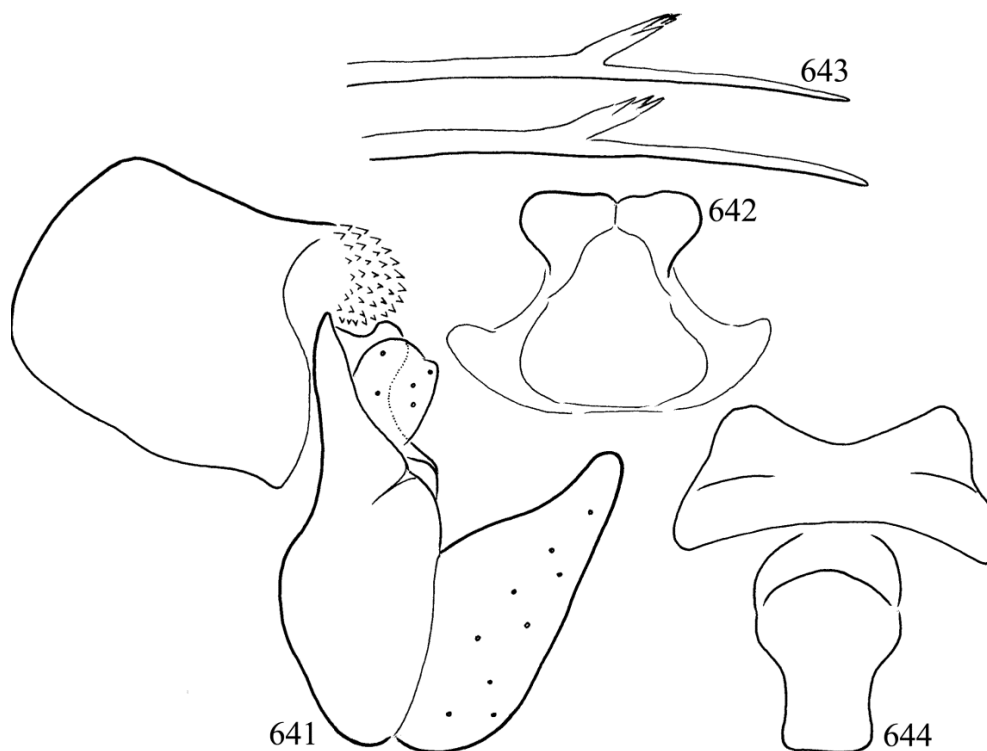
Figures 641–644. *Drusus osogovicus* Kumanski, 1980. 641 = male genitalia in left lateral view, 642 = paraproct in caudal view, 643 = paramere in left lateral view, 644 = tergite IX and dorsal profile of vaginal sclerite complex in dorsal view.

Drusus pallidus **Kumanski, 1988 stat. nov.**

(Figures 645–648)

Drusus rectus McLachlan, 1868: 295. "Pyrenees (Rev. T. A. Marshall), 1♂." Klapálek 1913: 16. "Jezero pod Musallou, 31.VII.2♂, neobycejne malé kusy, majici v rozpeti 16 mm." P. Chvojka'translation: "Lake below Musala Mt., remarkably small specimens, wing-span 16 mm)." Musala is in the alpine zone of the Rila Mts. Misidentification!

Drusus rectus rectus McLachlan, 1868: Schmid 1956: 61. established *D. rectus rectus* and *D. rectus nigrorectus* subspecies and considered Klapálek's record from Bulgaria as probably a mistake.

Drusus discophorus Radovanovic, 1942: Botosaneanu & Sykora 1963: 22–24. Revised and drawn Klapálek's specimen from Rila Mts. and compared with Schmid drawings of *Drusus discophorus*. Misidentification!

Drusus discophorus Kumanski, 1979: 68. Misidentification!

Drusus discophorus pallidus Kumanski, 1989: 19–20. "Holotype chosen among males of a large sample (20♂ and 5♀) from the Rila Mountains, the Lower Elensko Lake (*ca*. 2300 m alt.), 31.VII.1965, leg. A. Popov. The holotype and a large series of paratypes (altogether 50♂ and 25♀) from 20 localities in the three above mentioned mountains (Pirin, Rila, Vitosha) is kept in the collection of the National Museum of Natural History, Sofia"

Material examined. **Bulgaria**: Rila, Mesta basin, side-brook of the Stream Ropalica below the Grănčar mountain hut, 2100m, 7.IX.2005, leg. D. Murányi (1 male, HNHM). Rila, Maritza basin, spring of Stream Prava Maritza below Mt. Zavračitza, 2518m, N42°09'38.8", E23°37'16.2", 8.IX. 2005, leg. D. Murányi (1 male, HNHM). Sofia Region, Rila Mts, Borovetz resort, sidetorrent of Prava Maritza Stream beneath Zavračitza hut, 2030 m, N42°10.652', E23°38.438', 13.VIII.2005, leg. D. Murányi (2 males, HNHM). Vitosha Mts., Kladnitsa, Sv. Nikola, Tanchovitsa, N42°34'02.9", E23°11'41.4", 1100 m, 3.X.2011, light, leg. Á. Ecsedi, T. Kovács, G. Puskás, (1♂, OPC).

Diagnosis. Kumanski 1989: 19, "Rather small insects, very variable in size; length of forewing (♂,♀) 5.5–9.0 mm. Coloration pale-yellow to yellow-brownish, in general much lighter than in the other subspecies (*D. discophorus rhodopaeus*).

Additional diagnosis. We have found *D. pallidus* restricted to the Vitosha and Rila Mts. Specimens from the Pirin Mts. represent a new sibling species: *Drusus tovises* sp. nov.
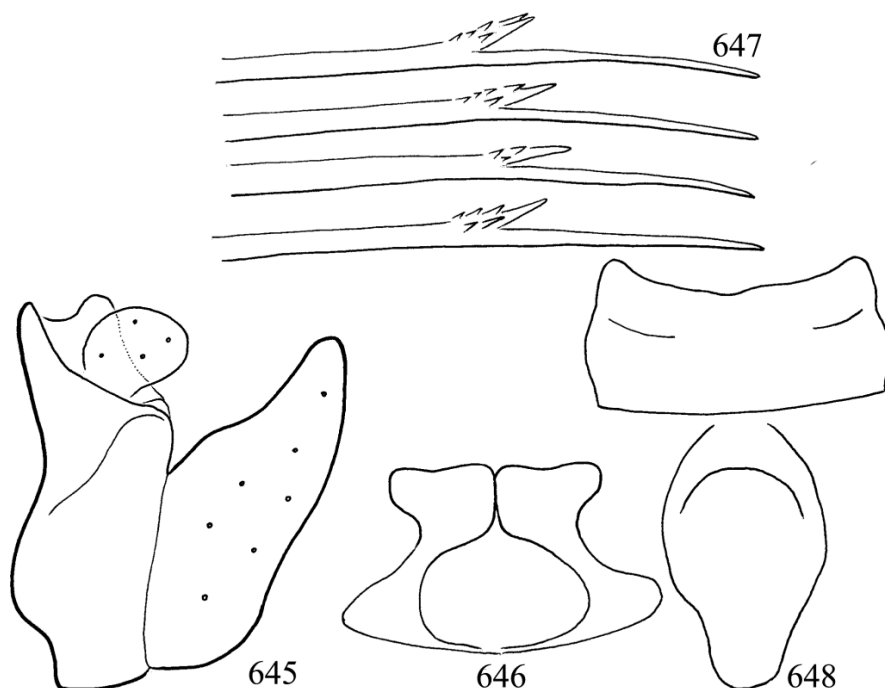
Figures 645–648. *Drusus pallidus* Kumanski, 1988. 645 = male genitalia in left lateral view, 646 = paraproct in caudal view, 647 = paramere in left lateral view, 648 = tergite IX and dorsal profile of vaginal sclerite complex in dorsal view.

Drusus rhodopeus **Kumanski, 1989 stat. nov.**

(Figures 649–655)

Drusus discophorus Rad. ssp. ? Kumanski & Malicky 1976: 104. "Die Tiere aus dem Rhodopen unterscheiden sich insofern leicht von der namenstypischen Form, als sie deutlich dunkler gefarbt sind. Da aber in den Kopulationsarmaturen keine Unteschiede zu finden sind und auch die geographische Isolation von den anderen Populationen nicht sehr ausgepragt ist, verzichten wir darauf, dieser Form einen eigenen Namen zu geben. Es sei aber immerhin auf den Sachverhalt hingewiesen"

Drusus discophorus rhodopeus Kumanski, 1989: 20. "Holotype ♂ and a couple (♂ and ♀) of paratypes (streamlets in the vicinity of the mountain hut "Erkyupriya", 1300–1700 m, 26.V.1969, leg. D. Braasch) in the collection of the National Museum of Natural History, Sofia; 1♂ paratype (same region, 1.–2.IX.1971, leg. D. Braasch) and 1♀ paratype (River Shirokolashka, upper stream, 1200-1600 m, 21.-31. VIII. 1971, leg D. Braasch) in coll. Malicky, Lunz am See, Austria".

Material examined. Holotype and allotype. **Bulgaria**, Rhodope Mts. Einzugsgebiet der Sabardska Reka inkl. Nebenbachen, bei der Hütte Ekuprija, 1300–1700 m, 26.V. 1969. leg. D. Braasch (Holotype male, allotype female, paratype male; NNHM).

Diagnosis. Kumanski 1989: 20. "Also small insects, but less variable than *D. d. pallidus* ssp. nov.; forewing length (♂,♀) 7.5–9.5 mm. General coloration rather fuscous. Except for the smaller size, the new subspecies is morphologically less different from the nominate form than *D. d. pallidus*. Its main distinctive feature remains the geographic isolation of the population."

Additional diagnosis. Close to *D. pallidus* and *D. tovises* sp. nov. but differs by the shape of paraproct both in lateral and caudal view.

Female description. Genitalia. Tergite of segment IX forming short tube, open ventrally, with wide V-shaped mesal excision and triangular apical margin of the lateral lobes in dorsal view; the lateral setose lobe of sternite IX rounded elongate and continuing into setaless less pigmented downward section. Segment X membranous and embedded inside segment IX and encircling anus; supragenital plate of segment X well-developed and quadrangular in lateral view with produced ventroapical corner. Dorsal profile of the vaginal sclerite complex narrowing anterad.
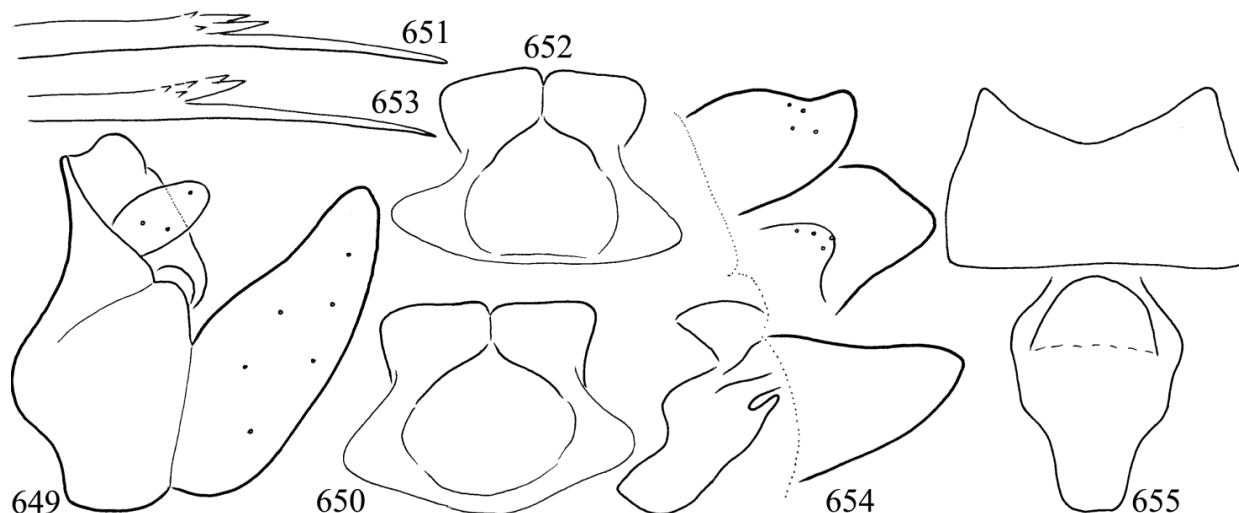
Figures 649–655. *Drusus rhodopeus* Kumanski, 1989. Holotype: 649 = male genitalia in left lateral view, 650 = paraproct in caudal view, 651 = paramere in left lateral view. Paratype: 652 = paraproct in caudal view, 653 = paramere in left lateral view. Allotype: 654 = female genitalia with vaginal sclerite complex in left lateral view, 655 = tergite IX and dorsal profile of vaginal sclerite complex in dorsal view.

Drusus tovises Olah & Chvojka, sp. nov.

(Figures 656–661)

Material examined. Holotype: **Bulgaria**, Blagoevgrad Region, Pirin Mt, left side brook of Vasilashki Potok, N41° 44'32.08", E23°26'24.45", 3.VII.2016, leg. K. Harmos, T. Kovács & G. Magos (1 male, OPC). Allotype: same as holotype (1 female, OPC). Paratypes: same as holotype (10 males, 1 femle; OPC). Bulgaria, Blagoevgrad Region, Pirin Mt, Bansko – Demianitsa hut, left side stream of Demianitsa Reka, 2.VII.2016, leg. K. Harmos, T. Kovács & G. Magos (4 males, OPC). Bulgaria, Blagoevgrad Region, Pirin Mt, Bansko – Demianitsa hut, left side brook of Demianitsa Reka, N41°46'15.3", E23°27'44.3", 3.VII.2016, leg. K. Harmos, T. Kovács & G. Magos (3 males, OPC). Bulgaria, Pirin Mts., Bela Reka stream (1800–1900 m), 19.IX.1990, leg. P. Chvojka (26 males, 31 females, NMPC; 6 males, 6 females; OPC).

Diagnosis and description. This new species is widely distributed in the crenon and hypocrenon habitats of high elevations in the Pirin Mts. A sibling species of *D. pallidus* and *D. rhodopeus*, but differs from both species by the shape of paraproct; the apical arms of the dorsal branches of the paraproct is slightly anterad angled, not rounded blunt of *D. rhodopeus* or simple hump of *D. pallidus* in lateral view; in caudal view the apical arms are very low with concave dorsum, not very high of *D. pallidus* or high with staright dorsum of D. rhodopeus.

Female description. Genitalia. Tergite of segment IX forming short tube, open ventrally, with very sallow mesal excision and low apical margin of the lateral lobes in dorsal view; the lateral setose lobe of sternite IX large, rounded elongate and continuing into setaless less pigmented downward section. Segment X membranous and embedded inside segment IX and encircling anus; supragenital plate of segment X well-developed and regular quadrangular in lateral view. Dorsal profile of the vaginal sclerite complex very long and narrowing anterad.

Etymology. „*tovises*",from „tövises", spiny in Hungarian, refers to the paramere with subapical spine bunch of many spines as well as to the paramere shaft anterad of the subapical spine bunch covered with numerous tertiary spines.

Drusus sp.

(Figures 662–672)

Material examined. **Serbia**, Sveti Nikola, 27. VI. 2016, leg. A. Bilalli & H. Ibrahimi (1 male, OPC). Serbia, Mosul, Besna Kobila, 28. VI. 2016, leg. A. Bilalli & H. Ibrahimi (1 male, OPC).
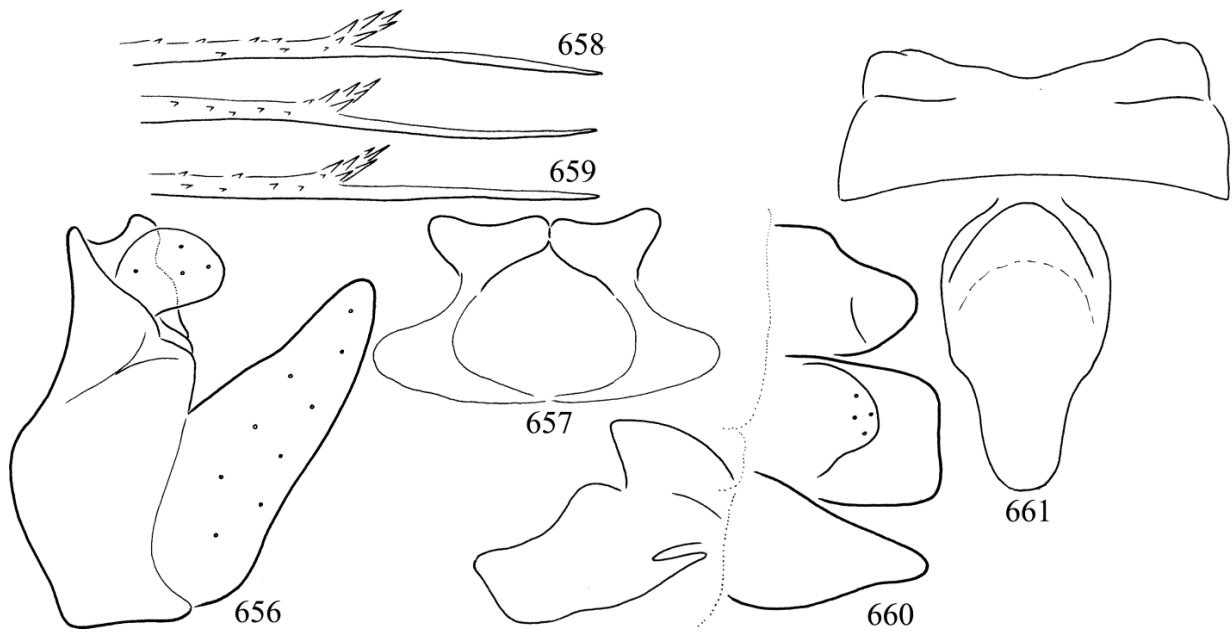
Figures 656–661. *Drusus tovises* Oláh & Chvojka, sp. nov. Holotype: 656 = male genitalia in left lateral view, 657 = paraproct in caudal view, 658 = paramere in left lateral view. Paratype: 659 = paramere in left lateral view. Allotype: 660 = female genitalia with vaginal sclerite complex in left lateral view, 661 = tergite IX and dorsal profile of vaginal sclerite complex in dorsal view.
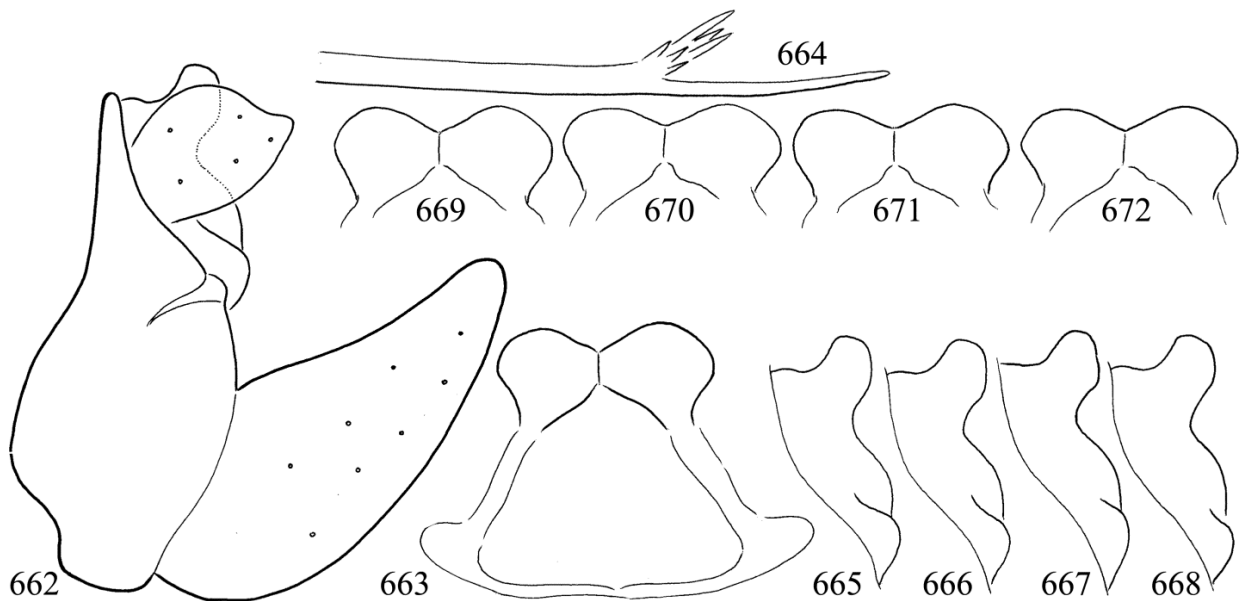
Figures 662–672. *Drusus* sp. 662 = male genitalia in left lateral view, 663 = paraproct in caudal view, 664 = paramere in left lateral view. 665–672 = Combined effect of redrawings and the inevitable and unovoidable slight drawing plane alterations on paraproct figures of *Drusus* sp. in lateral and caudal views. A visual demonstration of variability range of drawing procedure produced by subjective capability

Diagnosis. This species is most close to *Drusus osogovicus*, but distingushed by having the apical arms of the dorsal branches of paraproct differently shaped both in lateral and caudal view. In lateral view the arms are longer and less anterad angled, in caudal view higher and the dorsum is with wide V-shaped excision. At *D. osogovicus* the arms are shorter and more angled anterad in lateral view as well as lower and almost straight horisontal, not excised mesally in caudal view. Here we realised a repeated redrawings of the same paraproct, both in lateral and caudal view, with slight drawing plane alterations to demonstrate its effect on variability ranges of the prepared drawings including subjectivity effect of each redrawing. The species is under description by the collector, Halil Ibrahimi from Kosovo.

Drusus destitutus species complex

Drusus destitutus species complex has dorsal branch of the paraproct with apicad directed long rod shaped apical arms in lateral view; fused or diverged apex in caudal view. The sibling pair of *D. destitutus* and *D. croaticus* has fused dorsal arms in lateral view; *D. melanchaetes* and *D. kronion* has diverging dorsal arms of paraproct. This species complex comprised of four species: *croaticus*, *destitutus*, *kronion*, *melanchaetes*.

Drusus croaticus Marinkovic, 1971

(Figures 673–676)

Drusus croaticus Marinkovic, 1971: 105–107. „Source of river Črna Reka, Plitvice, 30 m, 1 f, 13.V.1971.”

Material examined. Yugoslavia, Plitvice, 14.IX.1997 (1 male, loan from Malicky Private Collection).

Diagnosis. Marinkovic 1971: 107, „*Drusus croaticus* is, probably, a member of the group *discolor* according to the form of intermediate appendages, which are the most similar to those of *D. macedonicus* and *D. transylvanicus*.”

Additional diagnosis. Based upon the ancestral divergence of the paramere pattern *D. croaticus* has no close relation to any member of the *Drusus discolor* species group. Neither to *D. macedonicus*

of the *D. macedonicus* copmlex or to *D. romanicus* (*transylvanicus*) of the *D. romanicus* species complex. *Drusus croaticus* is a very close relative, a sibling of *D. destitutus*. Both species has fused apical arms of the dorsal branches of the paraproct.
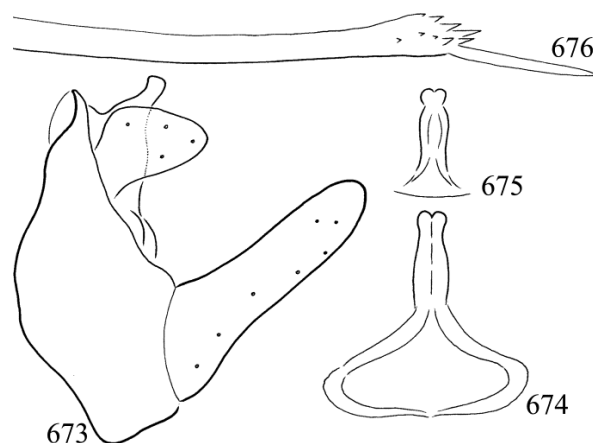
Figures 673–676. *Drusus croaticus* Marinkovic, 1971. 673 = male genitalia in left lateral view, 674 = paraproct in caudal view, 675 = apical arms of the dorsal branches of paraproct in dorsal view, 676 = paramere in left lateral view.

Drusus destitutus Kolenati, 1848

(Figures 677–680)

Stathmorphorus destitutus Kolenati, 1848: 60–61. "Habitat in Silesia, Elberfeld (Cornelius!)."

Halesus adustus McLachlan, 1867: 52–53. "Stelzing in Kärnthen, Juli (Zeller), 1♂."

Drusus destitutus (Kolenati, 1848): McLachlan 1876: 170–171. "I have only one ♂ from Carinthia (Stelzing, Zeller, in July). Kolenati records his *S. destitutus* from Silesia, and also from Elberfeld (Cornelius). I am informed by Brauer that the type in the Vienna Museum is specifically identified with my *H. adustus*, notwithstanding the obvious generic misplacement of the former. He also says that it occurs among Kolenati's types of *Hal. nigricornis* (vide ante p. 156)."

Drusus destitutus (Kolenati, 1848): Schmid 1956: 24. "Cette espèce est rare; elle a été signalée de Carinthie, de Silésie, d'Elberfeld et de Schwabhausen. Je ne la connais que par un dessin que m'a aimablement communiqué M. D. E. Kimmins."

Halesus adustus McLachlan, 1867: Fisher 1967: 175. A synonym of *Drusus destitutus* Kolenati.

Drusus destitutus (Kolenati ,1848): Malicky 2007: 51. "Die Situation is also: *Drusus destitutus* (Kolenati, 1848), species incerta, nec *Drusus destitutus* auctt. *Drusus adustus*
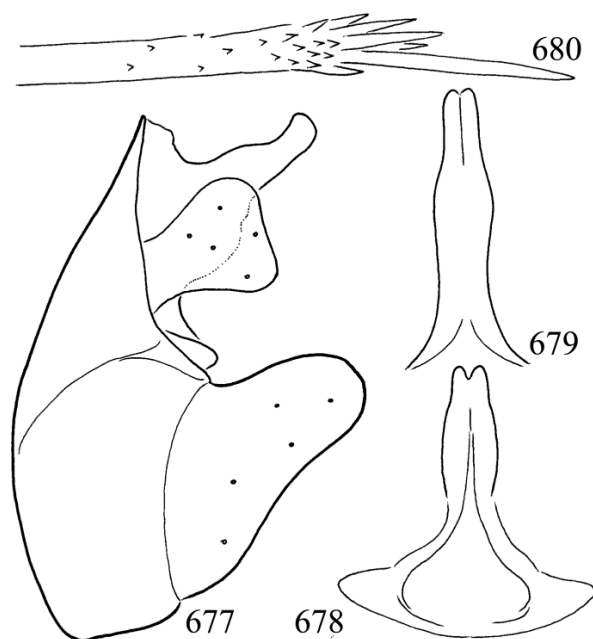
Figures 677–680. *Drusus destitutus* Kolenati, 1848. 677 = male genitalia in left lateral view, 678 = paraproct in caudal view, 679 = apical arms of the dorsal branches of paraproct in dorsal view, 680 = paramere in left lateral view.

(McLachlan 1867) = *Drusus destitutus* auctt." Opposite is right! *Drusus destitutus* has very distinct, very specific and easy to recognise characters! Brauer's determination is more reliable as accepted also by McLachlan than the location data of some old specimens. Similarly as we have documented the unreliability of old collecting data for *Chaetopteryx rugulosa*'s locus typicus established by commercial insect dealers (Oláh *et al.* 2015). *D. destitutus* in Silesia? We have to accept the conclusion of McLachlan (1876), Fischer (1967) and Schmid (1956) that *Drusus adustus* is a junior synonym of *Drusus destitutus*!

Material examined. **Austria**, Carinthia, Soboth, presented by W. Graf (1 male, OPC).

Diagnosis. Kolenati 1848: 60, "Nigro-fuscus, capite antice bituberculato, antennis nigro-fuscis, femoribus supra dimidium fuscis, palpis tibiisque testaceis, his nigro-spinosis, abdomine nigro-fusco, ad latera vitta rufa, tegminibus fusco-testaceis, nervis nigro-, interstitiis luteo-pilosis, thyridio et arculo obsolete albido, alis fusco-hyalinis, nervis fusco-testaceis, areola apicali quinta et in alis basi angustata."

McLachlan 1867: 53, "Diese Species steht *H. chrysotus* Rambur nahe, unterscheidet sich aber durch ihre viel dunklere Farbung und die Form der Appendices."

Schmid 1956: 25: "*Dr. destitutus* se reconnait facilement à ses appendices intermédiaires tres allongés et proéminents; il se place dans la groupe de *discolor*, mais est très nettement distinct des deux autres espèces."

Additional diagnosis. Based upon the ancestral divergence of the paramere pattern *D. destitutus* has no close relation to any member of the *Drusus discolor* species group, including *D. chrysotus*. *Drusus destitutus* is a very close relative, a sibling of *D. croaticus*. Both species has fused apical arms of the dorsal branches of the paraproct.

Drusus kronion Malicky, 2002

(Figures 681–685)

Drusus kronion Malicky, 2002: 6–7. Holotypus ♂: Frankreich, Isère, Chamrousse, Forsthaus Prémol, 1500 m, 45°07'N, 5°51'E, 10.VI.1986, leg. G. Vincon."

Material examined. **France**, Department Isére, Alpes, La Combe-de-Lancey, ru Combe Lancey le Grand Journal, 23. V.2015, leg. G. Coppa & J. Barnasson (2 males, OPC). Department Isére, Alpes, Sainte-Agnès, Ruisseau de Vorz le Chenevrey, 23.V.2015, leg. G. Coppa & J. Barnasson (2 females, OPC). Department Isére, Alpes, La Combe-de-Lancey, ru Combe Lancey le Grand Journal, 25.V.2015, leg. G. Coppa & J. Barnasson (1 female, OPC).

Diagnosis. Malicky 2002: 7, "Nach der auffallenden Form der mittleren und unteren Anhange steht diese Art ziemlich isoliert. Anlich lange, aber schlankere mittlere Anhange hat *Drusus alpinus* Meyer-Dür, 1875, bei dem aber die oberen Anhange viel grösser und die unteren Anhange in Lateralansicht spitz sind."

Additional diagnosis. Based upon the ancestral divergence of the paramere pattern *D. kronion* has no close relation to any member of the *Drusus alpinus* species group. It belongs to *D. monticola* species group, *D. destitutus* species complex and close to *D. melanchaetes*.
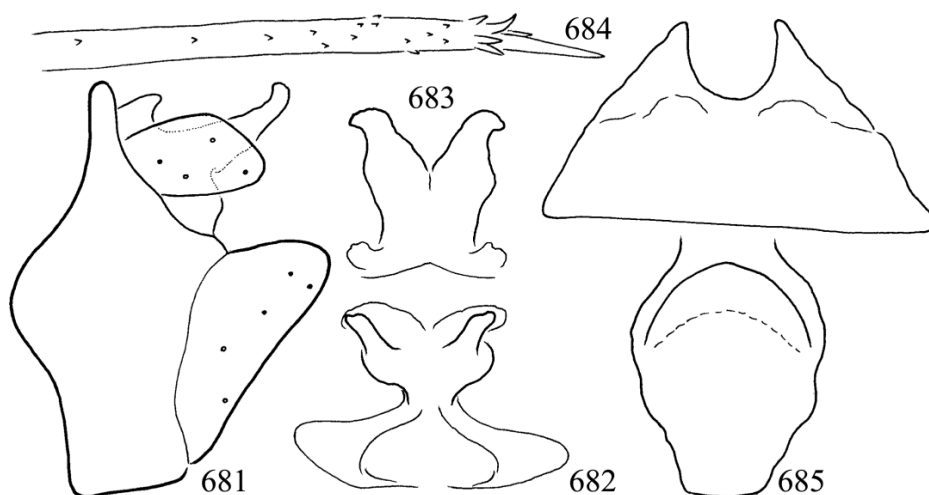
Figures 681–685. *Drusus kronion* Malicky, 2002. 681 = male genitalia in left lateral view, 682 = paraproct in caudal view, 683 = apical arms of the dorsal branches of paraproct in dorsal view, 684 = paramere in left lateral view, 685 = tergite IX and dorsal profile of vaginal sclerite complex in dorsal view.
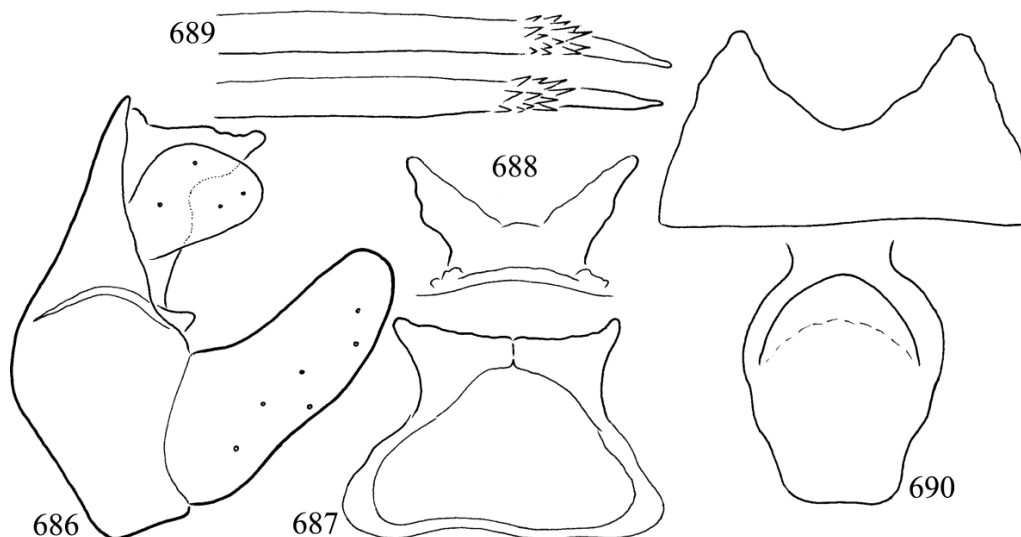
Figures 686–690. *Drusus melanchaetes* McLachlan, 1876. 686 = male genitalia in left lateral view, 687 = paraproct in caudal view, 688 = apical arms of the dorsal branches of paraproct in dorsal view, 689 = parameres in left lateral view, 690 = tergite IX and dorsal profile of vaginal sclerite complex in dorsal view.

Drusus melanchaetes McLachlan, 1876

(Figures 686–690)

Drusus melanchaetes McLachlan, 1876: 177.: „Switzerland (Gotthard, July, Frey-Gessner; Monte Rosa, Saudinger; Furca, Stainton;Ticino, Bremi; in Hagen's collection). Tyrol (Seefeld, Eaton)."

Material examined. **Italy**, Bergamo, Valbondione, effluente Lago Gelt, 2550 m, 15.VII.2003, leg. Calandrina (5 males, 5 females; OPC). Sondrio, Chiesa in Valmalenco, Val Ventina, 1900 m, 6.VII.1995, leg. Fabbri (4 female, MCSNBG). **France**: Department of Savoie**,** Bonneval-sur-Arc, source Lenta, 14.VII.2007, leg. G. Coppa (2 males, 2 females; OPC). Italy,

Diagnosis. McLachlan 1876: 177, „Very similar to *D. nigrescens*. The males of this and *nigrescens* can be immediately separated by the anal parts; in the females these parts are less widely

distinct, but still differ, and the shorter discoidal cell of *Melanchaetes* is a good character."

Schmid 1956: 55, „Systematiquement, *Dr. melanchaetes* est une forme isolée, caractérisée par la proéminence et la longueur des appendices inferieurs et par ses appendices intermediaires en forme de deux fines pointes divergentes. A cause de la forme de ces derniers, je le classe entre le groupe de *mixtus* et *Dr. cantabricus* n. sp."

Waringer *et al.* 2008: Based on larval morphology *D. melanchaetes* was demonstrated as most close to *D. destitutus*.

Additional diagnosis. Based upon the ancestral divergence of the paramere pattern *D. melanchaetes* has no close relation to any member of the *Drusus mixtus* species group. It belongs to *D. monticola* species group, *D. destitutus* species complex and close to *D. kronion*.

Drusus monticola species complex

Drusus monticola species complex has dorsal branch of paraproct with enlarged round apical arms in lateral view; mesally touching broad plates in caudal view. This species complex comprised of three species: *monticola*, *neltel* sp. nov., *nigrescens*. However, we have recorded divergences both in the lateral and dorsal profiles of the paraproct between the sampled Italian (Bolzano), Slovakian (Tatra Mts.) and Romanian (Maramures Mts.) populations. More sampling is required to establish their real taxonomic status.

Drusus monticola McLachlan, 1876

(Figures 691–707)

Drusus monticola McLachlan, 1876: 174–175. "Switzerland (Bergün, July, Zeller), Tyrol (Seefeld, Eaton), Noric Alps (Gross Glockner, in Stein's collection; Nassfeld, beginning of August, Palmén, in Helsingfors Museum). I have seen only a single example from each locality."

Material examined. **Austria**, Vorarlberg, Rappensee, 1. VII.1976, leg. Mende (3 males, 2 females; OPC). Kärnten, Glochner Gruppe, Pasterzen Kees, 2400 m, 28–30.VII.2006, leg. Morin, (1 male, MFSNU). **Czechoslovakia**, High Tatra, Zelené Lake, 6.VII.1982, leg. Nagy (1 male, 1 female; OPC). **Italy**, Bolzano, Moso in Passiria, Monteneve, 2500 m, 11. VII.1990, leg. Ghilardi, M. Valle (1 male, MCSNBG).

Bolzano, Moso in Passiria, Ponte segheria, 1600 m, 19.VI. 1993, leg M. Valle (1 female, MCSNBG). Bolzano, Moso in Passiria, dintorni Rifugio Monteneve, 20.VI.1993, leg. M. Valle (3 males MCSNBG). **Romania**: Maramureş county, Maramureş Mts. Borşa-Băile, Borşa, Stanchii spring, N47°40.762', E24°52.624', 1644 m; 22.V.2007 leg. Cs. Csuzdi, L. Dányi, J. Kontschán, & D. Murányi (2 males, 1 female, NHMB). **Slovakia**. N. Slovakia, High Tatras, Zelené Lake, 6.VII.1982, leg. Nagy (1 male, 1 female; OPC). N. Slovakia, West Tatras, pools above Rohácsky vodopad waterfall, 1.VII.1992, leg. P. Chvojka (4 males, 2 females; OPC). N. Slovakia, High Tatras, Mlynická dolina valley, Volie pliesko pool, 3.VII.1989, leg. P. Chvojka (2 males, 2 females; OPC). N. Slovakia, High Tatras, Javorinka stream, (1520 m), 2. VI. 1989, leg. P. Chvojka (3 males, 1 female; NMPC).

Diagnosis. McLachlan 1876: 175, "In its anal parts this species bears some considerable resemblance to *D. nigrescens*, but is very distinct in its larger size, very elongate wings, still longer discoidal cell, and fuliginous (instead of shining black) coloration of these wings."

Additional diagnosis. Close to *D. nigrescens*, but wing coloration is brown, not shining black, but in alcohol preserved specimens the colour contrast is not so pronounced. Among the examined populations the specimens from Romania exhibit shape divergences in the apical arms of the dorsal branch of paraproct, moreover the spine bunch on the paramere has longer stem, but more specimens are required for species delineation.

Drusus neltel Oláh, sp. nov.

(Figures 708–711)

Material examined. Holotype: **Italy**, Lombardia, Valbondione (BG), sorgenti fiume Serio, 13.VII.2001 (1 male, MCSNBG).

Diagnosis and description. We have a single male specimen from Lombardia, but with enough distinct divergences to describe it as a new species. The apical arm of the dorsal branch of paraproct with a very long basal constriction in lateral view, that is very short both at *D. monticola* and *D. nigrescens*. In dorsal view the apical arms form a rather peculiar shape pattern again very distinctly differs from both *D. monticola* and *D. nigrescens*. The pattern of the subapical spine bunch is highly modified, reduced to a small bunch almost without any basal stem.
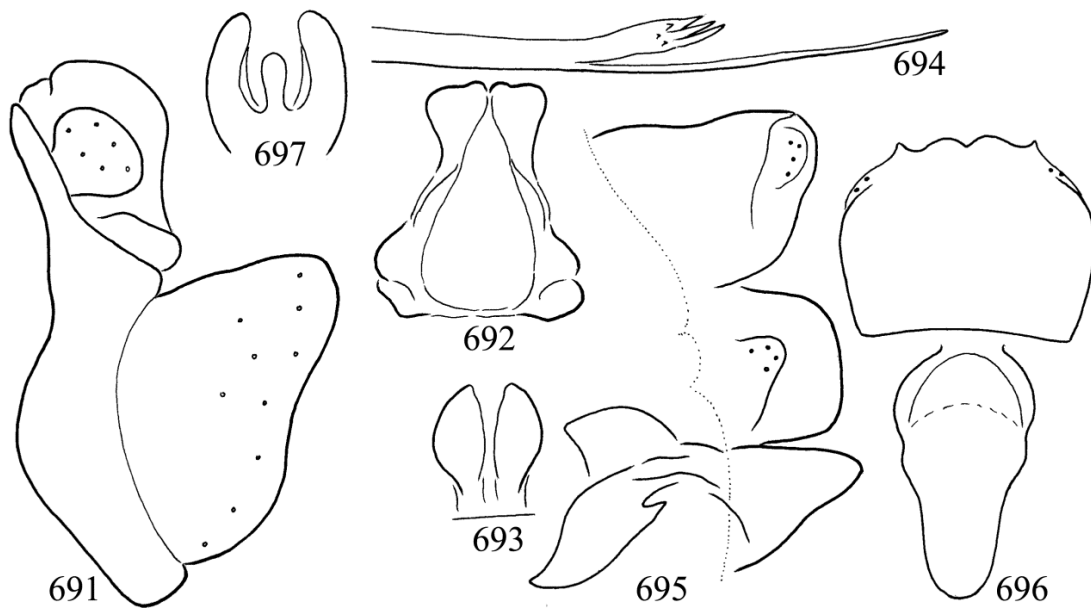
Figures 691–697. *Drusus monticola* McLachlan, 1876. Bolzano: 691 = male genitalia in left lateral view, 692 = paraproct in caudal view, 693 = apical arms of the dorsal branches of paraproct in dorsal view, 694 = parameres in left lateral view, 695 = female genitalia with vaginal sclerite complex in left lateral view, 696 = tergite IX and dorsal profile of vaginal sclerite complex in dorsal view, 697 = vulvar scale in ventral view.
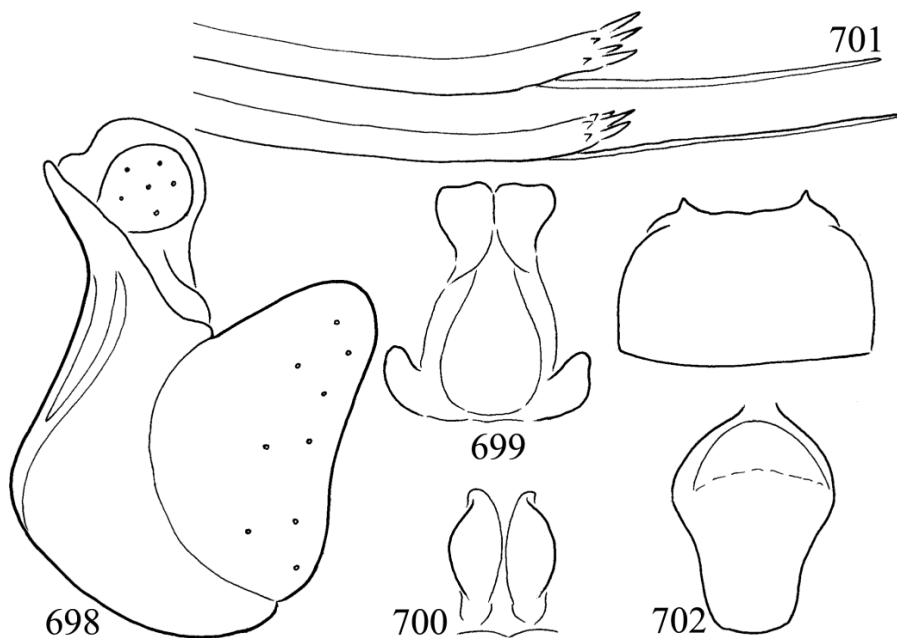

Figures 698–702. *Drusus monticola* McLachlan, 1876. Tatra Mts: 698 = male genitalia in left lateral view, 699 = paraproct in caudal view, 700 = apical arms of the dorsal branches of paraproct in dorsal view, 701 = parameres in left lateral view, 702 = tergite IX and dorsal profile of vaginal sclerite complex in dorsal view.
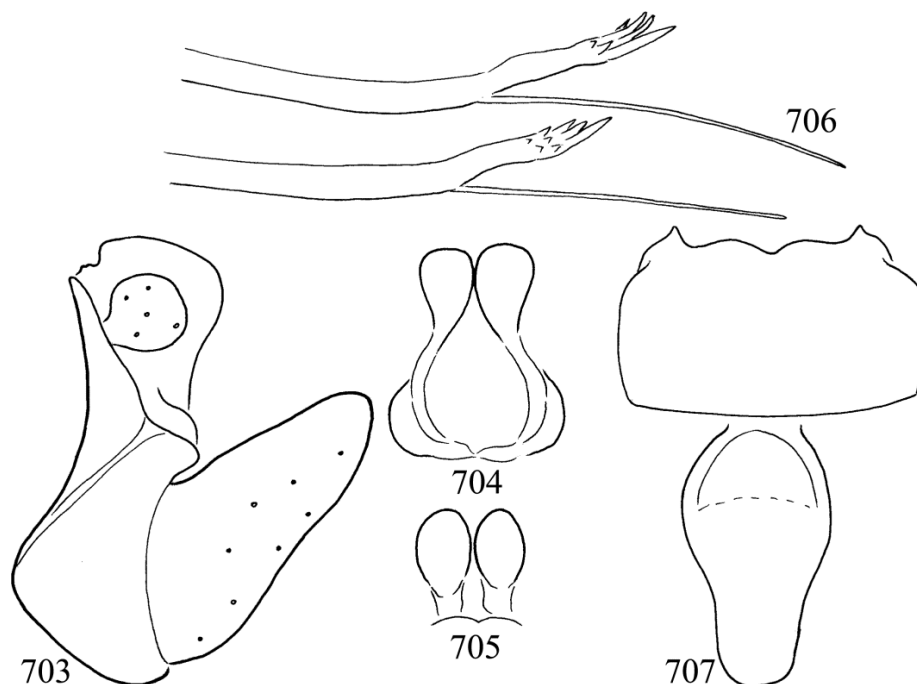
Figures 703–707. *Drusus monticola* McLachlan, 1876. Maramures Mts: 703 = male genitalia in left lateral view, 704 = paraproct in caudal view, 705 = apical arms of the dorsal branches of paraproct in dorsal view, 706 = parameres in left lateral view, 707 = tergite IX and dorsal profile of vaginal sclerite complex in dorsal view.
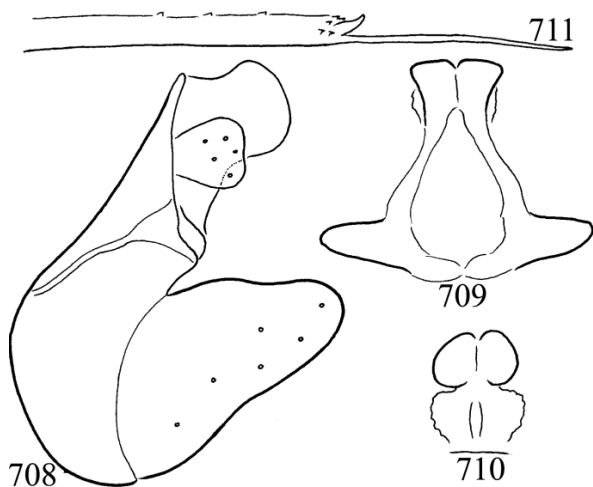
Figures 708–711. *Drusus neltel* Oláh, sp. nov. Holotype: 708 = male genitalia in left lateral view, 709 = paraproct in caudal view, 710 = apical arms of the dorsal branches of paraproct in dorsal view, 711 = paramere in left lateral view.

Etymology. „*neltel*",from „nyéltelen", without stem in Hungarian, refers to the subapical spine bunch without any stem.

Drusus nigrescens **Meyer-Dür, 1875**

(Figures 712–718)

Drusus nigrescens Meyer-Dür, 1875: 396. "Dischmathal und Davos in Bündten bei 4800' ü. M., im Lucendrothal in Tessin und an der Unteralp am Gotthard (Uri) in vielen Stücken von H. Dietrich gefangen.

Material examined. **Italy**, Bergamo, Premolo, sorgenti torrente Parina, 1750 m, 19.VI.2003, leg. Museo Bergamo (1 male, MCSNBG). Bergamo, Premolo, sorgenti torrente Parina, 1750–1900 m, 7.VII.2004, leg. O. Lodovici & P. Pantini (1 male, 2 females; MCSNBG). Chiesa in Valmalenco, Val Ventina, 1900 m, 6.VII.1995, leg. Fabbri (2 males, MCSNBG). Bergamo, Valbondione, torrente Trobio, 2000 m, 3.VII.1994, leg. Buttarelli & Pantini (5 males, 4 females; OPC). Bergamo, Valbondione, Val Cerviera, 2100 m, 7.VII. 2003, leg. Calandrina (3 males, 2 females; MCSNBG). Lombardia, Carona (BG), dintorni Rif. Calvi, 1900 m, 20. VI. 2009, leg. G. Federici (1 male, MCSNBG). **Switzerland**, Furkapass, N46°35.314', E8°25.814', 2348 m, 21.VII.2006, leg W. Graf (2 males, OPC).

Diagnosis. Meyer-Dür, 1875: 396, "Dem *Limnoph. hirsutus* P. oberflachlich sehr ahnlich. Dunkelschwarzlich, rauhhaarig, mit weisslichem
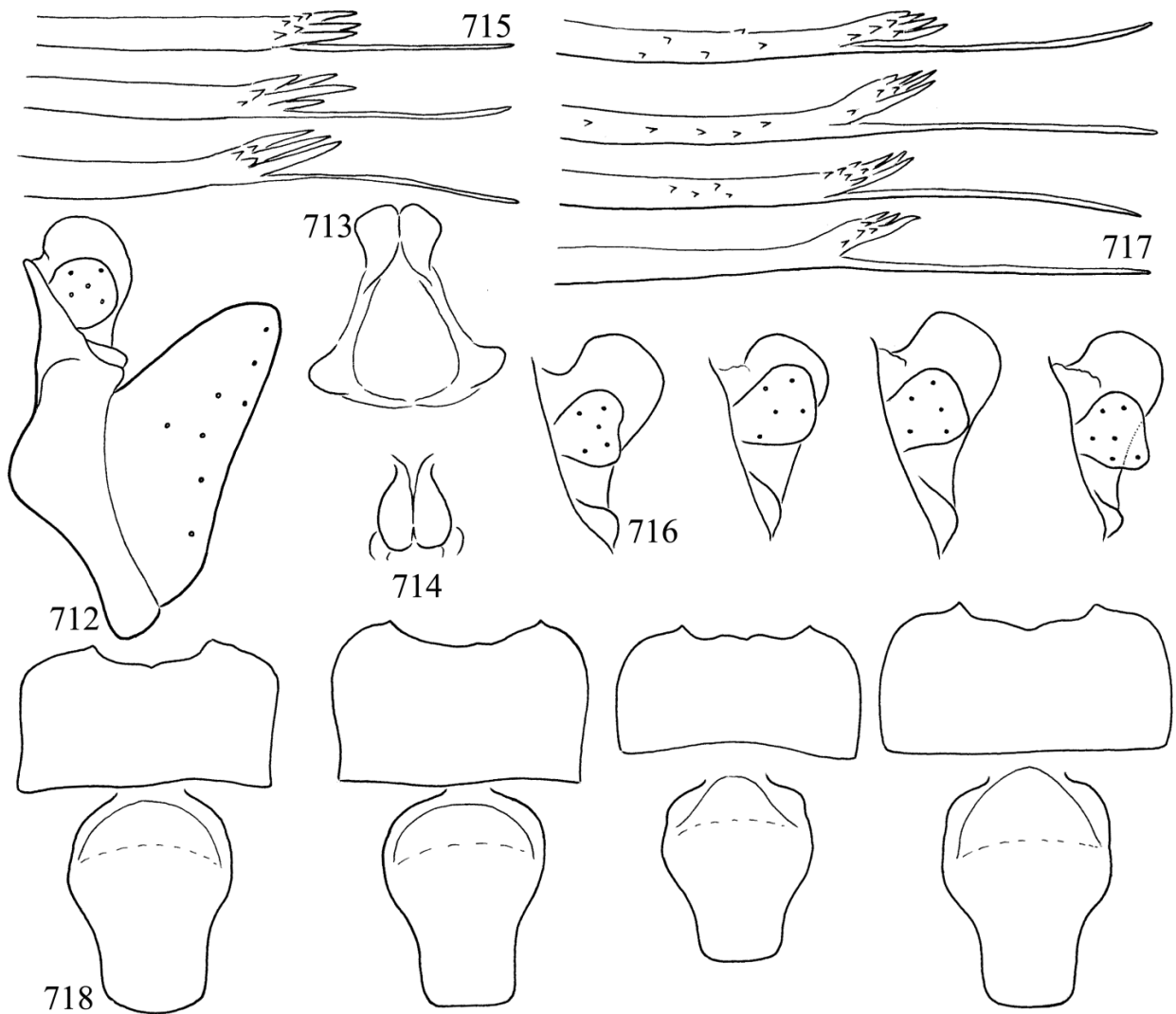
Figures 712–718. *Drusus nigrescens* Meyer-Dür, 1875. 712 = male genitalia in left lateral view, 713 = paraproct in caudal view, 714 = apical arms of the dorsal branches of paraproct in dorsal view, 715=parameres in left lateral view, 716 = cerci and paraproct in left lateral view, 717 = parameres in left lateral view, 718 = tergite IX and dorsal profile of vaginal sclerite complex in dorsal view.

Fleck am Thyridium und einem am Arculus, öfters auf den Forderflügeln mit zerstreuten, bleichen Punkten in den Apicalzellen."

Schmid 1956: 34, "*Dr. nigrescens* est extrêmement voisine de *monticola*, elle s'en distingue surtout par sa coloration presque noire, par sa taille plus petite et par la forme des appendices intermédiaires du ♂ qui sont moins fortement encastrés dans l'échancrure du VIIIe tergite; celui-ci forme des lobes proéminents et disposés à des niveaux différents."

Additional diagnosis. Besides the pronounced color and size differences *D. nigrescens* has the apical arms on the dorsal braches of paraproct more produced upwards from the short basal constriction.

Drusus mixtus species group

Drusus mixtus species group is integrated through ancestral divergence by subapical spine bunch having at least one larger primary upward arching spine and a stout abbreviated apical shaft.

175

This species group is enlarged by members of the synonymized *Metanoea* genus and comprised of ten species and three species complexes: *Drusus flavipennis* species complex, *Drusus mixtus* species complex, *Drusus spelaeus* species complex. The delineation of the species complexes in the species group is based on paraproct shape divergenses.

(1) *Drusus flavipennis* species complex has dorsal branch of the paraproct with upward directed digitiform apical arms in lateral view; laterally diverted in caudal view;

(2) *Drusus mixtus* species complex has dorsal branch of the paraproct with basal and apical converging lobes in lateral view; diverged apex in caudal view;

(3) *Drusus spelaeus* species complex has dorsal branch of paraproct with sharp or blunt hook on apical arms in lateral view; mostly fused in caudal view.

Drusus flavipennis species complex

Drusus flavipennis species complex has dorsal branch of the paraproct with upward directed digitiform apical arms in lateral view; laterally diverted in caudal view. According to the ancestral divergence of the spine pattern on the paraproct the members of the synonymized *Metanoea* genus

forms this species complex in the *Drusus mixtus* species group, except *Metanoea euphorion* which belongs to the *Drusus alpinus* species group. This species complex is comprised of five species: *apados* sp. nov., *flavipennis*, *malickyi*, *rhaeticus*, *vercorsicus*.

Drusus apados Olah & Coppa, sp. nov.

(Figures 719–725)

Material examined. Holotype: **France**, Drôme Department, Lus-la-Croix-Haute, Fontaine Mougious, 20.VIII. 2009, leg. G. Coppa & J. Le Doaré (1 male, CPC). Allotype: same as holotype (1 female, CPC). Paratype: same as holotype (5 males, 4 female, OPC).

Diagnosis and description. This new species forms a closely related sibling group together with *Drusus malickyi* and *Drusus vercorsicus. Drusus apados* sp. nov. has the apical arms directed upward, not backward like at *D. malicky*; the mesal posterad directed lobe on the fused basement of the dorsal branch of paraproct disappeared, present at *D. malicky*. The number of spines in the subapical spine bunch is reduced compared to *D. malickyi*. However, the sampled population may represent a mixed population in a contact zone between *D. apados* sp. nov. and *D. malickyi*.
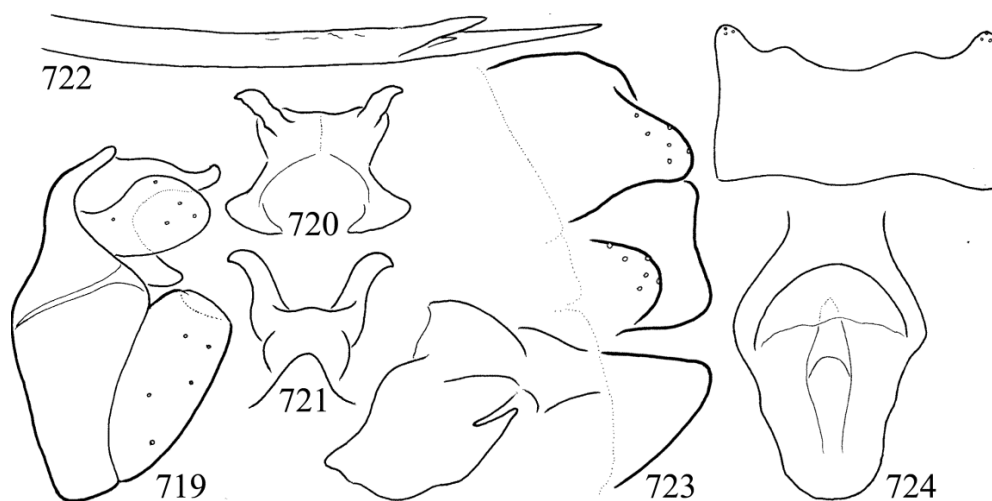
Figures 719–724. *Drusus apados* Oláh & Coppa, sp. nov. Holotype: 719 = male genitalia in left lateral view, 720 = paraproct in caudal view, 721 = apical arms of the dorsal branches of paraproct in dorsal view, 722 = paramere in left lateral view. Allotype: 723 = female genitalia with vaginal sclerite complex in left lateral view, 724 = tergite IX and dorsal profile of vaginal sclerite complex in dorsal view.
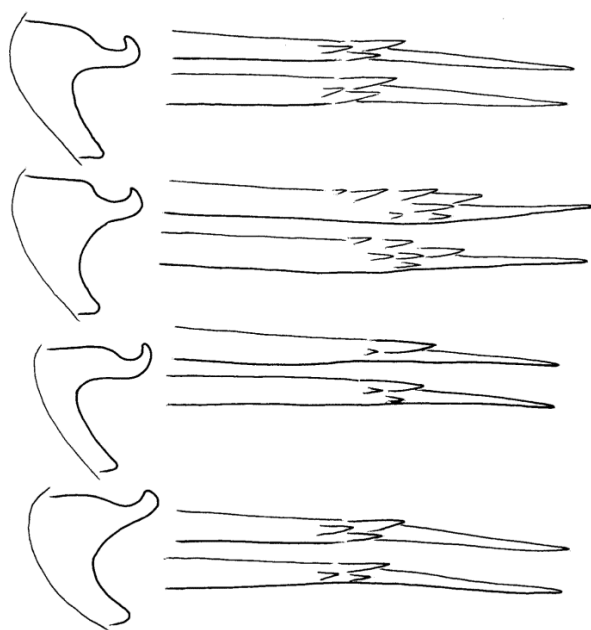
Figure 725. *Drusus apados* Oláh & Coppa, sp. nov. Paratypes: paraprocts and parameres in left lateral view.

Female description. Female genitalia. Tergite of segment IX forming short tube, open ventrally, with very sallow mesal excision and low rounded apical margin of the lateral lobes in dorsal view; the lateral setose lobe of sternite IX large, rounded. Segment X membranous and embedded inside segment IX and encircling anus; supragenital plate of segment X well-developed and quadrangular with slightly concave apical margin in lateral view. Dorsal profile of the vaginal sclerite complex long and narrowing anterad.

Etymology. apados, from „apadós", reduced in Hungarian, refers to reduced mesal posterad directed lobes and to the reduced number of spines in the subapical spine bunch.

Drusus flavipennis (Pictet, 1834) comb. nov.

(Figures 726–730)

Phryganea flavipennis Pictet, 1934: 155. "J'ai trouvé cette Phrygane, dont je ne connais pas la larve, dans le Val a'Iliers (Vallais) au milieu Juillet."
Halesus flavipennis (Pictet, 1834): McLachlan 1876: 148. "a very small delicate yellowish species, can hardly be considered congeneric, and is only retained here because it will not fit into *Drusus*, to which it is greatly allied."

Halesus flavipennis (Pictet, 1834): McLachlan 1876: 163. "very badly placed in *Halesus*, and its structural characters are those of *Drusus*, only that it wants the one essential, viz., the pouch in the posterior-wings of the ♂."
Metanoea flavipennis (Pictet, 1834): McLachlan 1880: 40. *Metanoea* gen. nov. "Characters as in *Drusus*, but the ♂ has no pouch and pencil of hairs in the posterior-wings. The position of the single species of this genus in *Halesus* is unnatural, and I have therefore decided upon removing therefrom. It is practically a *Drusus*, excepting in the absence of the pouch and pencil in the posterior-wings of the ♂."
Metanoea flavipennis (Pictet, 1834): Schmid 1956: 67–69. "R. McLachlan a confondu sous le nom de *flavipennis*: la vraie *flavipennis* de Pictet et une autre espèce. Malheureusement, il a figuré et décrit cette dernière. La vraie *flavipennis* a été ultérieurement redécrite par K. J. Morton sous le nom de *chapmani*. Aujourd'hui, il convient donc de mettre les choses au point: *chapmani* Morton entre en synonymie de *flavipennis* Pictet et je donne à la *flavipennis* de R. McLachlan (nec Pictet) le nouveau nom de *rhaetica*. Je n'ai pas vu les types de Pictet, ni chassé dans la localité typique, mais l'absence en Suisse romande de la *flavipennis* de R. McLachlan suffit à trancher la question."

Material examined. **Switzerland**, Val Münstair, 20.VII. 2006, leg. W. Graf (2 males, 2 females; OPC). **Italy**, Valbondione (BG) 862 m, Lago Barbellino T.L. 6.VIII.2003, leg. Calandrina (1 male, OPC).

Diagnosis. Pictet 1934: 155,: "Cette espèce se distingue facilement de toutes les autres parce qu'elle est petite, d'un fauve très clair, a les ailes peu arrondies et que les poils qui les couvrent sont en duvet court et serré."

Additional diagnosis. The nominate, name bearing species of the complex has the apical arms of the dorsal branches of the paraproct particularly elongated and pointed.

Drusus malickyi (Sipahiler, 1992) comb. nov.

(Figures 731–735)

Metanoea malickyi Sipahiler, 1992: 285–286. "I am pleased to dedicate this new species to my colleague Doz. Dr. Hans Malicky."

Material examined. Holotype and allotype: R-190, **France**, Alpes, Isére, montagne de Jacou, ruisseau affluent de l'Ebron àla station de ski de Lalley-le-Jacou (col de la Croix-Haute), 1500 m, 29.VIII.1988, leg. Vincon (1 male, 1 female; ZSM). Here we have given the collecting date written on the label present in the vial with the Holotype.
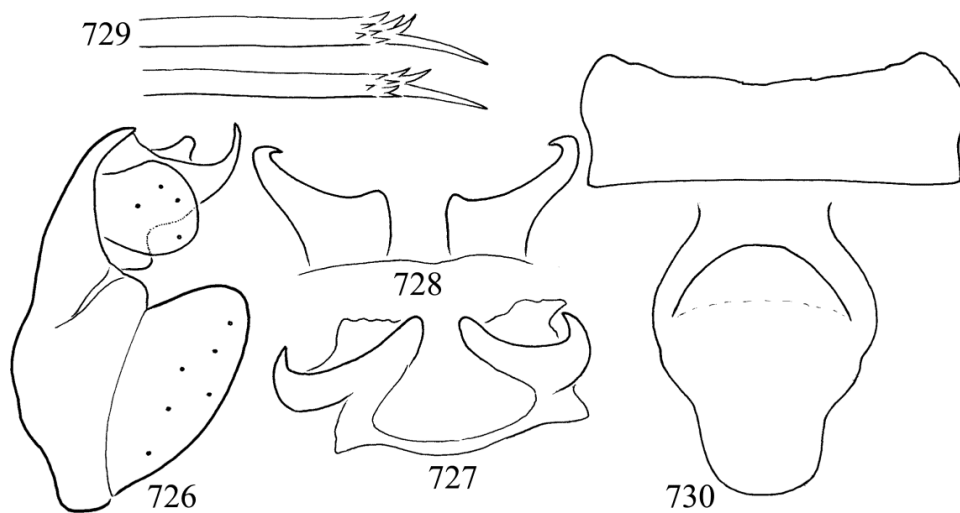
Figures 726–730. *Drusus flavipennis* (Pictet, 1834). 726 = male genitalia in left lateral view, 727 = paraproct in caudal view, 728 = apical arms of the dorsal branches of paraproct in dorsal view, 729 = parameres in left lateral view, 730 = tergite IX and dorsal profile of vaginal sclerite complex in dorsal view.
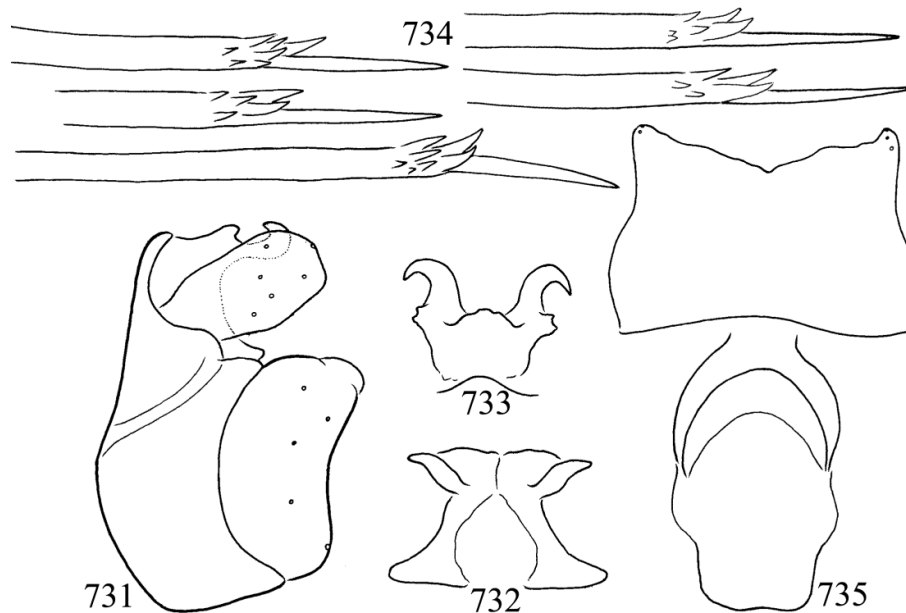
Figures 731–735. *Drusus malickyi* (Sipahiler, 1992). 731 = male genitalia in left lateral view, 732 = paraproct in caudal view, 733 = apical arms of the dorsal branches of paraproct in dorsal view, 734 = parameres in left lateral view, 735 = tergite IX and dorsal profile of vaginal sclerite complex in dorsal view.

However, the collecting date is 13.VI.1988 in the published species description. Both the holotype and allotype is over-cleared, completely depigmented. The dorsal profile of the vaginal sclerite complex is very feable, just discernible. New material: France, Drôme Department, Romeyer, Source du Ray, 18. IV. 2005, leg. G. Coppa (2 males, OPC). France, Drôme Department, Die, Prés de l'Abbaye de Valcroissant, 22. IV. 2005, leg. G. Coppa (2 males, OPC).

Diagnosis. Sipahiler 1992: 286, "*Metanoea malickyi*, spec. nov., is the third species of the genus *Metanoea* from the Alps and is well distinguished from the related species *M. flavipennis* Pictet from the western Alps and *M. rhaetica* Schmid from the eastern Alps." "These three species of *Metanoea* have very different genitalia

and no close relationship between them is evident."

Additional diagnosis. On the holotype and also on the newly collected specimens the posterad directed mesal lobe is well developed, the apical arms are distinctly anterad directed. Based upon the ancestral divergence of the spine pattern on parameres as well as on the basal architecture of the paraproct, all the three species, *D. flavipennis*, *D. malickyi*, and *D. rhaeticus* are closely related.

Drusus rhaeticus (Schmid, 1956) comb. nov.

(Figures 736–740)

Metanoea rhaetica Schmid, 1956: 69–70. "Elle habite les Alpes de la Suisse orientale ou son aire de distribution prolonge sans discontinuité celle de flavipennis. J'en ai étudié un grand nombre d'exemplaires de Suisse orientale."

Material examined. **Italy**, Feltre (BL) 750 m, sorgenti Torr. Colmeda, 7.VIII.2002, leg. Museo BG (1 male, OPC). **Slovenia**, Upper Carniola, Trizic municipality, Karawankas, upper section of Kosutnik stream, N46°25.684' E14°23.888', 1135 m, 9.VII.2013 leg. D. Murányi et al. (1male, OPC).

Julian Alp, small tributary of Sava Bohinjka, 24.VI.1988 leg. J. Oláh (8 males, 14 females; OPC).

Diagnosis. Schmid 1956: 69–70. "Cette espèce, très voisine de *flavipennis*, a une aire répartition plus orientale que cette dèrniere. Cette espèce ne se différencie guère de *flavipennis* que par l'armature génitale; la coloration, la nervulation et les proportions des différents articles des membres sont identiques chez les deux espèces."

Drusus vercorsicus (Botosaneanu & Dumont, 2003) comb. nov. and stat. restit.

(Figure 741)

Metanoea vercorsica Botosaneanu & Dumont, 2003: 236. **France** "Parc Naturel Regional du Vercors, 14. VII.2002 (B. Dumont), sur le cours d'eau Archiane, affluent du Bez, bassin versant de la Drome, environ 660 m d'altitude. En alcool, mais genitalia dans un petit tube à glycérine; dans les collection du Musée zoologique d'Amsterdam."

Metanoea vercorsica Botosaneanu & Dumont, 2003: Malicky 2005a: 569. Synonymised with *Metanoea malickyi*.
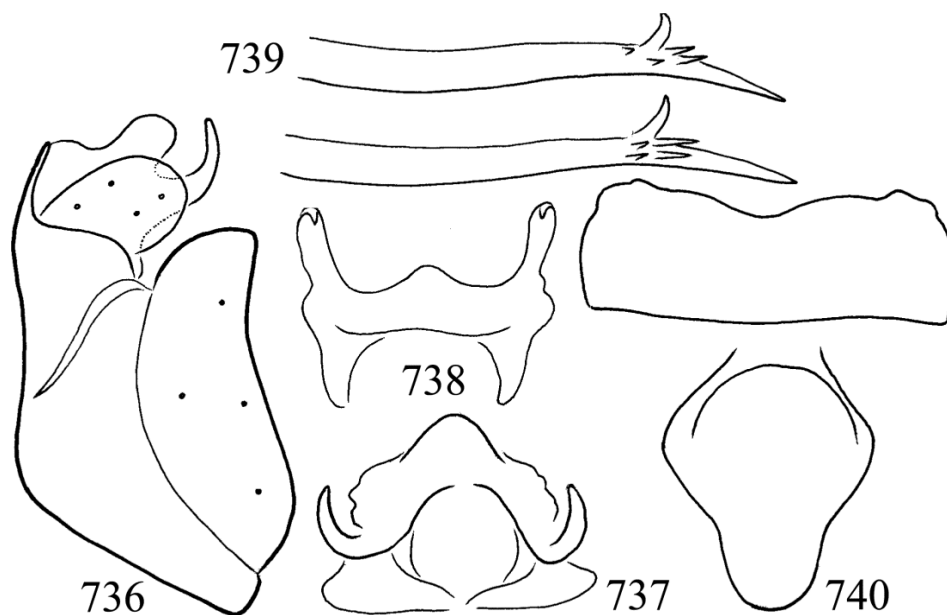
Figures 736–740. *Drusus rhaeticus* (Schmid, 1956). 736=male genitalia in left lateral view, 737=paraproct in caudal view, 738= apical arms of the dorsal branches of paraproct in dorsal view, 739=parameres in left lateral view, 740=tergite IX and dorsal profile of vaginal sclerite complex in dorsal view.
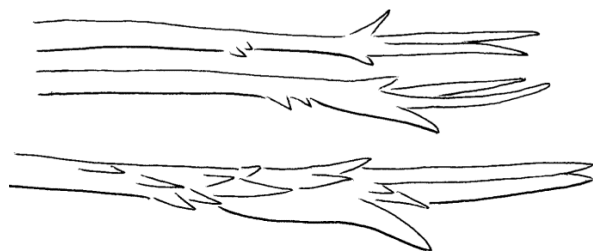
Figure 741. *Drusus vercorsicus* (Botosaneanu & Dumont, 2003). Parameres in left lateral view.

Diagnosis. Botosaneanu & Dumont 2003: 236, "Parmi les 5 espèces de *Metanoea* décrites a ce jour, *M. vercorsica* n. sp. se rapproche le plus de *M. malickyi* Sipahiler, 1992, espèce connue de deux localités des Alpes francaises et d'une de la cordillère Cantabrique, et ceci surtout par la structure curieuse des gonopodes avec leur importante concavité médiane et leur petite concavité apicale. Elle s'en distingue amplement, surtout par l'aspect nettement différent de la zone de tubercules noirs du segment VIII, et par celui - aussi nettement différent – des appendices intermédiaires et de leur "racine"."

Additional diagnosis. The species was described from a single holotype and deposited in the Zoological Museum of Amsterdam. The holotype was not available for a detailed paramere study, however Botosaneanu & Dumont (2003) have examined and have drawn the fine structure of the paramere very carefully. We have examined the paramere fine structure of the *D. malickyi* holotype and four more *D. malickyi* males from two different populations, other than locus typicus. The paraproct and paramere fine structures in the three *D. malickyi* populations were stable and different. The particularly diverged shape of the paraproct and the higly diverged setal pattern of the paramere with doubled terminal modified setae clearly demonstrate the incipient sibling species status of *Drusus vercorsicus* and here we reinstate its species status.

Drusus mixtus species complex

Drusus mixtus species complex has dorsal branch of the paraproct with basal and apical converging lobes in lateral view; diverged apex in caudal view. The nominate species complex is comprised of two species: *biguttatus*, *mixtus*.

Drusus biguttatus (Pictet, 1834)

(Figures 742–746)

Phryganea biguttata Pictet, 1834: 144. "J'ai trouvé cette espèce dans la même localité et à la même époque que la précédente. " (*P. guttulata*: "dans la vallée d'Abondance au mois de Juillet)."

Material examined. **Albania**: North Albanian Alps (Prokletije Mts.), Cerem, 42°29'48"N, 19°°56'55"E, 1225 m, 29. VII.2016, light leg. Z. Varga (1 female, OPC). **Austria:** Weissbach bei Lofer, Saalach Stream at the entranceof the Lambrechtshönle, 47°31.573'N, 12°44.351'E, 675 m, 26. VIII.2013, leg. L. Dányi (1 female, OPC). **Italy:** Valle d'Aosta, Camporcher (AO), Torr. Ayasse c/o Rif. Dondena, 45°37'4"N, 7°33'45"E, 2150m, 12.VII.2006, leg. Baldizzone (20 males, MCSNBG). Piemonte, Balme (TO), Cornetti, Rio Paschiet, 1550m, 18.VIII.2004, leg. F. Vaccarino (6 males, 13 females; OPC). Piemonte, Crissolo (CN), 1700 m, Pian della Regina f. Po T.L. 2.IX.1997, leg. M. Valle (6 males, 4 females, MCSNBG). Ossana (TN), Fucine 978 m, Torrente Vermigliana, T.L., 14.VIII.1998, leg. Bertuetti (1 male, 2 females, MCSNBG). Lombardia, Valbondione (BG), 2100 m, fiume Serio sotto L. Naturale, T.L., 15.VII.2003, leg. Calandrina (3 males, 2 females, MCSNBG). Friuli Venezia Giulia, Claut (PN) 500 m, torr. Cellina tr.lum. 16.IX.1996, leg. P. Pantini & M. Valle (4 males, 6 females; MCSNBG). Valle d'Aosta, Camporcher (AO), torrente Ayasse c/o Rifugio Dondena, 45°37'4"N, 7°33'45"E, 2150 m, 12.VII. 2006, leg. Baldizzone (2 females, MCSNBG). Friuli Venezia Giulia, Lusevera (UD), 320 m, torr. Torre, T.L., 20.IX.1996, leg. P. Pantini & M. Valle (10 males, 23 females; MCSNBG). Lombardia, Cusio (BG) Piani dell'Avaro, 1750 m, 46°00'44"N, 9°35'59"E, 22.VI.2005, leg. M. Massaro & P. Paleni (3 males, 13 females, MCSNBG). Lombardia, Ardesio (BG) Rif Alpe Corte, 1400 m, 15.VIII.1983, leg. CAI Bergamo (3 males, 9 females, MCSNBG). Friuli Venezia Giulia, Paularo (UD), 670 m, torr Chiarsò T.L., 18.IX.1996, leg. P. Pantini & M. Valle (6 males, 3 females; MCSNBG). Veneto, Feltre (BL), 750 m, sorgenti torr. Colmeda, T.L. 12.VI.2003, leg. O. Lodovici & P. Pantini (17 males, 11 females; MCSNBG). Lombardia, Mezzoldo (BG), 1800 m, Alpe Ancogno amb. Sorgentizio, T.L., 30.VII.1994, leg. Bertuetti (15 males, 8 females, MCSNBG; 12 males, 6 females; OPC). Veneto, Cesiomaggiore (BL), 530 m, Val Canzoi, torrente Caorame, T.L., 12.VI.2003, leg. O. Lodovici & P. Pantini (2 males, 18 females; MCSNBG). Lombardia, Bergamo Province, Mezzoldo, Alpe Ancogno, hygropetric habitat,1850 m a.s.l. 4.VIII.2010, singled leg. O. Lodovici & J. Oláh (2 males, 1 female, OPC). Friuli Venezia Giulia, Pordenone, Claut, torr Cellina, 680 m, 23.VIII.1996, leg. Pantini & Valle (6 females, OPC). Friuli Venezia Giulia, Udine, Lusevera, torrente Vedronza, 330 m, 24.V.1996, leg. Pantini & M. Valle (5 females, MCSNBG). Piemonte, Torino, Balme,Cornetti, Rio Paschiet, 1410 m, 18.VIII.2004 leg. F. Vaccarino (1 female, MCSNBG). **Montenegro**: Kolašin municipality, Manastir Morača, karst spring and its
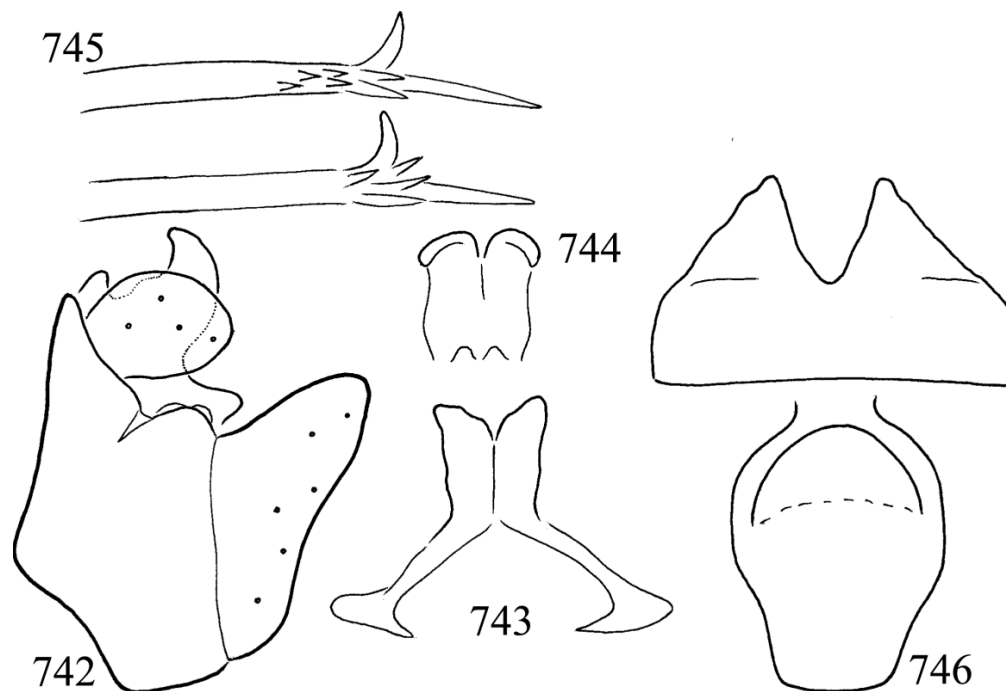
Figures 742–746. *Drusus biguttatus* (Pictet, 1834). 742 = male genitalia in left lateral view, 743 = paraproct in caudal view, 744 = apical arms of the dorsal branches of paraproct in dorsal view, 745 = parameres in left lateral view, 746 = tergite IX and dorsal profile of vaginal sclerite complex in dorsal view.

outlet at the monastery, N42°45.942', E19°23.436', 300 m, 14.06.2012 leg. Z. Fehér, T. Kovács, D. Murányi(2 males, OPC). **Romania**: Rodna Mts. Borsa-Statiunea Borsa, garden, 878m, N47°36'48.0", E24°46'55.8", 28–29.VI.2005, light trap leg. J. Kontschány, D. Murányi & K. Orci (3 males, NHMB). **Slovakia**: West Tatra Mts., Bela River, 3.VIII. 1976. light trap, leg. Nagy (1 male, OPC). High Tatra Mts., Mlynica stream, 17.VII.1966, leg. J. Oláh (3 males, OPC). **Slovenia**: Julian Alp, Radovna stream, 22.VI.1988, singled leg. J. Oláh (17 males, 6 females, HNHM).

Diagnosis. Pictet 1834: 144, "Cette espèce diffère de la *villosa* et de la *tuberculosa* par l'absence de poils soyeux, et de la *testacea* parce que ses ailes sont moins arrondies, d'un fauve plus uni et plus luisant, et parce qu'elles ont la tache blanche don't nous avons parlé"

Schmid 1956: 45, "La coloration de cette espèce est très variable, mais l'armature génitale présente une grande stabilité. Si voisine de mixtus qu'elle soit, il ne saurait être question de réunir les deux formes, car les caractéres distinctifs sont toujours tres nets."

Drusus mixtus (Pictet, 1834)

(Figures 747–749)

Phryganea mixta Pictet, 1834: 142–143. "J'ai trouvé cette espèce dans la Divonne, au pied du Jura"

Drusus mixtus (Pictet, 1834): MacLachlan 1876: 172–173. "I am inclined to adopt Pictet's implied suggestion that his *mixta* and *sericea* were one and the same species."

Material examined. **France**: Department Jura, Foncine le Haut, Jura la Saine, 21.V.2008 leg. G. Coppa (7 males, OPC). Department Doubs, Mouthe, Doubs en aval de la résurgence, 24.IX.2009 leg. G. Coppa (1male, 3 females; OPC).

Diagnosis. Pictet 1834: 142, "Description. La tête, le thorax et l'abdomen sont noirs, avec quelques poils de la même couleur; les palpes et les antennes sont noirs."

McLachlan 1876: 173, "the ♂ is immediately recognisable by the very peculiar intermediate appendages, which have no analogy to those of any other species."
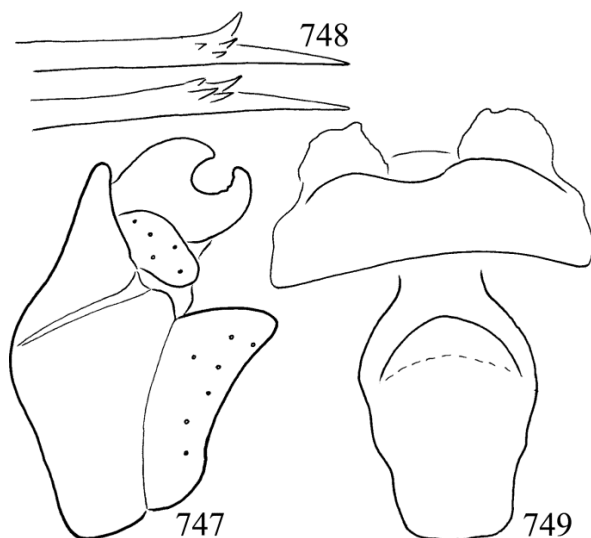
Figures 747–749. *Drusus mixtus* (Pictet, 1834). 747 = male genitalia in left lateral view, 748=parameres in left lateral view, 749=tergite IX and dorsal profile of vaginal sclerite complex in dorsal view.

Schmid, 1956:43: "*Drusus mixtus* est extrêmement voisin de *biguttatus*, mais sa coloration est constante, les poils du repli sont très clairs, la zone de spinules du VIIIᵉ tergite est bilobée et les deux pointes des appendices intermédiaires sont séparées par une échancrure hémicirculaire."

Drusus spelaeus species complex

Drusus spelaeus species complex has dorsal branch of paraproct with sharp or blunt hook on apical arms in lateral view; mostly fused in caudal view. This species complex is comprised of three species: *buscatensis*, *spelaeus*, *valserinensis*. *Drusus spelaeus* and *D. valserinensis* sp. nov. forms a closely related sibling group. However *D. buscatensis* has apical arms with blunt head and the paramere spine pattern is more diverged by having rather dissolved state of the subapical spine bunch. But desintegration of the subapical spine bunch seems a character state in this species complex.

Drusus buscatensis Botosaneanu, 1952

(Figures 750–754)

Drusus buscatensis Botosaneanu, 1960: 369–370. „Holotypus ♂: Baisoara – Muntele Buscat (Rumanische West-

liche Karpâten – Muntii Apuseni); Neben einer Quelle, 21.V.1956 (leg. Kiss Béla, Sammlung L. Botosaneanu). Paratypus ♂: selber Ort, 16.V.1956 (leg. L. Botosaneanu, Samlung F. Schmid)."

Drusus buscatensis Botosaneanu, 1960: Botosaneanu 1975: 97–98. „*Drusus buscatensis* Bots. ist einerseits vom Apuseni-Gebirge, anderseits vom Cibin- oder Cindrel-Gebirge (Südkarpaten) bekannt. Frühlingsart (Mai); lebt in Quellen und Bachlein in der Fichtenwaldzone (etwa 1400-1600 m).

Drusus buscatensis Botosaneanu, 1960: L. Újvárosi (pers. comm.) has collected 1♂ near locus typicus in 21.V.2012 (Romania, Cluj county, Apuseni, Muntele Baisorii, Buscat, springs 46.537505°N, 23.291260°E 1529 m 12.V.2012) and 1♂ near Paltinis, Muntii Cindrel in 2.VI.2012, (Romania, Sibiu county, Southern Carpathians, Complex Paltinis, Cibin, Batrana springs 45.620050°N, 23.893600°E, 1720 m 2.VI.2010)."

Material examined. **Romania**, Cindrel Mts. Pǎltiniș, spring streams of stream Bǎtrâna Micǎ, N45°37.716', E23°55.248', 1583 m, 28.V.2013, singled leg. J. Oláh, E. Bajka, Cs. Balogh & G. Borics (1 male, 2 females; OPC). Apuseni Mts. Muntii Gilǎului, Stațiunea Muntele Bǎişorii, Muntele Mare (Öreghavas), Iara (Jára) spring area, N46°28.914', E23°13.294', 1750 m, 19.VI.2015, singled leg. J. Oláh, Cs. Balogh, & P. Juhász (2 males, OPC).

Diagnosis. Botosaneanu 1975: 97–98, "Sicherlich nahe mit *D. doehleri* verwandt, die ihre Schwesterart ist. Es ware interessant zu wissen, wann und unter welchen Umstanden die Artaufsplitterung stattgefunden hat."

Drusus spelaeus (Ulmer, 1920)

(Figures 755–758)

Metanoea spelaea Ulmer, 1920: 308–309. "Frankreich: Dép. De la Drôme, Gritte de-Plan-de-Baix, Cant. De Crest-Nord, Argod-Vallon leg., 21.X.1912, 4♂, No. 588."

Drusus spelaeus (Ulmer, 19210): Schmid 1956: 45–46. "Cette espèce n'est connue que de la grotte de Plan-de-Baix (Drôme, France), 21.X.1912. J'ai étudié un ♂."

Material examined. **France**: Department Isère, Saint-Gervais, Le Drevenne, 18.VII.2012 leg. G. Coppa (1 male, OPC). Department Isère, Sarcenas, Ru de Fontfroide, 20. VIII.2010 leg. G. Coppa (1 male, 1 female; OPC). France, Bruyant Eugius, 45°8'47.60"N, 5°37'1.51."E, 7.VII.2012, leg. W. Graf (1 male, 1 female; OPC).

Diagnosis. Ulmer 1920: 309, "Die Art erinnert in den Genitalorganen etwas an *Drusus trifidus* Mc Lach., doch sind die Append. Praean., die
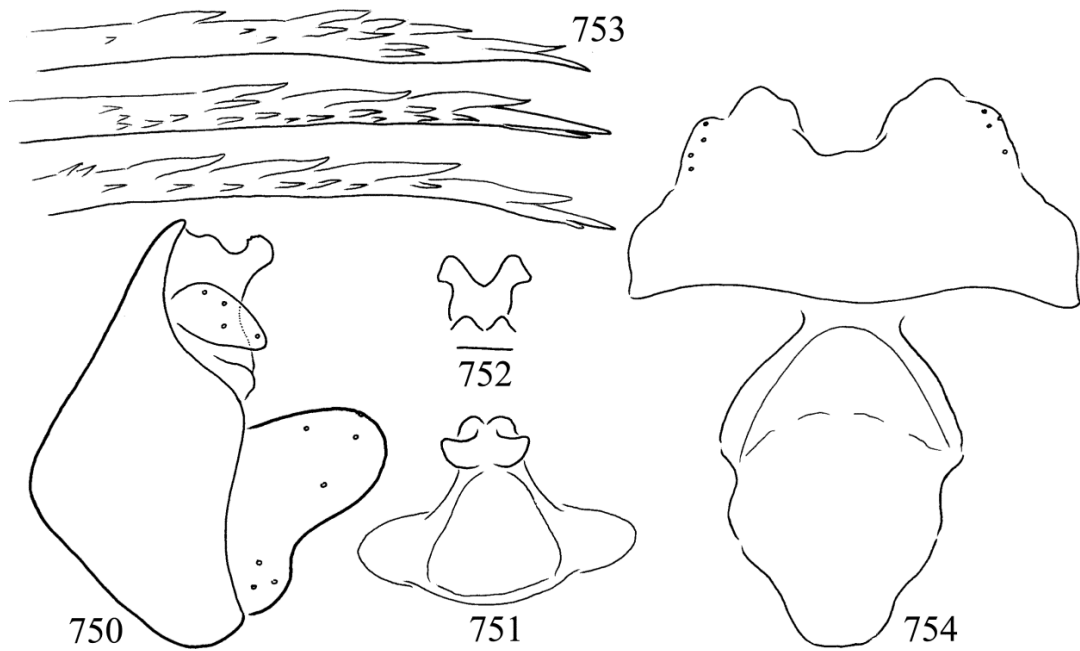
Figures 750–754. *Drusus buscatensis* Botosaneanu, 1952. 750 = male genitalia in left lateral view, 751 = paraproct in caudal view, 752 = apical arms of the dorsal branches of paraproct in dorsal view, 753 = parameres in left lateral view 754 = tergite IX and dorsal profile of vaginal sclerite complex in dorsal view.
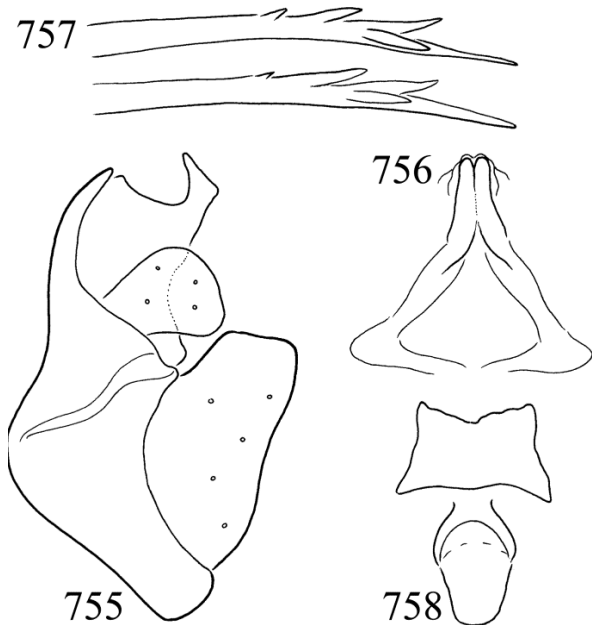
Figures 755–758. *Drusus spelaeus* (Ulmer, 1920). 755 = male genitalia in left lateral view, 756 = paraproct in caudal view, 757 = parameres in left lateral view, 758 = tergite IX and dorsal profile of vaginal sclerite complex in dorsal view.

Klauen des X. segments und die mittlere schwarze Partie des VIII. Tergits abweichend. Von den beiden anderen *Metanoea*-Arten unterscheidet sich diese, aufser in der dunkleren, mehr an *Drusus discolor* erinnernden Flügelfarbung, durch etwas breiter Flügelform und besonders durch den Bau der Genitalorgane. Eine Haartasche im Hinterflügel ist nicht sichbar (wenn diese vorhanden ware, würde es sich um eine neue *Drusus*-Art handeln)."

Schmid 1956: 45–46. "*Dr. spelaeus* n'est certainement pas une forme cavernicole, ni même un trogloxème régulier. Il est presque certain qu'on le découvrirait dans les Alpes francaises le long des torrents d'altitude." "*Dr. spelaeus* est caractérisé par sa grande taille et la forme de la pointe apicale des appendices intermédiaires, qui est seule présente. Son plus proche parent est *improvisus*, mais il n'a guère de caractères communs avec les *Metanoea*."

Additional diagnosis. Based upon the ancestral divergence of the spine pattern on the paramere *Drusus spelaeus* is a member of *Drusus spelaeus*

species complex in the *Drusus mixtus* species group and has no relation to *Drusus improvisus*, to the nominate species of the *D. improvisus* species complex in the *Drusus bosnicus* species group.

Drusus valserinensis Coppa & Olah, sp. nov.

(Figures 759–766)

Material examined. Holotype: **France**, Department Ain, Mijoux, source Perissode Valserine, 1008 m, 25.VIII.2014, leg. G. Coppa (1 male, OPC). Allotype: same as holotype (1 female, OPC). Paratype: same as holotype (1 male, OPC).

Diagnosis and description. We have two males and a single female specimens of this new species close to *Drusus spelaeus*, but differs by having the lateral profile of the entire dorsal branch of the paraproct diverged, differently shaped: the very apices are rounded hooked, not hooked in right angle; there is a pair of basal hump-like lobes developed very pronounced; there is subapical pair of small lobes; as a result the shape of dorsal excision in the lateral profile is completely different.

Female description. Female genitalia. Tergite of segment IX forming short tube, open ventrally, with rounded mesal excision and low rounded apical margin of the lateral lobes in dorsal view; the lateral setose lobe of sternite IX vertical. Segment X membranous and embedded inside segment IX and encircling anus; supragenital plate of segment X well-developed and quadrangular with slightly concave apical margin in lateral view. Median lobe of the vulvar scale (lower vaginal lip) present, triangular half as long as the latral lobes. Dorsal profile of the vaginal sclerite complex long, narrowing anterad.

Etymology. named after the locus typicus.

Drusus tenellus species group

Drusus tenellus species group is integrated through ancestral divergence by the remarkable basal fusion of the paramere pair with spine pattern similar to the *D. mixtus* species group. This unique and important ancestral character state transformation of paramere was overlooked,
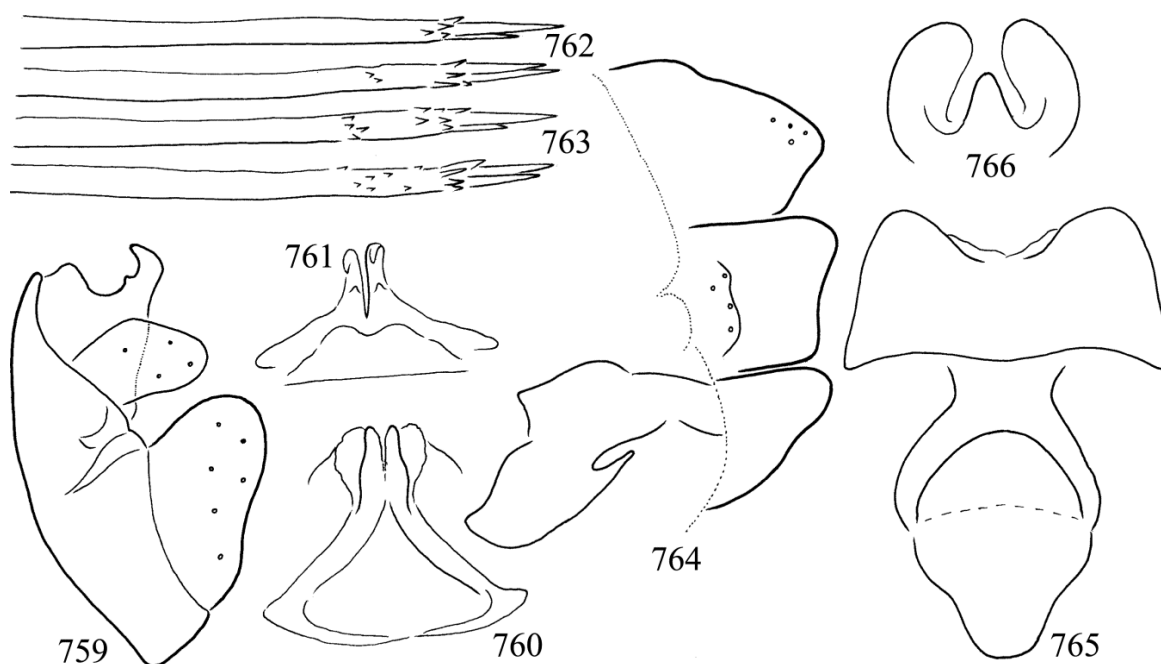
Figures 759–766. *Drusus valserinensis* Coppa & Oláh, sp. nov. Holotype: 759 = male genitalia in left lateral view, 760 = paraproct in caudal view, 761 = apical arms of the dorsal branches of paraproct in dorsal view, 762 =paramere in left lateral view. Paratypes: 763 = parameres in left lateral view. Allotype: 764 = female genitalia with vaginal sclerite complex in left lateral view, 765 = tergite IX and dorsal profile of vaginal sclerite complex in dorsal view, 766 = vulvar scale in ventral view.

not recognised properly in the taxonomy of the subfamily. This mere fact demonstrates very clearly how much and why the paramere and most fine structure have been neglected in the phenomics to differentiate between taxa due to over-financed focus with resources and attention to the genomics of the blind neutral DNA markers in the western taxonomy.

Drusus botosaneanui Kumanski, 1968

(Figures 767–770)

Drusus botosaneanui Kumanski, 1968: 214–216. "Fundort: Vitosa-Gebirge, Bojanski-Bach bei der Berghütte "Bor" (1.600 m Höhe), 3. IX. 1967. Holotypus (mit getrenntem Abdomen) und 2 Paratypen (alles in Alkohol) in der sammlung des Autors."

Material examined. **Albania**: Dibre county, Korab Mts, open stream above Fushe Korabit, 6 km E of Radomire, 1945 m, N41.49215°, E20.32738°, 28.VI.2007, leg. L. Dányi, Z. Fehér & D. Murányi (2 males, 1 female, HNHM). Erseke county, Grammos Mts, 2.8 km E of Starje, valley of Ali-kolare stream NW of Mt. Qukapeci, 1864 m, N40.361280° E20.754580°, 19.VII.2006, leg. Z. Barina, G. Király, Cs. Németh & D. Pifkó (1 male HNHM). Skrapa county, Backe, stream under the pass between Mt. Frengu and Mt. Faqekuq, 1913 m, 4.VII.2005, leg Z. Barina, D. Pifkó & D. Schmidt (5males, 2 females HNHM). **Bulgaria**: Vitosha Mts., Kladnitsa, Sv. Nikola, Tanchovitsa, N42°34'02.9", E23°11'41.4",

1100 m, 3.X.2011, light, leg. Á. Ecsedi, T. Kovács, G. Puskás, (3♂, OPC). Rhodopi, Yadenitza above Golyamo Belovo, 1167 m, N42°06'15", E23°54'11", 6.IX.2012, at lamps, light traps leg. S. Beshkov & M. Beshkova, (1 male, 1 female, NMNHS). Eastern Rhodopi, above Shumnatitza Village, Kirkovo District, 470 m, N41°16'32", E25°21'48", 11.X.2012, at lamps, light traps leg. S. Beshkov & M. Beshkova, (10 males, NMNHS, 8 males, OPC). Central Stara Planina, Central Balkan national Park, below the parking place of Pleven Chalet above Apriltzi Village, 865 m, N42°45'34", E24°54'29", 12.VIII.2012, at lights leg. S. Beshkov & M. Beshkova, (3 males, NMNHS). Iskar Gorge-Rzhana, near Brezov Dol-Osenovlag Village, 818m, N42.96697°E, 23.49273°, 8.IX.2012, at lamps, light traps leg. S. Beshkov & M. Beshkova, (28 males, 4 females, NMNHS, 18 males, 4 females, OPC). Rhodopi, on the road to Milevi Skali from Semchinovo, 941 m, N42°09'13", E24°04'12", 5.IX.2012, at lamps, light traps leg. S. Beshkov & M. Beshkova, (18 males, 12 females, NMNHS). E Rhodopi, Kirkovo distr., above Shumnatitza Village, 572 m, N41°15'53", E025°21'17" 14.VII.2015, light leg. S. Beshkov, B. Zlatkov & C. Plant (2 males, OPC). **Macedonia**, Pelagonia region, Pelister Mts, Nižepole, open brook at the ski station, N40°58.787', E21°15.218', 1375 m, 2.X.2013, leg. T. Kovács, D. Murányi, (2 males, 3 females; OPC). **Serbia**, Dolina reke Pcinje, Vrazji Kamen near Trgovishte Village, 663 m, N42°23'06", E022°03'06" 21.IX.2015, light leg. S. Beshkov & A. Nahirnic (1 male, OPC).

Diagnosis. Kumanski 1968: 214–216, "*Drusus botosaneanui* gehört zur Gruppe von *annulatus* (nach Schmid 1956) und steht *tenellus* am nachsten."
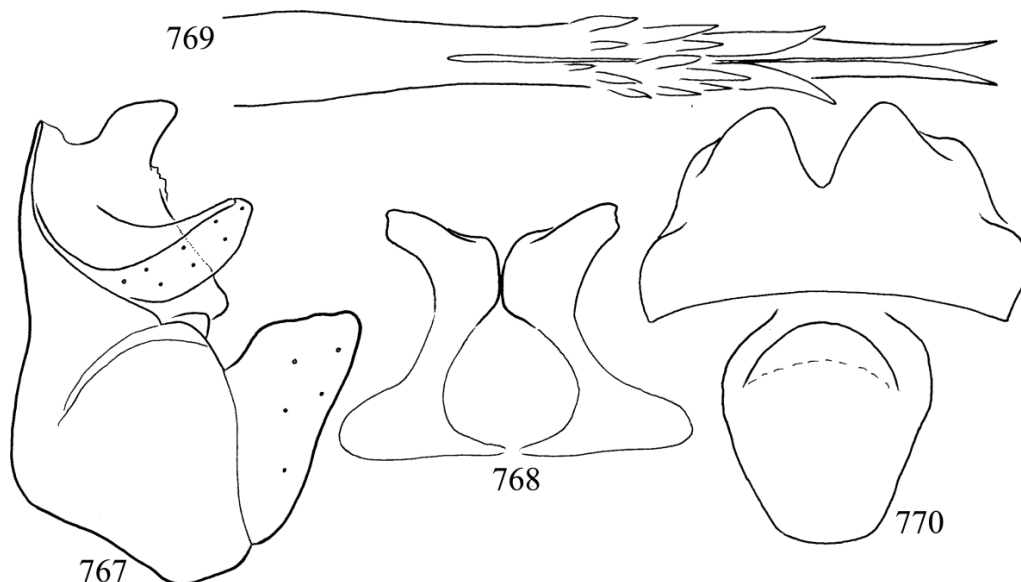
Figures 767–770. *Drusus botosaneanui* Kumanski, 1968. 767 = male genitalia in left lateral view, 768 = paraproct in caudal view, 769 = parameres in dorsal view, 770 = tergite IX and dorsal profile of vaginal sclerite complex in dorsal view.

Additional diagnosis. Based upon the ancestral divergences of the spine pattern on parameres *Drusus botosaneanui* belongs to the *Drusus tenellus* species group and has no close relation to the *D. annulatus* species group.

Drusus schmidi Botosaneanu, 1960

(Figures 771–775)

Drusus schmidi Botosaneanu, 1960: 288–290. „6♂ et 1♀ de Trescavica et 3♂ et 1♀ de Trnovo; le holotype ♂ et l'allotypes ♀ ont été choisis parmis les exemplaires de Trescavica (F. Schmid); 2 paratypes ♂: Deutsches Entomologisches Institut, Berlin; 4♂ et 1 ♀ parat.: L. Botosaneanu."

Material examined. **Bosnia & Herzegovina**: Bistrica, Dobro Polje, N43.59483°, E8.49553°, 12.VII.2008, leg. M. Bálint & S. Lelo (8 males, 4 females, OPC).

Diagnosis. Botosaneanu 1960: 288–290, "En comparant minutieusement les ♂ de *D. tenellus* qu'il avait capturé en Macédoine (Perister) et en Bosnie (Trescavica et Trnovo), le Dr. Schmid constata qu'en réalité seulement les premiers peuvent être considérés comme appartenant réel-lement à l'espèce de Klapalek, en ce qui concerne les exemplaires bosniaques "...la zone de spinules du VIIIe tergite est assez petite, indivise et située sur la ligne médiane. En comparant les exem-plaires bosniaques à celui de Macédoine et aux exemplaires de *D. tenellus* provenant de Rouma-nie (Retezat et Banat) je suis moi-même arrivé à la conclusion qu'il s'agit d'une nouvelle espèce, très proche de *tenellus*."

Drusus tenellus (Klapálek, 1898)

(Figures 776–779)

Catadice tenella Klapálek, 1898: 188–189. „Hungary, Vom Hochgebirge Retyezát, 2♂, 1♀".
Drusus tenellus (Klapálek, 1898): Mosely 1933: 499. *Catadice* synonymised with *Drusus*.
Drusus tenellus (Klapálek, 1898): Botosaneanu 1959: 71. Retezat, 800 m altitudine: 12.VIII, Valea Cernei: 1–2. VIII, Belareca spre varsarea in Cerna (de la Mehadia pina la confluenta): 31.VII. „Dintre toate speciile de *Drusus* din materiale noastre, este cea care coboara cel mai jos (pina la altitudini in jur de 150 m) si care populeaza gama cea mai euriterma de ape (riurile Belareca, Cerna, probabil riurile rezultate din unirea torentilor Rete-zatului)."
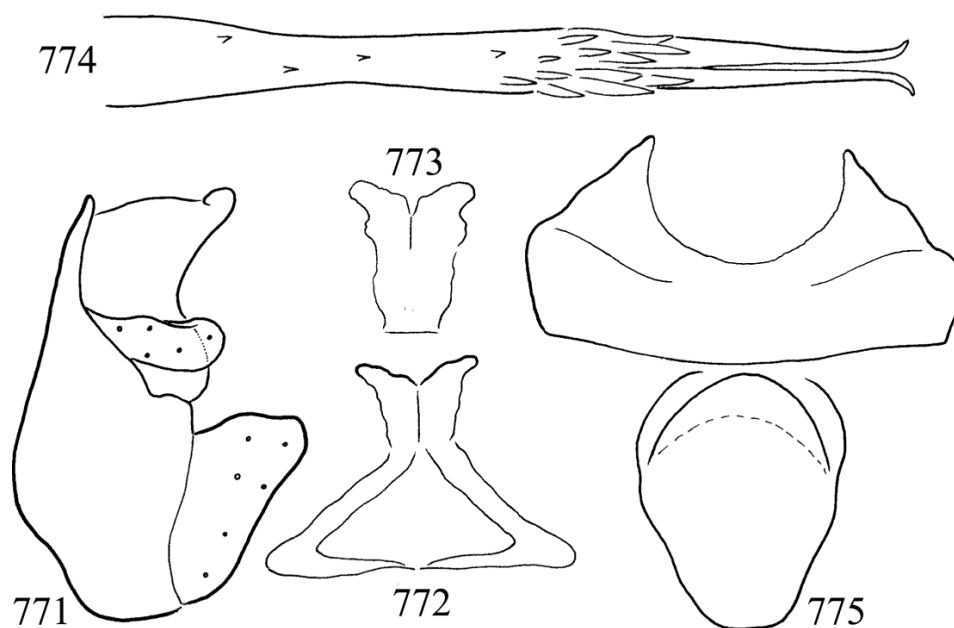
Figures 771–775. *Drusus schmidi* Botosaneanu, 1960. 771 = male genitalia in left lateral view, 772 = paraproct in caudal view, 773 = apical arms of the dorsal branches of paraproct in dorsal view, 774 = parameres in dorsal view, 775 = tergite IX and dorsal profile of vaginal sclerite complex in dorsal view.
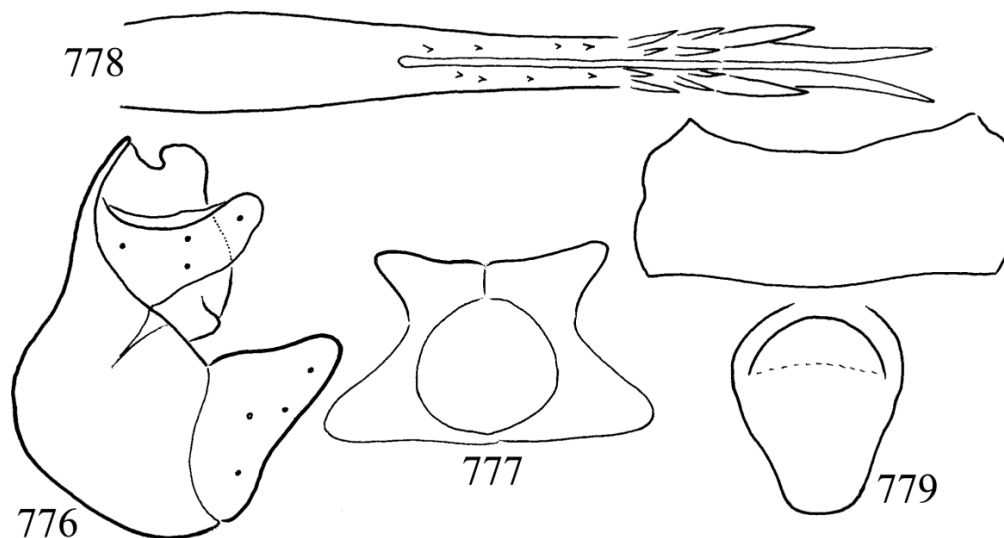
Figures 776–779. *Drusus tenellus* (Klapalek, 1898). 776 = male genitalia in left lateral view, 777 = paraproct in caudal view 778 = parameres in dorsal view, 779 = tergite IX and dorsal profile of vaginal sclerite complex in dorsal view.

Material examined. **Macedonia**, Vardar region, Jakupica Mts, Nežilovo, Babuna Stream S of the village, N41°38.238', E21°27.368', 630 m, 3.X.2013, leg. T. Kovács, D. Murányi, (15 males, 5 females; OPC). Southwestern region, Ohrid Lake Basin, Šum (Shum), Šum Spring Lake in the village, N41°10.974', E20°37.938', 705 m, 7.V.2014, T. Kovács, D. Murányi (1 male, OPC). **Romania**: Apuseni Mts. Somesul Cald la Obirec, 21–22.VII.2008, leg. C. Ciubuc, (12 males, 3 females; OPC). Retezat Mts. Gura Zlata, 13–14.VIII.2005, leg. C. Ciubuc (1 male, 1female; OPC). Argeş county, Făgăraş Mts, Căpătânenii Ungureni, small springlake by the Capra Stream along road No.7C, N45°34.605', E24°37.060', 1405 m, 29.VIII.2012 leg. T. Kovács, D. Murányi, J. Oláh (5 males, 1 female; OPC).

Diagnosis. Klapálek 1898: 188–189, "Körper rötlich gelbbraun, mit gelbbraunen Harchen, denen aber auf dem Scheitel und neben deen Augen schwarze Harchen beigemischt sind. Die obere anhänge schmal, länglich, schwach gekrümmt, in der Ansicht von oben stumpf dreieckig und ausgehöhlt; die mittleren Anhange verwachsen; untere Anhänge stark, aber kurz, kegelförmig, daher in der Seiten- und Rückenansicht dreieckig, stumpf."

Drusus vargai Oláh, sp. nov.

(Figures 780–782)

Material examined. Holotype: **Montenegro**, Durmitor Mts. Zabljá́k, 21–25.VII.1965, leg. Z. Varga (1 male, OPC).

Diagnosis and description. This new species is close to *Drusus schmidi*, but differs by having the paraproct diverged, differently formed. In lateral view the paraproct is slender, not robust; in dorsal view the slender apical arms of the dorsal branches of the paraproct form a deepp V-shaped apical excision that is lacking in *D. schmidi*; the lateral margins are smooth concave, not supplied with lateral humps. In caudal view the ventral branch of paraproct is high and narrow, not low and wide as well as the laterad directed arms are robust, not tapering.

Etymology. This beautiful yellow winged single male specimen was collected more than half century ago by our friend Prof. Zoltán Varga, renown lepidopterologist and oustanding theorist of speciation processsses during his balkan expedition together with his wife in the Durmitor Mts. This particular specimen has a rather remarkable history. The specimen was presented to the first author of this revision and its genitalia was cleared and its new species taxonomic position was established and the name of *Drusus flavus* was given in the year of 1965 by him. Later the new species was examined by Prof. Hans Malicky during his visit, who has recognised that the phallic apparatus with both adaeagus and the parameres has been lost. In spite of the lacking phallic organ here we desribe this new species and dedicate it to the collector, Prof. Z. Varga.
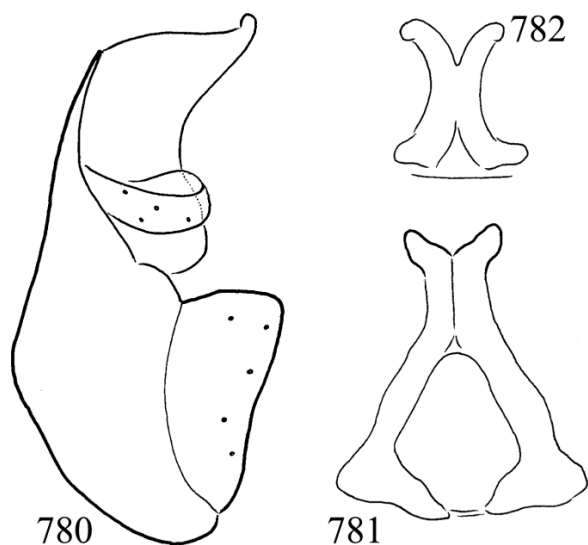
Figures 780–782. *Drusus vargai* Oláh, sp. nov. Holotype: 780 = male genitalia in left lateral view, 781 = paraproct in caudal view, 782 = apical arms of the dorsal branches of paraproct in dorsal view.

Drusus budtzi species group

Drusus budtzi species group is integrated through ancestral divergence by shifting all the spines to the very top of the paramere and as a consequence the loss of the apical shaft of the paramere preserved and present in all of the other species groups. It is remarkable how this two known species, *D. budtzi* of Corsica and Sardinia and *D. maculosus* of the Caucasus comprising this species complex, are related by both the male and female gross genital morphology and by the genital fine structure. Both species have similar architecture of the periphallic organs: (1) cerci are more or less integrated to paraproct, a unique character state partially present also in the *D. causcasicus* species complex of the *D. caucasicus* species group; (2) gonopods are vertically produced. Both species have similar gross morphology of female genital structures: (3) tergite IX short; (4) lateral setose lobes of sternite IX enlarged; (5) supragenital plate of segment X bipartite; (6) vaginal sclerite complex rather produced; (7) lateral profile of the vaginals sclerite complex is high and short; (8) presence of extremely enlarged dorsal articulation structure be

tween the supragenital plates and the vaginal sclerit plate; (9) and/or the presence of enlarged ventral articulation slerites between the internal continuation of the lateral lobes of the vulvar scale (lower vulvar lip) and the vaginal sclerite plate. (10) The most spectacular characte state transformation organised by integration at both species is the ancestral divergence in the paramere spine pattern. The single organising centre of the spine patters is shifted to the very terminal position on the paramere. *Drusus budtzi* species group is comprised of two species: *budtzi, maculosus*.

Drusus budtzi (Ulmer, 1913) comb. nov.

(Figures 783–788)

Potamorites budtzi Ulmer, 1913: 17–19. "Material; 1♂, Corsica, V. Budtz, 1912 leg.; aus der Sammlung der Herrn Esben Petersen mir freundlichst überlassen."

Leptodrusus budtzi (Ulmer, 1913): Schmid 1956: 82–83. *Leptodrusus budtzi* n'est connu que par deux spécimens, capturés à de nombreuses années d'intervalle en Corse. J'ai étudié le type."

Material examined. **France**, Corse, forêt domaniale de Valdu Niellu, tributary of the Golo River along the road D84, N42.292080°, E8.888240°, 1330 m, 4.V.2006, leg. Z. Barina (1 male, HNHM). Mausoleo, Haute-Corse, Sorgenti f. Tartagine m 1450, TL 21.IV.2000 leg. B. Salmini (1 male, OPC). Corsica –Mausoleo m 1200 torr. Tartagine T.L., 30. V.2000, leg. Bertuetti et al. (2 male, 1 female; OPC). **Italy**, Sardegna, torrente c/o sorg. Monte Limbara, 9.XII.2004, leg O. Lodovici & P. Pantini (3 males, 1 female; OPC).

Diagnosis. Ulmer 1913: 19, "Die Art is keine echte *Potamorites*; die langen Fühler, die fehlende faltentasche, die genitalfüsse des ♂ würden spater die Aufstellung einer neuen Gattung wohl rechtfertigen."

Schmid 1956: 82–83, "Les appendices intermédiaires ont la forme de deux forts ergots, assez largement distants l'un de l'autre, dirigés obliquement vers le haut, puis recourbés à angle droit vers l'avant; il sont très pointus à leur extrémité, ils sont soudés au bord interne des appendices supérieurs et il n'y a pas de corps du Xe segment individualisé." "…très peu proéminentes par rapport è ceux des autres espèces de la sous-famille."
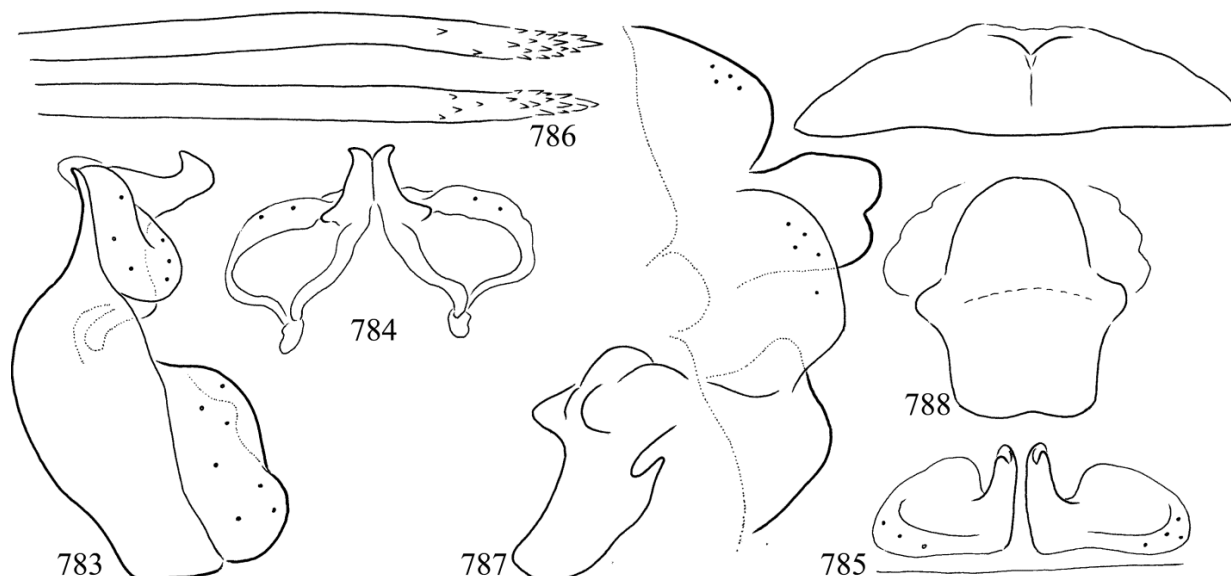
Figures 783-788. *Drusus budtzi* (Ulmer, 1913). 783 = male genitalia in left lateral view, 784 = paraproct in caudal view, 785 = apical arms of the dorsal branches of paraproct in dorsal view, 786 = parameres in dorsal view, 787 = female genitalia with vaginal sclerite complex in left lateral view, 788 = tergite IX and dorsal profile of vaginal sclerite complex in dorsal view.

Drusus maculosus **Malicky & Oláh, 1979**

(Figures 789–794)

Drusus maculosus Malicky & Oláh, 1979: 831–834. „Holotype (♂) and paratypes (2♀): Caucasus, Abhazia, stream flowing into Lake Mzy (2000 m), 17.VIII. (L. Zhilzovae), deposited into the Zoological Institute, Leningrad."

Material examined. Holotype and allotype: Caucasus, Abhazia, stream flowing into Lake Mzi, 17.VIII. (L. Zhilzovae), deposited in the Zoological Institute, Leningrad.

Diagnosis. Malicky & Oláh 1979: 834, „The systematic position of this extraordinarily striking species is not yet conclusive. Very probably it will become necessary to erect a new genus for it, but this must be reserved to a revision of the Drusinae on the basis of much more new material. Drusinae, without any other exception, are characterized by their very thin and delicate aedeagus and parameres. But *D. maculosus* sp. nov. imposes by its gigantic parameres and also with its distally broadly dilated aedeagus. Correspondingly the genital atrium of the female is also very wide. One could really ask oneself whether this species belongs indeed to the subfamily Drusinae. There are also some other characters which are unusual in Drusinae, such as the arrangement of the spiny patches on tergite 8, the size and form of subanal plate, the lack of the pencil pocket on the male hindwings, etc. But, as no character really contradicts to Drusinae (except, of course, the size of the parameres), the species is considered by us to be nevertheless as true Drusinae."

Additional diagnosis. Based on our ranking system this species, together with the nominate species *D. budtzi,* forms an independent lineage of the *Drusus budtzi* species group. The enlargement of paramere shaft is coupled with the shift of spine organising centre to the paramere terminal. The gigantic paramere, itself, is only one of the several ancestral paramere divergences in the *Drusus* genus: (1) basal fuse of parameres in the *D. tenellus* species group; (2); paramere enlargement in the *D. budtzi* species group; (3) complete loss of spines of setal origin in the *Drusus alpinus* species group; (4) miniuarization or abbreviation of the paramere in the *D. chauviniana* species group; (5) complete loss of paramere in the *D. torosensis* specie group.
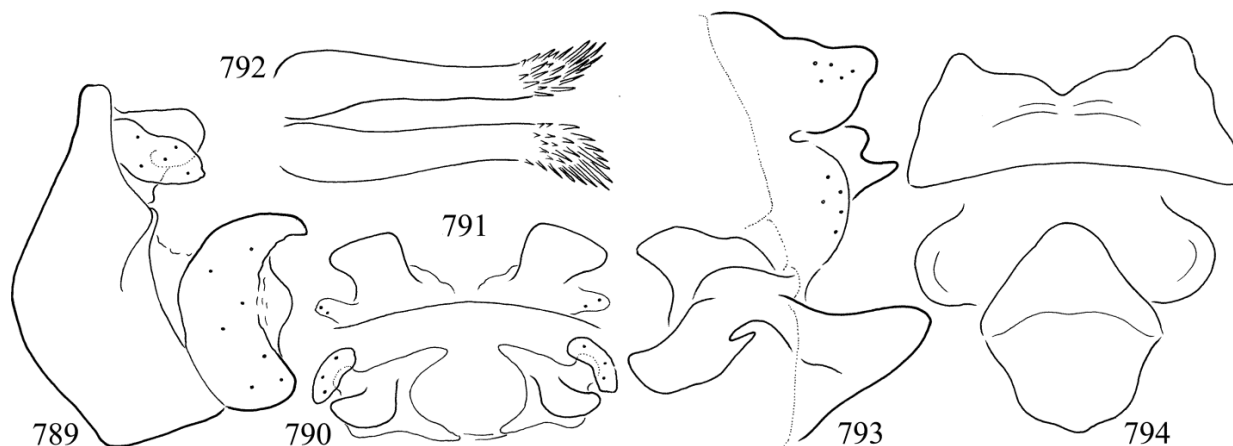
Figures 789–794. *Drusus maculosus* Malicky & Oláh, 1979. Holotype: 789 = male genitalia in left lateral view, 790 = paraproct in caudal view, 791 = apical arms of the dorsal branches of paraproct in dorsal view, 792 = parameres in dorsal view. Allotype: 793 = female genitalia with vaginal sclerite complex in left lateral view, 794=tergite IX and dorsal profile of vaginal sclerite complex in dorsal view.

Drusus alpinus species group

Drusus alpinus species group is integrated through ancestral divergence by the complete loss of all the paramere spines, that is by the loss or at least by the inactivation of the single spine organising centre, creating the bare paramere shaft without any spine. This particular paramere divergence, coupled with paraproct architecture as well as by female genital structures brings together into a well defined specis group the representatives of three formerly independent generic lineages: the valid genus *Drusus*, and the synonymized genera of *Cryptothrix* and *Metanoea*. *Drusus alpinus* species complex comprised of five species and two species complexes. The delineation of the species complexes in the species group is based on the paramere length and on the length of the IX tergite of female genitalia.

(1) *Drusus alpinus* species complex has long spineless paramere and long female IX tergite;

(2) *Drusus nebulicola* species complex has short spineless paramere and short female IX tergite.

Drusus alpinus species complex

Drusus alpinus species complex has long spineless paramere and long female IX tergit and comprised of three species: *alpinus*, *carpathicus*, *franzi*.

Drusus alpinus Meyer-Dür, 1875

(Figures 795–797)

Drusus alpinus Meyer-Dür, 1875: 395. "Herr Dietrich sammelte diese neue Art ziemlich zahlreich um den 19. Juni im Ursernthal und Unteralp am Gotthardt, unter *Potamorites biguttatus*."

Material examined. **Italy**, Torino, Traversella, Fondo, spring at Burdeivier tributary, 1350 m, 12.VII.2012. leg. Vincon (1 male, OPC). Piemonte, Tavigliano (BI), 1450 m, rivolo sorgentizio prima di Alpe Montuccia, N43.6683°, E8.0489°, 28.VI.2012, leg. O. Lodovici, P. Pantini & M. Valle (2 males, 1 female; OPC).

Diagnosis. Meyer-Dür, 1875: 395, Bei geschlossenen Flügeln hätte ich sie auch aus den grössern Stücken jener sehr veränderlichen Art kaum herauserkannt, wäre nicht die abweichende Spornzahl 1. 3. 3. (gegenüber von *Potamorites* 1. 2. 2 mir bei der genauem Durch-musterung aufgefallen. Die grislige Behaarung an Scheitel und Prothorax, die stark gebräunten Allerenden und Schrägadern am Thyridium, sowie die braune Längsstrieme in der Area clavalis machen indess die Art leicht kenntlich. Doch scheint sie ebenfalls mancher Veränderlichkeit unterworfen und sind jedenfalls über einige dieser sehr variabeln alpinen Arten die Acten noch nicht geschlossen.

Schmid 1956: 38, "Cette espèce est la seule de la sous-famille qui présente un fort dimorphisme sexuel dans la coloration."
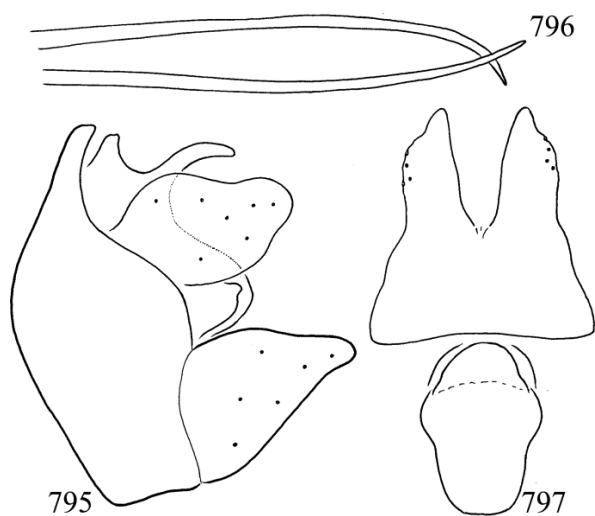
Figures 795–797. *Drusus alpinus* Meyer-Dür, 1875. 795 = male genitalia in left lateral view, 796=parameres in dorsal view, 797=tergite IX and dorsal profile of vaginal sclerite complex in dorsal view.

Drusus carpathicus Dziedzielewicz, 1911

(Figures 798–801)

Drusus carpathicus Dziedzielewicz, 1911: 206–209. „In Karpathibus Orientalibus in regione alpina (Pini Mughi) apud fontes. Mons Chomiak 27.V.–11.VI.1909 (supra 1300 m.s.m.). Czarnohora in montibus Dancerz et Howerla 30.V.1909.–10.VI.1910."

Drusus carpathicus Dziedzielewicz, 1911: Szczesny 1980: 462. Specimens in Cracow Museum: „1♂; this specimen is labelled with the following notes: „Czarnohora, Dancerz 31.V.1911" and „*Drusus carpathicus* Dz. ♂ ver. C. Tomaszewski", and is registered in the inventory under number 8/25. Dziedzielewicz(1911) desdribed the species on the basis of specimens collected „near the summit of Chomiak by springs of the stream Roskolski during the period 27.V.-11.VI.1909 and at Czarnohora near Howerla and Dancerz on the days 30.V.1909 and 10.VI.1910". Dziedzielewicz also noted that all the specimens collected in this period were deposited in the museum at Lvov. Therefore the male deposited at Cracow does not belong to this series of specimens which enabled Dziedzielewicz to decsribe a new species, nevertheless it does come from the „locus typicus".

Drusus carpathicus Dziedzielewicz, 1911: Szczesny & Godunko 2007: 33. "3♂♂, 3♀♀; East carpathians, Czarnohora Massif, Gorgany Massif (Chomiak); 1♂ and

1♀ collected on slopes of Chomiak Mt, 3.VI.1909 and 11.VI.1909, respectively (No E24.12.06.04/02 and 03), and 1♀ caught 9.VI.1910 in the Czarnohora massif (No E24.12.06.04/01) belong to the series of specimens on base of which Dziedzielewicz had described the species; the male from Chomiak is designated as a lectotype herein. To that series belong also several specimens stored in NMP (Chvojka, pers.comm.)."

Drusus carpathicus Dziedzielewicz, 1911: Szczesny & Chvojka 2008. Altogether 2♂♂ and 4♀♀ paraletotype specimens were collected during 27.V.–11.VI.1909 in the East Carpathians (Chomiak) and deposited in NMP.

Material examined. **Romania**, Maramureş county, Maramureş Mts. Borşa - Băile Borşa (Borşa - Borsabánya), brooks between Stanchi hut and Mt. Cearcănul, N47°39.801', E24°52.663', 1687 m; 22.V.2007, leg. Cs. Csuzdi, L. Dányi, J. Kontschán & D. Murányi (6 males, 1 female, HNHM). Maramureş county, Maramureş Mts, Borşa – Băile Borşa, Vulcănescu brook and alpine grassland at Mt. Preluca Cerbului, N47°38.674, E24°52.045', 1703 m; 23.V.2007, leg. Cs. Csuzdi, L. Dányi, J. Kontschán & D. Murányi (2 males HNHM). Munţii Iezerului, 1050 m, N45.45°, E25.02°, 4.VIII.2006, leg. M. Bálint (4 males, OPC). Radnei Mts. near Prislop Pass, N47°36'27.61", E 24°52'00.32", 1407 m, leg. Cs. Balogh (1 male, OPC).

Diagnosis. Dziedzielewicz 1911: 206, "Habitu coloreque *Druso bosnico* Klap. similis. Capita nigro, in fronte et occipite nigro piloso; protorace rufo, nigro piloso; meso et metathorace nigris; abdomine griseo. Appendices praeanales maris oblongae, lappaceae, pilosae; ungues praeanales perlongi, recti, apice hamato; pedeg genitales bipartiti, in aspectu supero excavati, apice arcuato exciso, in aspectu laterali conici, paullulum curvat."

Drusus franzi Schmid, 1956

(Figures 802–805)

Drusus franzi Schmid, 1956: 40–41. "Holotype ♂: Alpes orientales (Glünalpe, Hochalp), 7.X.1892 (H. Franz), déposé dans la collection Döhler."

Material examined. **Austria**, Styria, Hebalm, Filzmoos 1400 m, 17.V.1988, leg. H. Malicky (1 male, OPC).

Diagnosis. Schmid 1956: 41, "Dr. franzi est très voisin d'*alpinus*; il s'en distingue principalement par ses ailes antérieures fortement marquées de brun, par la très grande zone spinulifère du VIIIe tergite et par la forme des 3 paires d'appendices génitaux."
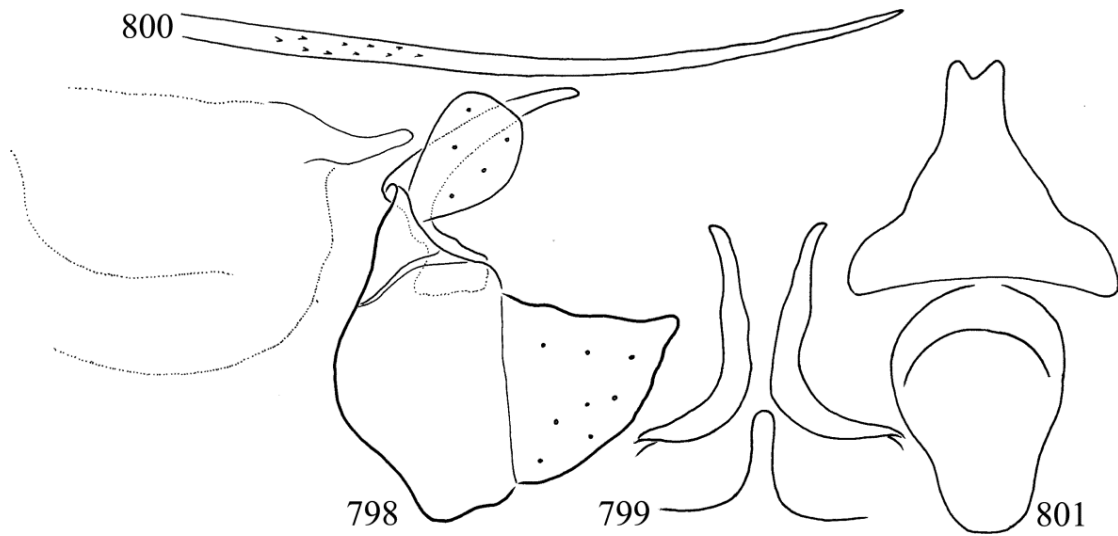
Figures 798–801. *Drusus carpathicus* Dziedzielewicz, 1911. 798 = male genitalia in left lateral view, 799 = apical arms of the dorsal branches of paraproct in dorsal view with the apicomesal digitate process of tergite VIII, 800 = paramere in dorsal view, 801 = tergite IX and dorsal profile of vaginal sclerite complex in dorsal view.
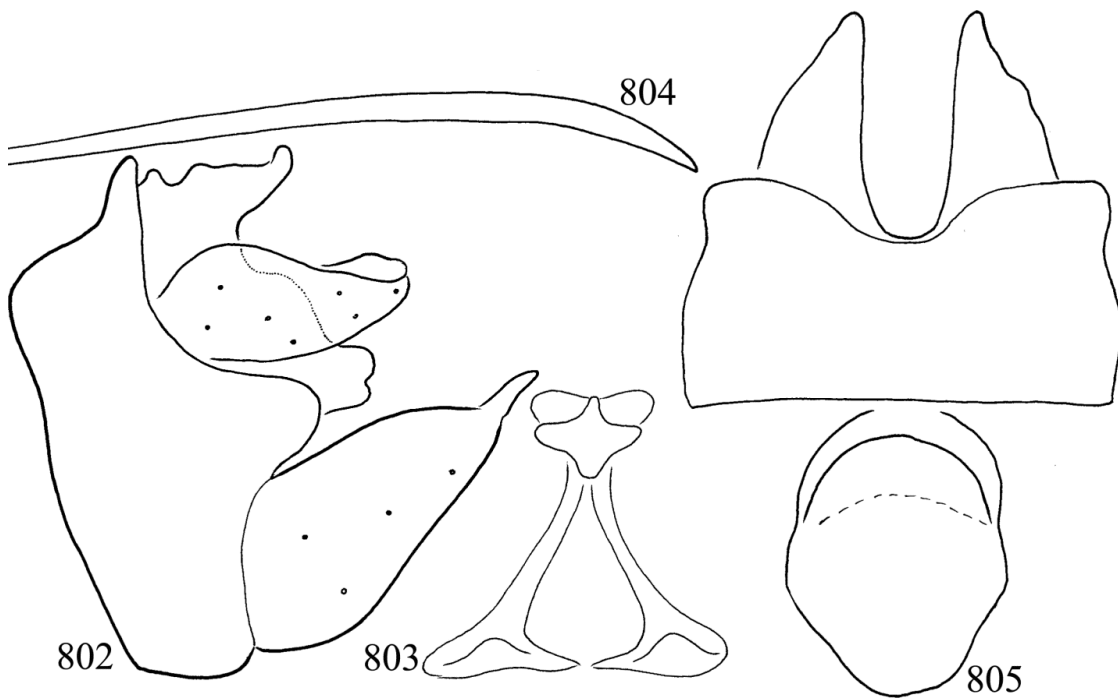
Figures 802–805. *Drusus franzi* Schmid, 1956. 802 = male genitalia in left lateral view, 803 = paraproct in caudal view 804 = paramere in dorsal view, 805 = tergite IX and dorsal profile of vaginal sclerite complex in dorsal view.

Drusus nebulicola species complex

Drusus nebulicola species complex has short spineless paramere and short female IX tergit and comprised of two species: *euphorion*, *nebulicola*.

Drusus euphorion (Malicky, 2002) comb. nov.

(Figures 806–809)

Metanoea euphorion Malicky, 2002: 7. "Holotypus: ♂ und 1♂, 1♀ Paratypen: France, Alpes-Maritimes, Wildbach an der östlichen (E) Auffahrt zum Col de Turini, 1200 m, 43°59'N, 7°25'E, 29.VI.2001."

Material examined. Holotype on loan from Malicky Private Collection.

Diagnosis. Malicky 2002: 7, "Obwohl auch dieser Art dem einfachen Muster der ♂ Kopulationsarmaturen der Drusinae folgt, ist sie an dem kleinen paarigen Dornenfeldern des 8. Tergits sofort kenntlich; ich kenne keine andere Drusinae-Art mit diesem Merkmal. *Metanoea* stelle ich sie wegen ihres Habitus mit der einheitlich gelben Farbung, mit der sie sehr an *M. rhaetica* Schmid, 1955 und *M. flavipennis*, Pictet 1834 erinnert, die ganz anders geformte Dornenflecken am 8. Tergit haben."
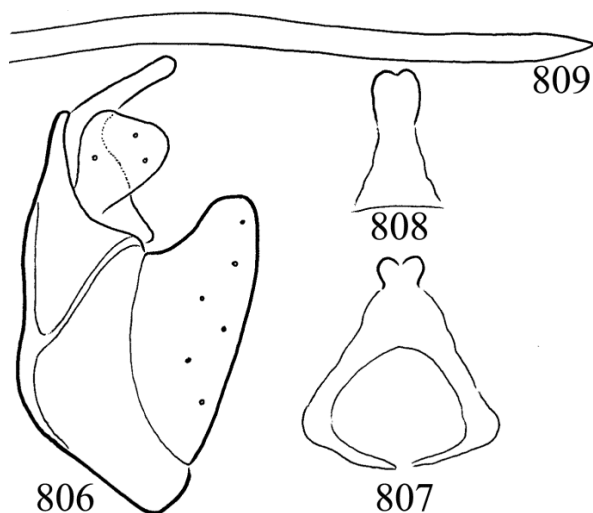
Figures 806–809. *Drusus euphorion* (Malicky, 2002). 806 = male genitalia in left lateral view, 807 = paraproct in caudal view, 808 = apical arms of the dorsal branches of paraproct in dorsal view 809 = paramere in dorsal view.

Drusus nebulicola (McLachlan, 1867) comb. nov.

(Figures 810–813)

Cryptothrix nebulicola McLachlan, 1867: 56–57. "Ein Mann von der Maienwand (Canton Wallis) ist in Hagen's Sammlung unter dem M. S. Namen *Enoicyla nebulicola*. Ein Weib von Brévent (Savoien) ist in der Sammlung von Pictet's Typen im britischen Museum, ist aber in Pictet's Werk nicht beschrieben. Ich besitze 5 Mannchen und 5 Weibchen, von Stainton am 25. Juli bei Disentis (Graubündten) 3835 ü. M. gefanden, wo die Art an Rosen- und Hollundergestrauch an den Ufern des Baches daselbst gemein vorkam."

Cryptothrix nebulicola McLachlan, 1867: McLachlan 1876: 182. "Savoy (Brevent, Pictet). Switzerland (Dissentis in July, Stainton, common; Maienwand, in Hagen's collection; Hospice St. Bernard; Lucendrothal, Gotthard, July, Dietrich; Gadmenthal, July, Meyer-Dür). Tyrol (Meran, in Hagen's collection)."

Cryptothrix nebulicola McLachlan, 1867: Schmid,1956: 75. Cette espèce a été signalée de Suisse, Savoie, Tyrol et Bade. En Suisse, elle est extrêmement commune et vole parfois en grande quantité. Avec Met. Flavipennis, c'est une des rares espèces de la sous-famille que l'on trouve durant tout l'été."

Drusus alpimar Botosaneanu & Giudicelli, 1983: 174–176. "Matériel et localité. – Plusieurs exemplaires des deux sexes, capturés le 8.IX.1982 par J. Giudicelli sur le Jalorgues, affluent de la Tinée (bassin du Var, Alpes Maritimes, France), au dessus de Saint Delmas-le-Selvage. Matériel conservé en alcool; holotype ♂ et allotype ♀, aux abdomens préparés au KOH, gardés au Zoölogisch Museum de l'Université d'Amsterdam; des paratypes (3♂, 1♀) sont dans la collection de J. Guidicelli à Marseille." "Il nous semble assez évident que la nouvelle espèce appartient au "groupe de *mixtus* Pictet"." Sipahiler 1993: 68, synonymised with *Cryptotrix nebulicola*.

Chryptotrix nebulicola McLachlan, 1867: Pauls *et al.* 2008: 781. "*C. nebulicola* is basal to a highly supported clade comprising members of the genus *Drusus*."

Chryptotrix nebulicola McLachlan, 1867: Vitecek *et al.* 2015: 85–86. "Material examined. 1 male: Italy, Torino, Traversella, Fondo, Burdeivier brook; leg. Vincon; 12.VII.2012. 12 males: Italy, San Marco Pass; leg. Graf; 14.VIII.2000; in coll WG. Type locality. Switzerland, Canton of Valais, Maienwand (Grimselpass)."

Material examined. **Italy**, Lombardia, Carona (BG), Val Sambuzza, 15.VII.1994, leg. Federici (5 males, 2 females; OPC). Mezzoldo (BG) 1400 m, affluente fiume Brembo Pra del Muto, 15.VIII.1997, leg. Albrici (2 males, 4 females; OPC). Lombardia, Valbondione (BG), 1862 m, Foce Trobio-Lago Barbellino, 16.VII.1990, leg. Calandrina (1 male, OPC). **Switzerland**, Val Münstair, 20. VII. 2006, leg. W. Graf (5 males, 1 female; OPC).
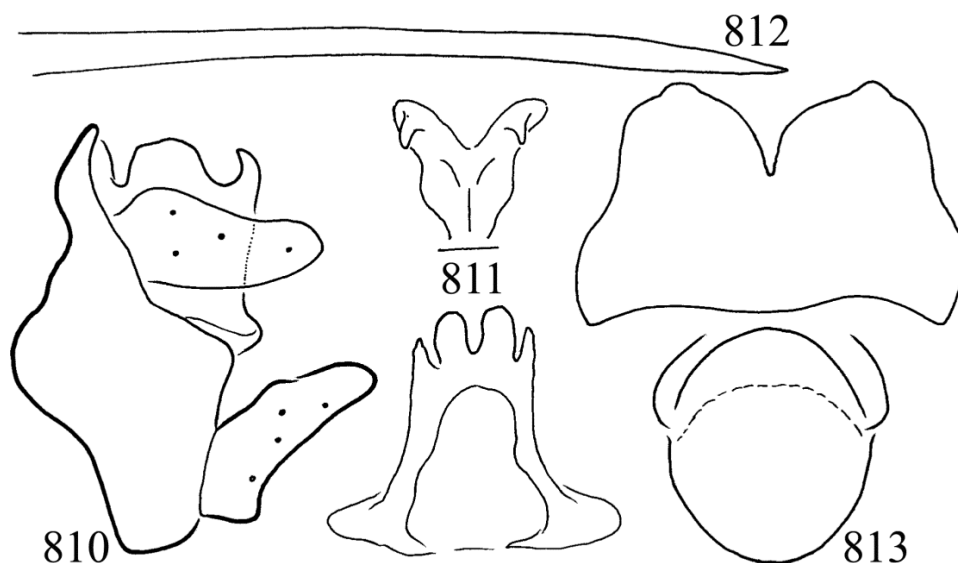
Figures 810–813. *Drusus nebulicola* (McLachlan, 1867). 810 = male genitalia in left lateral view, 811 = paraproct in caudal view and the apical arms of the dorsal branches of paraproct in dorsal view, 812 = paramere in dorsal view, 813 = tergite IX and dorsal profile of vaginal sclerite complex in dorsal view.

Diagnosis. McLachlan 1867: 56–57, "Eine sehr bemerkenswerthe Gattung; die Behaarung der Flügel ist starker als bei irgend einer andern Gattung der Limnephilidae (Chaetopterygidae) und gleicht derjenigen von *Sericostoma*. Die langen Haare der beiden Costulae hinter der Faltentasche der Hinterflügel des Mannchen sind im Rühezustand verborgen, stehen aber aufrecht, sobald dieselben ausgespannt werden. Dieses Genus kömmt wahrscheinlich vor *Apatania* zu stehen."

Drusus chauvinianus species group

Drusus chauvinianus species group is integrated through ancestral divergence by the miniaturization of the entire paramere. This species complex is comprised of one species: *chauviniana*.

Drusus chauvinianus (Stein, 1874) comb. nov.

(Figures 814–820)

Anomalopteryx chauviniana Stein, 1874: 251–252. "Ich sah drei Parchen, welche von Fraulein Marie von Chauvin, der zu Ehren ich die Art zu benennen mir erlaube, in Schlesien, vemuthlich unweit Warmbrunn, gefanden sind."

Anomalopterygella Fischer, 1966: 131. New name for *Anomalopteryx* Stein, 1874. Preoccupied by Reichenbach, 1853 in Aves.

Material examined. **Czech Republic**, E Bohemia, Orlické hory Mts, Bela river above Skuhrov (420 m), 19.VIII.1996 leg. P. Chvojka (3 males NMPC; 1 male, OPC). S Bohemia, Sumava Mts, Vydra river, Rejstejn (560 m), 20.VIII.1990 leg. O. Hovorka (1 male, NMPC); Vydra river, Antygl (900 m), 27.VII.1991 leg. P. Chvojka (1 female, NMPC). **France**, Massif-Central, Department Cantal, Laveissière, Alagnon Camping, 900 m, 17.VIII.2011, leg. G. Coppa, (8 males, 2 females; OPC). Massif-Central, Department Cantal, Laveissière, Alagnon, 920 m, 13.IX.2014, leg. G. Coppa, (2 males, 1 female; OPC). Massif-Central, Department Ardèche, Sainte Eulalie, La Loire le Long D116, 1220 m, 15.VIII.2012, leg. G. Coppa, (3 males, 1 female; OPC). Pyrénées, Department Pyrénées-Orientales, Escaldes, Ru du Lac Sobirans Estang Sobirans, 2340 m, 19.VIII.2011, leg. G. Coppa, (3 males, 1 female; OPC). Pyrénées, Department Pyrénées-Orientales, Escaldes, Angoustrine-Villeneuve-des-Escaldes, Torent d'Esparbe amont Lac Bouilleuse, 2150 m, 26.VIII.2011, leg. G. Coppa, (3 males, OPC). Pyrénées, Department Pyrénées-Orientales, Porte Puymorens, Angoustrine-Villeneuve-des-Escaldes, Ru d'en Gardia, 1980 m, 21.VIII.2011, leg. G. Coppa, (1 male, OPC). Department Vosges, Le Valtin, La Combe, 900 m, 19.X.2013, leg. G. Coppa, (1 male, OPC).
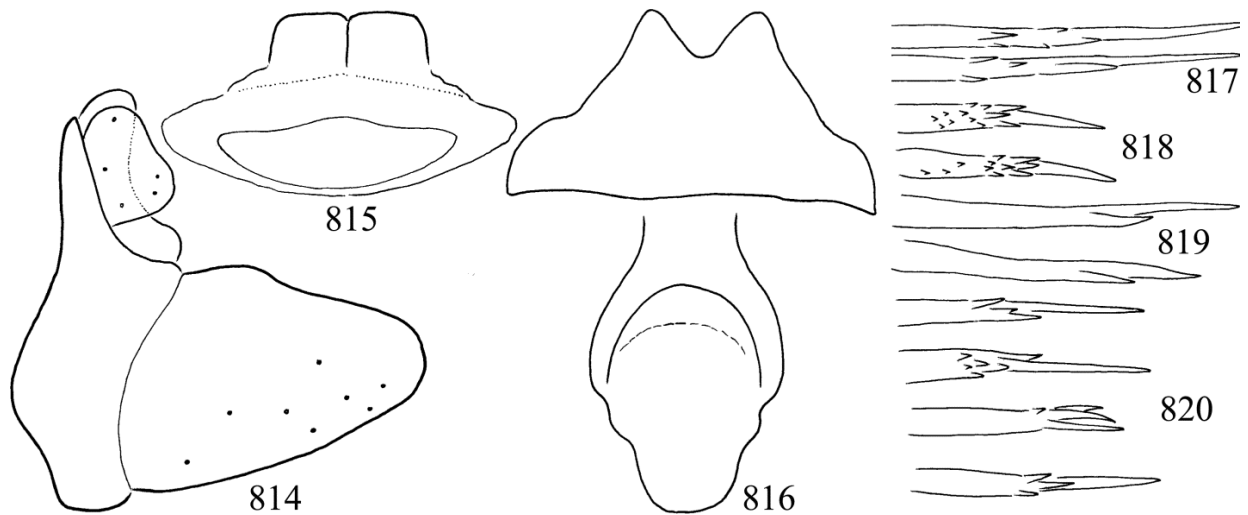
Figures 814–820. *Drusus chauvinianus* (Stein, 1874). 814 = male genitalia in left lateral view, 815 = paraproct in caudal view, 816 = tergite IX and dorsal profile of vaginal sclerite complex in dorsal view. Parameres in left lateral view from various mountain ranges: 817 = Pyrenées, 818 = Massive Centrale, 819 = Vosges, 820 = Sumava.

Diagnosis. Stein,1874: 251–252, "Das Tier ist der Unterhalfte entlang scherbengelb, oben mehr braun; die Flügel blass strohgelb; da indessen beide Gesclechter in Form und Farbung einzelner Theile etwas verschieden sind, wird es zweckmassiger sein, jedes für sich zu beschreiben."

Additional diagnosis. This is a true *Drusus* species having only brachyptery of sexual dimorphism as a result of stochastic genomic processes coupled to the adaptive integration in the reproductive isolation by sexual selection. We have found divergences in the caudal profile of the paraproct and especially in the pattern of paramere spine structure between poulations sampled in Pyrenées, Massive Central, Vosges and in Czeckia. However we need more population sampling to establish their incipient sibling species status.

Drusus torosensis **species group**

Drusus torosensis species group is integrated through ancestral divergence by the complete loss of the parameres. This species group comprised of one species: *torosensis*.

Applying our character ranking system the genus *Hadimina* was synonymized with the genus *Drusus* and downgraded here as an independent species group based on the ancestral divergence of the paramere loss. Originally the genus *Hadimina* was erected by eight character states: (1) the 4-segmented maxillary palps of females; (2) the partially notched apical part of the antennae; (3) the lobes of tergit 8 bifurcate; (4) the shape of segment 9; (5) the location of inferior appendages with sclerotized apical parts; (6) the sclerotized dorsal parts of the preanal appendages; (7) the short and ventrad curved aedeagus; (8) and the lacking parameres.

According to our character ranking system supported by theoretical background, elaborated and adapted to the Drusinae subfamily the original eight generic level character states are either stochastic body modifications, secondary sexual traits or species level characters and occuring also in other species groups of the *Drusus* genus.

Drusus torosensis **(Sipahiler, 2002) comb. nov.**

(Figures 821–822)

Hadimina torosensis Sipahiler, 2002: 240–248. "Type material: Holotype ♂, and paratypes (7 ♂ and 5 ♀), Turkey, Konya, Hadim, Koruala, Yenice Köyü, Borini cave,

Toros Mountains, 1700 m, 23.VI.1998, other paratypes (22♂, and 5♀), same place 27.VI.2000, (36°58'N, 32°25'E), leg. and coll. Sipahiler; 1 ♂ and 1 ♀ paratype deposited in the Museum für Naturkunde Berlin."

Material examined. The single male and female paratype deposited in the Museum für Naturkunde Berlin were available on loan for the present study.

Diagnosis. Sipahiler 2002: 243–248, "The new genus *Hadimina* has many aberrant characters, which make the relationship to the subfamily difficult. In the subfamily Drusinae the antennae are filiform and never notched; the preanal appendages are never sclerotized; the aedeagus is smooth, long and cylindrical, bearing always parameres and the female have 5-segmented maxillary palps. The new genus *Hadimina* is unique for having 4-segmented maxillary papls of females within Limnephilidae. The segments of the apical part of the antennae are notched, the preanal appendages are sclerotized on the dorsal parts and the short aedeagus is curved towards ventral, lacking the parameres. Nevertheless, because of the similarities on the venation of the wings, the genitalia in general and larval characters, the new genus is assigned to the subfamily Drusinae. It differs from the other genera of the subfamily Drusinae in having many different characteristics in the male genitalia, especially apical lobes of tergit 8, the shape of segment 9, the location of inferior appendages with sclerotized apical parts and a short and curved aedeagus lacking the parameres. The new genus *Hadimina* appears the most primitive genus in the subfamily Drusinae in having the following features: The wings are dilated and rounded apically, radius is almost straight, complex development of tergite 8, segment 9 is broadly curved inwards, basal lobes of the imtermediate appendages, sclerotized preanal appendages, locating caudally and the short and curved aedeagus.

Among the genera of the subfamily Drusinae, the new genus has some affinities to the genus *Anomalopterygella* Fischer, 1970. Although the male of *Anomalopterygella* has reduced fore wings, the fore wings of the female *Anomalopterygella* are large and rounded apically similar to that of *Hadimina*, which is a primitive feature

in the Limnephilidae (Schmid 1956). In both genera the fore wings possess erected hairs on the veins. In *Hadimina torosensis* the first tarsal segment of the fore legs of the males is short and as broad as the tibia, like *Anomalopterygella*, that has also short and broad first tarsal segment on the fore leg. The adults of both genera have abdominal tracheal gills. In *Hadimina* the amount of the abdominal gills are variable but found in a large number between the first and 8th segments locating dorsal, medium and ventral part of the pleural region; *Anomalopterygella* has fewer gills from the first to eight segments. In other genera of the subfamily Drusinae only the male of the genus *Cryptotrix* possesses a few abdominal gills locating on the first, third and the fourth segments. To have abdominal gills could be ralated to the mode of life of *Hadimina torosensis* sp. nov., which seems very dependent to the water and the humidity. The alive collected 20 specimens died in half an hour. Shrinking of abdominal gills of these specimens was observed."

Additional diagnosis. All of the original generic state characters are either species group or species level characters in the *Drusus* genus. Wing shape, maxillary palp and antennal modifications are stochastic body alteration integrated in long isolation by neutral and random genomic, epigenomic, and eco-evo-devo processes, under the internal and external flux of mutations, permutations, transmutations and perturbations. Similarly, most of the shape divergences in the genital structures are random, some divergence, like paramere loss, are fixed in adaptive genomic processes of reproductive isolation by sexual selection.

Unplaced *Drusus* taxa!

Here we have presented the available taxonomic documentation of five species we were unable to receive for examination in spite of several trials to borow types or any specimens form the authors. The published drawings were not enough to establish their exact taxonomical position according to our ranking system. Without fine structure drawings, especially without paramere drawings of high resolution it is impossible to determine their species group character status.

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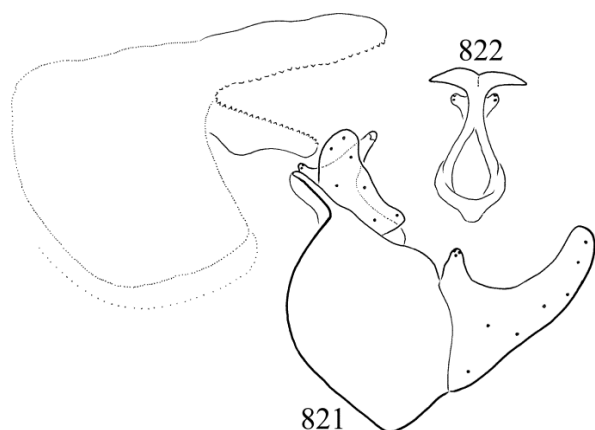
Figures 821–822. *Drusus torosensis* (Sipahiler, 2002). 821 = male genitalia in left lateral view, 822 = paraproct in caudal view.

Drusus anatolicus (Sipahiler, 1986) comb. nov.

Metanoea anatolica Sipahiler, 1986: 116–118. "Holotype ♂, allotype ♀ and paratypes (5♂♂, 1♀): Turkey, Rize, Ikizdere, Basköy, 2080 m, 19.VII.1984 leg. and coll. Sipahiler. Other paratypes (5♂♂, 2♀♀) the same place, 2200 m, 20.VII.1984 leg. and coll. Sipahiler."

Material examined. No type or other material was available for study!

Diagnosis. Sipahiler 1986: 116–118, "Differs from the other two species in the dark colour of the body and the length of wings. Schmid (1956) stated in his revision of the subfamily Drusinae that thes pecies of *Metanoea* can easily be recognised by their small size very light color and slender and delicate appearance. However *Metanoea anatolica* does not display the above features and may be mistaken for *Drusus* were it not for the fact that *Metanoea* does not possess the pouch and pncil of hairs on the posterior wing which is a very distinctcharacteristic of the genus *Drusus*"

Drusus demirsoyi Sipahiler, 1983

Drusus demirsoyi Sipahiler, 1983: 240–241. "Holotype ♂, allotype ♀ and paratypes (1♂, 1♀): Bolu, Yedigöller. 750 m, 6.VI.1981, leg. and coll. Cakin."

Material examined. No type or other material was available for study!

Diagnosis. Sipahiler 1983: 241, "This species is well characterized by the shape of most pieces of the genitalia of males, especially the sclerotized zone of the 8th tergite and the intermediate appendages. It is somewhat similar to *Drusus bureschi* from Bulgaria (Kumanski 1973). The differences in the sclerotited zone, intermediate and inferior appendages are evident."

Drusus gueneri Sipahiler, 1995

Drusus gueneri Sipahiler, 1995: 217–219. "Holotype ♂, allotype ♀ and paratypes (27♂♂, 8♀♀): Turkey, Ispara, 10 km south of Yenisarbademli, Dedegöl mountains, 1500 m, cave Pinargözü, 37°37'N, 31°17'E, 31.V.1993, same place, 5.VIII.1993 1♂; Beyschir, Kurucuova, direction to the summit of the Dedegöl mountains, before Karagöl, 1700 m, 37°40'N, 31°19'E, 6.VIII.1993, 10♂♂, 1♀, leg. and coll. Cakin."

Material examined. No type or other material was available for study!

Diagnosis. Sipahiler 1995: 218–219, "*Drusus gueneri* sp. nov. is related to *D. serbicus* Marinkovic, 1971 (Marinkovic-Gospodnetic 1971c) and *D. siveci* Malicky, 1981 from the Balkans and can easily be distinguished from these species by several parts of the male genitalia; differences in the shape of the spinulose zone, intermediate appendages and inferior appendages are especially evident."

Drusus hackeri Malicky, 1986

Drusus hackeri Malicky, 1986: 4–6. "Material. – Holotypus ♂: Türkei: Provinz Bolu, 40°40'N, 31°21'E, Abant Silsilesi, 1000 m, 4 km NE von Abant gölü, 3.IX.1985, H. Hacker leg. – In meiner Sammlung."

Material examined. No type or other material was available for study!

Diagnosis. Malicky 1986: 4–6, "Diese Art gehört zu der auf der Balkanhalbinsel und in Kleinasien vorkommenden Gruppe um *D. discophorus* Radovanovic, 1942 und steht von den derteit bekannten Arten sicherlich *D. demirsoyi* Cakin, 1983 am nachsten (Malicky 1983: 164). Bei diesem sind aber die mittleren Anhange in Kaudalansicht nicht breit rechteckig, sondern

spitz. Auch *D. muchei* Malicky, 1986 (Sipahiler & Malicky i. Dr.) von Izmir steht ihr ferne, obwohl dieser sofort durch die andere Form des Dornenfeldes des 8. Tergits und das Fehlen der Dornen an den mittleren Anhangen unterscheidbar ist."

Drusus serbicus Marinkovic-Gospodnetic, 1971

Drusus serbicus Marinkovic-Gospodnetic, 1971c: 107–108. "Stream which is an affluent of the river Glosnica (near Nova Varos, west Serbia), 13 m, 1 f, 30.V.1970"

Material examined. No type or other material was available for study!

Diagnosis. No diagnosis is given in the original species description.

Ecclisopteryx Kolenati, 1848

Ecclisopteryx Kolenati, 1848: 74. "Character essentialis: Tibiae intermediae bi-, posticae tricalcaratae, tegminum apex parabolicus, alarum forum cubitale modice dilatatum, radio subcostalis paule crassiori; tibiae: 1.2.3. Una species arctica." Type species: *Ecclisopteryx dalecarlica* Kolenati (monobasic).

Diagnosis. Schmid 1955: 121, "Appendices intermédiaires absents ou fortement réduits; ils sont remplacés ou renforcés par un bourrelet issu de la partie interne des appendices supérieurs."

Schmid 1956: 76, "Le genre *Ecclisopteryx* est assez différent de *Drusus*, mais tous ses caractères génériques sont localisés dans l'armature genitale." "La repli est présent, assez bien développé et du type perfectionné de la plupart des *Drusus*." "Cavité génitale est largement tapissée par les appendices supérieurs qui présentent une partie externe, proéminente, et une partie interne, relevée en un bourrelet peu chitineux, situé sur la ligne médiane et remplacant les appendices intermédiaires."

Additional diagnosis. McLachlan (1876) has early recognised, mostly on the structure of the anal parts (genitalia) that this genus is less nearly allied to *Drusus* than the other genera. Schmid (1956) has clearly emphasized the taxonomic importance of the significant alteration of paraproct structure. In the generic ranking of the Drusinae subfamily we have recognised the importance of adaptive ancestral architectural divergences both in the paraproct and in the paramere structures. Only the *Ecclisoptery* genus has modified radically the basic architecture of the ancestral periphallic organs and integrated them to generic level of ranking.

The paraproct of *Ecclisopteryx*, both its ventral and dorsal branches, have almost completely disappeared. The stimulatory function of the lost paraproct at the *Ecclisopteryx* genus has been taken over by the modified head of the gonopods. The generic status of *Ecclisopteryx* is also supported by an ancestral divergence in the paramere structure. The ancestral spine pattern on the paramere is produced by a single organising centre in the *Drusus* genus, but it is organised by two organising centres in the *Ecclisopteryx* genus. The *Ecclisopteryx* genus is comprised of 14 species and two species complexes. Two species, *E. asterix*, *E. madida* form independent lineages. One unique species, *E. malickyi* with character states of both the *Drusus* and *Ecclisopteryx* genera needs further analysis. The delineation of the two species complexes in the genus is based on shape of the stimulatory organ on the apicocaudal surface of the gonopods.

(1) *Ecclisopteryx dalecarlica* species complex has stimulatory organ on the apicocaudal surface of the gonopods developed into a variously pronounced vertical ridge.

(2) *Ecclisopteryx guttulata* species complex has stimulatory organ on the apicocaudal surface of the gonopods developed into variously formed clavate or capitate structure.

Ecclisopteryx asterix Malicky, 1979

(Figures 823–826)

Ecclisopteryx asterix Malicky, 1979: 4–5. "Holotype ♂ and two paratypes ♂: Austria, Carinthia, northern slope of Loiblpass, 800 m, 18.VI.1977, leg. & coll. Malicky."

Material examined. **Slovenia**, Julian Alps, Radovna stream, 21.VI.1988 leg. J. Oláh (2♂, 4♀; OPC). Slovenia, Julian Alps, small tributary to Radovna stream, 21.VI.1988 leg. J. Oláh (13♂, 8♀; OPC). Slovenia, Upper Carniola, Kamnik municipality, Kamnik Alps, small forest brook S of Podvolovljek Pass, N46°16.250', E14°41.325', 980 m, 9. VII. Leg. D. Murányi & I Sivec (4 males, 3 females; OPC).
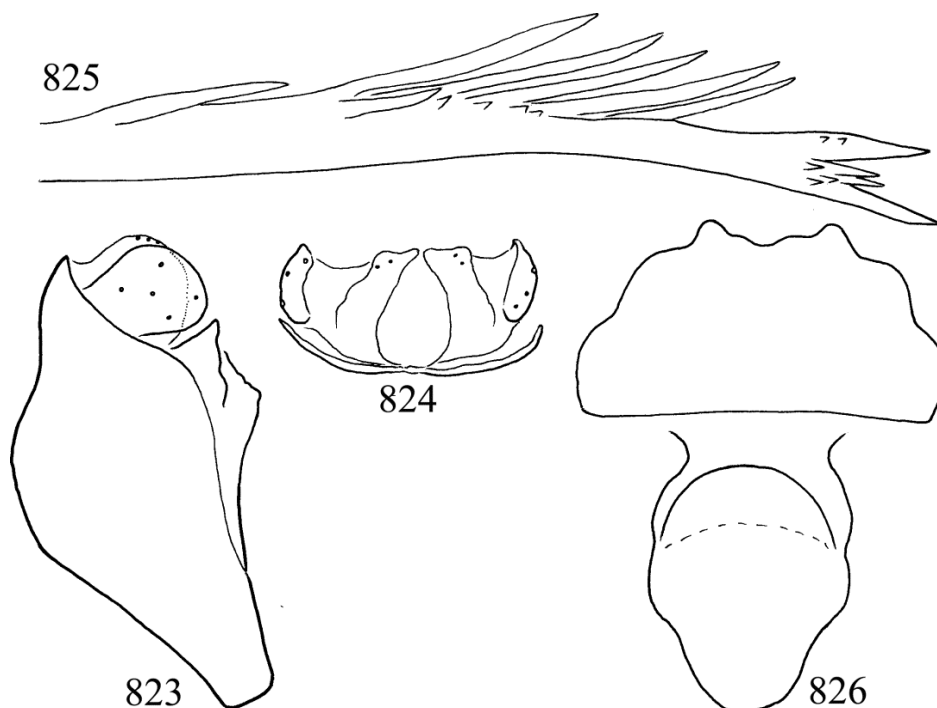
Figures 823–826. *Ecclisopteryx asterix* Malicky, 1979. 823 = male genitalia in left lateral view, 824 = cercal complex and the vestigial paraproct in caudal view, 825 = paramere in left lateral view, 826 = tergite IX and dorsal profile of vaginal sclerite complex in dorsal view.

Diagnosis. Malicky 1979: 5, "This species resembles *Metanoea rhaetica* in colour and general appearance. In the genus *Ecclisopteryx* (Schmid, 1956) it is somewhat isolated because segment 9 is closed ventrally, whereas in the other three species interrupted."

Additional diagnosis. The first basal spine pattern organising centre on the paramer is very pronounced, fully packed with strong and long spines, especially well discernible at male specimens with erecting, not recumbent spine position. The second organising centre moved to the very top of the paramere shaft.

Ecclisopteryx dalecarlica species complex

Ecclisopteryx dalecarlica species complex has stimulatory organ on the apicocaudal surface of the gonopods developed into a variously developed vertical ridge. This species complex is comprised of seven species: *aksu*, *alkon* sp. nov., *dalecarlica*, *ivkae*, *keroveci*, *loudai* sp. nov. *oylat*.

Ecclisopteryx aksu Sipahiler, 2015

Ecclisopteryx aksu Sipahiler, 2015: 70–71,73, "Material. Holotype male and paratypes (4 males, 3 females): Turkey, Isparta, Egirdir, Aksu, Aksu River, 1350 m a.s.l., 37°49'N, 31°06'E, 17.VI.2002, leg. and coll. Sipahiler"

Material examined. No types or any specimen were available for study.

Diagnosis. Sipahiler, 2015: 70, 73, "*Ecclisopteryx aksu* sp. nov. is closely related to *Ecclisopteryx dalecarlica* Kolenati, 1848."

Ecclisopteryx alkon Oláh & Oláh, sp. nov.

(Figures 827–836)

Ecclisopteryx dalecarlica Kolenati, 1848: Oláh & Kovács 2015: 109. A single male specimen from Montenegro. Misidentification!

Ecclisopteryx dalecarlica Kolenati, 1848: Oláh & Beshkov 2016: 101. Male and female specimens from Western Rhodopi and Central Stara Planina Mts. Misidentification!

Material examined. Holotype: **Romania**, Lotru Mts, Obirsia Lotrului, dawn swarm along Lotru River, 30.VI. 2016, leg. J. Oláh & J. Oláh jr. (1 male, OPC). Allotype: same as holotype (1 female, OPC). Paratypes: **Bulgaria** Western Rhodopi, Surnena Reka near crossroad to Zmeitza, 1245m, N41°39'20", E24°13'44", 16.VI.2012, at lamp, light traps leg. S. Beshkov M. Beshkova & V. Gashtarov, (1 male, 1 female, NMNHS). Central Stara Planina Mts. Elenova Gora Reserve near Skobelevo Village, Mazalat Forestry, 872 m, N42°44'34", E025°08'50", 1.VIII.2014, leg. S. Beshkov (1 male, 3 females; OPC). **Montenegro**: Mojkovac munici-pality, Sinjajevina Mts, Gornja Polja, Zoljski Ljevak Stream above the village, N42°57.808', E19°31.597', 880 m, 14.06. 2012, leg. Z. Fehér, T. Kovács, D. Murányi (1 male, OPC). **Romania**, same as holotype (4 males, 3 females, OPC). Rodna Mts. Borsa-Statiunea Borsa, garden, 878 m N47°36'48", E24°46'55.8", 28–29.VI.2005, light trap J. Kontschán, D. Murányi, K. Orci (2 males, NHMB). Maramaros Mts. tributaries at Visó spring area, 15.VI.1993 leg. J. Oláh (6 females, OPC). Apuseni Mts, Direction to Scarisoara, 30.V.2006, leg. M. Bálint (14 males, OPC). Apuseni Mts. Muntii Gilaului, Muntele Baisorii, stream Valea Gera, N46°33.001', E23°20.014', 1055 m, 18.VI.2013, light leg. J. Oláh, Cs. Balogh, & S. Fekete (1 male, 1 female; OPC). Apuseni Mts., Bihor Mts., Crisul Pietros, Boga, Valea Bulz and Valea Galbena, N46°35'23.25", E22°37'54.74", 450 m, 4.VII.2013, light leg. Cs. Balogh, (1 male, OPC). Apuseni Mts. Bihor Mts. Bubesti-Cobles, tributary P. Cobles, N46°29'56.08", E22°43'48.64" 902 m, 14.05.2014, leg. Cs. Balogh & B.V. Béres (1 male, OPC). Cupas Mts, Cupas Valley, Locu Rosu, 14.VII.1981 leg. L. Peregovits & L. Ronkay (4 males, 2 females; HNHM). Bucegi Mts. Cocora stream, N45.394969°, E25.443993°, 1564 m, 15.VII.2015, light trap, leg. Z. Baczó & J. Kecskés (14 males, 182 females; OPC). Bucegi Mts. Cocora stream, N45.3402125°, E25.443147°, 1680 m, 16.VII.2015, leg. Z. Baczó & J. Kecskés (1 male, 1 female; OPC). Vâlcea county, Parâng Mts, Obrâşia Lotrului, open spring area, 500 m along Transalpina (67C) road, downstream from N45°22'27.7", E23°39'4.0", 1915 m, 30.VI.2016, leg. J. Oláh & J. Oláh jr. (1 female, OPC). Lotru Mts, Obirsia Lotrului, 1578 m, N45.463°, E23.620°, 29.VI.2016, singled leg. J. Oláh & J. Oláh jr. (1 female, OPC). Lotru Mts, Obirsia Lotrului, 1578 m, N45.463°, E23.620°, 29.VI.2016, light trap leg. J. Oláh & J. Oláh jr. (5 females, OPC). Lotru Mts, Obirsia Lotrului, 1578 m, N45.463°, E23.620°, 30.VI.2016, light trap leg. J. Oláh & J. Oláh jr. (3 females, OPC). Lotru Mts, Obirsia Lotrului, side stream of River Lotru, 29.VI.2016, dawn swarm, leg. J. Oláh & J. Oláh jr. (5 males, 105 females; OPC). Lotru Mts, Obirsia Lotrului, side stream of River Lotru, 30.VI.2016, light trap, leg. J. Oláh & J. Oláh jr. (119 females; OPC). Retezat Mts., Chele Butii, 936 m, N45°18'07.30", E22°58'27.92". 9.VII.2013, leg. E. Bajka, Cs. Balogh, G. Borics, P. Borics, (3 males, 2 females, OPC). Retezat Mts., Chele Butii, 910 m, N45°18'06.96", E22°58'31.48", 9.VII.2013, light leg. E. Bajka, Cs. Balogh, G. Borics, P. Borics, (28 males, 141 females; OPC). Muntii Sibiului, Rau Sadu, 700 m N45.64°, E24.06°, 3.VII.2007,

leg. M. Bálint (1 male, OPC). Caras-Severin county, Tarcu Mts. Poina Marului, upper section of Sucu Stream, S of the village, 955 m, N45°20.907', E22°31.073', 08.VI.2011, leg. T. Kovács, D. Murányi & G. Puskás, (16 females, HNHM). **Serbia**, Dolina reke Pcinje, Below Vrazji Kamen near Trgovishte Village, 586 m, N42°22'59", E022°03'00", 10. VII.2016, leg. S. Beshkov & A. Nahirnic (1 male, OPC).

Diagnosis and description. This very abundant species was routinely identified earlier as *Ecclisopteryx dalecarlica* sampled from Romania, Bulgaria, Serbia and Montenegro. Population sampling enabled us to examine large series of specimens from several populations. The carefully examined apicodorsal stimulatory organs on the gonopods as well as the fine structure analysis of paramere spine pattern applying high resolution revealed subtle, but stable divergences in the shape of the adaptive speciation traits of gonopods as well as of the paramere spine pattern. This finding was predictable from our discoveries on the speciation traits of limnephilids (Oláh *et al*. 2015b, Oláh *et al*. 2016).

This new species is a close incipient sibling species of *E. dalecarlica*, but differs by having different lateral profile of the gonopods; gonopod apex is monolobed, not bilobed; produced mono-lobe on the ventral corner of the gonopod apex is a decisive character state of *E. alkon* sp. nov.; *E dalecarlica* has bilobed gonopod apex, *i.e.* there is an additional, smaller lobe on the dorsal corner of the gonopods; this different pattern of the lateral profile of the gonopods is the result of the modi-fied position of the heavily pegged vertical ridge of the stimulatory organ; actually the small lobe of the dorsal corner is present also on *E. alkon* sp. nov. but the vertical ridge moved or shifted higher masking or decreasing the apparent lobeness of the dorsal corner of the gonopods.

The presence of two spine pattern oganising centres on the paramere shaft is well discernible in all populations of the various mountain ranges. The subapical spine pattern organising centre has integrated two – three spines into a small cluster. The subbasal spine pattern organising centre has integrated two – three larger secondary spines and numerous smaller tertiery spines along the basal half of the shaft in a scattered position. The differ-
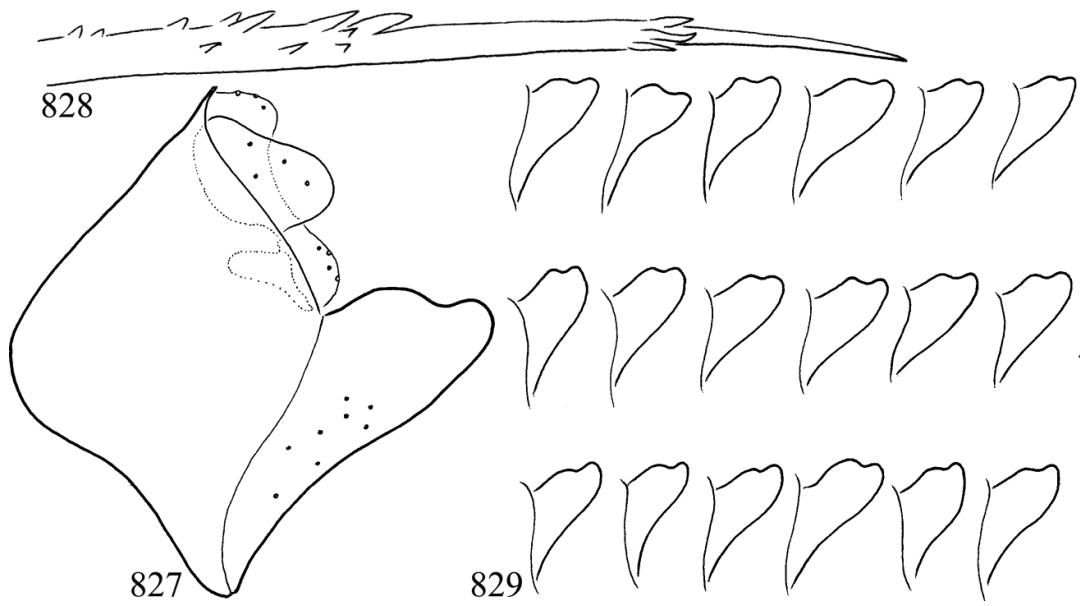
Figures 827–829. *Ecclisopteryx alkon* Oláh & Oláh, sp. nov. Holotype: 827 = male genitalia in left 828 = paramere in left lateral view. 829 = Gonopods in left lateral view from various montain ranges.
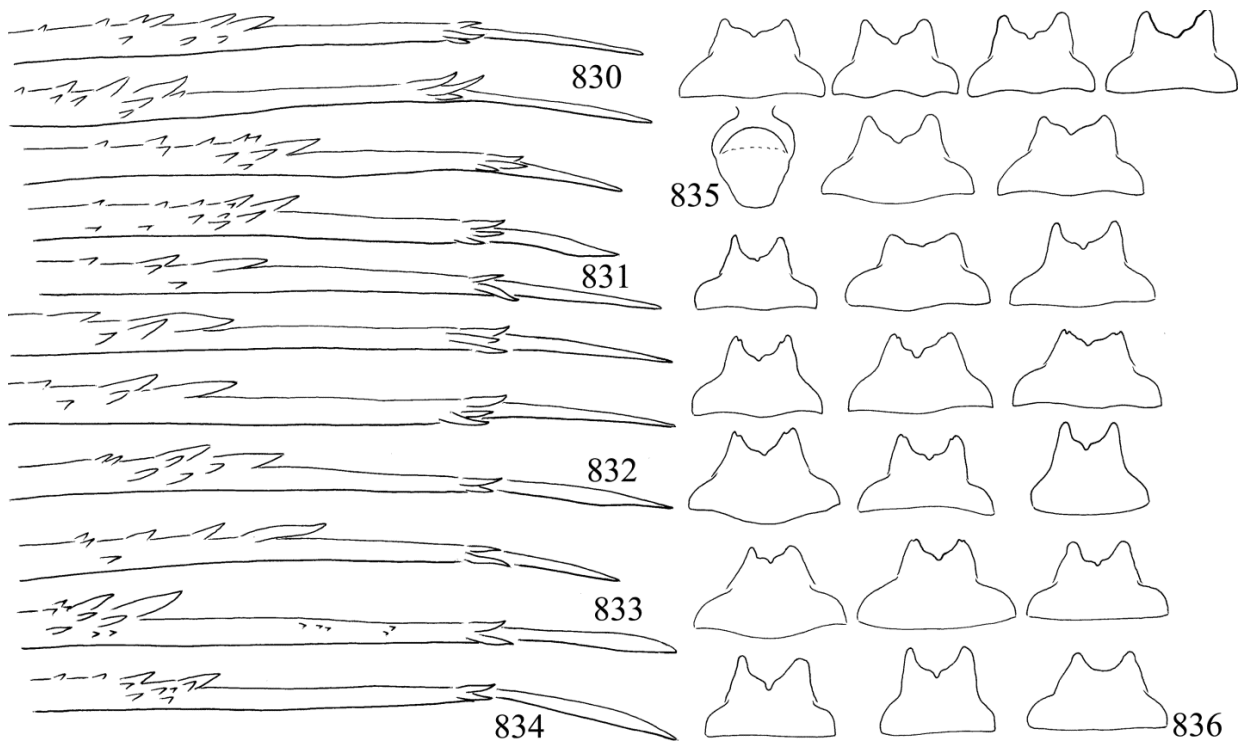
Figure 830–836. *Ecclisopteryx alkon* Oláh & Oláh, sp. nov. 830 = holotype paramere in left lateral view. Paratype parameres in left lateral view from various montain ranges: 831 = Lotru, 832 = Bucegi, 833 = Apuseni, 834 = Retezat.
Allotype: 835 = tergite IX and dorsal profile of vaginal sclerite complex in dorsal view.
Paratypes: 836 = tergite IX in dorsal view from various montain ranges.

ence in the spine patterns between the two siblings is less pronounced, but *E. alkon* sp. nov. has smaller subapical spine cluster and more heavily developed subbasal scattered spine pattern, compared to *E. dalecarlica*.

Etymology. "alkon",from „alkony", nightfall in Hungarian, refers to the mass swarming habit of this new species in the dusk of the nightfall. We have experienced clouds of heavy swarmings at nighfall in Apuseni, Bucegi, Lotru and Retezat mountains.

Ecclisopteryx dalecarlica Kolenati, 1848

(Figures 837–838)

Ecclisopteryx dalecarlica Kolenati, 1848: 75. "Habitat in Dalecarlia (Schönherr!)"
Ecclisopteryx guttulata dalecarlica Kolenati, 1848: Schmid 1955: 121. Reduced to subspecies of *Ecclisopteryx guttulata*.
Ecclisopteryx dalecarlica Kolenati, 1848: Botosaneanu & Malicky1978: 349. "*Dalecarlica* und *guttulata* sind offenbar gute Arten, aber ihre Verbreitung ist unvollstandig bekannt."

Material examined. **Czech Republic**, W Bohemia, Libocky potok stream below Kacerov, (425 m), VI–VIII. 2006, malaise trap, leg. P. Chvojka (1 male, 3 females; OPC). N Bohemia, Jizerské hory Mts. Raseliniste Jizery, Jizera River, (840 m), V–VI.2003, malaise trap, leg. P. Vonicka & J. Preisler (4 males, 4 females; OPC). N Bohemia, Bohemian Switzerland NP, Krinice River, (285m), V–VII.2009, malaise trap, leg. M. Tryzna (2 males, 3 females; OPC). **France**, Department Doubs, Cléron, Ru de Valbois TM7, 8.VI.2010, leg. G. Coppa (1 male, 1 female; OPC). Department Doubs, Cléron, Ru de Valbois TM8, 24.VI.2010, leg. G. Coppa (4 males, OPC). Department Puy-de-Dôme, Chastreix, Ru de la Montagne Prairie et Petite Saulai, 1299 m, 15.VI.2015, leg. G. Coppa (3 males, OPC). Department Puy-de-Dôme, Messeix, Chalameyroux sur la Dordogne, 590 m, 21.VI. 2010, leg. G. Coppa (1 male, 1 female; OPC). Department Haute-Saône, Belonchamp, Ognon pont D97, 377 m, 3.V. 2011, leg. G. Coppa (3 males, 2 females; OPC). Department Lozère, Recoule d'Aubrac, Le Bes Pont du Gournier, 1065 m, 22.V.2011, leg. G. Coppa (1 male, 1 female; OPC). Department Ardennes, Fumay, Alize vers le milieu et l'ardoisière, 3.VI.2007, leg. G. Coppa (2 males, 1 female; OPC). **Hungary**, Jósvafő Mts., 14–16.VI.1986, light leg. J. Oláh (1 male, OPC). Zemplén Mts. Telkibánya, 1–7.VIII. 1984, light leg. J. Oláh (26 males, 19 females; OPC). **Poland**, Gorce Mts., Kamienica stream, 26.VI.1985, leg. J. Oláh (2 males, OPC). **Slovakia**, Oravské Beskydy Mts. Polhoranka stream above Oravská Polhora (750 m), 29.VI. 1992, leg. P. Chvojka (3 gmales, 5 females; OPC).
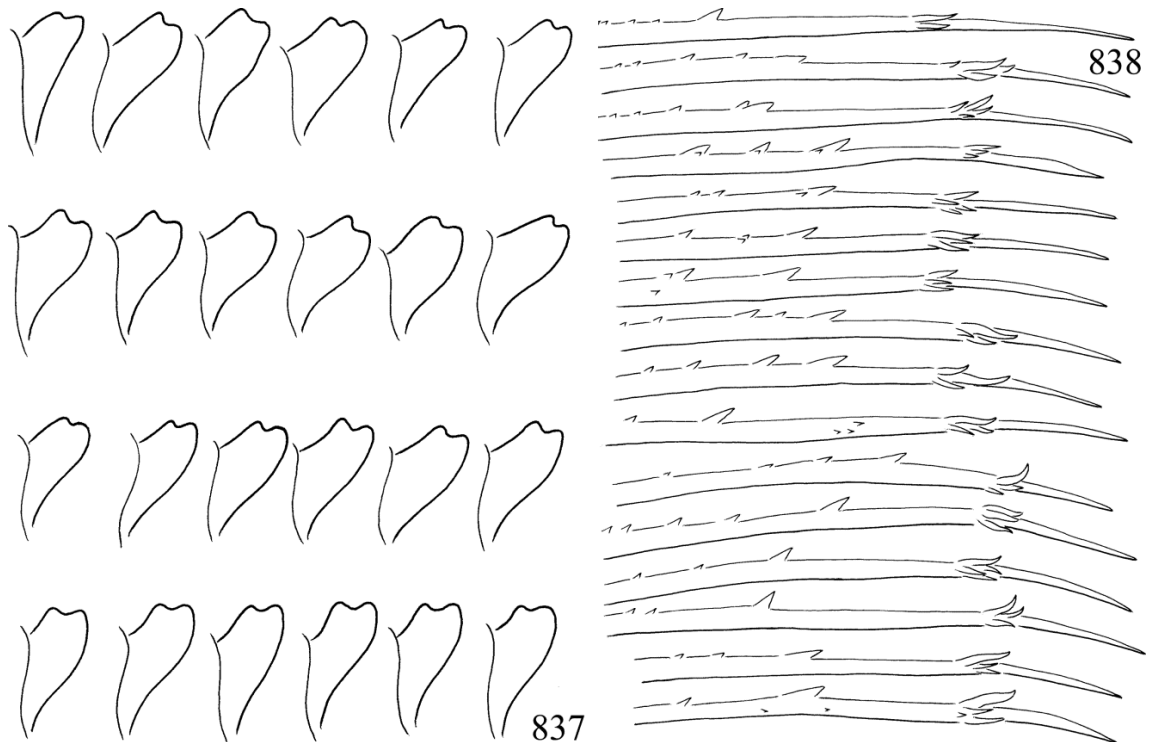
Figure 837–838. *Ecclisopteryx dalecarlica* Kolenati, 1848. 837 = gonopods in left lateral view from various montain ranges, 838 = parameres in left lateral view from various montain ranges.

Diagnosis. Kolenati 1848: 75, "Fusco-testacea, corpore fusco, pronoto rufo, antennis fusco-annu-latis, femeribus griseis, palpis tibiisque testaceis, his nigro-spinosis, tegminibus fusco-testaceis, brunneo-nervosis, thyridio, arculo et punctis ob-soletis in areolis apicalibus pallidis, alis fusco-hyalinis, testeceo-nervosis, anastomosi in alis et tegminibus antica nimis obliqua."

Schmid 1956: 79. Compared to *Ecclisopteryx guttulata*: "La coloration du corps est plus foncée. Les ailes antérieures sont plus sombres et plus brunes." "La zone spinulifere est légèrement plus grande et les spinules y sont plus denses." "Les appendices inférieurs ont une forme semblable è ceux de cette dernière sous-espèce, mais ont une position différente."

Ecclisopteryx ivkae Previsic, Graf & Vitecek, 2014

Ecclisopteryx ivkae Previsic, Graf & Vitecek, 2014, in Previsic *et al.* 2014: 319–320. "Type material. *Ecclisopteryx ivkae* sp. nov. Holotype ♂: Cetina River, Glavas spring, N43.976697°, E16.430150°, 386 m asl,. 2. VI.2011, leg. Previsic A.; deposited in the Biology Centre, Oberösterreichisches Landesmuseum, Linz, Austria. Paratypes: 4♂ and 2♀, same data; 1♂ and 1♀ 31.V.2005, leg Previsic A.; 1♀ 7.VI.2007, leg Graf W.;

2♀, 2.VI.2012, leg. Previsic A.; deposited in the first author's collection at the Faculty of Science in Zagrab, 8 5th instar larvae, same location, 4.X.2013 (N=4, leg. Kucinic M.) and 7.XI. 013 (N=4, leg. Previsic A.)."

Examined material. No types or any specimens were available for study in spite of our several loan requests.

Diagnosis. Previsic *et al.* 2014: 320, "Posterior edge of tip of inferior appendages more or less straight in lateral view, lacking a clear ventral elongation, tips in dorsal view with distinct shoulder."

Ecclisopteryx keroveci Previsic, Graf & Vitecek, 2014

(Figures 839–842)

Ecclisopteryx keroveci Previsic, Graf & Vitecek, 2014, in Previsic *et al.* 2014: 317–319: "Type material. *Ecclisopteryx keroveci* sp. nov. Holotype ♂: Bosnia and Herzegovina, mouth of Jabucica River, N43.29022°, E18.61733°, 765 m asl,. 4.VII.2012, leg. Previsic A., M. Ivkovic, Z. Mihaljevic, M. Milisa; deposited in the Biology Centre, Oberösterreichisches Landesmuseum, Linz, Austria. Paratypes: 39♂ and 49♀, same data; deposited in the first author's collection at the Faculty of Science in Zagrab, 10 5th instar larvae, same location, 14. V.2008 and 2.VI.2009, leg. Previsic A., W. Graf."
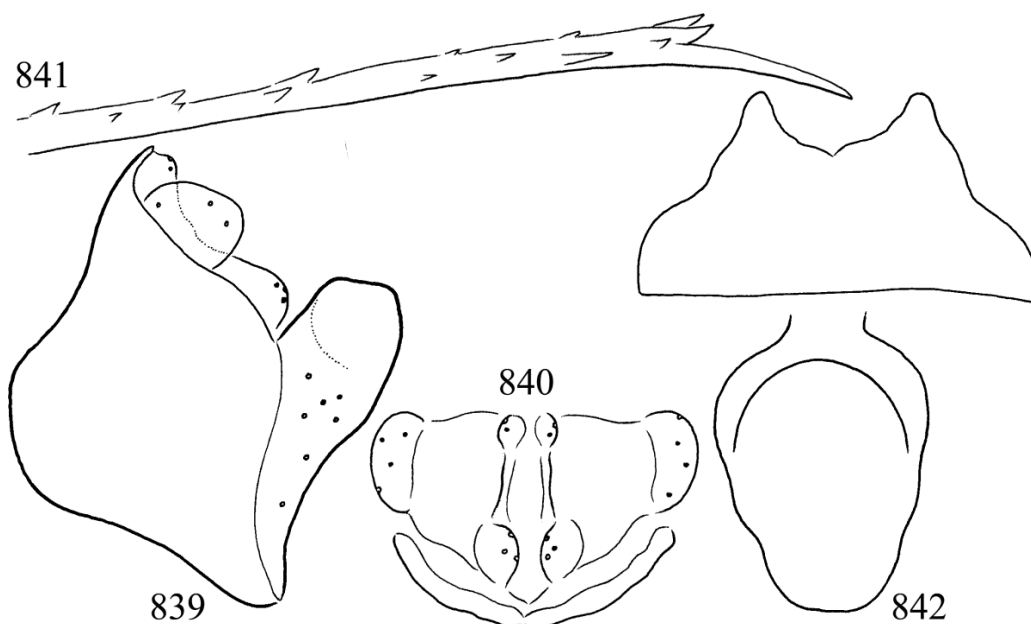
Figures 839–842. *Ecclisopteryx keroveci* Previsic, Graf & Vitecek, 2014. 839 = male genitalia in left lateral view, 840 = cercal complex and the vestigial paraproct in caudal view, 841 = paramere in left lateral view, 842 = tergite IX and dorsal profile of vaginal sclerite complex in dorsal view.

Material examined. **Macedonia**: Polog region, Šar Planina, Brodec, Tetovska Reka (Pena) in the village, N42° 03.375', E20°53.561', 980 m, 24.VI.2014, P. Juhász, T. Kovács & D. Murányi (1 male, 1 female; OPC). Southwestern region, Jablanica Mts, Vevčani, Vevčani Springs and outlet stream at the city, N41°14.371', E20°35.056', 935 m, 26.VI.2014, P. Juhász, T. Kovács & D. Murányi (2 males, 1 female; OPC).

Diagnosis. Previsic *et al.* 2014: 320: "Posterior edge of tip of inferior appendages ventrally elongated and arched dorsally, tips in dorsal view lacking distinct shoulder."

Additional diagnosis. The two spine pattern organising centres are more diffused at the examined three males.

Ecclisopteryx loudai Oláh, sp. nov.

(Figures 843–846)

Material examined. Holotype: **Greece**, Metsovo, 1100 m, 39.77°N, 21.18°E, 13.VII.2012 leg. J. Louda (1 male, MCSNBG). Allotype: same as holotype (1 female, MCSNBG). Paratypes: same as holotype (3 females, MCSNBG; 1 male, 1 female, OPC).

Diagnosis and description. This new species is a close incipient sibling species of *E. alkon* sp. nov. and *E. dalecarlica* but differs by having different lateral profile of the gonopods; the smaller lobe on the dorsal corner of the gonopods has completely reduced, that is disappeared at both the holotype and at the single male paratype. The gonopod is narrowing apicad into a single lobe, that is the gonopod head is produced into the apical terminal of the vertical stimulatory organ in lateral view. The presence of two spine pattern oganising centres on the paramere shaft is well discernible. The subapical spine pattern organising centre has integrated a large hook-like spine and three smaller spines; the subbasal spine pattern organising centre is reduced to a single secondary spine and a few tertiary spines.

Etymology. The species was named after Josef Louda, Czech entomologist, who has collected this new species.
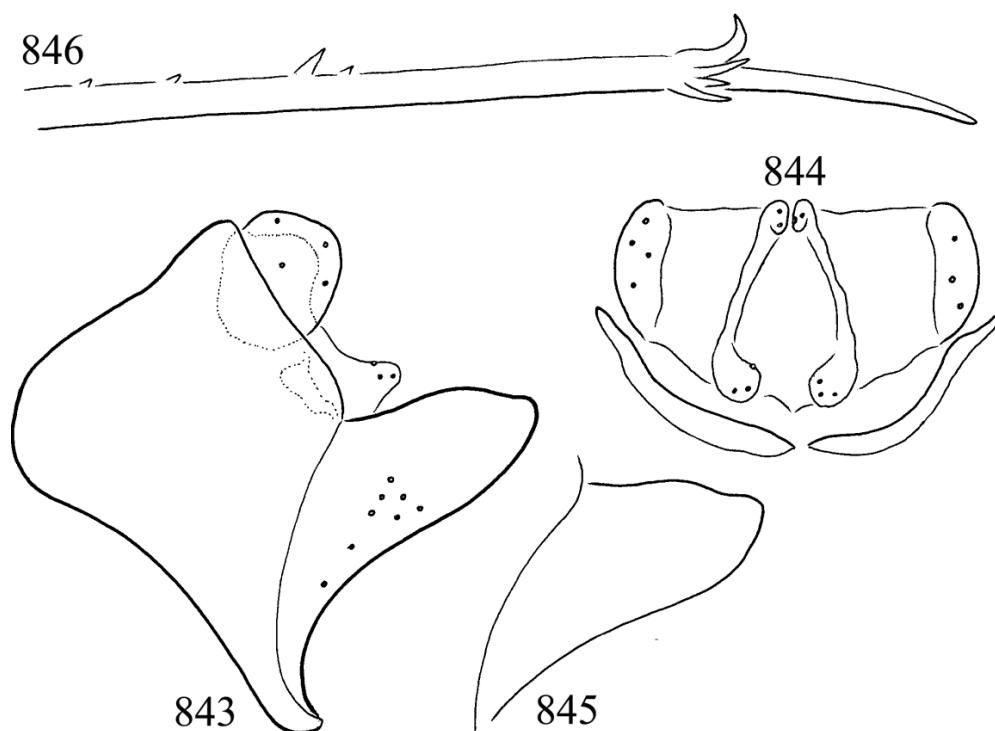
Figures 843–846. *Ecclisopteryx loudai* Oláh, sp. nov. Holotype: 843 = male genitalia in left lateral view, 844 = cercal complex and the vestigial paraproct in caudal view, 845 = paratype gonopod in left lateral view, 846 = paramere in left lateral view.

Ecclisopteryx oylat Sipahiler, 2015

Ecclisopteryx oylat Sipahiler, 2015: 70–71, 73. "Material. Holotype male and paratype female: Turkey, Bursa, Oylat, Kozluca direction, 10 km east of Saadet Village, 630 m a.s.l., 40°05'N, 29°03'E, 19.V.1994, leg. and coll. Sipahiler"

Material examined. No types or any specimens were available for study.

Diagnosis. Sipahiler, 2015: 70, 73: "*Ecclisopteryx oylat* sp. nov. is closely related to *Ecclsopteryx dalecarlica* Kolenati, 1848."

Ecclisopteryx guttulata species complex

Ecclisopteryx guttulata species complex has stimulatory organ on the apicocaudal surface of the gonopods developed into variously formed clavate or capitate structures. The shape divergences of the clavate or capitate stimulatory organ are subtle and stable. As we have documented (Oláh *et al.* 2015b) this subtle and stable pattern of divergences seems to be a solid general mechanism of the integration of the adaptive speciation trait. We have examined female specimens of the siblings species of the species complex, but the evaluation of between species delimitation needs more studies. Earlier, all members of this species complex have been determined routinely as *Ecclisopteryx guttulata* sampled from France, Italy, Britain, Belgium, Germany, Slovenia, Switzerland, Austria, Czech Republic and Poland. The subtle shape divergences of the stimulatory organ was not recognised properly neither in lateral or caudal view, because this small structure is disposed in an oblique plane between sagittal and transversal planes. To realise its exact shape we examined and drawn every specimens in a view perpendicular to this oblique plane. This species complex is comprised of four species: *guttulata*, *kunkor* sp. nov., *legeza* sp. nov., *tolda* sp. nov.

Ecclisopteryx guttulata (Pictet, 1834)

(Figures 847–855)

Phryganea guttulata Pictet, 1834:143-144: "J'ai trouvé cette espèce dans la vallée d'Abondance au mois de Juillet; sa larve, que je ne connais pas, vivait vraisemblablement dans la Dranse, car la phrygane voltigeait sur les buissons qui bordent cette rivière."
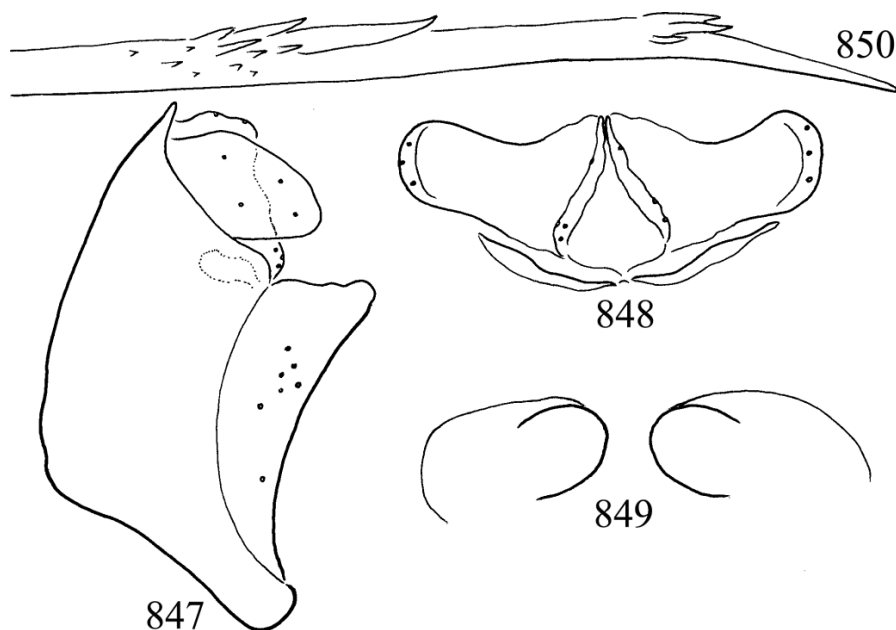
Figures 847–850. *Ecclisopteryx guttulata* (Pictet, 1834). 847 = male genitalia in left lateral view, 848 = cercal complex and the vestigial paraproct in caudal view, 849 = gonopod apex with the stimulatory organ in perpendicular laterocaudal view, 850 = paramere in left lateral view.

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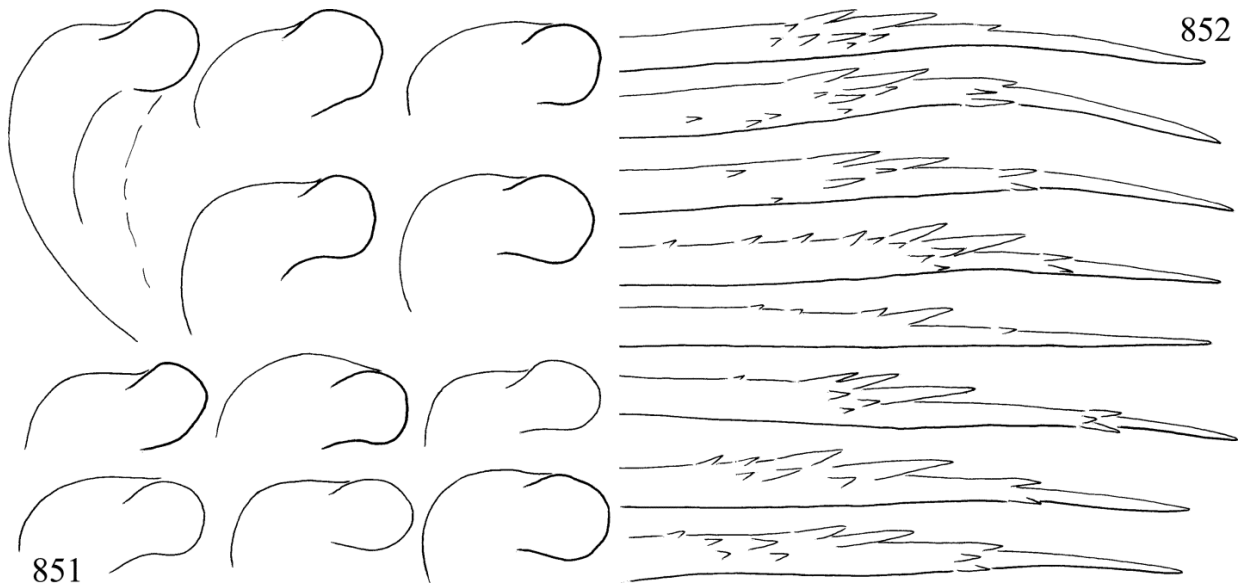
Figure 851–852. *Ecclisopteryx guttulata* (Pictet, 1834). 851= gonopod apex with the stimulatory organ in perpendicular laterocaudal view from various regions, 852 = parameres in left lateral view from various regions.

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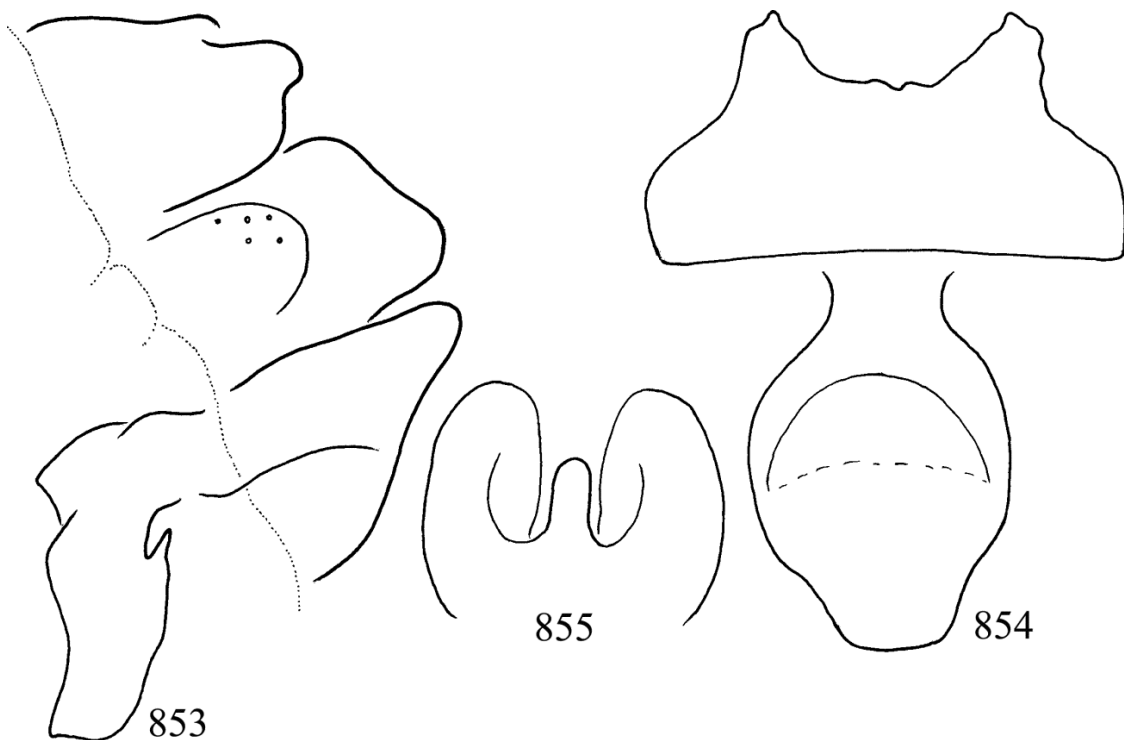
Figures 853–855. *Ecclisopteryx guttulata* (Pictet, 1834). 853 = female genitalia with vaginal sclerite complex in left lateral view, 854 = tergite IX and dorsal profile of vaginal sclerite complex in dorsal view, 855 = vulvar scale in ventral view.

Material examined. **Austria**: Karawanks, Vellach stream, 25.VII.1989 leg. J. Oláh (1 male, OPC). Raxalpe Mts. Kaiserbrunn, Höllental, Schwarza River at Abbrenn bridge, 3.VI.2006, leg. L. Dányi & Á Vári (5 males, HNHM). **Italy**, Veneto, Cesiomaggiore (BL), 590 m, torrente Caorame, light trap, 7.VIII.2002, leg. Museo BG (5 males, 4 females; OPC). Lombardia, Valvestino (BS), 500 m, fiume Toscolano, light trap, 5.VII.2009, leg. E. Ferrario, M. Gaini & P. Pantini, (5 males, 4 females, OPC). Lombardia, Valgoglio (BG), 1300 m, Valsanguigno torrente, light trap, 7.VIII.2009, leg. S. Cerea (5 males, 3 females, OPC). Trentino Alto Adige, Bedollo (TN), 1200 m, Valle di Piné, light trap, 18.VII.2015, leg. A. Andreotti (2 males, OPC). Piemonte, Oncino (CN), c/o viadotto Fiume Po, 19.VIII.1998, leg. O. Lodovici (5 males, 5 females; OPC). **Slovenia**, Julian Alps, Radovna stream, 23.VI.1988 leg. J. Oláh (1 female, OPC).

Diagnosis. Pictet 1834: 143–144, "Moyenne, brune; antennes et pattes fauves; ailes brunâtres, couvertes de petites gouttelettes blanchâtres peu visibles."

Schmid 1956: 78, "Les appendices supérieurs sont de grande taille et tapissent largement cette dernière; leur partie externe est arrondie et bien proéminente; leur bord interne est relevé en un fort bourrelet dont les deux extrémités sont très saillantes; l'angle supérieur forme un lobe arrondi et l'angle inférieur constitue une forte languette convexe, dirigée vers le bas. Il est probable que les appendices intermédiaires aient disparu et que la languette décrite ci-dessus appartienne bien aux appendices supérieurs."

Additional diagnosis. The nominate, name bearing species of the complex has an almost circular rounded capitate stimulatory organ in all of the examined populations. The subbasal spine pattern organising cetre has integrated two-three secondary spines with several tertiary spines.

Ecclisopteryx kunkor Oláh, sp. nov.

(Figures 856–864)

Material examined. Holotype: **Italy**, Calabria, Spezzano della Sila (CS), 1350 m, Vivaio Sbanditi, light trap, 5.VI.2015, leg. S. Scalercio & M. Infusino (1 male, MCSNBG). Allotype: Basilicata, Chiaromonte (PZ), 1600 m, sorg. Rummo, light trap, 1.VIII.1993, leg. Pantini & M. Valle (1 female, MCSNBG). Paratypes: same as allotype (2 males, 3 females, MCSNBG; 2 males, 1 female; OPC). Emilia Romagna, Corniglio (PR), 1000 m, bosco torrente Parma di Lago Santo, light trap, 16. VIII. 1997 leg. R. Fabbri (5 males, 1 female, OPC).
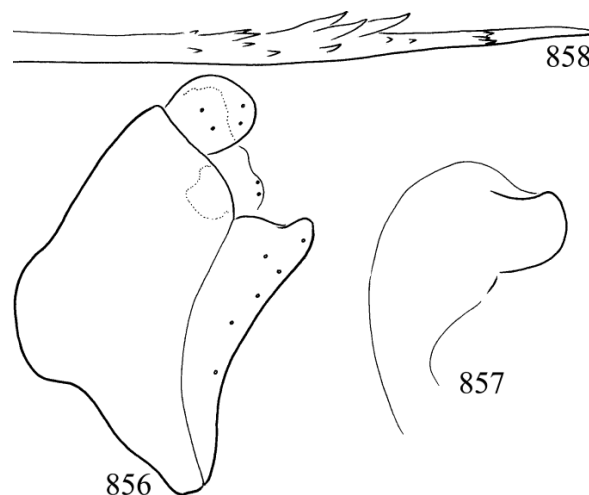
Figures 856–858. *Ecclisopteryx kunkor* Oláh, sp. nov. Holotype: 856 = male genitalia in left lateral view, 857 = gonopod apex with stimulatory organ in perpendicular laterocaudal view, 858 = paramere in left lateral view.
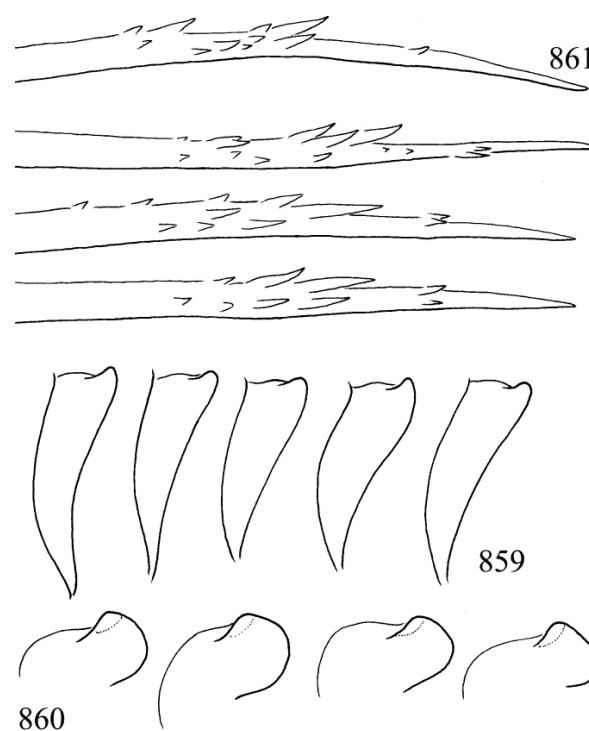
Figures 859–861. *Ecclisopteryx kunkor* Oláh, sp. nov. 859 = paratype gonopods in left lateral view, 860 = paratype gonopod apex with the stimulatory organ in perpendicular laterocaudal view, 861 = paratype parameres in left lateral view.

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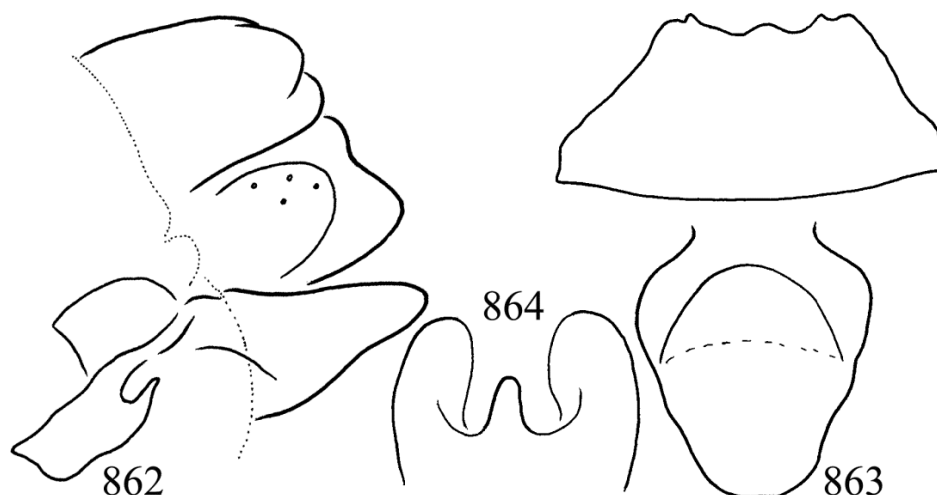
Figures 862–864. *Ecclisopteryx kunkor* Oláh, sp. nov. Allotype: 862 = female genitalia with vaginal sclerite complex in left lateral view, 863 = tergite IX and dorsal profile of vaginal sclerite complex in dorsal view, 864 = vulvar scale in ventral view.

Diagnosis and description. This new incipient sibling species of the complex form Peninsular Italy has a capitate stimulatory organ with decisive curly dorsal lobe in all of the examined populations both from Calabria, Basilicata and from Emilia Romagna. The subapical spine pattern organising centre has integrated a less developed spine cluster comprised of one – two small spines.

Etymology. "kunkor",from „kunkor", curly in Hungarian, refers to the small dorsal lobe developed on the dorsum of the stimulatory capitate organ, looks curly inlateral profile.

Ecclisopteryx legeza Oláh & Lodovici, sp. nov.

(Figures 865–874)

Material examined. Holotype: **Italy**, Piemonte, Vinadio, Alps, 44.305 7.171, 1200 m, 11.VII.2007, leg. N.−K. NAGY & M. BÁLINT (1 male, MCSNBG). Allotype: same as holotype (1 female, OPC). Paratypes: **Italy**: Piemonte, Ormea (CN), conf. Negrone-Tanarello, light trap, 18. VIII. 2001, leg. Museo Caffi BG (1 male, 2 females MCSNBG; 1 male, 3 females; OPC). **France**, Department Alpes-Maritimes, Belvédère, La Grange a Colonel, 8. VII. 2012, leg. G. Coppa (1 male, OPC). Department Alpes-Maritimes, Tende, Ru de la Minière Passerelle du Gias Viore, 1580 m, 6. VII. 2006, leg. G. Coppa (2 males, 1 female; OPC). Department Alpes-Maritimes, Tende, Ru de la Minière Passerelle du Gias Viore, 1580 m, 13. VII. 2009, leg. G. Coppa (2 males, OPC). Department Alpes - Maritimes,
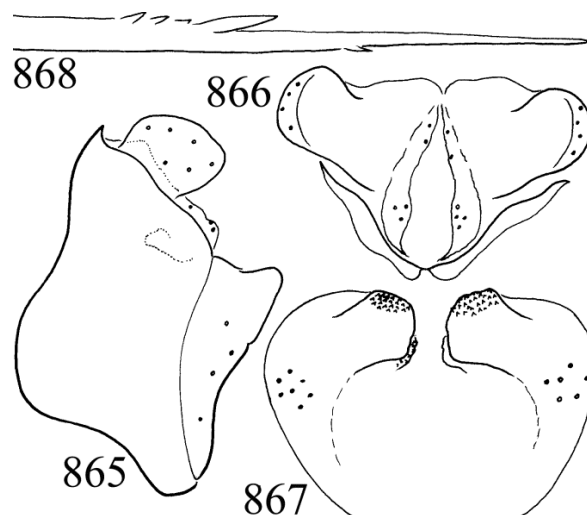
Figures 865–868. *Ecclisopteryx legeza* Oláh, sp. nov. Holotype: 865 = male genitalia in left lateral view, 866 = cercal complex and the vestigial paraproct in caudal view, 867 = gonopods with stimulatory organs in caudal view, 868 =paramere in left lateral view.

Belvédère, La Gordolasque sans autre précision, 10. VII. 2012, leg. G. Coppa (1 female, OPC). Department Alpes-Maritimes, Tende, la Bieugne sur Fond des Plans Castérino, 1500 m, 14. VII. 2009, leg. G. Coppa (2 males, 1 female; OPC). Department Alpes-Maritimes, Tende, Col de Tende, 1500 m, 6. VII. 2012, leg. G. Coppa (1 male, OPC).

Diagnosis and description. This new incipient sibling species of the complex form Piemonte of
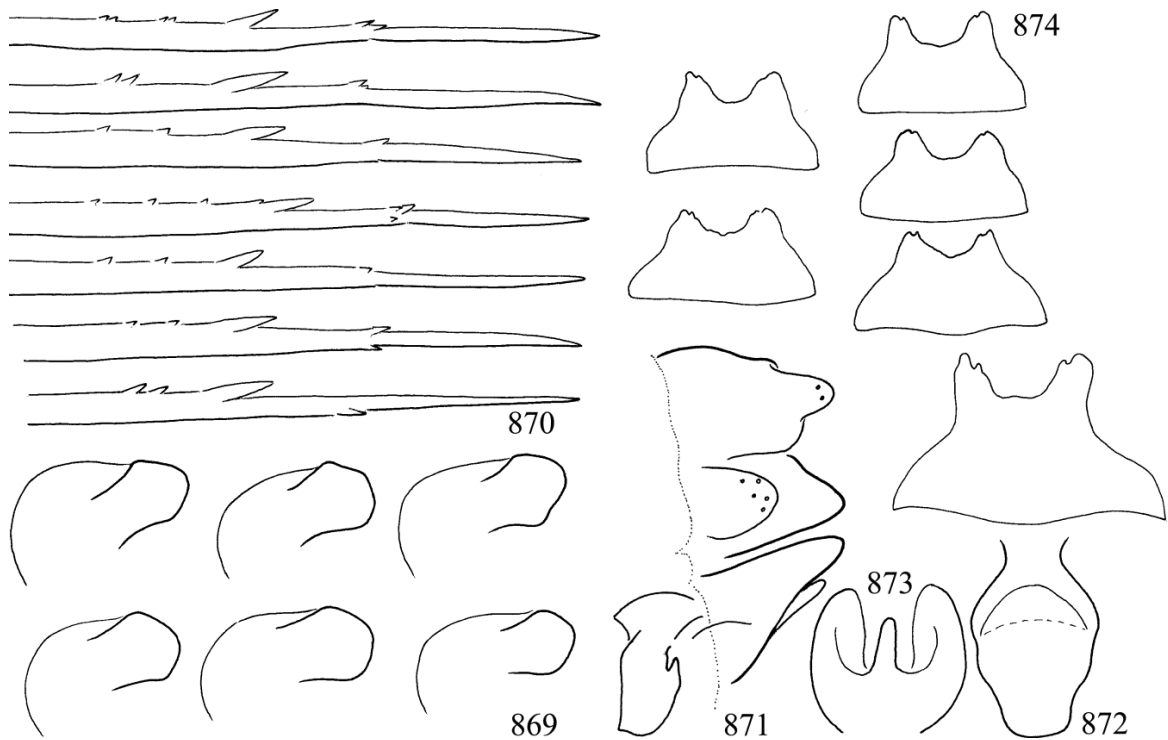
Figures 869–874. *Ecclisopteryx legeza* Oláh, sp. nov. 869 = paratype gonopod apex with the stimulatory organ in perpendicular laterocaudal view, 870 = paratype parameres in left lateral view. Figures 871-874. Allotype: 871 = female genitalia with vaginal sclerite complex in left lateral view, 872 = tergite IX and dorsal profile of vaginal sclerite complex in dorsal view, 873 = vulvar scale in ventral view. Paratypes: 874 = tergite IX in dorsal view.

Italy and from the Departement Alpes-Maritimes in France has a capitate stimulatory organ with decisive fan shape in all of the examined populations from cross border area in Italy and in France. The fan shape refers to a somehow elongated constricted basal part diverting in apical direction and ended in a rounded triangular apical margin. Both the subbasal and subapical spine pattern organising centres have integrated only few spines; very short spines in the subapical area and a single large secondary spine accompanied by a few small tertiary spines in the subbasal area.

Etymology. "legeza", from „legyező", fan in Hungarian, refers to the perpendicular shape of the stimulatory organ.

Ecclisopteryx tolda Oláh & Coppa, sp. nov.

(Figures 875–882)

Material examined. Holotype: **France**, Department Hautes-Pyrénées, Tramezaigues, Rioumajou près du parking Frecandon, 18.VII.2012, leg G. Coppa (1 male, OPC). Allo-
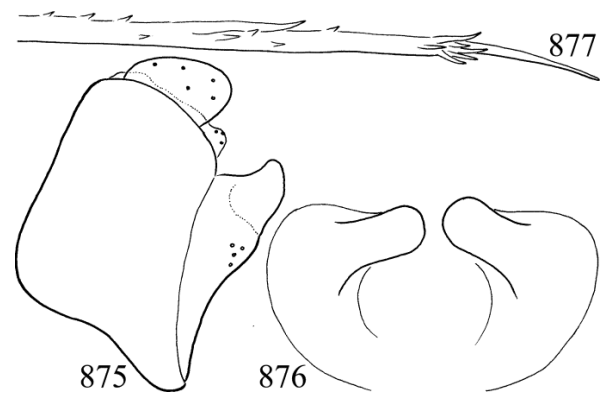
Figures 875–877. *Ecclisopteryx tolda* Oláh & Coppa, sp. nov. Holotype: 875 = male genitalia in left lateral view, 876 = gonopods with stimulatory organs in caudal view, 877 = paramere in left lateral view.

type: same as holotype (1 female, OPC). Paratypes: same as holotype (4 male, 2 females; OPC). Department Hautes-Pyrénées, Gèdre, Estaube avant Pont Source, 26.VII.2010, leg G. Coppa (3 males, OPC). Department Pyrénées-Atlantiques, Laruns, Gave de Bious, 13.VII.2010, leg G. Coppa (1 male, 1 female; OPC).

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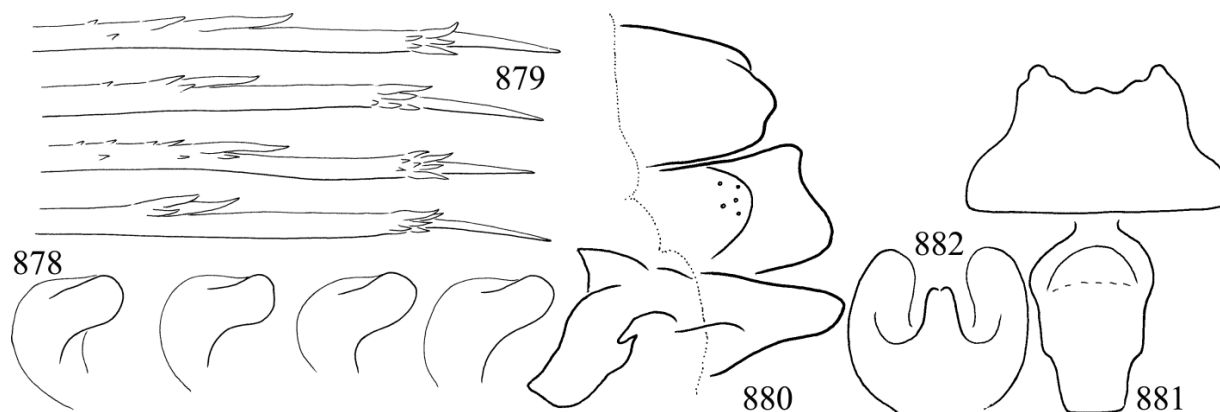
Figures 878–882. *Ecclisopteryx tolda* Oláh & Coppa, sp. nov. 878 = paratype gonopod apex with the stimulatory organ in perpendicular laterocaudal view, 879 = paratype parameres in left lateral view. Allotype: 880 = female genitalia with vaginal sclerite complex in left lateral view, 881 = tergite IX and dorsal profile of vaginal sclerite complex in dorsal view, 882=vulvar scale in ventral view.

Diagnosis and description. This new incipient sibling species of the complex from Pyrenées has a capitate stimulatory organ of an elongated shape in all of the examined populations. The elongated stimulatory organ has a rounded terminal ending. The paramere is characterized by a rather developed subapical spine cluster.

Etymology. "tolda",from „told", elongate in Hungarian, refers to the elongated shape of the stimulatory organ.

Ecclisopteryx madida (McLachlan, 1867)

(Figures 883–886)

Halesus madidus McLachlan, 1867: 53. "Stelzing in Kärnthen, Juli (Zeller), 2♂, 3♀."

Ecclisopteryx madida (McLachlan, 1867): McLachlan 1876: 187: "Carinthia (Stelzing, in July). Silesia (Reinerz, July) in Hagen's collection."

Material examined. **Hungary**, Zemplén Mts. Lászlótanya, 1.X.1982, at light leg. J. Oláh (2 males, 2 females; OPC). Zemplén Mts. Telkibánya, 9.X.1982, at light leg. J. Oláh. Zemplén Mts. Lászlótanya, 6–8.VII.2010 lightrap leg. Z. Varga (1 female, OPC). **Poland**, Podhale, small stream, 20.VIII.1986, leg. J. Oláh (3 males, 1 female; OPC). High Tatra Mts., Chocholowska Valley, 22.VIII.1989 leg. J. Oláh (3 males, 4 fgemales; OPC). **Romania**, Maramures county, Ignis Mts. Desesti, Statiunea Izvoare, open brook with spring bog on the Valhani Plateau, 1040m, N47°43'44", E23°44'39", singled leg. J. Oláh & L. Szél, 8.VIII.2012 (5 males, 1 females; OPC). Maramures county, Maramaros Mts. Frumuseaua stream, 764 m, N47°52'43'', E24°18'22'',

7.VIII.2012, light trap leg. J. Oláh & L. Szél (6 males, OPC). Apuseni Mts. Sebes Körös valley, Suncuius, near Izbandis spring, 26.X.2009 leg. J. Oláh & M. Bálint (29 males, 3 females, OPC). Apuseni Mts. Muntii Gilaului, Statiunea Muntele Baisorii, La Mocirle, spring streams, N46°30.241', E23°15.550', 1552 m, 19–20.VI.2015, singled leg. J. Oláh, Cs. Balogh, & P. Juhász (1 male, OPC). Apuseni Mts. Vadul Crisul, 17.IX.2014, light leg. Cs. Balogh (24 males, 16 females; OPC). Cupas Mts. Valley Cupas, Lacu Rosu, 22. VII.1981 leg. L. Peregovits & L. Ronkay (1 male, HNHM). Lotru Mts. N45°25'7.091", E23°40'44.314", 1583 m, 30.VII.2015 leg. J. Kecskés, & Zs. Pap (5 males, 7 females; OPC). Lotru Mts, Obirsia Lotrului, 1578 m, N45.463°, E23.620°, 30.VI.2016, light trap leg. J. Oláh & J. Oláh jr. (1 male, OPC). Retezat Mts., Chele Butii, 910m, N45°18' 06.96", E22°58'31.48" 9.VII.2013, light leg. E. Bajka, Cs. Balogh, G. Borics, P. Borics, (2 males, 18 females; OPC). **Slovakia**, Hnilec stream, 27.VII.1964, leg. J. Oláh (1 male, OPC). Biela Voda, 22.VII.1966, leg. J. Oláh (1 male, 1 female; OPC). Banskobystrický region, Javorie Mts, Stará Huta, Blýskavica, Tisovník Stream, N48°27.553', E19° 18.048', 671 m, 7–9.X.2013, singled leg. J. Oláh & L. Szél (6 females, OPC). Banskobystrický region, Javorie Mts, Stará Huta, Blýskavica, Stara Rieka Stream, N48°25.248', E19°17.822', 764 m, 7–9.X.2013, singled leg. J. Oláh & L. Szél, (1 male,2 females; OPC). Spisske Bystre (Hernádfalu), Bystra stream, N48°58'45", E20°13'23", 769 m, 9.VII.2012 light trap, leg. P. Boda, B.A. Lukács, I. Szivák & G. Várbíró (1 female; OPC).

Diagnosis. McLachlan 1867: 53, "Wie die vorhergehende gehört auch diese Art der Gruppe mit einem Haarpinsel am Hinterflügel an."

McLachlan 1876: 187, "Very distinct in appearance from any variety of *E. guttulata*; a much more delicate insect, with more regularly parabolic anterior-wings, and peculiar anal structure."
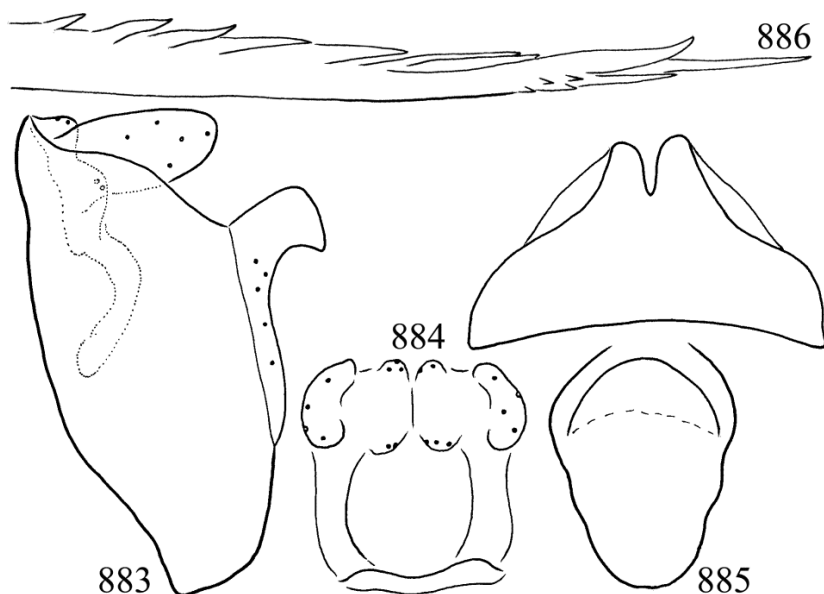
Figures 883–886. *Ecclisopteryx madida* (McLachlan,1867). 883 = male genitalia in left lateral view, 884 = cercal complex and the partially vestigial paraproct in caudal view, 885 = paramere in left lateral view, 886 = tergite IX and dorsal profile of vaginal sclerite complex in dorsal view.

Unplaced *Ecclisopteryx* species

Ecclisopteryx malickyi **Moretti, 1991**

Ecclisopteryx malickyi Moretti, 1991: 393. "Holotype ♂, allotype ♀, Trentino – Alto Adige, ruisseau Sega di Ala, Trento, 1230 m, 9.VII.1979, leg. Mason (Musée des Sciences Naturelles de Verona)." According to the information from Museo Civico di Scienze Naturali "E. Caffi", Bergamo, Italy, the holotype is preserved at Perugia University.

Diagnosis. Moretti 1991: 393, "Les appendices intermédiaires sont bien développés et fortement sclérifiés, rêches, noircis et recourbés vers le haut comme ceux de *Drusus*, alors que les appendices inférieurs, sont nettement tordus vers l'intérieur et presque entièrement soudés au IXe segment. L'apex de ces appendices est armé de tubercules coniques noirs, forts et épais, caractère qui n'est pas présent chez *Drusus*. Le IXe tergite est fortement bombé et spinuleux, noirci et bilobé aux parties latérales. Poche androconiale de l'aile postérieure du type perfectionné de la plupart des Drusus avec un pinceau de longues sétules. Eperons 1,2,2." "…d'une espèce intéressante qui unit les caractères taxonomiques de deux genres, *Ecclisopteryx* et *Drusus*."

Additional diagnosis. Unfortunalety we have been unable to locate the holotype, the only known male specimen of this species. New specimens have to be collected to establish the taxonomic position of this strange species more reliably. *Ecclisopteryx malickyi* is characterized with combined traits of the *Drusus* and *Ecclisopteryx* genera and needs further study. The presence of regular paraproct relates it to *Drusus* genus and its pegged gonopod relates it to the *Ecclisopteryx* genus. The detailed examination of the fine structure of the paramere would help to understand more its taxonomic position. In the species description the original paramere drawings are not detailed enough. Form these drawings it seems discernible that this unique species has only one organising centre of spine pattern on the paramere. This is a ranking character of the *Drusus* genus. Moreover, as visible on the drawings, the discernible ancestral paramere divergence of the multidivision, that is the transformation of the single subapical spines into spine bunch with various number of spines, as well as together with the paraproct architecture, relate this species to the *Drusus monticola* species group and to the *Drusus balcanicus* species complex. It seems this species is rather a *Drusus* and not an *Ecclisopteryx*.

Table 1. *Drusus* samplings in the Bucegi Mts., Southern Carpathians, Romania

Locality	Coordinate	Methods	Date	*Drusus*	♂	♀
Ialomița stream	45.397N, 25.446E	net	14.VII.2015	*brunneus*	5	2
Ialomita s	45.425N, 25.444E	net	15.VII.2015	*brunneus*	27	7
Ialomița s	45.416N, 25.416E	lighttrap	15.VII.2015	0	0	0
Ialomița s	45.416N, 25.416E	net	15.VII. 2015	*brunneus*	8	4
				discolor	4	7
Cocora s.	45.340N, 25.443E	net	16.VII.2015	*brunneus*	3	
Cocora s.	45.394N, 25.443E	lighttrap	16.VII.2015	0	0	0
Ialomița s	45.402N, 25.443E	net	16.VII.2015	*discolor*	3	12
Brătei s.	45.383N, 25.385E	net	13.VII.2016	*brunneus*	2	1
				discolor	1	2
Negru s.	45.383N, 25.350E	net	14.VII.2016	*brunneus*	1	
				discolor	1	1
Negra s.	45.383N, 25.350E	lighttrap	14.VII.2016	0	0	0
Negra s.	**45.383N, 25.350E**	**net**	**14.VII.2016**	***romanicus***	**1**	**1**
Brătei Valley (la Baraj)	45.318023N,25.379547E	lighttrap	22–23.VII.2016	*brunneus*	1	
Neagra V.	45.382123N, 25.346601E	lighttrap	8-9.VIII.2016	*brunneus*	1	
Dudele S. (Stâna Dudele)	45.386128N, 25.375172E	lighttrap	26–27.VII.2016	*discolor*	3	2
Dudele S. (Stâna Dudele)	45.386128N, 25.375172E	lighttrap	27–28.VII.2016	*discolor*	2	1
Deleanu V.	45.368N, 25.374E	lighttrap	20–21.VII.2016	*discolor*	1	
Deleanu V.	45.368N, 25.374E	lighttrap	21–22.VII.2016	*discolor*	3	
Deleanu V.	45.368N, 25.374E	lighttrap	23–24.VII.2016	*discolor*	3	2
Deleanu V.	45.368N, 25.374E	lighttrap	24–25.VII.2016	*discolor*	4	2
Deleanu V.	45.368N, 25.374E	lighttrap	25–26.VII.2016	*discolor*	3	
Ialomița V. (Salvamont Peștera)	45.397947N, 25.440193E	lighttrap	01–02.VIII.2016	*discolor*		1
Piatra Arsă, izvor la Stână s.	45.386101N, 25.481898E	lighttrap	05–06.VIII.2016	0	0	0
Piatra Arsă, izvor la Stână s.	45.386101N, 25.481898E	lighttrap	06–07.VIII.2016	0	0	0
Piatra Arsă, izvor la Stână s.	45.386101N, 25.481898E	lighttrap	04–05.VIII.2016	0	0	0
Dobrești, V. Brătei, amonte confl. Ialomița V.	45.292055N, 25.403428E	lighttrap	21v22.VII.2016	0	0	0
Dobrești, V. Brătei, amonte confl. Ialomița V.	45.292055N, 25.403428E	lighttrap	22–23.VII.2016	0	0	0
Bușteni (Centrul de Vizitare) V.	45.408986N, 25.526779E	lighttrap	21–22.VII.2016	0	0	0
Bușteni (Centrul de Vizitare) V.	45.408986N, 25.526779E	lighttrap	22–23.VII.2016	0	0	0
Bușteni (Centrul de Vizitare) V.	45.408986N, 25.526779E	lighttrap	23–24.VII.2016	0	0	0

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