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Lineage sorting by parameres in Limnephilinae subfamily (Trichoptera): with description of a new tribe, new genera and new species

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Abstract. The discovery of the new *Agaphylax* genus with unique paramere organisation has initiated our lineage sorting of tribes by parameres in the Limnephilinae subfamily applying the principles and procedures of fine phenomics in order to establish transformation series of the polarized plesiomorphy-apomorphy character states for each limnephiline genera. According to the extraordinary high diversity the paramere that is the stimulatory and titillating structure of the phallic organ is a speciation supertrait. This adaptive trait is directly involved in the processes of reproductive isolation and diverging as subtle initial split of lineages producing the incipient sibling species in the recent past of contemporary speciation processes. Contrary, the drastic divergence of the *Agaphylax* plated paramere is much older, similarly to the many-spined parameres of the *Hesperophylacini* tribe. It has been initiated by drastic combined and synchronous external and internal stochastic effects, processed in ancestral sexual integrative adaptation as well as organised and fixed in older and deeper coalescence events and appears as a character with tribe ranking potential. To open a wider perspective, a systemic relational analysis is required in the future including other adaptive or neutral character transformation series, due to the burden of taxonomic incongruences grounded by chimerism in stochastic genetic reticulation. Traits of species are mixed products coming from various sources. Only character combinations can and ought to be analysed in terms how to classify taxa. We have polarized eight genitalic characters additional to parameres for a future analysis of the potential of character combinations.

Limnephilinae subfamily is composed of Limnephilini, Chilostigmatini, Chaetopterygini, Stenophylacini and Hesperophylacini tribes and here we established the new Agaphylacini tribe. Based on parameres we have delineated taxa in lineage sorting and described two new genera: *Fogophylax* gen. nov., *Simaphylax* gen. nov. and fourteen new species: *Anabolia alsoja*, *A. hepehupa*, *Asynarchus kimaros*, *Limnephilus kerekes*, *L. maghrebensis*, *L. oblos*, *Homophylax beges*, *H. coros*, *Chaetopteroides plackovicensis*, *C. rilaensis*, *Allogamus ketpar*, *Platyphylax beshkovi*, *Pycnopsyche letova* and *P. telea* spp. nov. The by-product of this survey is a world atlas of paramere drawings for the entire Limnephilinae subfamily.

Keywords. Paramere organisation, paramere polarization, paramere atlas, lineage sorting.

INTRODUCTION

This paramere survey enriched with other character transformation series was initiated by the discovery of the unique *Agaphylax* genus. Recently we have described a new European limnephiline genus *Agaphylax* characterized by surprisingly unique parameres of drastic shape divergence, almost incongruent to the known paramere patterns in the subfamily. This unusual paramere structure, the product of drastic divergence in integrative organisation could be a character with tribe ranking potential. Therefore it was suggested to conduct a comprehensive paramere revision on the entire subfamily (Oláh *et al.* 2018).

Here we survey the paramere organisation in each tribe of the Limnephilinae subfamily along the generic lineages by the principles and procedures of fine phenomics. According to the extraordinary high diversity the paramere is a speciation supertrait. How does the diversity of paramere, the stimulatory and titillating substructure of the phallic organ, influences the speciation processes and results in lineage sorting? Based on parameres we delineate taxa in lineage sorting and as a by-product we describe a new tribe, new genera and species accordingly, applying the shape organisation of this adaptive trait that is directly involved in the processes of reproductive isolation. To open a wider perspective, a systemic relational analysis is required on other adaptive or neutral character transformation series in the future, due to the burden of taxonomic incongruences grounded by chimerism in stochastic genetic reticulation. The analytic possibility of character combinations is established here by surveying the plesiomorphic or apomorphic states of eight basic genital substructures besides the parameres in each genus. The by-product of this survey is a world atlas of paramere drawings for the entire Limnephilinae subfamily.

Theoretical grounding

Such a large shape divergence must have been initiated by combined and synchronous external and internal stochastic effect, as well as organised

and fixed probably in older and deeper coalescence events and processed by ancestral sexual integrative adaptation (Oláh *et al.* 2018). Sexually adapted structures diverged in contemporary recent past exhibit usually more subtle, but nevertheless stable shape divergences of the initial split. They are particularly suitable to delineate the recent lineages of the new incipient sibling species. These speciation traits are useful and practical for taxonomist in converting the natural kind of divergences into nominal kind of taxonomic rank in early stages of speciation processes. The organisation of these adaptive structures is processed frequently in post-mating prezygotic copulatory mechanisms like cryptic female choice with over 25 known mechanisms (Eberhard 2010) including gametic incompatibilities. The divergence of speciation traits, like any kind of divergences, is initiated stochastically by random environmental effects, but stabilised on molecular level by complex adaptive and integrative mechanisms (Oláh *et al.* 2017, Oláh & Oláh 2017).

If the adaptive paramere shape divergence is drastic and the morphological differences are great, as we have detected in *Agaphylax* genus, it was probably produced by deeper coalescence events during older and drastic stochastic accidents and fixed by ancestral integration and not by contemporary one. The combination of gross and fine paramere shape divergences may have real potential and unexplored capacity to utilise in the lineage sorting of multiple nodes by the gross phenomics of ancestral traits and by the fine phenomics of contemporary more subtle speciation traits. This possibility inspired us to elaborate an outline of working hypothesis for a future comprehensive and systemic revision of paramere organisation in the Limnephilinae subfamily (Oláh *et al.* 2018).

But what we can really gain by elaborating paramere trees of limnephiline genera if clouds of endless trait trees exist inside each species trees frequently contradicting to each other (Oláh *et al.* 2019)? Can we sort lineages and delineate phylogenetic species directly by the trees of the adaptive paramere divergences? Yes, if these particular traits are supertraits representing the repro-

ductive barrier building by their shape divergences either in sympatry or more frequently in allopatry under strong genetic drift of small isolated populations.

These questions lead us to the basic problem of taxonomy. We are more and more aware of and faced with the reality of taxonomical incongruences. Traits of species are mixed products. They are integrated through random processes from various lineages. Every entity itself is the result of the chimerical reticulation (Oláh *et al.* 2019). The stochastic universe makes our ontology naturally incongruent and the various capacities of taxonomists produce additional incongruences in an ever probabilistic epistemology.

The discovery in growing number of conflicting gene/trait trees obscures the species relationships of the containing species tree resolvable only by probabilism of phylogenetic inferences and systematics (Siddal & Kluge 1997, Haber 2005). Fundamental problem arises how to reconcile conflicting trait trees into one species tree that is into the containing species tree. Individual morphological/gene traits depart from species tree and frequently differ from each other due to epistemic reasons: (1) virtual model manipulations; (2) tree-building errors, as well as to ontic or ontological reasons: (3) gene duplication/loss; (4) undetected paralogy, (5) horizontal gene transfer, (6) introgression, (7) incomplete lineage, (8) ancestral polymorphism when within-species polymorphism lasts longer than the time between two successive speciations. Concatenation, the supermatrix approaches do not help to solve inconsistency rather it increases the conflict in the presence of incomplete lineage sorting (ILS). New ILS-aware coalescent algorithms correcting or smoothing for ILS were developed in the virtual industry. But again, as usual the new models were supported by theoretical, not empirical arguments. The new models of concatenation versus coalescence versus "concatalescence" were assessed, increasingly used and vehemently criticized (Scornavacca & Galtier 2017). The real question how can we apply paramere trees for lineage sorting with the contradictory within-

species trees of many other morphological traits remains ambiguous.

Recombination, genetic drift, genetic draft, gene flow, lateral transfer, introgression and many more, innumerable, unknown and unnamed mechanisms and their multiple interactions allow different parts of the genome, and their coded and expressed phenomic traits, to have different genealogical histories. Environment dictates how some characters are under directional integration for change while others are exposed to stabilizing integration to remain unchanged. Some characters are loosely, others are tightly integrated. The arbitrary nature of boundaries between single characters, character complexes and hierarchies as well as the interdependence amongst structurally and functionally integrated parts create highly varying and interwoven character weights in calculating phylogenetic relationships giving higher weights to characters unlikely to change (Kemp 2016).

Incongruences between genes or morphological traits are central issue both in phylogeny and in taxonomy. In reductionist (atomistic) models characters are taken to be independent rather than structurally or functionally linked and equally susceptible to divergences. Modular models of character clusters manipulate with semi-independent characters and correlated models calculate with dependent characters having potential to integrate.

In spite of the rich arsenal of alterations, coalescent theory tries to modelise how gene variants sampled from a population may have originated from a common ancestor. Accordingly a single gene or phenomic trait stands in proxy for each species, but in reality different genes can produce different lineages in the evolutionary trees. In our scientific media-besotted era the oversimplified unrealistic models of coalescent theory assumes no recombination, no natural integration, and no gene flow or population structure, meaning that each gene/phenomic trait variant is equally likely to have been passed from one generation to the next. The model looks backward in time, merging alleles into a single

ancestral copy according to a random process in coalescence events. In reality true gene trees are actually distinct from each other, and from the species tree. Genetic variation shared between closely related species may be due to retention of ancestral polymorphisms because of incomplete lineage sorting and/or introgression following secondary contact and realised in multiple of alteration and protection mechanisms by the background integrative organisation.

Stochastic ontology and probabilistic epistemology lead us to the growing number of conflicting trees resolvable only by probabilism of phylogenetic inferences and systematics (Siddal & Kluge 1997, Haber 2005). Trait tree parsimony, which, given a set of trait trees, seeks a species tree that requires the smallest number of evolutionary events to explain the incongruence of the trait trees. In limnophilid genera the “*conflicting within-species character states*” of the periphallid organs, cerci, paraprocts, gonopods as well as aedeagus and parameres of the phallic organ seem to be a general rule. Incongruences and discordances among individual character trees are detected in the every-day practices of taxonomists by bewildering exuberance of empirical evidences as produced by idleness, curiosity and ambiguity in the everydayness of the inauthentic condition of present-day taxonomy.

MATERIAL AND METHODS

Appendicular terminology of genital substructures

We used our functional appendicular terminology and not the conventional anatomical directional terminology to describe the genital structures in species description (Oláh & Johanson 2008). Polyphorae has the most plesiomorphic state of the superanal complex in the Limnophiloidea superfamily (Vshivkova 2007). Segment X (XI) is most produced and the genitalia primitively comprise 7 pairs of appendages: (1) dorsomesal lobes of segment IX; branches on segment X (XI): (2) preanal appendages; (3)

external branches; (4) internal or intermediate branches; (5) inferior branches; (6) subanal plate; (7) inferior appendages on segment IX. These structures are variously present or absent in different genera; some of them often lost through specialization by simplification that could be an inherent complexity increase (Oláh *et al.* 2017). Complexity could arise, not only by incremental addition but by incremental subtraction in the Apataniidae, Uenoidae families and in the Dicosmoecinae subfamily of the limnophiloid Polyphorae. At Oligophorae taxa the number of branches on segment X(XI) is reduced/fused and consistently comprised only 4 pairs of appendages: (1) cerci, one or the fused forms of setose cercal appendages (praeanal appendages and external branches of segment X(XI)); (2) paraproct appendages (the fused internal and inferior branches of segment X)(XI); (3) membranous or less pigmented subanal plate as well as (4) the subphallic complex of inferior appendages on segment IX with its basal plate. In Oligophorae limnophilids the *paraproct complex* is formed by the fusion of internal and inferior branches of segment X (XI) due to the further body reduction of segment X (XI). The paraproct complex is represented by variously produced remnants of these branches and named in four different directional terminologies: (1) internal and inferior branches of Schmid (1955), (2) apparent dorsal and ventral branches of Vshivkova (2007), (3) apical and basal branches or (4) horizontal and vertical branches. Dorsal branches are produced caudad and more or less horizontal, ventral branches oriented more or less dorsoventrad. Combining the four directional nomenclatures of the paraproct branches we may summarize that the dorsal branch is internal (bilobed in plesiomorphy: external and internal), apical and horizontal; the ventral branch is inferior, basal and vertical. Branches may be partially or completely fused in various shape and forming a completely or partially sclerotized ring around anus. This paraproct complex could be fused with dorsum IX, segment X and with cerci forming together the *superanal genitalic complex* of Vshivkova (2007).

Polarization of basic genital substructures

A systemic relational analysis is necessarily probabilistic due to the taxonomic incongruences. It requires, besides the adaptive parameres, several additional adaptive or neutral traits for character combination. The future possibility of character combination is initiated and supported here by surveying the character polarization, the plesiomorphy-apomorphy transformation series of some basic genital structures:

(1) Absence (plesiomorphic) or presence (apomorphic) of spinulose protuberance or any neoforation on tergite VIII;

(2) Produced (plesiomorphic) or reduced (apomorphic) state of tergite IX;

(3) Setose inerm (plesiomorphic) or more sclerotized variously dentate (apomorphic) state of cerci;

(4) Produced (plesiomorphic) or reduced (apomorphic) state of the dorsal branch of paraproct;

(5) Separate free from each-other (plesiomorphic) or fused to-each-other (apomorphic) state of the dorsal branch of paraproct;

(6) Separate free-from-cerci (plesiomorphic) or fused to-cerci (apomorphic) state of the dorsal branch of paraproct;

(7) Produced (plesiomorphic) or reduced (apomorphic) state of the ventral branch of paraproct;

(8) Separate free from each-other (plesiomorphic) or fused to each other (apomorphic) state of the ventral branches of paraproct.

Depositories

Here we give some background information for the Oláh Private Collection that stands for its own identity. Its donation to the Hungarian Natural History Museum is declared and firmly committed purely on loyalty, but conditions and details are not contracted yet. The collection is installed and curated at the first author's residence until he and his son János Oláh jr. continue research on caddisflies. The collection was built up and still being built intensively by organising collecting trips from private resources. During research activities we have visited and expe-

rienced many caddisfly collections of large museums in Europe and USA. Unfortunately the natural history museums, „the place for the Muses (moussa)”, „the museum (mouseion) of sciences”, have lost their founding ideology. They are converted into interactive baby-sitter centres based on the pervasive ideology of resentment. They are suffering the consequences of research and financial inadequacy all over the western world loaded by climate change with rapidly declining biodiversity. We agree with visitors that our private caddisfly collection is the best organised and properly curated one. Unfortunately this is a sad and absurd scenario of the present devastated state of taxonomy. We hope that the primordial idea of ontology and epistemology will return into the natural history museums. At least on a long run the Hungarian Natural History Museum will regain its historical quality to curate properly our caddisfly collection.

List of abbreviations

- Canadian National Collection, Ottawa, Canada (CNC)
- Clemson University Arthropod Collection, USA (CUAC)
- Department of Plant Protection, Henan Institute of Science and Technology, China (DPP-HIST)
- Hungarian Natural History Museum, Budapest, Hungary (HNHM).
- Museum der Natur, Gotha, Germany (MNG)
- Museum for Natural History of the Humboldt University of Berlin, Germany (ZMB).
- National Museum of Natural History, Sofia, Bulgaria (NMNHS)
- National Museum of Natural History, Smithsonian Institution, Washington, (NMNH)
- Natural Institute of Biological Resources, Incheon, Korea (NIBR).
- Oláh Private Collection, Debrecen, Hungary (OPC) under national protection of the Hungarian Natural History Museum.
- Royal Ontario Museum, Toronto, Canada (ROM)
- Ruitter Private Collection, Oregon, USA
- Swedish Museum of Natural History, Stockholm, Sweden (SMNH)
- Zoological Institute, Leningrad, Russia (ZIL)

TAXONOMY

In this survey we have realised partial lineage sorting by parameres in the Limnephilinae subfamily based upon the established transfor-

mation series of paramere states for each limnephiline genera. Our main goal was to outline briefly the paramere organisation in the subfamily without a systematic relational analysis. Transformation series appears from ancestral complex plesiomorphic state of shape and compositional diversity to the specialisation by simplification of incremental subtraction. This apparent simplification could be an inherent complexity increase by complementary qualities associated with decrease in the shape diversity and in the number of structural units. This partial lineage sorting with paramere transformations has produced some actual changes (new tribe, new genera, new species) in the taxonomy of the Limnephilinae subfamily without however, a systematic presentation of taxonomic history as well as of the taxonomical relations of the taxa.

In the Limnephilinae subfamily five tribes have been established (Limnephilini, Chilostigmatini, Chaetopterygini, Stenophylacini, Hesperophylacini) and here we delineate and describe the sixth tribe Agaphylacini based on the unique paramere organisation of monobasic genus *Agaphylax*.

The tribe definitions in the Limnephilinae subfamily are based on rather general statements on general body characters (Schmid 1955). (1) Limnephilini tribe is characterised by anastomose disposition, massive male genitalia and appendages on female genitalia; (2) Stenophylacini tribe by less massive and more variable male genitalia; (3) Chaetopterygini tribe by robust and spiny body features; (4) Chilostigmatini tribe by particular ancestral genital features. (5) Only Hesperophylacini, a newly established tribe has been grouped inside the Limnephilinae subfamily by paramere organisation: the three species of the tribe have short paramere shaft and armed apically with broom-like burst of strongly sclerotized, long and recurved spines (Vshivkova et al. 2007). Below, we detail the tribe definition with characteristics of paramere organisations in each tribe.

Limnephilini tribe

In the Limnephilini tribe the basic plesiomorphic state of parameres is the rod-like sclerotized shaft terminating in dilated/enlarged bilobed apex composed of apical setose lobes/branches in dorso-subapical (proximal) and apical (distal) position. These bilobed apices are usually heavily setose and the terminal lobes/branches are variously shaped, curved and oriented. Apical setae are present as unmodified fine sensory structures and/or variously modified spine-like stimulatory structures. Most of the genera in the tribe have species with this bilobed plesiomorphic paramere state: *Anabolia*, *Anisogamodes*, *Arctopora*, *Asynarchus*, *Clistoronia*, *Glyphotaelius*, *Grammotaulius*, *Halesochila*, *Lenarchus*, *Lepnevaina*, *Limnephilus*, *Philarctus*, *Platycentropus*; the small *Nemotaulius* genus has only setose unilobous paramere and the monobasic *Leptophylax* and *Sphagnophylax* genera has setose spiniform parameres. In the *Limnephilus* genus one lobe becomes occasionally membranous erectile. This basic pattern of rod-like sclerotized paramere with apical complex of setose lobes/branches could be modified with simplification of incremental subtraction forming variously enlarged monolobed setose apical portion in several genera (*Anabolia*, *Asynarchus*, *Clistoronia*, *Grammotaulius*, *Leptophylax*, *Lenarchus*, *Leptophylax*, *Nemotaulius*, and *Philarctus*). Further simplification has produced simple spiniform paramere shaft with few setal structures (*Limnephilus*, *Sphagnophylax*) or spiniform paramere shaft without any structure of setal origin (*Limnephilus*). Final stage leads to paramere lost occurring in some genera (*Limnephilus*, *Platycentropus*).

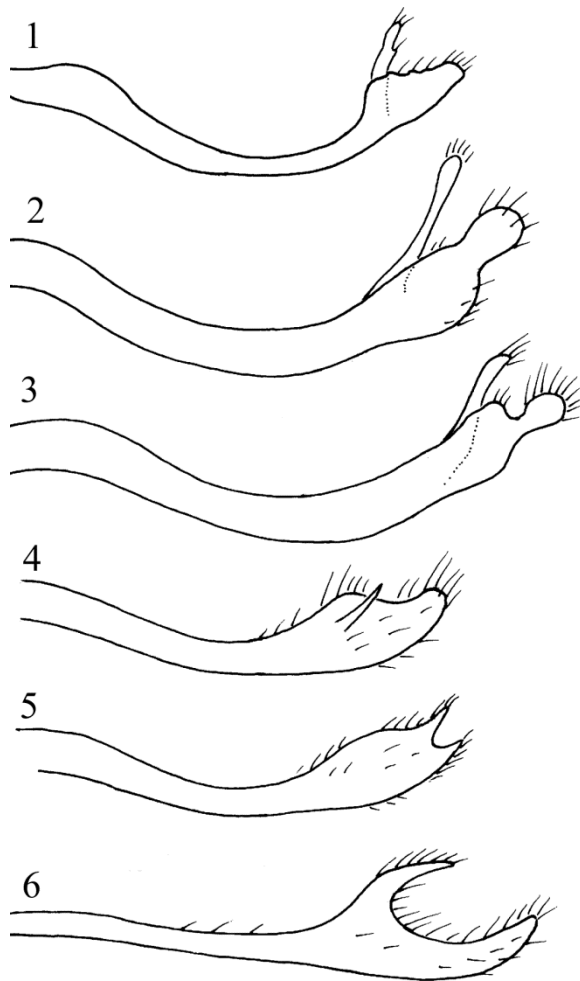
This simplification type of transformation series of character states seems to occur on most taxonomical levels of hierarchy: tribus, genus, and species group or species complex.

Anabolia Stephens, 1837

Rivulophilus Nishimoto, Nozaki & Ruitter, 2000:377–386. Monobasic. Type species: *Rivulophilus sakaii* sp. nov. **New Synonym!**

Original differential diagnosis. Heavy-bodied, rust-colored species. Formal delineation is not given.

Relation. *Anabolia* is more related to *Limnephilus* (Schmid 1955).



Figures 1–6. Ancestral *Anabolia* lineage with bilobed plesiomorphic paramere. *Anabolia nervosa* species group. 1 = *A. anatolica*, 2 = *A. brevipennis*, Hungary, Duna-Dráva N. P., 3 = *A. brevipennis*, Hungary Aggtelek N. P., 4 = *A. ozburni* drawn by Schmid, 5. *A. ozburni* drawn by Nimmo, 6 = *A. taibaishanica*.

Genital character state combinations. (1) Absence (plesiomorphic) of spinulose protuberance or any neoformation on tergite VIII; (2) Reduced (apomorphic) state of tergite IX; (3) Sclerotized variously dentate (apomorphic) state of cerci; (4) Produced (plesiomorphic) state of the dorsal branch of paraproct; (5) Separate free from each other (plesiomorphic) state of the dorsal branch of paraproct; (6) Separate free-from-cerci (plesiomorphic) state of the dorsal branch of paraproct; (7) Reduced (apomorphic) state of the ventral branch of paraproct; (8) Separate free from each other (plesiomorphic) state of the ventral branches of paraproct.

Parameres organisation. According to the parameres there are two lineages in the genus. (1) The ancestral lineage has plesiomorphic ancestral complex-headed bilobed parameres. In species with variously complex bifid parameres the apical lobes usually supplied with slender sensory types of setae and the dorso-subapical lobes usually armed with stronger spine-like stimulatory types of modified setae. (2) The derived lineage has apomorphic simple-headed monolobed parameres. A few species both in Nearctic and in Asia regions have lost the bifid subdivision of the paramere head and simplified into variously shaped monolobed ending with mostly slender sensory type of setae.

Ancestral *Anabolia* lineage with bilobed plesiomorphic paramere

***Anabolia nervosa* species group**

(Figures 1–6)

Parameres have heavily setosed bilobed apex in this ancestral lineage with wide holartctic distribution including the Chinese palaeartctic area: *anatolica*, *brevipennis*, *concentrica*, *furcata*, *laevis*, *lombarda*, *nervosa*, *oculata*, *ozburni*, *servata*, *subquadrata*, *taibaishanica*. Until now the fine phenomics of the paramere was not examined and our knowledge is very limited how stable are the paramere fine structure in the isolated population of this species group. Parameres of natural

hybridization in contact zones between *Anabolia nervosa* and *A. furcata* are rather variable exhibiting wide ranges of intermediate structures (Mey 1982). Paramere drawings of *Anabolia ozburni* published by Schmid (1950) and Nimmo (1971) are very different. It is more different that could be explained by different drawing styles. We have recorded significant interpopulation differences at *Anabolia brevipennis*.

***Anabolia brevipennis* (Curtis, 1834)**

(Figures 2–3)

Material examined. Hungary, Aggteleki Mts. Aggtelek National park, Jósvalő, Karst Research Station, 5.VII.1983, light leg. J. Oláh & Z. Varga, (1 male, 1 female; OPC). Hungary, Aggteleki Mts. Aggtelek National park, Jósvalő, Karst Research Station, VII–VIII.1984, light leg. J. Oláh (7 males, 1 female; OPC). Hungary, Duna-Dráva National Park, Gyékényes, Lankóci Forest, Alnus swamp, Grófi út N 46° 13' 51", E 17° 03' 02", 8.VI.2010 light leg. J. Oláh & Á. Uherkovich (4 males, 2 females, OPC).

Remarks. In the examined two populations of *Anabolia brevipennis* located in different faunal regions in Hungary the bifid ancestral complex head of the parameres is rather variable with significant fluctuating asymmetry, reflecting developmental instability and indicating strong internal genetic or external environmental impacts.

Intermediate *Anabolia* lineage with inflated paramere head

***Anabolia bimaculata* species group**

(Figures 7–11)

In this species group with intermediate paramere head the ancestral plesiomorphic bilobed parameres is getting mostly monolobed but still the terminal part is inflated/expanded into a widened head of various shapes: *abriel*, *bimaculata*, *schmidi*, *semenovi*, *sordida*, *tibetana*.

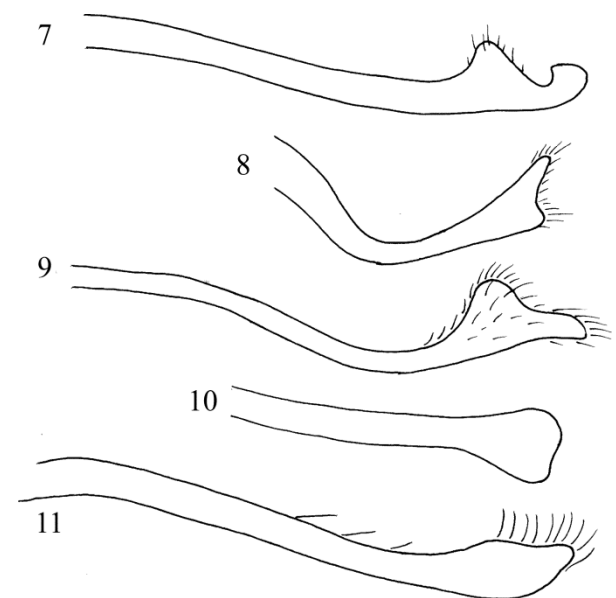
***Anabolia tibetana* (Schmid, 1966) comb. nov**

(Figure 11)

Asynarchus tibetanus Schmid, 1966:366–367: “*Asynarchus tibetanus* est certainement voisin de *Anabolia oculata* Mart. du Tibet oriental, que je transporte ici dans le genre *Asynarchus*. A vrai dire, il est difficile de classer ces deux espèces de façon satisfaisante. Leur coloration les range sans conteste permis les *Asynarchus* tandis que leurs genitalia sont ceux d’*Anabolia* peu orthodoxes.”

Material examined. India, Sikkim, Goma Sechen 3.VI.1959, black light leg. F. Schmid. Paratype ♂ CNC No. 8900 (1 male, CNC).

Remarks. According to the genital structure, *Asynarchus tibetanus* Schmid is an *Anabolia* species. The paramere head is simplified monolob forming a broadening shape slightly upward directed.



Figures 7–11. Intermediate *Anabolia* lineage with inflated paramere head. *Anabolia bimaculata* species group.
7 = *A. abriel*, 8 = *A. bimaculata*, 9 = *A. schmidi*,
10 = *A. semenovi*, 11 = *A. tibetana*.

Derived *Anabolia* lineage with apomorphic monolobed parameres

***Anabolia consocia* species group**

In this species group with derived lineages the ancestral plesiomorphic bilobed state of parameres are reduced to an apomorphic monolobed state by simplification of incremental substraction. The species group is composed of two species complexes based upon the divergences in the curvature of the paramere shaft: *Anabolia sakaii* species complex and *Anabolia consocia* species complex.

***Anabolia sakaii* species complex**

(Figures 12–16)

In this species complex the ancestral bilobed state of parameres are reduced to an apomorphic setose monolobed state with slightly produced curvatures of paramere shaft. The species complex populates limited area of the Palaearctic and Oriental regions: *alsoja* sp. nov., *continentis*, *hepehupa* sp. nov., *sakaii*, *yunnanensis*.

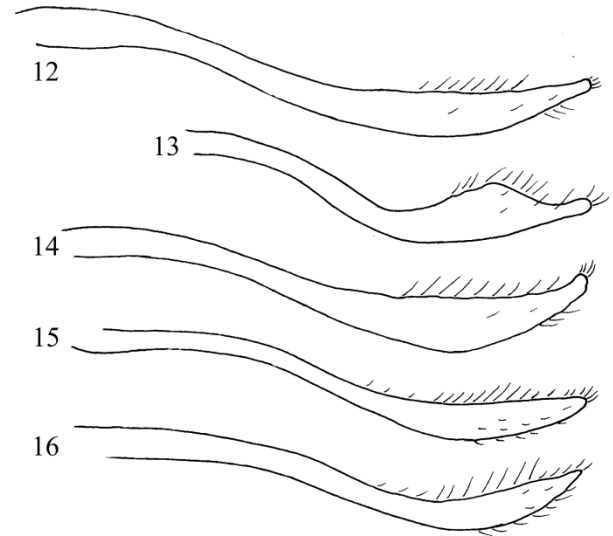
***Anabolia sakaii* (Nishimoto, Nozaki & Ruiter, 2000) comb. nov.**

(Figure 15)

Rivulophilus sakaii Nishimoto, Nozaki & Ruiter, 2000: 378.

Material examined. **Japan**, Numappara mire, Kuroiso-shi Tochigi, pupae collected on 18.VIII.1999, adult emerged on 1–25.IX.1999, reared by T. Nozaki (2 males, OPC).

Remarks. *Rivulophilus* genus, a synonym of the *Anabolia* genus with apomorphic parameres, is a derived lineage, and forms the *Anabolia sakaii* new species complex in the *Anabolia consocia* species group. This is supported also by neutral traits of periphallallic organs, especially by the finger-like lateral profile of the gonopods.



Figures 12-16. Derived *Anabolia* lineage with apomorphic monolobed parameres. *Anabolia consocia* species group.

Anabolia sakaii species complex. 12 = *A. alsoja*, 13 = *A. continentis*, 14 = *A. hepehupa*, 15 = *A. sakaii*, 16. *A. yunnanensis*.

***Anabolia alsoja* Oláh, sp. nov.**

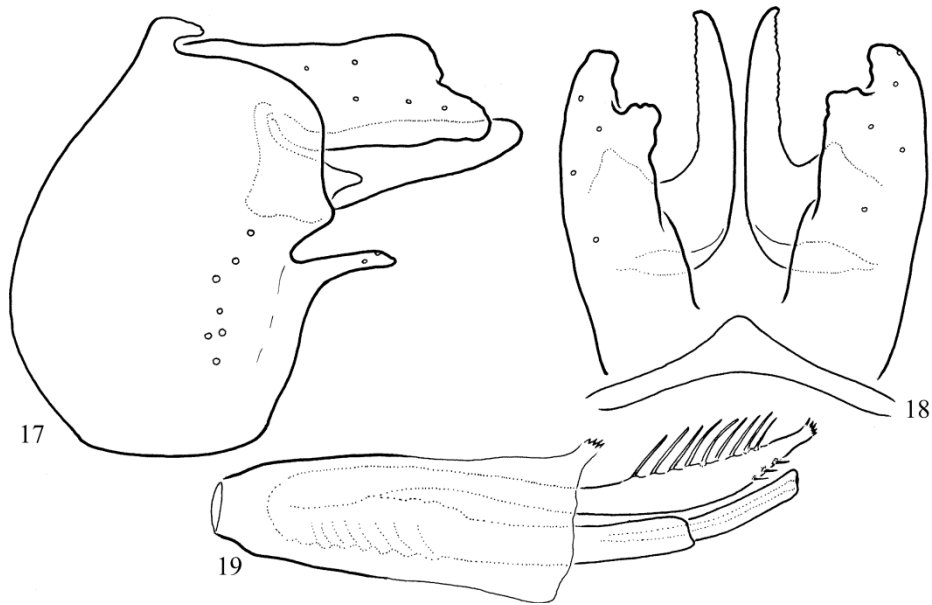
(Figures 12, 17–23)

Material examined. Holotype: **Taiwan**, Nantou Province, 5 km SW of Tayüling, N24.09° E121.17°, 2900m, 8.X.1995, leg. T. Csövári & P. Stéger, (1 male, OPC). Allotype: same as holotype (1 female, OPC). Paratypes: same as holotype (1 male DPP-HIST)

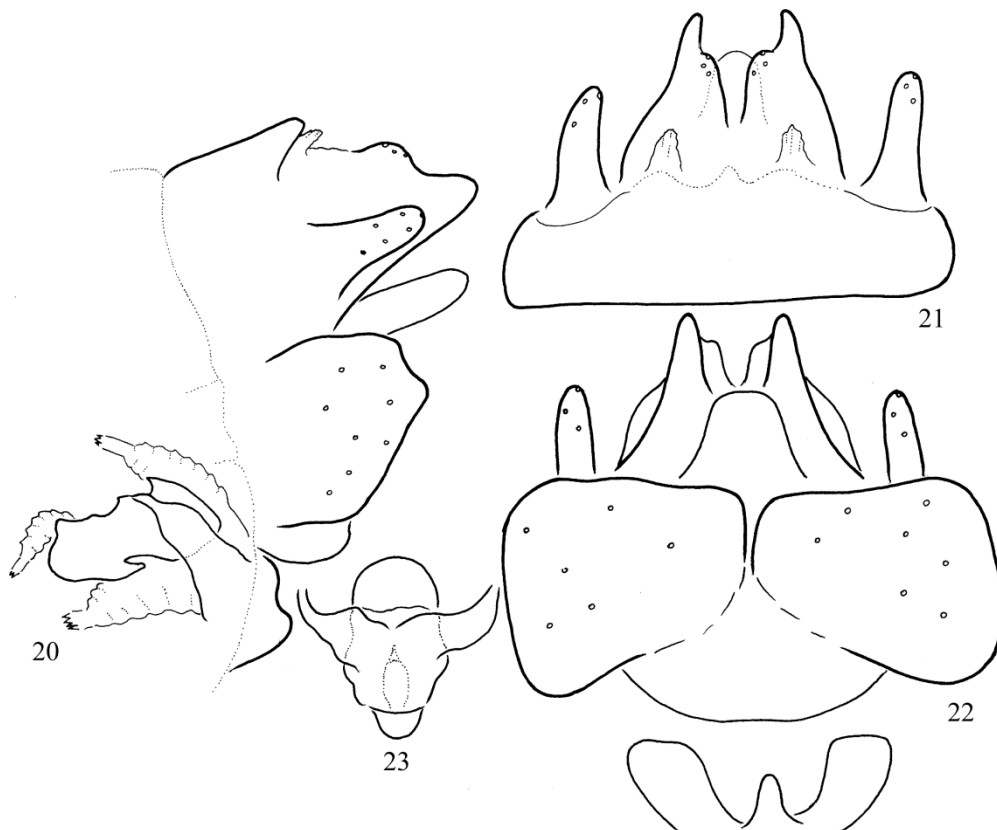
Diagnosis. This new species is close to *Anabolia hepehupa* sp. nov., but differs by having apical margin of cerci with produced ventroapical corner, not evenly bumpy apical margin, and paraproct slender, not robust.

Description. Male (in alcohol). Large-sized, rust-coloured animal; forewing rust-coloured ferruginous without any discernible speckled dark spots or light-coloured spots, but faded in alcohol. Spurs: 134. Forewing length 18 mm.

Male genitalia. Tergite VIII spinule-free, without any anchoring strong setae, short spines or pegs that is without any setate or spinate area.



Figures 17–19. *Anabolia alsoja* Oláh sp. nov. Holotype male: 17 = genitalia in left lateral view, 18 = cerci and paraproct in dorsal view, 19 = phallic organ in lateral view.



Figures 20–23. *Anabolia alsoja* Oláh sp. nov. Allotype female: 20 = genitalia with the vaginal sclerite complex in left lateral view, 21 = genitalia in dorsal view, 22 = genitalia in ventral view, 23 = vaginal sclerite complex in dorsal view.

Segment IX long almost subovoid in lateral view with low and short dorsal strap. Cerci robust, heavily sclerotized, subquadrangular, its ventroapical corner produced. Paraproct slightly longer than cerci. Gonopods digitiform, short. Parameres of the phallic organ broad subapicad, apices with tiny dense setal brush.

Female genitalia. There is no closed “anal tube” formed by the complex of the fused tergite IX and segment X; the tube that is more or less closed at many limnephilid females. Tergite IX with long, heavily setosed digitiform apicolateral processes widely separated in dorsal view; there is a pair of irregular membranous small dorsal process at the apical margin of tergite IX. Sternite IX setose subtriangular in lateral and quadrangular in ventral view; ventrally produced mesad, almost touching; the mesal plate constricted posterad, widened anterad; this glabrous ventral surface of sternite IX functions like the upper vaginal lip present as a free supragenital plate. Segment X represented by heavily sclerotized, black tergum, a basally fused pair of L-shaped processes and the free flapping rounded ventral elongated plate; in lateral view the ventral plate of segment X visible as a long digitiform structure closely lying on the dorsum of sternite IX. The open tubing function around the proctal opening of anus is realised by the sclerotized dorsum and the ventral plate of segment X. The lower vaginal lip, the vulvar scale visible somewhat separated from sternite VIII by its more sclerotized structure. Dorsal vaginal sclerite complex and the membranous vaginal chamber short, reaching only half length of sternite VIII.

Etymology. *alsoja* from “alsója” “its lower” in Hungarian, refers to the backward produced lower corner of the cerci in lateral view.

***Anabolia hepehupa* Oláh, sp. nov.**

(Figures 14, 24–26)

Material examined. Holotype: **Taiwan**, Nantou Province, 1 km of Tatchia peak, N23.33° E120.53°, 2520m, 13.X.1995, leg. T. Csövári & P. Stéger, (1 male, OPC). Paratypes: same as holotype (2 males, DPP-HIST; 1 male, OPC)

Diagnosis. This new species is close to *Anabolia yunnanensis* Leng & Yang, 2004, but differs by having apical margin of cerci bumpy convex, not plane concave and paraproct with blunt apex, not with tapering apex.

Description. Male (in alcohol). Large-sized, rust-coloured animal; forewing rust-coloured ferruginous without any discernible speckled dark spots or light-coloured spots, but faded in alcohol. Spurs: 134. Forewing length 18 mm.

Male genitalia. Tergite VIII spinule-free, without any anchoring strong setae, short spines or pegs, that is without any setate or spinate area. Segment IX long almost subovoid in lateral view with short dorsal strap. Cerci robust, heavily sclerotized, subquadrangular, its apical margin bumpy. Paraproct longer than cerci. Gonopods digitiform. Parameres of the phallic organ broad subapicad, apices with tiny dense setal brush.

Etymology. *hepehupa* from “hepehupás” “bumpy” shaped in Hungarian, refers to the pattern profile on the apical margin of cerci.

***Anabolia consocia* species complex**

(Figures 27–29)

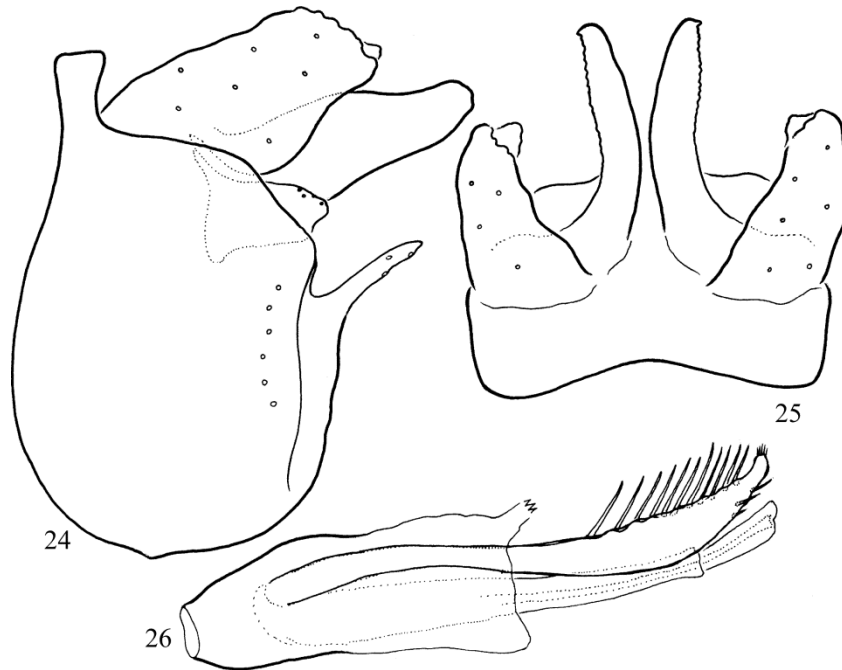
In this small species complex the ancestral bilobed state of parameres are reduced to an apomorphic setose monolobed state with strongly produced curvatures of the paramere shaft. The species complex populates the Holarctic fauna region: *apora*, *appendix*, *consocia*. Parameres were redrawn from published drawings.

***Anisogamodes* Martynov, 1924**

(Figure 30)

Anisogamodes Martynov, 1924:364, a new monobasic genus established for *Anisogamus flavipunctatus* Martynov, 1914; generotype: *A. flavipunctatus*.

Original differential diagnosis. Short-winged species with large cerci and long paraproct. Formal delineation is not given.



Figures 24–26. *Anobolia hepehupa* Oláh sp. nov. Holotype male: 24 = genitalia in left lateral view, 25 = cerci and paraproct in dorsal view, 26 = phallic organ in lateral view.

Relation. This species resembles *Anisogamus difformis* and *Stenophylax mitis* (Martynov, 1914), some characters are similar to *Stenophylax* (Schmid, 1955). Monobasic genus still with a single species.

Genital character state combinations. (1) Presence (apomorphic) of spinulose protuberance on tergite VIII; (2) Reduced (apomorphic) state of tergite IX; (3) Sclerotized variously dentate (apomorphic) state of cerci; (4) Produced (plesiomorphic) state of the dorsal branch of paraproct; (5) Separate free from each-other (plesiomorphic) state of the dorsal branch of paraproct; (6) Separate free-from-cerci (plesiomorphic) state of the dorsal branch of paraproct; (7) Reduced (apomorphic) state of the ventral branch of paraproct; (8) Separate free from each-other (plesiomorphic) state of the ventral branches of paraproct.

Parameres. Martynov 1914:11 “The shape of the penis and titillatores can not be seen in our specimen distinctly enough; penis slender, thickened at the apex, titillatores seem to be divided at the end into two branches.” Based on the flattened parameres having thin hair-like setae along their

margin as well as on the well developed central vulval scale, the *Anisogamodes* genus was removed from the Stenophylacini tribe and placed in the Limnephilini tribe (Grigorenko 2002). The entire paramere is rather stout robust. The robust setose bilobed head of the paramerese preserved the ancestral plesiomorphic state.

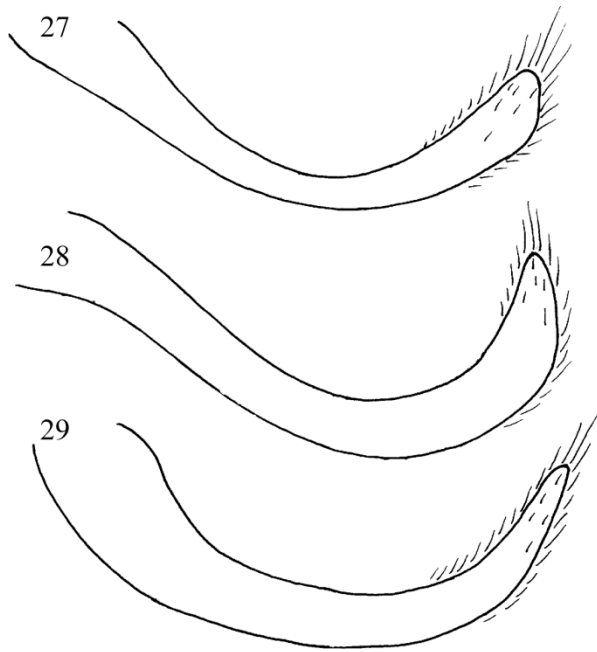
Anisogamodes flavipunctatus (Martynov, 1914)

(Figure 30)

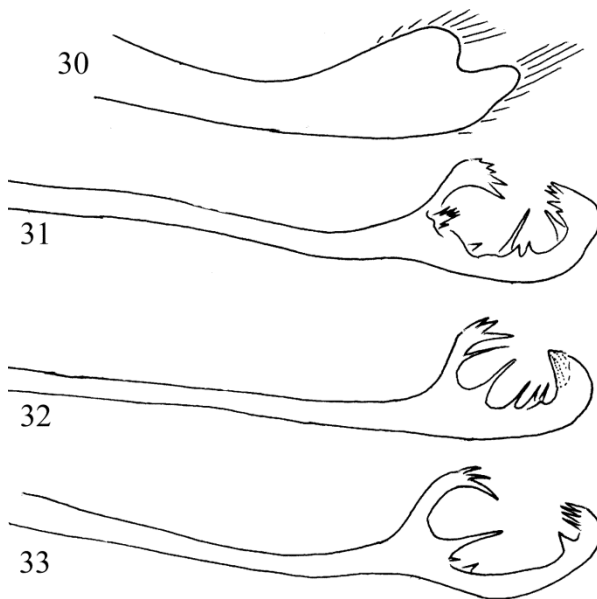
Anisogamus flavipunctatus Martynov, 1914c:82: “In the sape of genital appendages this species resembles *Anisogamus* Mc Lach. (*A. difformis* Mc Lach.) and also some species of *Stenophylax* like *S. mitis* Mc Lach. Having no females I am not sure in referring this species to *Anisogamus*; perhaps it could be separated into a new genus.”

Anisogamodes flavipunctatus: Martynov 1924:364, a new genus established for *Anisogamus flavipunctatus*.

Material examined. No specimen was available for examination. The paramere drawing was produced from the paramere picture taken by S. Chuluunbat.



Figures 27–29. Derived *Anobolia* lineage with apomorphic monolobed parameres. *Anobolia consocia* species group. *Anobolia consocia* species complex. 27 = *A. apora*, 28 = *A. appendix*, 29 = *A. consocia*.



Figures 30–33. Parameres of *Anisogamodes* and *Arctopora* genera. 30 = *Anisogamodes flavipunctatus*, 31 = *Arctopora pulchella*, 32 = *A. salmon*, 33 = *A. trimaculata*.

Arctopora Thomson, 1891

(Figures 31–33)

Original differential diagnosis. Small cool-adapted arctic and circumboreal species with wings fairly wide. Formal delineation is not given.

Relation. Wing has resemblance to *Limnephilus* and male genitalia to *Lenarchus*, but more primitive (Schmid 1955). This small genus is known with three species: *pulchella*, *salmon*, *trimaculata*.

Genital character state combinations. (1) Presence (apomorphic) of spinulose protuberance on tergite VIII; (2) Produced (plesiomorphic) state of tergite IX; (3) Sclerotized variously dentate (apomorphic) state of cerci; (4) Produced (plesiomorphic) state of the dorsal branch of paraproct; (5) Separate free from each-other (plesiomorphic) state of the dorsal branch of paraproct; (6) Separate free-from-cerci (plesiomorphic) state of the dorsal branch of paraproct; (7) Reduced (apomorphic) state of the ventral branch of paraproct; (8) Separate free from each-other (plesiomorphic) state of the ventral branches of paraproct.

Parameres. Paramere is ancestral plesiomorphic, bilobed, but rather subdivided and very complex, slender with widened head forming an almost semicircular indentation bearing rows of hairs and divided into several points. The basic architecture of the paramere head is similar at all the three species (*pulchella*, *salmon*, *trimaculata*), but diverged in fine structure. The stability of fine pattern has been not examined.

Arctopora pulchella (Banks, 1908)

(Figure 31)

Material examined. **Canada**, Ontario, Black Sturgeon Lake, 21-31.VII.1965, leg. S. Bleszynski (1 male, CNC). Canada, Alberta, Banff National Park, Alta, 3 mi. s. L. Louise Jct., 4600', 7.VII.1955, leg. R. Coyles (2 males, 2 females; OPC). Ontario, Kenora Dist, Kiruna Lake,

54°55'N 84°55'W, small stream in muskeg, 22.VII.1981, 810061b, leg. E. Fuller (1 male, ROM). Ontario, Kenora Dist, Kiruna Lake, 54°30'N 84°55'W, light:2300h, 6.VIII.1981, 810061b, leg. E. Fuller (1 female, ROM).

***Arctopora trimaculata* (Zetterstedt, 1840)**

(Figure 33)

Material examined. Norway, Hedmark (HEN), Follidal, Stadsbuøyen, 62.0364345°N 10.0075637°E, 8.VII.1988 1967 net leg. T. Andersen (1 male, OPC). Norway, Finnmark, Kautokeino Lahpoluoppal, Nahpoljohka ved bru, 69.21029°N 23.76200°E, 320 moh, 24.VII.-6.VIII.2010, Malaisiet trap 4 leg. Finnmarksprosjektet (4 males, OPC).

***Asynarchus* McLachlan, 1880**

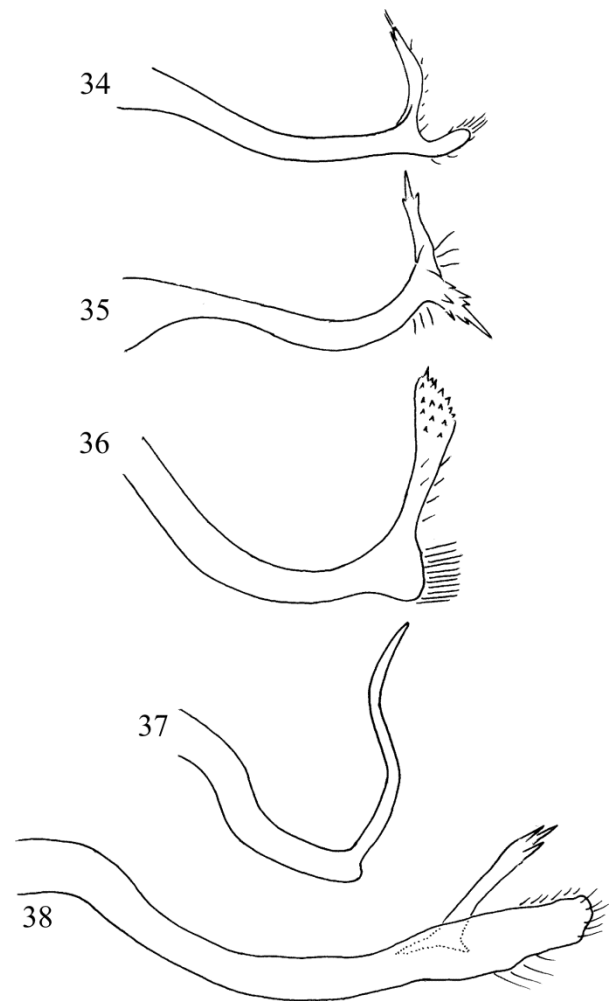
(Figures 34–47)

Original differential diagnosis. “Of *Limnophiliform* aspects, but with shorter and broader anterior-wings. Separated from *Stenophylax* (typically) by the anterior-wings being somewhat less parabolic at the apex.” Formal delineation is not given.

Relation. Has resemblance to *Limnephilus* and *Anabolia* (Schmid, 1955).

Genital character state combinations. (1) Absence (plesiomorphic) of spinulose protuberance or any neof ormation on tergite VIII; (2) Reduced (apomorphic) state of tergite IX; (3) Sclerotized variously dentate (apomorphic) state of cerci; (4) Produced (plesiomorphic) state of the dorsal branch of paraproct; (5) Separate free from each-other (plesiomorphic) state of the dorsal branch of paraproct; (6) Separate free-from-cerci (plesiomorphic) state of the dorsal branch of paraproct; (7) Reduced (apomorphic) state of the ventral branch of paraproct; (8) Separate free from each-other (plesiomorphic) state of the ventral branches of paraproct.

Parameres. Paramere is ancestral complex, slender with usually bilobed/bifid apex; dorso-subapical branch with stronger spines or pointed processes, apical branch with more and finer setae. Certain state transformation with simplification is detectable at *Asynarchus impar* and *A. pacificus* having partially (*impar*) or entirely (*pacificus*) lost the bifid terminal structure of the paramere producing elongated filament. The bifid apex is distinct although in different pattern at *A. circopa* and *A. contumax*.



Figures 34–38. Parameres of *Asynarchus* genus. 34 = *A. amurensis*, 35 = *A. circopa*, 36 = *A. contumax*, 37 = *A. impar*, 38 = *A. kimaros*.

Asynarchus amurensis (Ulmer, 1905)

(Figure 34)

Material examined. **North Korea**, North Pyongan Province, Mt. Myohyang-san, Hotel Myohyang-san, 11.X.1987. Collected on lampshade at the hotel, leg. Z. Korsós & L. Ronkay (2 males, HNHM). Chagang Province, Mt. Myohyang-san, Hotel Myohyang-san, 13. IX. 1980. Singled in the vicinity of the hotel, mainly at lamps standing around the hotel, leg. L. Forró & Gy. Topál (1 male, OPC).

Asynarchus impar (McLachlan, 1880)

(Figure 37)

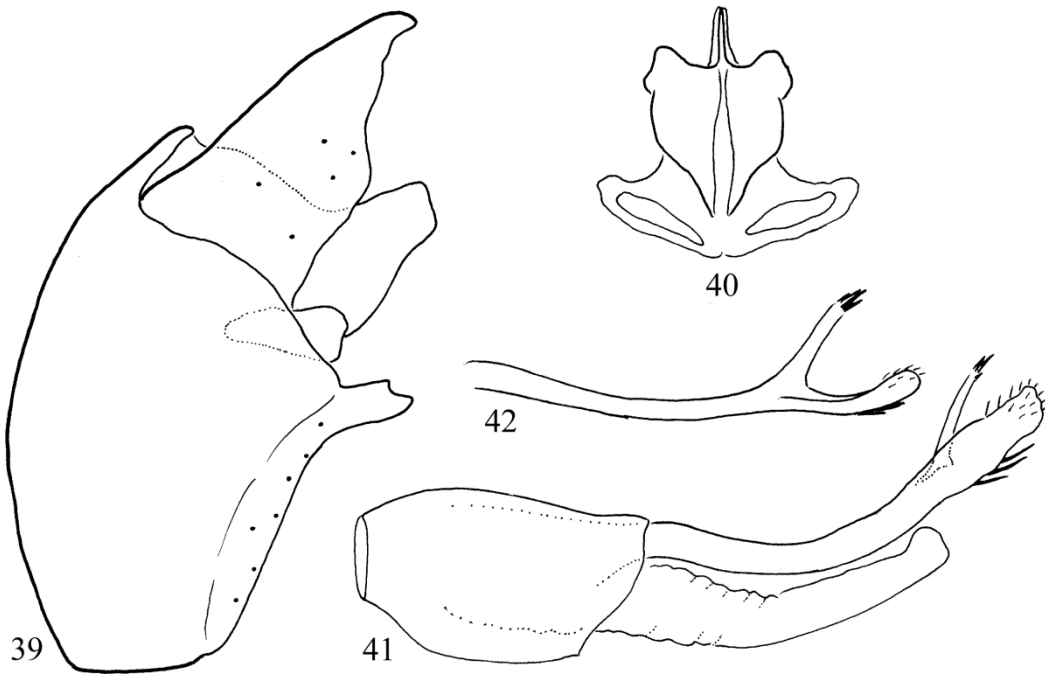
Material examined. **Norway**, Finnmark, Kautokeino Lahpoluoppal, ved innsjø, 69.20992° N 23.757661°E, 320 moh, 25.VI.–9.VII.2010, Malaiset trap 3 leg. Finnmarksprosjektet (4 males, OPC).

Asynarchus kimaros Oláh & Johanson, sp. nov.

(Figures 38, 39–42)

Material examined. Holotype: **Norway**, Akershus, Nesodden, Fagerstrand, 1–2.IX.1997, leg. S. Kobro (1 male, SMNH).

Diagnosis. The new species belongs to the *Asynarchus lapponicus* species group of Schmid. The lateral profile of the cerci resembles *A. lapponicus* and *A. mongolicus*, but differs by having directed vertically and having no any teeth or lobes ventrally. The lateral profile of the paraproct with its truncate apex similar to the *A. impar* and *A. thedenii*, but more robust and more vertically directed. The paramere differs from all the know species of the genus by having the bifurcated apex diverging in horizontal, not in vertical plane.



Figures 39–42. *Asynarchus kimaros* Oláh & Johanson, sp. nov. Holotype male: 39 = genitalia in left lateral view, 40 = paraproct in caudal view, 41 = phallic organ in lateral view, 42 = paramere in dorsal view.

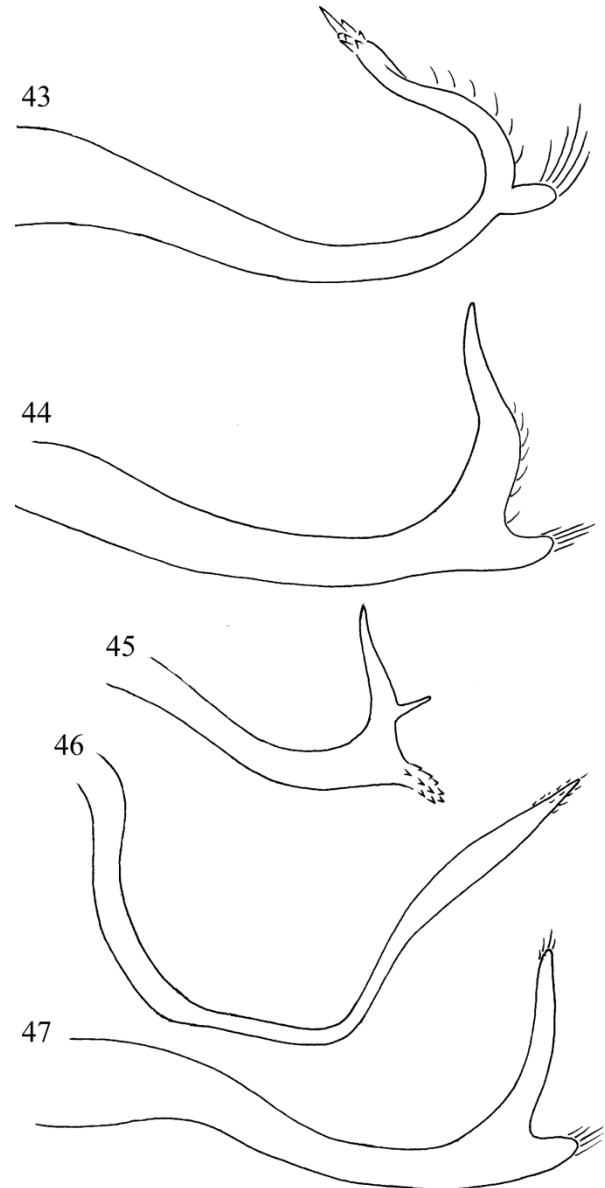
Description. Small animal. The single male specimen stored in alcohol over twenty years faded brown. The forewing length only 9 mm. Segment IX very short dorsad longer ventrad, although the demarcation line between segment IX and gonopods just discernible. Cerci very large, subtriangular, without ventral lobe. The paraproct truncate apicad and enlarged in size, its dorsal branch especially large; its ventral branch reduced in size and forms a pair of closed triangulums. Gonopod lateral profile characterized with smaller dorsal and longer ventral apical lobe. Phallic organ composed of phallosome (phallobase), endothenca, aedeagus, endophallus and parameres. The parameres characterized by a horizontal extension; its horizontally bifid apex composed of the vertically flattened setose apex of the basal shaft in lateral position and the digitiform mesal process with apical spines; the length of the lateral and mesal process almost identical.

Etymology. *kimaros* from *chimaros* male goat and *chimaira* female goat in Greek and coined in Hungarian, a Greek mythical creature with body parts taken from various animals. A symbol to describe anything composed of very disparate parts. Here it refers to taxonomical incongruence with structural units coming from different species.

***Asynarchus lapponicus* (Zetterstedt, 1840)**

(Figure 43)

Material examined. **Norway**, Nordland (NSI), Saltdal, Solvågli, 66.8228695°N 15.5178944°E, August 1967 net. leg. A. Fjeldså (1 male, OPC). **Finnmark (FN)**, Vardø, Persfjord, 70.41994°N 30.79179°E, 8.VII 1989 net. leg. A. Fjellberg (1 female, OPC). **Finnmark**, Sør-Varanger, Svanhovd forskningsstasjon, 69.45403°N 30.04057°E, 46 moh, 29.IX.2010, light trap Finnmarksprosjektet, leg. T. Andersen (2 males, OPC). **Russia**, Chaunskaya Gulf, Ajon Island, N69.552140 E169.18236, 14–27.VII.2015. Malaise trap, leg. P. Mortensen. (2 males, 1 female, SMNH; 2 males, OPC).



Figures 43–47. Parameres of *Asynarchus* genus. 43 = *A. lapponicus*, 44 = *A. mongolicus*, 45 = *A. nigriculus*, 46 = *A. pacificus*, 47 = *A. thedenii*.

***Asynarchus mongolicus* Oláh, 2018**

(Figure 44)

Material examined. Holotype: **Mongolia**, Gorkhi-Terelj National Park, N47°58'58.81" E107°27'07.10", 1550-1600 m, 20.VII–15.VIII. 1986, leg. Z. Varga (1 male, OPC).

Remarks. Most close to *A. lapponicus*, but differs by the differently formed neutral trait of cerci and gonopods and by the diversified fine structure of the paramere. The cerci are very large, subtriangular, its ventral lobe located middle and blunt, not near the basement and not pointed. The paraproct is reduced in size, its dorsal arm especially small and triangular in lateral view. Gonopod lateral profile is characterized with pointed dorsal and very blunt ventral apical lobe. Phallic organ composed of phallosome (phallobase), endotheca, aedeagus, endophallus and parameres. The parameres are characterized by an upward and forward turning spine-like dorsal arm and the more setose horizontal ventral arm. The new species is most close to *A. lapponicus*, but differs by having differently shaped lateral profiles both of the cerci and gonopods as well as easily distinguished by the diversified fine structure of the parameres.

***Asynarchus nigriculus* (Banks, 1908)**

(Figure 45)

Material examined. USA, Colorado, Independence Pass, Lake Co. 12100', tundra, 7.VIII.1961, leg. C. H. Mann (1 male, 1 female; OPC).

***Asynarchus pacificus* (Banks, 1900)**

(Figure 46)

Material examined. USA, Oregon, Wetmore Campground, Baker Co. 3.VII.1965, black light leg. E. & I. Munroe (1 male, CNC). Oregon, Wetmore Campground, Baker Co. 29.VI.1965, black light leg. E. & I. Munroe. With yellow label: Barcode of Life, DNA voucher specimen 09CNCTR-0064, BOLD ID CNCTR064-09 (1 male, CNC).

***Asynarchus thedenii* Wallengren, 1879**

(Figure 47)

Material examined. Sweden, Sorsele, Ammarnäs, 27.VIII.1911, leg. D. Saunitz (1 male, SMNH). Sweden, Sundsvall, 27.VIII.1937, (1 male, SMNH). Sorsele (1 male, OPC).

***Clistoronia* Banks, 1916**

(Figures 48–50)

Original differential diagnosis. The genus was established by a key: "Large full winged species, membrane not granulate". Formal delineation is not given.

Relation. Has resemblance to *Limnephilus* and differs only by the genital structure (Schmid 1955).

Genital character state combinations. (1) Absence (plesiomorphic) of spinulose protuberance or any neof ormation on tergite VIII; (2) Reduced (apomorphic) state of tergite IX; (3) Sclerotized variously dentate (apomorphic) state of cerci; (4) Produced (plesiomorphic) state of the dorsal branch of paraproct; (5) Separate free from each-other (plesiomorphic) state of the dorsal branch of paraproct; (6) Separate free-from-cerci (plesiomorphic) state of the dorsal branch of paraproct; (7) Reduced (apomorphic) state of the ventral branch of paraproct; (8) Separate free from each-other (plesiomorphic) state of the ventral branches of paraproct.

Parameres. Paramere is ancestral complex, plesiomorphic, stout with usually variously bifid setose apex; transformation with simplification to monolobed apex present.

***Clistoronia formosa* (Banks, 1900)**

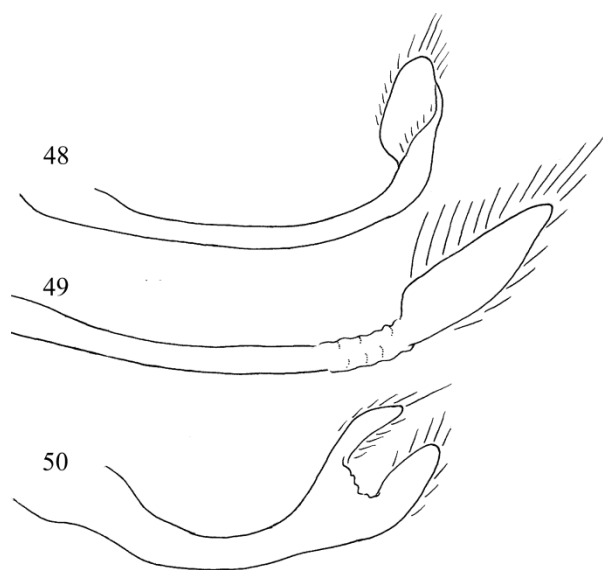
(Figure 48)

Material examined. USA, New Mexico, Cimarron Canyon, Sangre de Cristo Mts., Colfax County, 7900 ft., 6.VII.1962, black light leg. E. & I. Munroe (1 male, CNC). Arizona, Greer, White Mts., Apache County, 8500', 4.VIII.1962, black light leg. E. & I. Munroe (1 male, OPC).

***Clistoronia maculata* (Banks, 1904)**

(Figure 49)

Material examined. USA, Arizona, Greer, White Mts., Apache County, 8500', 4.VIII.1962, black light leg. E. & I. Munroe (1 male, CNC).



Figures 48–50. Parameres of *Clistoronia* genus. 48 = *Clistoronia formosa*, 49 = *C. maculata*, 50 = *C. magnifica*.

***Clistoronia magnifica* (Banks, 1899)**

(Figure 50)

Material examined. **Canada**, British Columbia, Vancouver, 30.IX.1951, leg. A. L. Turnbull, V2600, 55, 13, *Clistoronia magnifica* (Banks) Det. C.B. Wiggins 1963 ♂ (1 male, CNC).

***Glyphotaelius* Stephens, 1837**

(Figure 51)

Original differential diagnosis. Formal delineation is not given.

Relation. Has resemblance to *Limnephilus* and differs by the apex of the forewing (Schmid 1955).

Genital character state combinations. (1) Presence (apomorphic) of spinulose protuberance on tergite VIII; (2) Reduced (apomorphic) state of tergite IX; (3) Setose inerm (plesiomorphic) state of cerci; (4) Produced (plesiomorphic) state of the dorsal branch of paraproct; (5) Separate free from each-other (plesiomorphic) state of the dorsal branch of paraproct; (6) Separate free-from-cerci (plesiomorphic) state of the dorsal branch of

paraproct; (7) Reduced (apomorphic) state of the ventral branch of paraproct; (8) Separate free from each-other (plesiomorphic) state of the ventral branches of paraproct.

Parameres. Paramere is ancestral complex, stout with variously bifid setose apex.

***Glyphotaelius pellucidus* Retzius, 1783**

(Figure 51)

Material examined. **Hungary**, Aggtelek Mts. Aggtelek National Park, Szelcepuszta, 2.VI.1983, light leg. J. Oláh (2 males, 1 females; OPC).

Remarks. The complex ancestral head of the paramere bilobed and typically the apical lobe supplied with thin hair-like sensory setae and the dorso-subapical lobe armed with strong and stout more modified spine-like setae.

***Grammotaulius* Kolenati, 1848**

(Figures 52–53)

Original differential diagnosis. Formal delineation is not given.

Relation. Related to the to *Limnephilus* genus (Schmid 1955).

Genital character state combinations. (1) Absence (plesiomorphic) of spinulose protuberance or any neof ormation on tergite VIII; (2) Reduced (apomorphic) state of tergite IX; (3) Sclerotized variously dentate (apomorphic) state of cerci; (4) Produced (plesiomorphic) state of the dorsal branch of paraproct; (5) Separate free from each-other (plesiomorphic) state of the dorsal branch of paraproct; (6) Separate free-from-cerci (plesiomorphic) state of the dorsal branch of paraproct; (7) Reduced (apomorphic) state of the ventral branch of paraproct; (8) Separate free from each-other (plesiomorphic) state of the ventral branches of paraproct.

Parameres. Paramere is ancestral complex, plesiomorphic, stout with variously bifid setose apex. The apical lobe supplied ventrally with thin and short hair-like sensory setae and dorsally

with long stronger setae. The dorso-subapical lobe armed with even stronger and very stout modified spine-like setae. Transformation with simplification to monolobed apex present: *betteni*, *lineatipennis*, *lorettae*.

***Grammotaulius nigropunctatus* (Retzius, 1783)**

(Figure 52)

Material examined. Hungary, Zemplén Mts. Kemence valley, Kemence stream, 2.VI.1983. singled leg. J. Oláh (1 male, OPC).

***Grammotaulius nitidus* (Müller, 1764)**

(Figure 53)

Material examined. Hungary, Aggtelek Mts. Aggtelek National Park, Szelcepuszta, 2.VI.1983. light leg. J. Oláh (1 male, OPC).

***Halesochila* Banks, 1907**

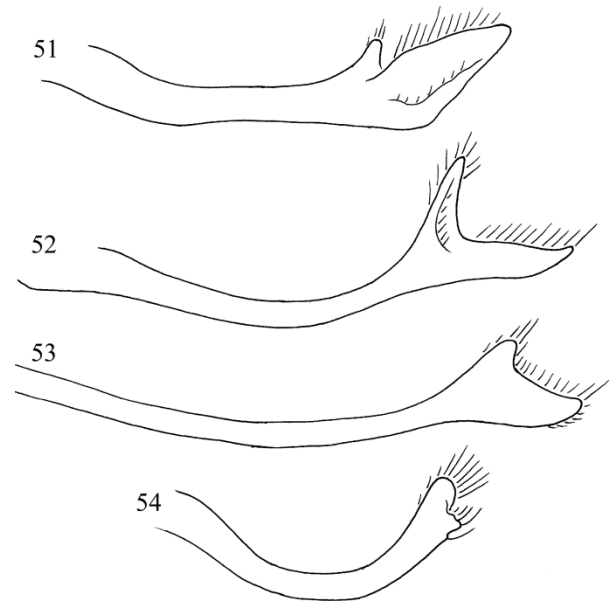
(Figure 54)

Original differential diagnosis. Formal delineation is not given.

Relation. Related to the *Limnephilus* genus (Schmid 1955).

Genital character state combinations. (1) Absence (plesiomorphic) of spinulose protuberance or any neof ormation on tergite VIII; (2) Produced (plesiomorphic) state of tergite IX; (3) Sclerotized variously dentate (apomorphic) state of cerci; (4) Produced (plesiomorphic) state of the dorsal branch of paraproct; (5) Separate free from each-other (plesiomorphic) state of the dorsal branch of paraproct; (6) Separate free-from-cerci (plesiomorphic) state of the dorsal branch of paraproct; (7) Produced (plesiomorphic) state of the ventral branch of paraproct; (8) Separate free from each-other (plesiomorphic) state of the ventral branches of paraproct.

Parameres. Paramere is ancestral complex, stout with bifid setose apex.

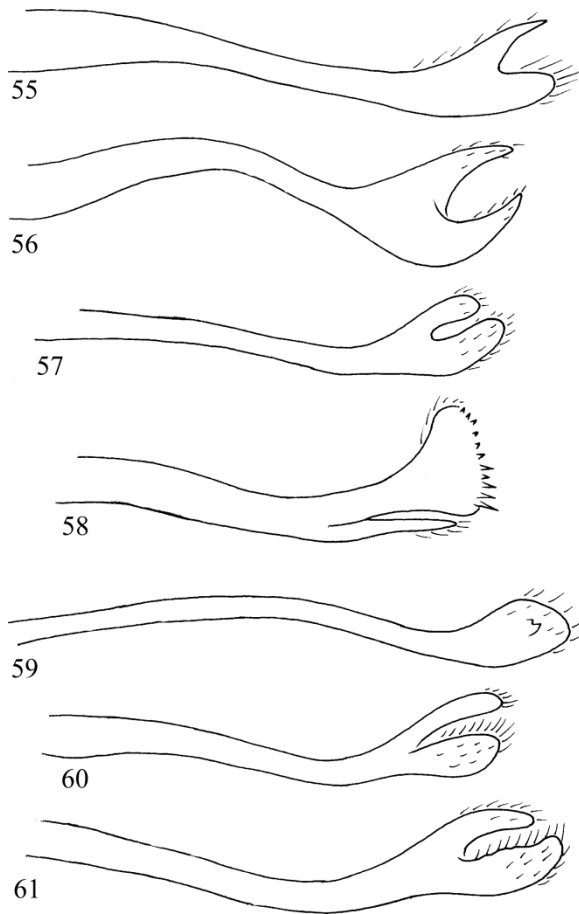


Figures 51–54. Parameres of *Glyphotaelius*, *Grammotaulius* and *Halesochila* genera. 51 = *Glyphotaelius pellucidus*, 52 = *Grammotaulius nigropunctatus*, 53 = *G. nitidus*, 54 = *Halesochila taylori*.

***Halesochila taylori* (Banks, 1904)**

(Figure 54)

Material examined. USA, Oregon, Benton County, Coleman Creek, at Glenbrook Road, N44.31304°, W123.48135°, 859 feet, 27.X.2014, leg. C. D. Kerst, (1 male, OPC). Oregon, Lane County, Too Deep Lake, 3 mi. n. Waldo Lake, 6000', benthos, 15.IX.1976, leg. Sedell & Cummins, (1 male pupa, ROM). Oregon, Clackamas County, near Estacada, 20.X.1968, leg. K. Goeden, (1 male, ROM). Oregon, Clatsop County, Vic. Gronnel Rd., ca 2 mi. e. Elsie, 1.XI.1963, leg. S. G. Jewett, (1 female, ROM). Oregon, Clatsop County, Vic. Gronnel Rd., ca 2 mi. e. Elsie, 24.X.1964, leg. S.G. Jewett, (1 female, OPC). Oregon, Lane County, 12 mi. s.e. Eugene, 25.X.1966, leg. K. Goeden (1 male, OPC). Canada, British Columbia, Marion Lake, Univ. Brit. Col. Forest, Haney, 24.X.1969, leg. Winterbourn (1 female, ROM).



Figures 55–61. Parameres of *Lenarchus* genus. 55 = *Lenarchus devius*, 56 = *L. expansus*, 57 = *L. gravidus*, 58 = *L. keratus*, 59 = *L. productus*, 60 = *L. rillus* 61 = *L. vastus*.

***Lenarchus* Martynov, 1914**

(Figures 55–61)

Original differential diagnosis. Formal delineation is not given.

Relation. According to Martynov (1914a) by habitus *Lenarchus* is close to *Asynarchus*, but differs greatly by the genital structure: segment IX, cerci, gonopod, penis (aedeagus) and titillator (parameres) are differently constructed.

Genital character state combinations. (1) Absence (plesiomorphic) of spinulose protuberance or any neof ormation on tergite VIII; (2) Produced (plesiomorphic) state of tergite IX; (3) More sclerotized variously dentate (apomorphic) state of cerci accompanied by partial or complete

fusion at the most advanced lineages (“*Paralenarchus*”); (4) Produced (plesiomorphic) state of the dorsal branch of paraproct; (5) Separate free from each-other (plesiomorphic) state of the dorsal branch of paraproct; (6) Separate free-from-cerci (plesiomorphic) state of the dorsal branch of paraproct; (7) Produced (plesiomorphic) state of the ventral branch of paraproct at the most ancestral lineages (*Prolenarchus*, *Paralenarchus*); (8) Separate free from each-other (plesiomorphic) state of the ventral branches of paraproct.

Parameres. Paramere is ancestral complex, plesiomorphic, stout with bifid setose apex of converging lobes/branches. The paramere is monolobed in a single species *L. productus*, the second lobe reduced to its possible remnants in the form of a bifid pointed process moved to the middle of the enlarged monolobed apex.

***Lenarchus devius* (McLachlan, 1880)**

(Figure 55)

Material examined. Type: **Russia**, North-Western Siberia (Hautaika, District of the Yenesei, (68°5’N, 15th July, J. Sahlberg, 2♂, 1♀), pinned with genitalia separate mounted in permanent slide (1 male, SMNH).

***Lenarchus expansus* Martynov, 1914**

(Figure 56)

Material examined. **USA**, Alaska, Barrow Mesic, 71.301529°N, 156.760032°W, 18–19.VII.205, leg D.E. Ruitter (1 male, 1 female; OPC).

***Lenarchus gravidus* (Hagen, 1861)**

(Figure 57)

Material examined. **USA**, Kalifornia, Sierra County, SF St. Univ. 5700’ Highway 49, 28.VI.-1.VII.1999, leg. P. Opler & Buckner (1 male, OPC).

***Lenarchus keratus* (Milne, 1935)**

(Figure 58)

Material examined. **Canada**, Quebec, Knob Lake, 54°47’ 66°47’, 27.VII.1948, leg. E. & I. Munroe, CNC280128 (1 male, CNC).

***Lenarchus productus* (Morton, 1896)**

(Figure 59)

Material examined. Sweden, Töfsingdalens National Park, no more detailed collecting data. (1 male, SMNH).

***Lenarchus rillus* (Ross, 1938)**

(Figure 60)

Material examined. USA, Kalifornia, Mendocino County, Dunlap Campground, 18 mi. E. Ft. Bragg, 1000', 19.VIII.1965, black light leg. E. & I. Munroe, CNC280123 (1 male, CNC).

***Lenarchus vastus* (Hagen, 1861)**

(Figure 61)

Material examined. USA, Oregon, Jefferson County, Santiam, Pass, 20.IX.1993, UV light leg. P. Hammand, (1 male, 1 female; OPC).

***Lepnevaina* Wiggins, 1987**

(Figure 62)

Original differential diagnosis. Formal delineation is not given.

Relation. Possible assignment both to *Limnephilini* and *Stenophylacini* tribes was discussed. According to the paramere organisation this genus is close to the *Limnephilini* tribe.

Genital character state combinations. (1) Absence (plesiomorphic) of spinulose protuberance or any neoformation on tergite VIII; (2) Reduced (apomorphic) state of tergite IX; (3) More sclerotized dentate (apomorphic) state of cerci; (4) Reduced (apomorphic) state of the dorsal branch of paraproct; (5) Fused to each-other (apomorphic) state of the dorsal branch of paraproct; (6) Separate free-from-cerci (plesiomorphic) state of the dorsal branch of paraproct; (7) Produced (plesiomorphic) state of the ventral branch of paraproct; (8) Fused to each-other (apomorphic) state of the ventral branches of paraproct.

Parameres. Paramere is ancestral complex, "terminating in an inflated scoop-shaped lobe bearing an elongate apical point and a shorter dorsal point".

***Lepnevaina signata* Wiggins, 1987**

(Figure 62)

Material examined. No specimen was available for direct examination. However detailed, well presented and interpreted drawings permitted the presentation of the character state combination of this rare species.

***Leptophylax* Banks, 1900**

(Figure 63)

Original differential diagnosis. Formal delineation is not given.

Relation. A cold-adapted genus with small narrow wings. The genital structure of both the male and female is close to the *Anabolia* genus (Schmid 1955).

Genital character state combinations. (1) Absence (plesiomorphic) of spinulose protuberance or any neoformation on tergite VIII; (2) Reduced (apomorphic) state of tergite IX; (3) More sclerotized dentate (apomorphic) state of cerci; (4) Produced (plesiomorphic) state of the dorsal branch of paraproct; (5) Separate free from each-other (plesiomorphic) state of the dorsal branch of paraproct; (6) Separate free-from-cerci (plesiomorphic) state of the dorsal branch of paraproct; (7) Reduced (apomorphic) state of the ventral branch of paraproct; (8)) Separate free from each-other (plesiomorphic) state of the ventral branches of paraproct.

Parameres. The derived paramere simplified into a simple arching digitiform structure with setose apical region.

***Leptophylax gracilis* Banks, 1900**

(Figure 63)

Material examined. USA, Minnesota, Kittson County, Hallock, 26.VI.1936, light trap leg. D.G.

Denning (1 male, OPC). Illinois, Algoquin, 10. VII. 1909, leg. Nason (1 female, OPC).

***Limnephilus* Leach, 1815**

Original differential diagnosis. Formal delineation is not given.

Relation. Schmid 1955:133, “Le genre compte un certain nombre de **groupes** d’espèces naturels, le nombre des **formes** isolées est très grand et rend toute classification claire et commode impossible.”

Genital character state combinations. (1) Presence (apomorphic) of spinulose protuberance or any neoformation on tergite VIII; (2) Reduced (apomorphic) state of tergite IX; (3) More sclerotized dentate (apomorphic) state of cerci; (4) Produced (plesiomorphic) state of the dorsal branch of paraproct; (5) Separate free from each other (plesiomorphic) state of the dorsal branch of paraproct; (6) Separate free-from-cerci (plesiomorphic) state of the dorsal branch of paraproct; (7) Reduced (apomorphic) state of the ventral branch of paraproct; (8)) Separate free from each other (plesiomorphic) state of the ventral branches of paraproct.

Paramere organisation. The large *Limnephilus* genus is more diverse with more isolated lineages and accompanied with more frequent chimeric incongruences than the similarly large genera of *Rhyacophila* and *Hydropsyche*. In the present survey on parameres we demonstrate the infra-generic organisation of paramere structure from complex to simple or to the complete reduction resulted in paramere lost. We instantiate the transformation series and directions of paramere organisation with selected species or species groups. The bilobed heavily setose ancestral, plesiomorphic state of paramere head dominates this large genus.

This ancestral state was simplified into a setose monolobed apex or further into a simple digitiform or spiniform structure or to the lost of parameres, producing a character state transformation series: (1) Ancestral bilobed plesio-

morphic; (2) Intermediate monolobed apomorphic; (3) Intermediate erectile apomorphic; (4) Spiniform apomorphic; (5) Paramere lost. This character transformation trend of simplification seems, as a general rule, to occur at any hierarchical levels of taxa, but with incongruencies as evidenced by stochastic ontology and probabilistic epistemology.

Besides this transformation series additional modifications further increase the diversity and specification of paramere morphology in any hierarchical level of taxa: (1) Abbreviation of paramere shaft; (2) Elongation of paramere shaft; (3) Thinning of paramere shaft; (4) Thickening of paramere shaft; (5) Additional shape variation of paramere head; (6) Variation in abundance of setae; (7) Variation in distribution of setae; (8) Modification of setae from thin sensory to thick stimulatory structures; (9) Orientation of the strong apical stimulatory modified setae.

Ancestral lineages of bilobed plesiomorphic paramere

(Figures 64–76)

Parameres have heavily setosed variously shaped bilobed apex in this ancestral lineage with wide holarctic distribution.

***Limnephilus algosus* McLachlan, 1868**

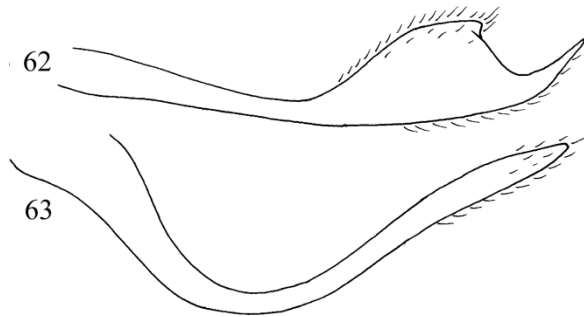
(Figure 64)

Material examined. **Sweden.** Exchange material from the Naturhistoriska Riksmuseet Stockholm, with 2 labels: *white label*: upper side with printed letters: DLR.IDRE NIPFJALL. lower side with written letters: bäck Y. A. 1.8.1928; *blue label* with 8020 E95+ (1 male, OPC).

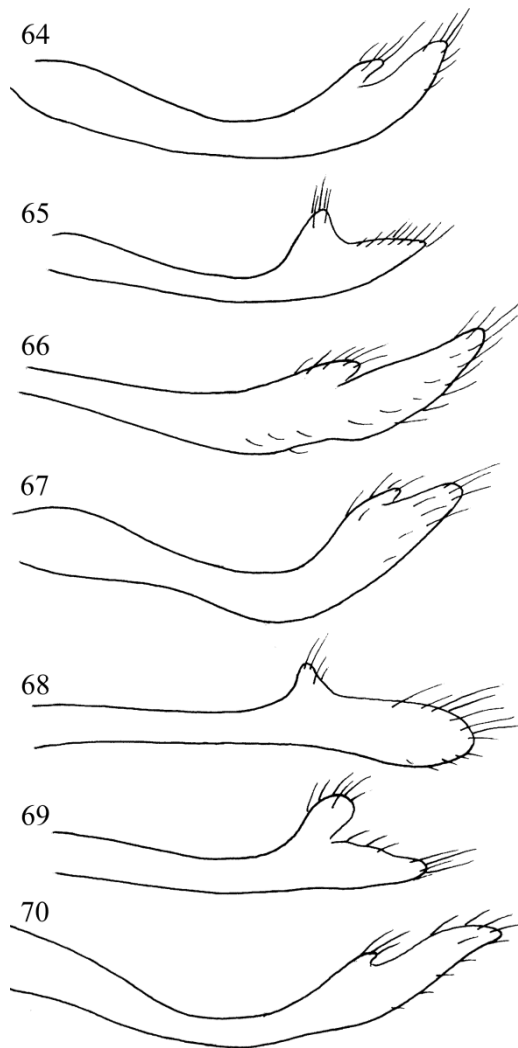
***Limnephilus argenteus* Banks, 1914**

(Figure 65)

Material examined. **Canada,** Newfoundland and Labrador, Hopedale, 10.VI.1928, leg. W.W. Perrett (1 male, CNC). Yukon Territory, Alaska Hwy., km. 1706 at Slims R. 60°59'N 138°27'W,



Figures 62–63. Parameres of *Lepnevaina* and *Leptophylax* genera. 62 = *Lepnevaina signata*, 63 = *Leptophylax gracilis*.



Figures 64–70. Ancestral *Limnephilus* lineage of bilobed pleiomorphic paramere. 64 = *Limnephilus algosus*, 65 = *L. argenteus* 66 = *L. centralis*, 67 = *L. fuscovittatus*, 68 = *L. orientalis*, 69 = *L. pantodapus* 70 = *L. picturatus*.

12.VII.1979, 791118b, leg. ROM Field Party (1 male, ROM). Ontario, Geraldton, Thunder Bay Dist., 15.VI.1966, u-v. light, leg. J.C.E. Riotte, L. *Argenteus*, det. G.B. Wiggins, 1966 (2 males, 5 females; OPC). Alberta, Banff National Park, Alta, roadside pond and stream Hwy. N of L. Luise, 21.VII.1962, leg. G.B. Wiggins (2 male, ROM).

***Limnephilus centralis* Curtis, 1834**

(Figure 66)

Material examined. **Bulgaria**, Rila Mts., Granchar (=Boris Hadzhusotirov) chalet above Yakoruda, 2187m., N42.1219°, E023.5925°, 22.IX.2018 lamps, light traps, leg. S. Beshkov & A. Nahirnic (2 males, 1 female; OPC). **France**, Le Pont-de-Montvert (department Lozère), 26.V.2015, ru Pouzets, E03°47'37", N44°22'48", 1301m, leg. G. Coppa (1 male, 1 female; OPC). Chambon-sur-Lac (department Puy-de-Dôme), Dent de la Rencune, 23.VI. 2012, E. 2°50'39".N.45°32'10", 1240m, leg. G. Coppa (3 males, 2 females; OPC). Chastreix (department Puy-de-Dôme); la Trentaine, 02.VII.2015, E02°14'55", N45°30'06", 1265m, leg. G. Coppa (2 males, OPC). France: Auzat (department Arriège), ru le Soulcem, 16.VII.2009, E.01°27'08", N.42°40'24", 1620m, leg. G. Coppa (1 female; OPC). Rosis (department Hérault), Fontalès, 14.IX.1999, E02°58'24", N43°35'59", 1043m, leg. G. Coppa (1 male, 1 female; OPC). Sévigny-la-Forêt (department Ardennes), ru Greffier, 19.V.2009, E04°30'15", N49°53'38", 362m, leg. G. Coppa (2 males, 2 females; OPC). Fleigneux (department Ardennes), Ru de la Hatrelle, 28.IX.2013, E04°57'45". N49°45'21", 269m, leg. G. Coppa (1 male, 1 female; OPC). Causerets (department Hautes-Pyrénées), lac d'Estom, 18.VII.2010, next to Lac d'Estom, E0°5'59", N42°48'32", 1785m, leg. G. Coppa (1 male, 1 female; OPC). Causerets (department Hautes-Pyrénées), Gave de Lutour, 17.VII.2010, E0° 05'43", N42°50'49", 1450m, leg. G. Coppa (1 male, OPC). Gavarnie (department Hautes-Pyrénées), Ossoue, 27.VII.2010, E0° 5'55", N42° 45'27", 1829m, leg. G. Coppa (1 male, 1 female; OPC). Montfiquet (department Calvados), Wood

Cerisy, 07.X.2010, 125m, leg. G. Coppa (1 male, 1 female; OPC). **Norway**, Vest-Agder, Mandal, Holmesland, 58.1402°N 7.5387°E, 1-4.VII.1988, leg. K.A. Johanson (12 males, 8 females; OPC). **Serbia**, Moravica district, Ivanjica, Golija Mts, forest stream and its sidebrook along road No.197, 1500m, N43°20.289' E20°15.059' leg. P. Juhász, T. Kovács & D. Murányi, 26.VI.2018 (2 males, 1 female; OPC). Serbia, Raška district, Novi Pazar, Golija Mts, Radaljica, spring brooks in forest edge by the settlement 1595m, N43°16.495' E20°20.896' leg. P. Juhász, T. Kovács, D. Murányi, 26.VI.2018, (3 females, OPC).

Remarks. The extraordinary variability of the body size and wing pattern is well known both between and inside the populations of *Limnephilus centralis*. Botosaneanu (2004) has detected conspicuous variability also in the male genitalia. He has published drawings of the apex of gonopod with variation in great amplitude even in the same population. This is the typical variability pattern of non-adaptive neutral traits that could be very significant especially in small effective population size. Here we have examined the variability range of parameres, a putative adaptive speciation trait. The bilobed paramere was remarkably stable even in populations far from each others in France, Norway, Bulgaria and Serbia.

***Limnephilus fuscovittatus* Matsumura, 1904**

(Figure 67)

Material examined. **Japan**, Tsukanoiri-ike, Itaka-cho, Neito-ku, Nagoya, Aichi, 2.IX.2010, leg. T. Nozaki (2 males, OPC). **North Korea**, Ryanggang Province, Samjiyon, 4.VI.1985, night collecting at blended light (250W), fed by a Honda generator in a Picea stand at an altitude of about 2100 m, leg. A. Vojnits & L. Zombori (2 males, HNHM, 1 male, OPC). Pyongyang City, Pyongyang, Hotel Potonggang, 13.X.1987, singled at light around the hotel, leg. Z. Korsos & L. Ronkay (2 females, HNHM, 1 female, OPC). Pyongyang City, Pyongyang, Ryongak-san, 21. IX.1994, singled at a lookout place, leg. Z. Mé-

száros & L. Zombori (1 male, HNHM). North Pyongan Province, Mt Myohyang-san, Hyangsan, 15.IX.1994, light trap, leg. Z. Mészáros & L. Zombori (2 males, HNHM). North Hwanghae Province, Sariwon, Samsal Hotel balcony, 29. IX.1994, light trap, leg. Z. Mészáros & L. Zombori (10 males, 4 females; HNHM). Kangwon Province, Mt Kumgang-san, Oe-Kumgang, 23.IX. 1994, sweeping path-side vegetation behind Kumgangsan Hotel, leg. Z. Mészáros & L. Zombori (1 male, HNHM). **Russia**, Kuril Is. Ketoi, Swamp west of Kaskad Waterfall, east of Cape Storozheva, 47°22.54'N, 152°27.47'E, 15.VIII. 19954, leg. N. Minakawa & P. O. Berg, KE-95-PO-061 (1 male, OPC).

***Limnephilus kerekes* Oláh, sp. nov.**

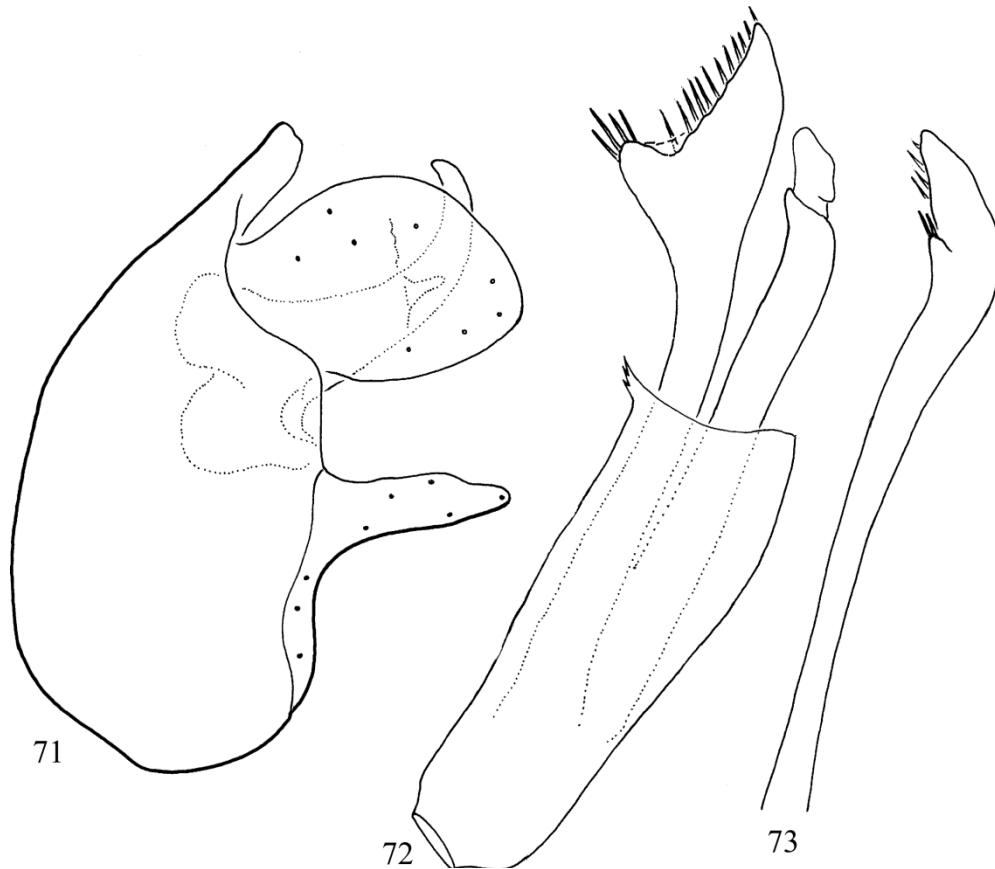
(Figure 71–76)

Material examined. Holotype: **Taiwan**, Province Taoyuan, 16 km E of Fuhsing, 121°24'E 24°50'N, 870 m, 5.X.1995, leg. T. Csóvári & P. Stéger (1 male, HNHM). Allotype: same as holotype (1 female, HNHM). Paratypes: same as holotype (2 males, 2 females, HNHM; 2 males, 1 female; OPC).

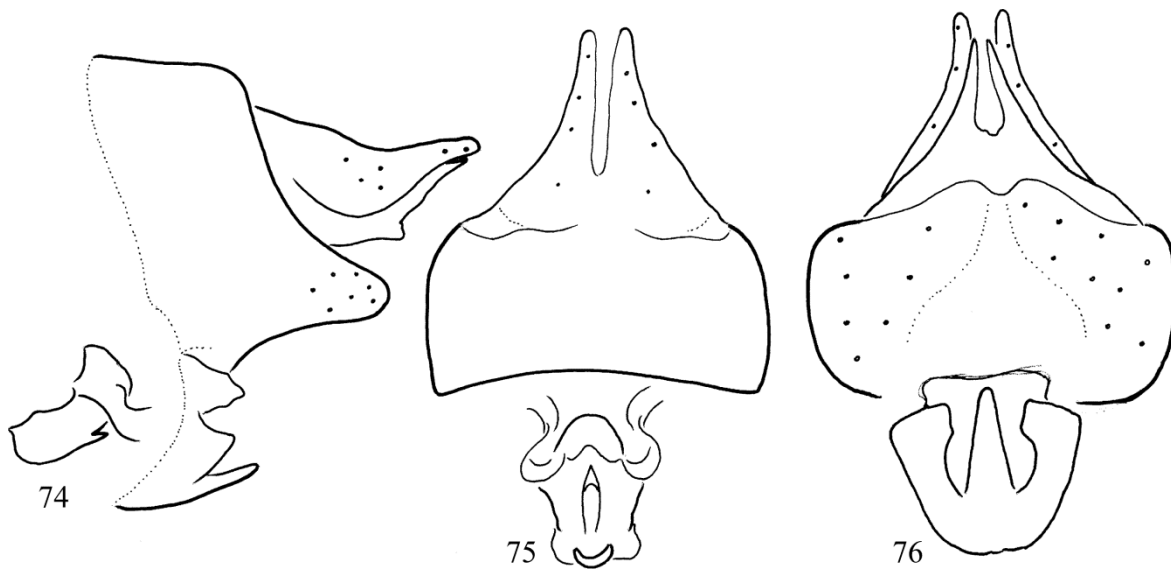
Diagnosis. This new species is close to *Limnephilus zhejiangensis* Leng & Yang, 2004 as a sibling, but differs by having cerci rounded not tapering apicad and the paraproct is upward curving in lateral view, not straight. Also the bilobed apex of the paramere differs both in lateral and in dorsal view.

Description. Male (in alcohol). Large-sized, brown-coloured animal; forewing with heavily pigmented large pterostigma and with speckled and streaked darke brown reticulation. Spurs: 134. Forewing length 17 mm.

Male genitalia. Tergite VIII with spinulose mesal protuberance. Segment IX long almost subovoid in lateral view with high and short dorsal strap. Cerci robust, heavily sclerotized, almost circular; its mesal vertical line supplied with a single large outgrowth. Paraproct slightly longer than cerci; slender in lateral view and regularly curving upward. Gonopods digitiform,



Figures 71–73. *Limnephilus kerekes* Oláh sp. nov. Holotype male: 71 = genitalia in left lateral view, 72 = phallic organ in lateral view, 73 = paramere in dorsal view.



Figures 74–76. *Limnephilus kerekes* Oláh sp. nov. Allotype female: 74 = genitalia with the vaginal sclerite complex in left lateral view, 75 = genitalia with the vaginal sclerite complex in dorsal view, 76 = genitalia in ventral view.

almost perpendicular, its apex slightly tapering. Parameres with bilobed apex.

Female genitalia. There is no closed “anal tube” formed by the complex of the fused tergite IX and segment X; the tube that is more or less closed at many limnephilid females, here formed by segment X and cleft deeply both dorsum and ventrum. Tergite IX long, sternite IX setose long subtriangular in lateral and sub quadrangular in ventral view; ventrally produced mesad, touching, forming a unified plate; the mesal plate constricted posterad, widened anterad; this glabrous ventral surface of sternite IX functions like the upper vaginal lip present as a free supragenital plate. The lower vaginal lip, the vulvar scale with long tapering mesal lobe is visible somewhat separated from sternite VIII by its more sclerotized structure. Dorsal vaginal sclerite complex and the membranous vaginal chamber is short, reaching only half length of sternite VIII.

Etymology. *kerekes* from “*kerekes*” circular in Hungarian, refers to the more rounded shape of the cerci in lateral view.

***Limnephilus orientalis* Martynov, 1935**

(Figure 68)

Material examined. **Russia**, Tokotan Bay, Urup, Kuril Islands, leg. S. Bergman (1 male, SMNH).

***Limnephilus pantodapus* R. McLachlan, 1875**

(Figure 69)

Material examined. Type of *Limnephilus asaphes* McLachlan, 1880: “North-Western Siberia (Platina, District of Jenesei, 14th July, J. Sahlberg, 1♂ 1♀). Deposited in SMNH.

Remarks. Grigorenko (2002) has synonymised *Limnephilus asaphes* with *L. pantodapus*.

***Limnephilus picturatus* McLachlan, 1875**

(Figure 70)

Material examined. **Russia**, Chaunskaya Gulf, Ajon Island, N69.552140° E169.18236°, 14–

27.VII.2015. Malaise trap, leg. P. Mortensen. (2 males, 1 female; OPC).

Derived lineages of monobed apomorphic paramere

(Figures 77–83)

Parameres have heavily setosed monolobed apex in this derived lineage with wide holartctic distribution.

***Limnephilus alienus* Martynov, 1914**

(Figure 77)

Material examined. **Japan**, Jizou-numa, Shizu Nishikawa-machi, Yamagata 10.IX.2003, leg. T. Hattori & T. Ito (2 males, OPC). **Russia**, Kuril Is. Iturup, Reidovoye Lake, near Reidovo, 45° 16.00'N 148°01.30'E, 18.VIII.1994, leg. R.I. Gara & N. Minakawa, IT-94-RG-09 (1 male, OPC).

***Limnephilus diphyes* McLachlan, 1880**

(Figure 78)

Material examined. **Russia**, Khabarovsk Territory, Slavyanka 5 km E Troitskoye, bog-margin in dec. forest, 18–19.VI.1993, light trap, leg. P. Lindskog & B. Viklund (1 male, SMNH; 1 male, OPC)

***Limnephilus lithus* (Milne, 1935)**

(Figure 79)

Material examined. **USA**, Colorado, Jefferson City, S. Platte River at Kasster Bridge, 24. IX. 2005, leg D. E. Ruitter (2 males, 2 females, OPC).

***Limnephilus nipponicus* Schmid, 1964**

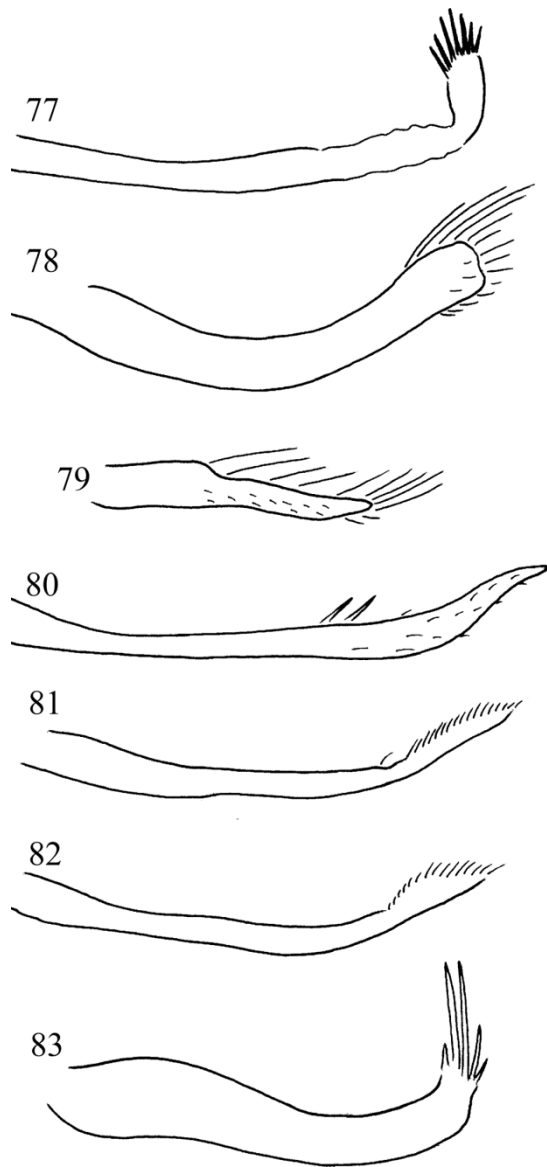
(Figure 80)

Material examined. **Japan**, Iyari-mire, Inao Taira, Omachi-shi, Nagano, 10.VII.1999. leg. W. Miyata. (2 males, OPC).

***Limnephilus quadratus* Martynov, 1914**

(Figures 81–82)

Material examined. **Japan**, Hokkaido, Kushiro, Kushiro River, Canoe Station, 43°06'26"N 144°



Figures 77–83. Derived *Limnephilus* lineage of monobed apomorphic paramere. 77 = *Limnephilus alienus*, 78 = *L. diphes* 79 = *L. lithus*, 80 = *L. nipponicus*, 81 = *L. quadratus*, Korea; 82 = *L. quadratus*, Japan; 83 = *L. sibiricus*.

28°15'E, 15.VIII.2007, leg. T. Ito (2 males, OPC). **North Korea**, Ryang-gang, Chann-Pay plateau, Sam-zí-yan, 1700 m, 27.VIII.1971, netting on lake shore, leg. J. Papp & S. Horvatovich (1 male, HNHM).

Remarks. There are pronounced divergences in the formation of the setose apex of the parameres

detectable between the populations of Korea and Japan. They most probably represent diverged incipient sibling species. More specimens from more populations are required for comparative trait stability studies.

***Limnephilus sibiricus* Martynov, 1929**

(Figure 83)

Material examined. **China**, Quinghai province, Gangca Dasi (lamasery), spring, river, 37°32.4–33.0'N 100°05.3–06.0'E, 3505–3840 m, 11.–12.VII.2005, leg. J. Hajek, D. Král & J. Růžička (1 male, OPC). **Mongolia**, Ulan-Baator, Bogdoul, 11.VII.1986, leg. L. Peregovits (2 females, HNHM).

Derived lineages of erectile paramere shaft or lobe

(Figures 84–86)

One lobe of the limnephiline paramere or the entire paramere shaft membranous and erectile.

***Limnephilus fuscinervis* (Zetterstedt, 1840)**

(Figure 84)

Material examined. **Russia**, LK/Karelska ASSR: Bus excursion around Upper Ladoga from Kexholm to Olonetz, 28-30.VII.1994, leg. B. Viklund (1 male, OPC).

***Limnephilus griseus* (Linnaeus, 1758)**

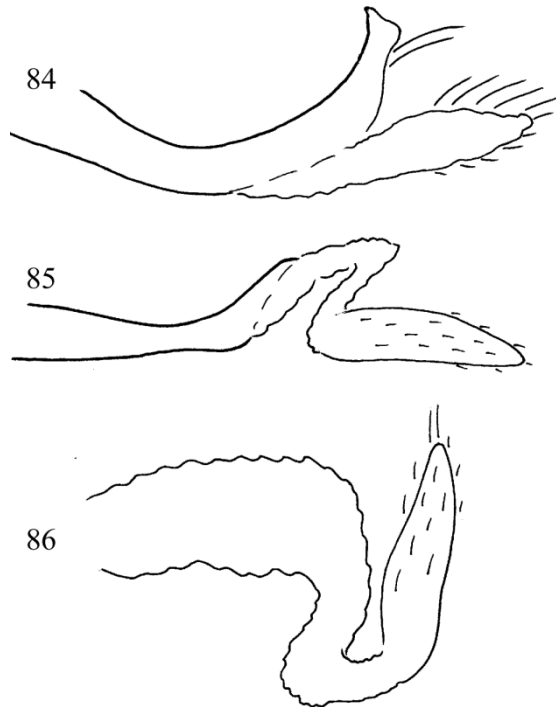
(Figure 85)

Material examined. **Iceland**, Fjaðrárgljúfur canyon, N63.7712°–W18.1716°, in Fjaðrá River, 15.VII.2015. leg. Z. Korsós (1 male, HNHM).

***Limnephilus sericeus* (Say, 1824)**

(Figure 86)

Material examined. **Russia**, Khabarovsk Territory, Slavyanka, 5 km E Troitskoya, bog-margin in dec forest, light trap, 12.VI.1993, leg. P. Lindskog & B. Viklund (1 male, OPC).



Figures 84–86. Derived *Limnephilus* lineages of erectile paramere shaft or lobe. 84 = *Limnephilus fuscinervis*, 85 = *L. griseus*, 86 = *L. sericeus*.

Derived lineage of spiniform paramere

Here we have selected and examined species to exemplify/instantiate the various shape modifications of the parameres in derived lineages with spiniform state produced by simplification of incremental substractions.

Limnephilus fenestratus species group

(Figures 87–88)

Limnephilus coloradensis (Banks, 1899)

(Figure 87)

Material examined. USA, Colorado, Park City, 4-Mile Fen, 11. VIII. 2009, leg D. E. Ruiter (2 males, 2 females, OPC).

Limnephilus fenestratus (Zetterstedt, 1840)

(Figure 88)

Material examined. Norway, Norge, Finnmark, Sør-Varanger, Svanhovd forskningsstasjon,

69.45403°N 30.04057°E, 46 moh, 7–8. IX.2010, light trap Finnmarksprosjektet, leg. T. Andersen (4 males, OPC).

Limnephilus incisus species group

(Figures 89–94)

Species of this group of the former *Colpo-*taulius** genus have been characterized with sinuous apical margin of the forewing, with very strong spur on the foreleg. Ruiter (1995) characterized the males by the following character combination: simple tergite VIII, short cerci, high paraproct and elongated cylindrical parameres; except *L. secludens* incongruent with short and membranous parameres. Females are characterized by tubular segment X and by the laterally divided segment IX.

Limnephilus asiaticus (McLachlan, 1874)

(Figures 89)

Material examined. Kazakhstan, Province Almaty, Kuluktau Mt., 1 km S of Uzunbulak, 1600 m, 28.IX.2002, light, leg. B. Benedek & T. Csővári (1 female, OPC). Province Almaty, Sugeti Mt., 8 km NW of Kok-Pek, 980 m, 25.IX.2002, light, leg. B. Benedek & T. Csővári (1 female, OPC). Zailiskiy Alatau Mts., 21.IX. 2002, light, leg. B. Benedek & T. Csővári (1 female, OPC). Turkestan, Kette, Ujugli, 1500 m, 4.V.1990, leg. F. Klima (1 male, ZMB).

Limnephilus incisus Curtis, 1834

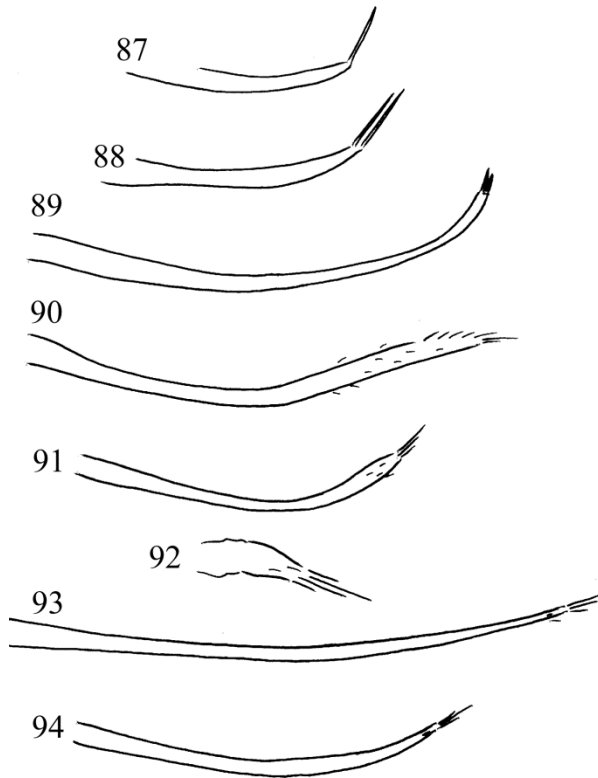
(Figures 90)

Material examined. Hungary, Debrecen, Józsa, Tócs stream, 6. VII. 2010, light leg J. Oláh (1 male, 2 females, OPC).

Limnephilus major Martynov, 1909

(Figures 91)

Material examined. Russia, Kamchatka, western side, Inland from 1.5 km south of Yavinskoya Lake, 51°35'N 156°30'E, 28.VII. 1999, leg. N. Minakawa & K. L. Kurowski (2 males, OPC).



Figures 88–94. Derived *Limnephilus* lineage of spini-form paramere. *Limnephilus fenestratus* species group: 87 = *Limnephilus coloradensis*, 88 = *L. fenestratus*; *Limnephilus incisus* species group: 89 = *Limnephilus asiaticus*, 90 = *L. incisus*, 91 = *L. major*, 92 = *L. secludens*, 93 = *L. submonilifer*, 94 = *L. tarsalis*.

***Limnephilus secludens* Banks, 1914**

(Figures 92)

Material examined. **USA**, Wyoming, Albany County, Laramie River at Woods Landing, N41.11004° W106.01167°, 13.VII.2011, leg D. E. Ruiter (1 male, OPC). **Canada**, Saskatchewan, picnic ground on Rt 14, ca. 2.8 mi. E. Foam L., 12.VII.1970, uv light ROM 700388, leg. ROM Field Party (1 male, ROM). Saskatchewan, sm. pond beside Rt 210 s. of Echo Valley Prov. Pk., 13.VIII.1969, ROM 690324, leg. ROM Field Party (1 male, 1 female; OPC). Saskatchewan, Balcarres, pond, 29.VI.1962, leg. G.B. Wiggins (1 male, ROM). Manitoba, Fort Garry, 11.IX.1957, light trap, leg. J.B. Wallis, Jr. (2 females, ROM).

***Limnephilus submonilifer* (Banks, 1920)**

(Figures 93)

Material examined. **USA**, Rhode Island, Washington County, Monument Pond, Block Island, Aaron Hunt, 16. V. 2017, leg D. E. Ruiter (1 male, 1 female; OPC).

***Limnephilus tarsalis* (Banks, 1920)**

(Figures 94)

Material examined. **USA**, Colorado, Gunnison City, Snodgrass Mts., 25. VIII. 1995, leg. D.E. Ruiter (2 males, 2 females, OPC).

***Limnephilus samoedus* species group**

This small group of species is characterised by the elongated almost perpendicular outgrowth of the gonopods. Similar rectangularly oriented gonopods are present, as a chimeric incongruent structure, in the small *Limnephilus iranus* species group, a species group in the *Limnephilus* genus with lost parameres. The most characteristic fine structure appears the most diverse in *Limnephilus samoedus* species group is a pair of downward and anterad curving lateral subapical spine-like strongly sclerotized hook formation on the head of the aedeagus.

The structure of the hook-like sclerite seems as a chimeric incongruent development present also, for instance, in the *Limnephilus fenestratus* species group of the Lemnephilini tribe, in the *Chilostigma* genus of the Chilostigmini tribe, in the *Annitella* genus of the Chaetopterygini tribe with lost paramere as well as appears in the small *Platyphylax* genus of the Stenophylacini tribe however with upward and anterad orientation. Orientation of flanking genes may contribute to the organisation of intergenic regions with *cis*-regulatory elements. The divergently transcribed bi-directional upstream sequences may be more constrained than those of uni-directional upstream

sequences displaying lower population mutation rate, as well as more low-frequency polymorphisms. Contrary uni-directional upstream regions have considerable variation in evolutionary rates, with putative signatures of adaptation and with higher number of adaptive fixation in phenotypic organisation.

In this species group the paramere organisation is characterized by simplification of incremental substruction resulted in a spiniform structure with diverse and specific apical divergences. Grigorenko (2002) has synonymised all of the known 5 species of the group with the well known lumpner's slogan as this is a polymorphic (variable) and widely distributed species. However, lumpers search for scalar similarities, not for vectorial differences (Oláh et al. 2019). Here we reinstate the species status of the five species and describe two new species based on the distinctive divergence combinations between the species (1) in the lateral profile of the paraproct, (2) in the lateral profile of the hook formation on the aedeagus as well as (3) in the fine structure of the paramere head.

Based on the lateral profile of the aedeagal hook, that seems the more effective stimulatory adaptive structure, there are two distinct lineages of species complexes in the species group and there is a species integrated under extreme adaptation: *Limnephilus samoedus* new species complex, *Limnephilus alaicus* new species complex and the extremely adapted *Limnephilus hovsgolicus*.

***Limnephilus samoedus* species group**

***Limnephilus samoedus* species complex**

(Figures 95–100)

This complex of species has the downward and anterad curving lateral subapical spine-like hook formation on the aedeagus located dorsad. Three known species belongs to this complex: *L. cheresnevi* (Russia: Chukotka Peninsula), *L. pallens* (Alaska), and *L. samoedus* (Russia: North-Western Siberia).

***Limnephilus cheresnevi* Nimmo, 1995 stat. restit.**

(Figures 95–96)

Limnephilus cheresnevi Nimmo, 1995:2–3: Holotype male: Russia, Chukotka, 10/7/74. Coll. Cheresnev. "Similar to *pallens* (Banks)".

Limnephilus cheresnevi Nimmo, 1995: Grigorenko 2002:110, *Limnephilus cheresnevi* Nimmo is synonymized with *Limnephilus samoedus* McLachlan.

Material examined. Type material was not available for study; divergences in paraproct, aedeagus and paramere are distinct from the original drawings.

Remarks. This species has very high lateral profile of the basic body of paraproct with very short narrowing apices; less developed dorsal subapical spine-like hook formation on the aedeagus directed more ventrad; spiniform paramere with vertically flattened upward curving apices without any additional spines.

***Limnephilus pallens* (Banks, 1920) stat. restit.**

(Figures 97–98)

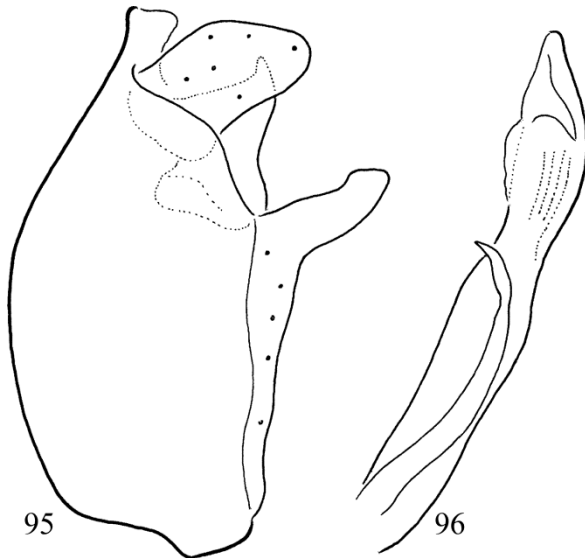
Zaporota pallens Banks 1920:342: "Alaska, Demarkation Point. 30 June (W. S. Brooks). "Related to *Colpotauius*."

Limnephilus pallens (Banks): Schmid 1955:133: *Zaporota* genus transferred to *Limnephilus* genus.

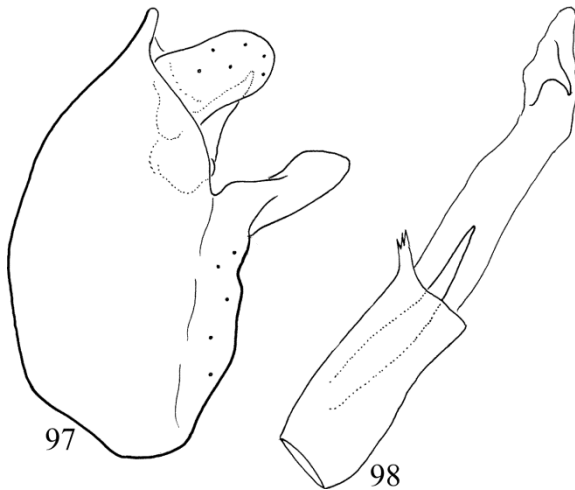
Limnephilus pallens (Banks): Grigorenko 2002:110, *Limnephilus pallens* (Banks) is synonymized with *Limnephilus samoedus* McLachlan.

Material examined. **Canada**, Southhampton Island, East Bay, 63.98703°N, 81.69661°W, 17. VII.2011. leg. D.E. Ruiter. (2 males, 1 female; OPC).

Remarks. This species has low lateral profile of the basic body of paraproct with long narrowing apices; less developed dorsal subapical spine-like hook formation on the aedeagus directed more ventrad; spiniform paramere with pointing apices without any additional spines.



Figures 95–96. Derived *Limnephilus* lineage of spiniform paramere. *Limnephilus samoedus* species group: *Limnephilus samoedus* species complex. *Limnephilus cheresnevi* Nimmo, 1995: 95 = genitalia in left lateral view, 96 = phallic organ in lateral view.



Figures 97–98. Derived *Limnephilus* lineage of spiniform paramere. *Limnephilus samoedus* species group: *Limnephilus samoedus* species complex. *Limnephilus pallens* Banks, 1920: 97 = genitalia in left lateral view, 98 = phallic organ in lateral view.

***Limnephilus samoedus* McLachlan, 1880**

(Figures 99–100)

Astratus samoedus McLachlan 1880:16–17, “North-Western Siberia (Dudinka 68°14’, N., District of

Yenesei, 25th July, J. Sahlberg, 1 ♂, 1 ♀).” “A less robust species than *A. asiaticus*.”

Material examined. Lectotype deposited in SMNH. North-Western Siberia (Dudinka, 69°14’, N., District of the Yenesei, 25th July, J. Sahlberg, 1 ♂, 1 ♀).

Remarks. This species has low lateral profile of the basic body of paraproct with long narrowing apices; less developed dorsal subapical spine-like hook formation on the aedeagus directed more anterad; spiniform paramere with pointing apices with 2–3 additional apical spines. The examined lectotype has parameres of fluctuating asymmetry with two apical spine on the left paramere and three apical spines on the right paramere.

***Limnephilus samoedus* species group**

***Limnephilus alaicus* species complex**

This species complex has downward and anterad curving lateral subapical spine-like hook formation on the aedeagus located ventrad. Four species belong to this complex: *L. alaicus* (Middle Asia), *L. maghrebensis* sp. nov. (Tunisia), *L. oblos* sp. nov. (Kazakhstan, Mongolia) and *L. tricalcaratus* (Tibet).

***Limnephilus alaicus* (Martynov, 1915) stat. restit.**

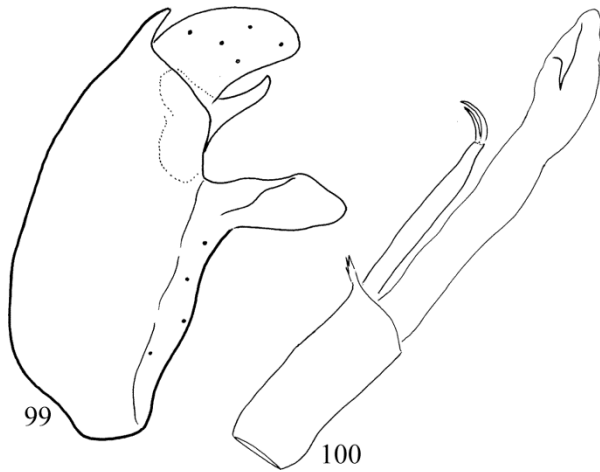
(Figures 101–103)

Astratus alaicus Martynov, 1915:417–421, “intermediate appendages broad at base, sharply attenuating to the apex, which is acute and diriged upwards.” “more allied to *Astratus samoedus* McLachlan., than to *Astratus asiaticus* McLachlan.” described from specimens from Karakul Ravine, Alai Mts.

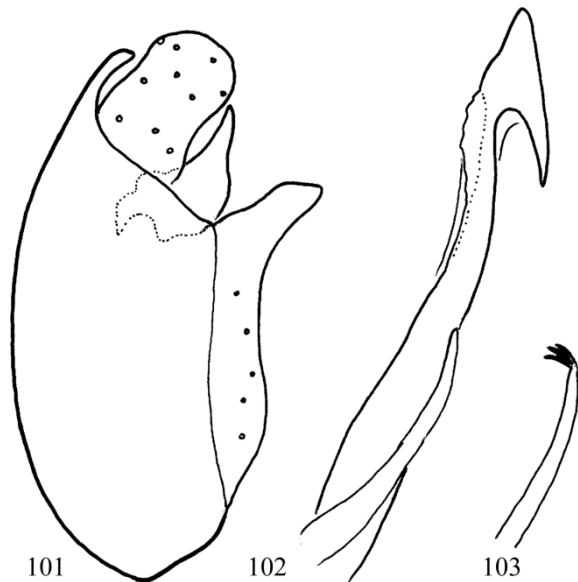
Astratus alaicus Martynov, 1915: Martynov 1927:486, “widely distributed in Turkestan, and found also in Semiretchje, in Pamir and near the Mount Ararat, Transcaucasia.”

Limnephilus alaicus (Martynov): Schmid 1955:133, *Astratus* genus transferred to *Limnephilus* genus.

Limnephilus samodeus (McLachlan, 1880): Grigorenko 2002:110, *Limnephilus alaicus* (Martynov) is synonymized with *Limnephilus samoedus* McLachlan.



Figures 99–100. Derived *Limnephilus* lineage of spiniform paramere. *Limnephilus samoedus* species group: *Limnephilus samoedus* species complex. *Limnephilus samoedus* McLachlan, 1880: 99 = genitalia in left lateral view
100 = phallic organ in lateral view.



Figures 101–103. Derived *Limnephilus* lineage of spiniform paramere. *Limnephilus samoedus* species group: *Limnephilus alaicus* species complex. *Limnephilus alaicus* (Martynov), 1915: 101 = genitalia in left lateral view, 102 = phallic organ in lateral view, 103 = paramere in dorsal view.

Material examined. Holotype: A male labelled with golden circle from the type series, designated by Grigorenko (2002) as lectotype for fixation of the application of the name. Labeled “Karakul Ravine, Alai Mts. 10.VII.1895, leg. Korzhinskiy.

Remarks. In Martynov’s drawings the paraproct (intermediate appendages) is clearly broad based and sharply narrowing, pointing to the apex as was pronounced in the original species description. We have examined the holotype male specimen from Karakul Lake and the lateral profile of the paraproct was identical with Martynov’s drawings. This species has low lateral profile of the basic body of paraproct with very long narrowing apices; well developed ventral subapical spine-like hook formation on the aedeagus directed more anterad forming low hook-sinus; spiniform paramere with pointing apices with 3 additional apical spines.

***Limnephilus maghrebensis* Mey & Oláh, sp. nov.**

(Figures 104–105, Picture 1)

Material examined. Holotype: **Tunesia**, Süd Tunesien, 5 km von Bir Thiethine, 40 km S Tataouine, 32°37N, 10°19E, 285 m, 13.IV.2001, Lichtfang, leg. H. Hoppe & T. Fischer (1 male, ZMB)

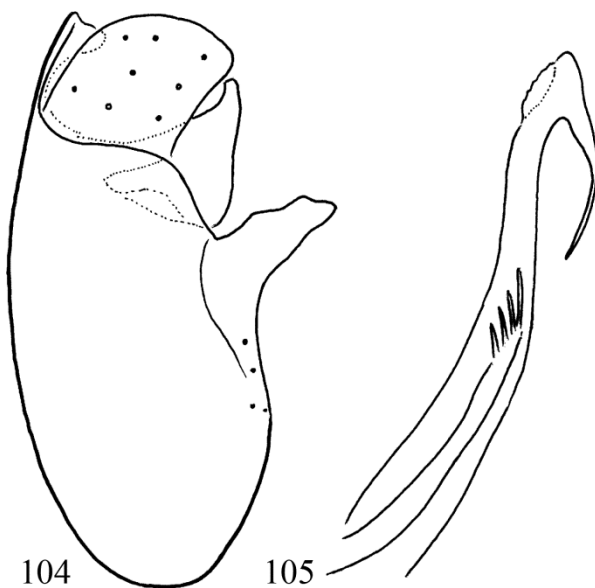
Diagnosis. This species has high lateral profile of the basic body of paraproct with short narrowing apices; well developed ventral subapical spine-like hook formation on the aedeagus directed more anterad forming low hook-sinus and characterized by extremely elongated filiform spine; spiniform paramere with pointing apices with 4 additional apical spines arranged consecutively.

Description. Male (in alcohol). Large-sized, light brown, yellowish coloured animal; forewing with less pigmented large pterostigma and unicoloured yellowish membrane without any pronounced pattern but with darker venation. Spurs: 234. Forewing length 16 mm.

Male genitalia. Tergite VIII with spinulose mesal protuberance. Segment IX long almost subovoid in lateral view with high and short dorsal strap. Cerci setose as usual, large, slightly elongated with downward turning ventroapical corner. Paraproct slightly shorter than cerci; its basic body is high with short narrowing apices in



Picture 1. *Limnephilus maghrebensis* Mey & Oláh, sp. nov. Habitus photo of the male Holotype and its label.



Figures 104–105. Derived *Limnephilus* lineage of spiniform paramere. *Limnephilus samoedus* species group: *Limnephilus alaicus* species complex. *Limnephilus maghrebensis* Mey & Oláh, sp. nov.: Holotype male: 104 = genitalia in left lateral view, 105 = phallic organ in lateral view.

lateral view. Gonopods broad digitiform, almost perpendicular, their apex obliquely truncate, slightly excised. Aedeagus with well developed ventral subapical very long spine-like hook formation on the aedeagus directed more anterad forming low hook-sinus. Parameres with four apical spines located consecutively.

Etymology. Named by the general region of type locality.

***Limnephilus oblos* Oláh, sp. nov.**

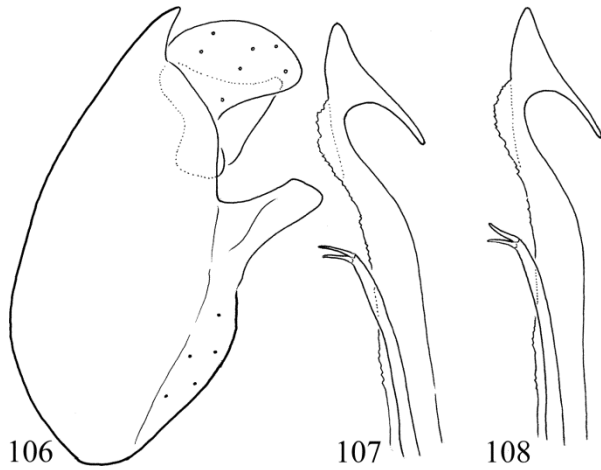
(Figures 106–108)

Material examined. Holotype: **Kazakhstan**, Province Almaty, Temerlik Mt., 10 km SW of Tuyuk, 79°20'E 43°05'N, 2100 m, 28.VIII.1997, leg. A. Orosz, *Limnephilus alaicus* Martynov, det. J. Oláh, 2005 (1 male, HNHM). Paratype: **Mongolia**, Kaszab Expedition, No.817 (Südgobi aimak: SW-R and des sees Dund gol, 1300 m, 18.VI.1967), CNC279997. *Limnephilus samoedus* McLachlan, det F. Schmid, 1969 (1 male, CNC).

Diagnosis. This species has low lateral profile of the basic body of paraprot with very long narrowing apices; well developed ventral subapical spine-like hook formation on the aedeagus directed more anterad forming low hook-sinus; spiniform paramere with pointing apices with 3 additional apical spines.

Description. Male (in alcohol). Large-sized, light brown, yellowish coloured animal; forewing with less pigmented large pterostigma and unicoloured yellowish membrane without any pronounced pattern but with darker venation. Spurs: 234. Forewing length 16 mm.

Male genitalia. Tergite VIII with spinulose mesal protuberance. Segment IX long almost subovoid in lateral view with high and short dorsal strap. Cerci setose as usual, large, slightly elongated with downward turning ventroapical corner. Paraproct slightly shorter than cerci; its basic body is high with very short narrowing apices in lateral view. Gonopods broad digitiform, almost perpendicular, their apex obliquely truncate.



Figures 106–108. Derived *Limnephilus* lineage of spiniform paramere. *Limnephilus samoedus* species group: *Limnephilus alaicus* species complex. *Limnephilus oblos* Oláh, sp. nov.: Holotype male, Kazakhstan, 106 = genitalia in left lateral view, 107 = phallic organ in lateral view; Paratype male, Mongolia: 108 = phallic organ in lateral view.

Aedeagus with well developed ventral subapical spine-like hook formation on the aedeagus directed more anterad forming very high hook-sinus. Parameres with two apical spines both on holotype from Kazakhstan and the paratype from Mongolia.

Etymology. *oblos* from “öblös” a wide bay, gulf or sinus in Hungarian, refers to the wide rounded internal shape of hook, that is the hook-sinus in lateral view.

***Limnephilus tricalcaratus* (Mosely, 1936) stat. restit.**

(Figures 109–111)

Astratus tricalcaratus Mosely, 1936:453–454, described close to *A. alaicus* from Western Tibet, but having only three spurs to the posterior leg.
Limnephilus tricalcaratus (Mosely). Schmid 1955:133, *Astratus* genus transferred to *Limnephilus* genus.
Limnephilus tricalcaratus (Mosely). Grigorenko 2002: 110, *Limnephilus tricalcaratus* (Mosely) is synonymized with *Limnephilus samoedus* McLachlan.

Material examined. Type material. Paratype male: Western Tibet, Pangur Tso, 14203 ft., 13–14.VIII.1932, leg. G. E. Hutchinson, Yale North

India Expedition. Type ♂ and paratypes ♂ and ♀ in the collection of the British Museum; other paratypes in the collection of the Yale University, U.S.A., all from the same locality.

Remarks. This species has high lateral profile of paraprot with long tapering apices; much developed subapical spine-like hook formation on the aedeagus and spiniform paramere with monofid apices in lateral view, but with triplet apices in dorsal view, that is having three apical spines on the paramere apical region in consecutive location indiscernible in lateral but well visible in dorsal view. According to Mosely (1936) resembles *L. alaicus* in the genitalia but differs vastly in general appearance and in having only 3 spurs to the posterior leg.

***Limnephilus samoedus* species group
integrated species with extreme adaptation**

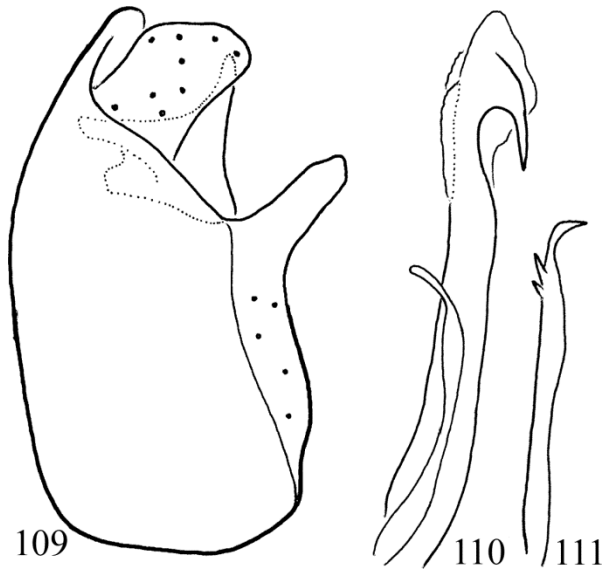
***Limnephilus hovsgolicus* Morse, 1999**

(Figures 112–113)

Limnephilus hovsgolicus Morse, 1999:253–257, this strange brachypterous “skating” *Limnephilus* species was a great discovery and record from the Lake Hövsgöl, northern Mongolia. This new species was placed into the *Limnephilus asiaticus* species group.

Material examined. **Mongolia**, Khövsgöl Aimag, Khvösgöl Nuur (=lake) at Khankh nr. Pier; 51°31'14"N, 100°38'45"E; elev. 1630m; 19.VII.1997, leg. J. Gelhaus, B. Hayford & party. The picture of the male genitalia with paramere was taken by S. Chuluunbat and served to draw the paramere.

Remarks. The adaptation to the skimming behaviour has initiated great morphological integration to function under the extreme habitat similarly to the brachypterous species in the genera of *Thamestes*, *Drusus* (*Anomalopterygella*), *Limnoecetis*, *Rhyacophila*. The basic architecture of the genitalia combined in the *L. samoedus* species group preserved, only the sclerous hook formation on the head of the aedeagus dissolved into sclerous stripes.



Figures 109–111. Derived *Limnephilus* lineage of spiniform paramere. *Limnephilus samoedus* species group: *Limnephilus alaicus* species complex. *Limnephilus tricalcaratus* (Mosely), 1936: 109 = genitalia in left lateral view, 110 = phallic organ in lateral view, 111 = paramere in dorsal view.

Derived lineage of lost paramere *Limnephilus iranensis* species group

In this small group of species the paramere is completely disappeared. Species in this group have been described in the new genus *Astratodes* near to the genus *Astratus*, but transferred to and listed among *Limnephilus* (Schmid 1955; Fisher 1968). This small species group contains three species: *hermonianus*, *iranensis*, *turanus*.

Limnephilus turanus (Martynov, 1928)

Material examined. **Turkmenistan**, Kopet-Dagh Mts., Firyuza, 13. X. 1991, leg Ronkay (28 males, 31 females; OPC). **Kazakhstan**, Zailiskiy Alatau Mt., 21.IX.2002, leg. B. Benedek & T. Csóvári (1 female, OPC).

Nemotaulius Banks, 1906

(Figure 114)

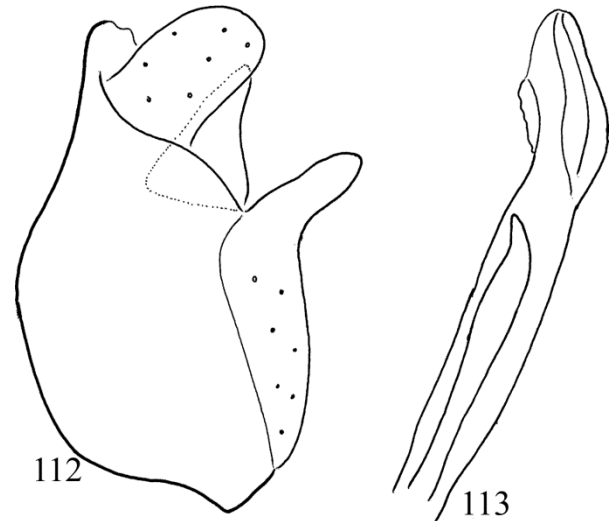
Original differential diagnosis. “In most respects similar to *Grammotaulius*, but in the hind

wings the first apical sector is connected to the radius or runs into it near tip.”

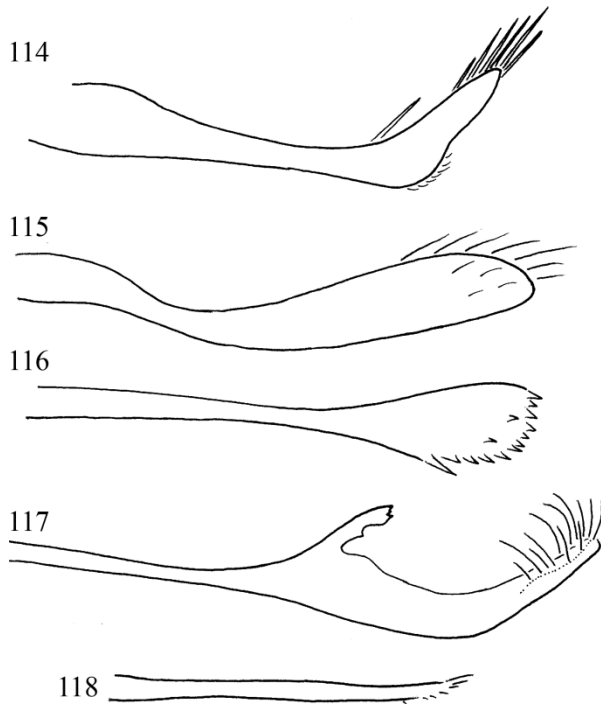
Relation. A cold-adapted genus with small narrow wings. The genital structure of both the male and female is close to the *Anabolia* genus (Schmid 1955).

Genital character state combinations. (1) Presence (apomorphic) of spinulose protuberance on tergite VIII; (2) Reduced (apomorphic) state of tergite IX; (3) More sclerotized dentate (apomorphic) state of cerci; (4) Produced (plesiomorphic) state of the dorsal branch of paraproct; (5) Separate free from each-other (plesiomorphic) state of the dorsal branch of paraproct; (6) Separate free-from-cerci (plesiomorphic) state of the dorsal branch of paraproct; (7) Reduced (apomorphic) state of the ventral branch of paraproct; (8) Separate free from each-other (plesiomorphic) state of the ventral branches of paraproct.

Parameres. The derived paramere simplified into a simple digitiform structure with setose apical region. A single species, *Nemotaulius brevilinea* has lost its paramere.



Figures 112–113. Derived *Limnephilus* lineage of spiniform paramere. *Limnephilus samoedus* species group: *Limnephilus alaicus* species complex. *Limnephilus hovsgolicus* Morse, 1999: 112 = genitalia in left lateral view, 113 = phallic organ in lateral view.



Figures 114–118. Parameres of *Nemotaulius*, *Philarctus*, *Platycentropus* and *Sphagnophylax* genera. 114 = *Nemotaulius coreanus*, 115 = *Philarctus asiaticus*, 116 = *P. bergrothi*, 117 = *Platycentropus radiatus* 118 = *Sphagnophylax meiops*.

***Nemotaulius coreanus* Oláh, 1985**

(Figure 114)

Material examined. Male holotype. **North Korea**, Mt Pektu-san, before Sam-zi-yan Hotel, lakeshore, wooded environment, collecting at Mv lamp, 20.VII.1977, (1 male, HNHM). **Russia**, Primorye, Khasan District, 3 km W Ryazanovka, 15.VII.1992, light trap, leg. P. Lindskog & A. Nilsson (1 male, SMNH).

Remarks. Martynov (1914a) has described from the lower Ussuriland a single male with question mark as similar to the Japanese *Glyphotelius admorsus* McLachlan. Based on his remarks and drawings we have concluded that his male specimen is *Nemotaulius coreanus* Oláh, 1985 (Oláh et al. 2018c). Here we have a single male specimen from Ussuriland of Russia and the direct examination and comparison with *Nemotaulius admorsus* from Japan confirm Martynov's question mark and our own conclusion. *N. admo-*

sus is present in Japan, and *N. coreanus* lives in South and North Korea as well as in Ussuriland/Amurland of Russia.

The Japanese species of *Nemotaulius admorsus* has cerci without dental projection on the apical margin. Contrary all the examined specimens of *Nemotaulius coreanus* from North and South Korea as well as from Ussuriland have characteristic dental projection on the apical margin of the cerci. The other periphallial organ the paraproct is band-like with tapering and slightly upward directed conical apex at *N. admorsus* and capitate or rather clavate and truncate at *N. coreanus* in lateral view. The fine structure of the parameres is even more diverged in the two species. *N. admorsus* has paramere apex with long setae both on the dorsal and ventral margin in lateral view. *N. coreanus* has long setae only on the dorsum of the paramere apex.

***Philarctus* McLachlan, 1880**

(Figures 115–116, 119–121)

Original differential diagnosis. “In most respects similar to *Grammotaulius*, but in the hind wings the first apical sector is connected to the radius or runs into it near tip.”

Relation. A cold-adapted genus with small narrow wings. The genital structure of both the male and female is close to the *Anabolia* genus (Schmid 1955).

Genital character state combinations. (1) Absence (plesiomorphic) of spinulose protuberance or any neof ormation on tergite VIII; (2) Produced (plesiomorphic) state of tergite IX; (3) Setose inerm (plesiomorphic) state of cerci; (4) Produced (plesiomorphic) state of the dorsal branch of paraproct; (5) Separate free from each-other (plesiomorphic) state of the dorsal branch of paraproct; (6) Separate free-from-cerci (plesiomorphic) state of the dorsal branch of paraproct; (7) Produced (plesiomorphic) state of the ventral branch of paraproct; (8) Separate free from each-other (plesiomorphic) state of the ventral branches of paraproct.

Parameres. The derived paramere simplified into a simple digitiform structure with setose scoop-shaped head emarginated by teeth or setae.

***Philarctus asiaticus* (Forsslund, 1934)**

(Figures 115, 119–121)

Platycentropus asiaticus Forsslund, 1934:1718, “Nervatur wie bei *P. maculipennis* KOL., doch ist die Querrippe M-Cu quer (nicht schräg). Das ♀ ist brachypter.

Philarctus asiaticus (Forsslund, 1934): Schmid 1955: 158, “Je place dans le même genre *Platycentropus asiaticus* Forssl. dont le type est détruit et qui, quoiqu’il soit probablement étranger aux *Philarctus*, y est tout de même moins mal à sa place que parmi les *Platycentropus*.”

Platycentropus asiaticus Forsslund, 1934: Grigorenko 2002:113, “It is advisable to return *P. asiaticus* to *Platycentropus* until re-examination of type material.”

Material examined. Holotype: **China**, S. Kansu: Tjeggala, Alpenweise, 3200 m, Sven Hedins

Exp. Ctr. Asien, leg. Hummel (1 male, SMNH).

***Philarctus bergrothi* McLachlan, 1880**

(Figure 116)

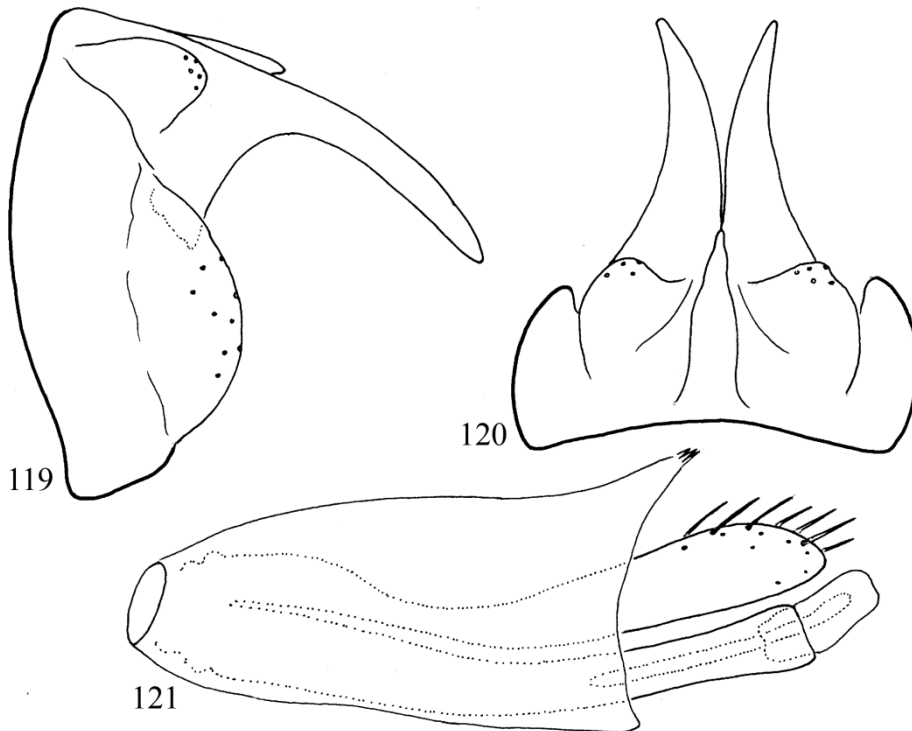
Material examined. **Canada**, Alberta, Banff Alta., 13.IX.1992, leg. C. B. D. Garrett (1 male, OPC). **Canada**, Saskatchewan, Saskatoon, 27.IX. 1948, leg. J. R. Vockeroth (1 male, CNC).

***Platycentropus* Ulmer, 1905**

(Figure 117)

Original differential diagnosis. This genus was established by the specialised mesoapical spur of the hind leg. This is a small genus of fairly large insects. The three known species are exclusively Nearctic in distribution populating large varieties of habitats from cold streams to warm ponds.

Relation. Has some relation to *Lenarchus* (Schmid 1955).



Figures 119–121. *Philarctus asiaticus* (Forsslund, 1934). Holotype: 119 = genitalia in left lateral view, 120 = genitalia in dorsal view, 121 = phallic organ in lateral view.

Genital character state combinations. (1) Absence (plesiomorphic) of spinulose protuberance or any neoformation on tergite VIII; (2) Produced (plesiomorphic) state of tergite IX; (3) Setose inerm (plesiomorphic) state of cerci; (4) Produced (plesiomorphic) state of the dorsal branch of paraproct; (5) Separate free from each-other (plesiomorphic) state of the dorsal branch of paraproct; (6) Separate free-from-cerci (plesiomorphic) state of the dorsal branch of paraproct; (7) Produced (plesiomorphic) state of the ventral branch of paraproct; (8) Separate free from each-other (plesiomorphic) state of the ventral branches of paraproct.

Paramere. At two species, *P. indistinctus* (Walker), *P. radiatus* (Say) the parameres have bilobed apex of ancestral limnephilini. The larger ventroapical lobe elongated club-shaped and heavily setose. The dorsal lobe forms somewhat flattened apex almost trough-like with ventral concavity and the apical margin armed with small pointed fringes, somewhat serrated. The third species of the genus, *P. amicus* (Hagen) has lost its paramere; it is reduced to small triangular, immobile stubs set dorsolaterad on the basement of the aedeagus.

***Platycentropus radiatus* (Say, 1824)**

(Figure 117)

Material examined. USA, North Carolina, Highlands 3800', 4–10.VI.1957, leg. J.R. Vockeroth (1 male, 1 female; OPC).

***Sphagnophylax* Wiggins & Winchester, 1984**

(Figure 118)

Original differential diagnosis. Detailed delineation trials on the taxonomic status of the new genus is presented (Wiggins & Winchester 1984).

Relations. Affinity of *Sphagnophylax* with the four tribes of Limnephilinae is evaluated in details (Wiggins & Winchester 1984). Habitus, short and thickened body, broad wings, long bristles on forewings are synapomorphic with chaetopterygin tribe, but male genital structure indicate some af-

finity to Stenophylacini tribe and female genital structure has similarity to Limnephilini tribe. Taxonomic status remained questionable and assigned as Limnephilinae *incertae sedis*. After discovery and description of the larval and pupal stages *Sphagnophylax* was assigned to the tribe Limnephilini based on larval gill structure, female genital structure and on the resemblance of male genitalia to *Philarctus* genus from the Limnephilini tribe (Winchester *et al.* 1993). Paramere organisation supports this relation to the Limnephilini tribe.

Genital character state combinations. (1) Absence (plesiomorphic) of spinulose protuberance or any neoformation on tergite VIII; (2) Reduced (apomorphic) state of tergite IX; (3) Setose inerm (plesiomorphic) state of cerci; (4) Produced (plesiomorphic) state of the dorsal branch of paraproct; (5) Separate free from each-other (plesiomorphic) state of the dorsal branch of paraproct; (6) Fused to-cerci (apomorphic) state of the dorsal branch of paraproct; (7) Produced (plesiomorphic) state of the ventral branch of paraproct; (8)) Separate free from each-other (plesiomorphic) state of the ventral branches of paraproct.

Parameres. Paramere is small only slightly more than half of the length of the aedeagus; slender spiniform with few apical setae accompanied mesad by 2–3 subapical setae.

Neoformation/innovation. Other than the character combination unique enough for genus ranking, the produced pair of coarsely granulated peg-packed roughened independent and freely movable ventral branch of paraproct is organised only as a real structural innovation of neoformation.

Taxonomic state. Unique combination of body and genital characters together with organisational novelty of the ancestral ventral branch of paraproct grounds a generic status of *Sphagnophylax*.

Remarks. In the original description the dorsal branch of paraproct was discussed as the mesal arm of the cercus and the ventral branch of paraproct was presented as the paraproct (intermediate

appendages). According to alternative transformation detected in several caddisfly lineages, the dorsal branches of the paraproct are frequently fused mesally to the cerci. The fused-to-cerci character state can be detected by surface texture of microsculpture, either by cuticular structures like sutures, or by vestitural projections like non-articulated cuticular projection, directly continuous with the cuticula like vestitural denticles or by articulated setal development. In *Sphagnophylax* the fused dorsal branch of paraproct has the same surface microsculpture of heavily sclerotized vestitural denticles than the ventral branch of the paraproct in contrast to the articulated setal vestitular projections of cerci.

***Sphagnophylax meiops* Wiggins & Winchester, 1984**

(Figure 118)

Material examined. **Canada**, North-West Territories, Involut Hills, 16 km NE Tuktoyaktuk, 69°29'N, 132°35'W, transient tundra pool, larva 25.VI.1983 reared to adult, 6.VII.1983, leg. N.N. Winchester (1 male, OPC). North-West Territories, Involut Hills, 16 km NE Tuktoyaktuk, 69°29'N 132°35'W, transient tundra pool, larva 25.VI.1983 reared to adult, 13.VII.1983, leg. N. N. Winchester (1 female, OPC).

Chilostigmini tribe

Basic pattern of parameres are rather simple thin spiniform, almost filiform without branches, lobes or setal structures. The dominating slender, slim, spiniform basic pattern of the parameres is modified in a few genera to an abbreviated thick pattern. (1) Paramere slender, slim, spiniform: *Brachypsyche*, *Chilostigma*, *Chilostigmodes*, *Desmona*, *Grensia*, and *Psychoglypha*; (2) Paramere abbreviated thick and much shorter than aedeagus: *Frenesia*, *Glyphopsyche*, and *Homophylax*.

This apomorphic, particularly simplified and derived basic paramere pattern is frequently accompanied with plesiomorphic ancestral character states of the produced tergite IX and the produced ventral branch of the paraproct.

***Brachypsyche* Schmid, 1952**

(Figures 122–123)

Original differential diagnosis. Intermediate between *Chilostigma* and *Psychoglypha*.

Relation. Cerci and gonopod are related to *Chilostigma* and the phallic organ is related to *Psychoglypha* (Schmid 1955).

Genital character state combinations. (1) Absence (plesiomorphic) of spinulose protuberance on tergite VIII at *Brachypsyche rara* and *B. sibirica*; presence (apomorphic) of spinulose protuberance on tergite VIII at *B. schmidi*; (2) Produced (plesiomorphic) state of tergite IX; (3) Setose inerm (plesiomorphic) state of cerci; (4) Produced (plesiomorphic) state of the dorsal branch of paraproct; (5) Separate free from each other (plesiomorphic) state of the dorsal branch of paraproct; (6) Separate free-from-cerci (plesiomorphic) state of the dorsal branch of paraproct; (7) Produced (plesiomorphic) state of the ventral branch of paraproct; (8) Separate free from each other (plesiomorphic) state of the ventral branches of paraproct.

Paramere. Paramere simplified into a slender spiniform slim structure. Equally thin along the entire length. At the examined two species the very tip of the parameres represents a vestigial seta attached to the shaft-end with alveolar remnants of sutures preceded by tiny cuticular spinules.

Neoformation/innovation. An important limnephiline character state transformation is the absence (plesiomorphic) or presence (apomorphic) of spinulose protuberance or any neoformation on tergite VIII. In this small genus the Korean species *B. schmidi* has the generic type of character combination and paramere structure except its tergite X is apomorphic, not plesiomorphic and spinulose protuberance is present with a particular innovation that is a deep mesal excision forming a bilobed spinulose apical margin of the tergite. Similar neoformation is organised also at the monobasic *Grensia* genus.

Taxonomic state. Combination of body and genital characters together with the slender thin spiniform, highly simplified parameres grounds the generic status of *Brachypsyche*.

***Brachypsyche schmidi* Choe, Kumanski & Woo, 1999**

(Figure 122)

Material examined. **South Korea**, Gyeonggi-do, Gapyeong-gun, Buk-myeon, Jomurakgol rd. N: 37°59'24.7" E: 127°26'76.0" 360 m, 4.XI. 2016, light trap, leg. J. Babics & B. Tóth (1 male, HNHM).

***Brachypsyche sibirica* (Martynov, 1924)**

(Figures 123)

Material examined. **Sweden**, Exchanged specimen from Naturhistoriska Riksmuseet, Stockholm, without collecting data (1 male, OPC).

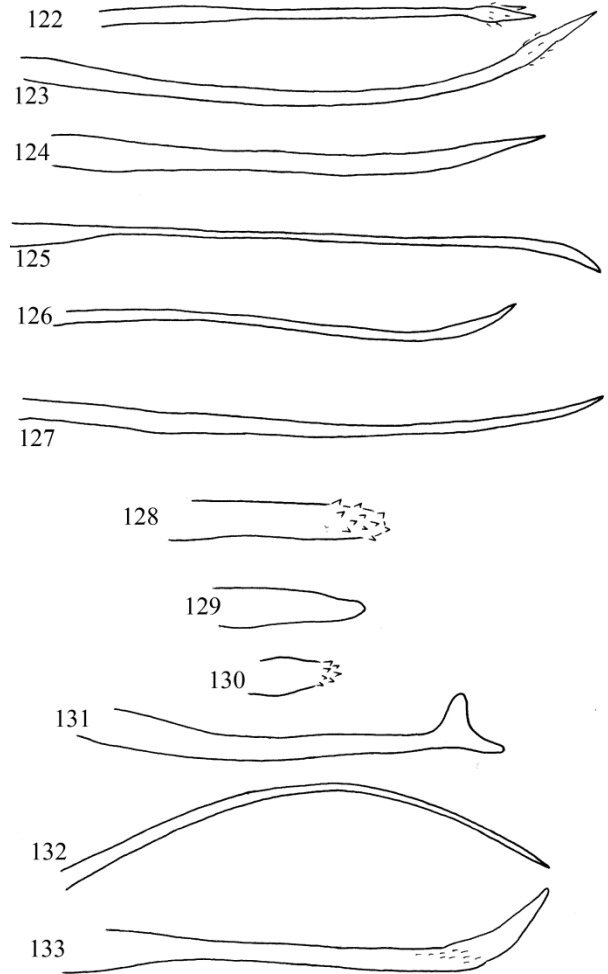
***Chilostigma* McLachlan, 1876**

(Figure 124)

Original differential diagnosis. The position of this genus is uncertain.

Relation. Close to *Grensia* by wing characters, but relates to *Brachypsyche* and *Psychoglypha* by genital characters (Schmid, 1955).

Genital character state combinations. (1) Presence (apomorphic) of spinulose protuberance on tergite VIII; (2) Reduced (apomorphic) state of tergite IX; (3) Setose inerm (plesiomorphic) state of cerci; (4) Reduced (apomorphic) state of the dorsal branch of paraproct; (5) Separate free from each-other (plesiomorphic) state of the dorsal branch of paraproct; (6) Separate free-from-cerci (plesiomorphic) state of the dorsal branch of paraproct; (7) Reduced (apomorphic) state of the ventral branch of paraproct; (8) Separate free from each-other (plesiomorphic) state of the ventral branches of paraproct.



Figures 122–133. Parameres of *Brachypsyche*, *Chilostigma*, *Chilostigmodes*, *Desmona*, *Frenesia*, *Glyphopsyche*, *Grensia*, *Phanocelia*, *Psychoglypha* genera. 122 = *Brachypsyche schmidi*, 123 = *B. sibirica*, 124 = *Chilostigma sieboldi*, 125 = *Chilostigmodes areolatus*, 126 = *C. forcipatus*, 127 = *Desmona bethula*, 128 = *Frenesia difficilis*, 129 = *F. missa*, 130 = *Glyphopsyche irrorata*, 131 = *Grensia preterita*, 132 = *Phanocelia canadensis*, 133 = *Psychoglypha bella*.

Paramere. Paramere simplified into a slender spiniform slim structure. Equally thin along the entire length.

Taxonomic state. Combination of body and genital characters together with the slender thin spiniform highly simplified parameres grounds the generic status of *Chilostigma*.

***Chilostigma sieboldi* McLachlan, 1876**

(Figure 124)

Material examined. Sweden, Exchanged specimen from Naturhistoriska Riksmuseet, Stockholm, without collecting data (1 male, OPC).

Chilostigmodes Martynov, 1914

(Figures 125–126)

Original differential diagnosis. Allied to *Chilostigma*, but differs by venation characters and by the extremely enlarged cerci.

Relation. A single genus having 1,1,1 spur formula in the entire family. Body and wing characters related to *Chilostigma* and *Grensia* (Schmid 1955).

Genital character state combinations. (1) Absence (plesiomorphic) of spinulose protuberance on tergite VIII; (2) Reduced (apomorphic) state of tergite IX; (3) Setose inerm (plesiomorphic) state of cerci; (4) Reduced (apomorphic) state of the dorsal branch of paraproct; (5) Fused to each-other (apomorphic) state of the dorsal branch of paraproct; (6) Separate free-from-cerci (plesiomorphic) state of the dorsal branch of paraproct; (7) Produced (plesiomorphic) state of the ventral branch of paraproct; (8) Fused to each-other (apomorphic) state of the ventral branches of paraproct.

Paramere. Paramere simplified into a slender spiniform slim structure. Equally thin along the entire length.

Taxonomic state. Combination of body and genital characters together with the slender thin spiniform highly simplified parameres grounds the generic status of *Chilostigmodes*.

***Chilostigmodes areolatus* (Walker, 1852)**

(Figure 125)

Material examined. Canada, Alaska, Anchorage, Eagle River Flats, 7.IV.1948, on snow, leg.

F. S. Blanton, (1 male, ROM). Manitoba, The Pass, 6.IV.1951, leg. W. Krivda (1 male, OPC).

***Chilostigmodes forcipatus* Martynov, 1914**

(Figure 126)

Material examined. Russia, Verhoyansk Oblast, Adychanskaya, Adycha River, 7.V.1927, leg. Tkachenko, det. Martynov (1 male, ROM). Kolymskij Territory, Verhoyansk Oblast, Tostah River, 4.V.1927, leg. Tkachenko, det. Martynov (1 male, OPC).

***Desmona* Denning, 1954**

(Figures 127)

Original differential diagnosis. “General appearance resembles *Hesperophylax*, but the genitalia and other characters are radically different.”

Relation. *Desmona* is part of a complex with *Chilostigma*, *Brachypsyche* and *Psychoglypha* (Wiggins & Wisseman 1990).

Genital character state combinations. (1) Absence (plesiomorphic) of spinulose protuberance on tergite VIII; (2) Reduced (apomorphic) state of tergite IX; (3) Setose inerm (plesiomorphic) state of cerci; (4) Reduced (apomorphic) state of the dorsal branch of paraproct; (5) Separate free from each-other (plesiomorphic) state of the dorsal branch of paraproct; (6) Separate free-from-cerci (plesiomorphic) state of the dorsal branch of paraproct; (7) Reduced (apomorphic) state of the ventral branch of paraproct; (8) Fused to each-other (apomorphic) state of the ventral branches of paraproct.

Paramere. Paramere simplified into a slender spiniform slim structure. Equally thin along the entire length.

Taxonomic state. Combination of body and genital characters together with the slender thin spiniform highly simplified parameres grounds the generic status of *Desmona*.

***Desmona bethula* Denning, 1954**

(Figure 127)

Material examined. USA, California, spring (B) entering Sagehen Cr. above Univ. of Calif Sta., 8 mi. n. Truckee, Nevada Co. 7.X.1966, leg. Wiggins, Yamamoto, Odum (1 male, OPC).

Frenesia Betten & Mosely, 1940

(Figures 128–129)

Original differential diagnosis. In the original genus description *Frenesia* was distinguished from *Chilostigma* by the shape of forewing, the proportionate lengths of the palpal joints, and by the structure of the foreleg of the male.

Relation. This is a small genus with only two known species found exclusively in the eastern Nearctic region along springs and streams.

Genital character state combinations. (1) Presence (apomorphic) of spinulose protuberance on tergite VIII; (2) Produced (plesiomorphic) state of tergite IX; (3) Setose inerm (plesiomorphic) state of cerci; (4) Produced (plesiomorphic) state of the dorsal branch of paraproct; (5) Separate free from each-other (plesiomorphic) state of the dorsal branch of paraproct; (6) Separate free-from-cerci (plesiomorphic) state of the dorsal branch of paraproct; (7) Produced (plesiomorphic) state of the ventral branch of paraproct; (8) Separate free from each-other (plesiomorphic) state of the ventral branches of paraproct.

Paramere. Paramere abbreviated, modified into thick rod-shape structure much shorter than aedeagus. The short paramere is equally thick along the entire length; its apical region is closely packed with short conical pointed pegs.

Taxonomic state. The produced plesiomorphic state of tergite IX is not the usual horizontally enlarged structure, but developed into a very wide vertical plate. Combination of body and genital characters together with thick rod-shaped highly modified parameres grounds the generic status of *Frenesia*.

***Frenesia difficilis* (Walker, 1852)**

(Figure 128)

Material examined. Canada, Quebec, Old Chelsea, King Mt. 1150', 16.X.1968, leg. J. F. McAlpine (2 females, CNC; 1 male, 1 female; OPC). Ontario, Arnprior, on snow, 25.XI.1920, leg. C. Macnamara (3 females, CNC). Mexico, State of Mexico, Ixtapan de La Sal, 5500', 9.VIII.1954, leg. J. G. Chillcott (1 male, CNC).

***Frenesia missa* (Milne, 1935)**

(Figure 129)

Material examined. Canada, Quebec, Fairy Lake, 14.XI.1928, leg. G.S. Walley (5 males, CNC; 1 male, OPC). Canada, Quebec, Old Chelsea, King Mt. 1150', 16.X.1968, leg. J.F. McAlpine (1 female; OPC).

***Glyphopsyche* Banks, 1904**

(Figure 130)

Original differential diagnosis. "Much resemblance to *Glyphotaelius*, but differs in more prominent pterostigma, in the much smaller prothorax, and different shape of head."

Relation. Large species of brown coloured and patterned forewings with Nearctic distribution found transcontinentally inhabiting still waters of marshes, ponds and small lakes. Close to *Frenesia* and convergence to *Psychoglypha*, but more specialised (Schmid 1955).

Genital character state combinations. (1) Presence (apomorphic) of spinulose protuberance on tergite VIII; (2) Reduced (apomorphic) state of tergite IX; (3) Setose inerm (plesiomorphic) state of cerci; (4) Produced (plesiomorphic) state of the dorsal branch of paraproct; (5) Fused to each-other (apomorphic) state of the dorsal branch of paraproct; (6) Free-from-cerci (plesiomorphic) state of the dorsal branch of paraproct; (7) Produced (plesiomorphic) state of the ventral branch of paraproct; (8) Separate free from each-other (plesiomorphic) state of the ventral branches of paraproct.

Paramere. The parameres are highly abbreviated, very small and thick with pegged tip and based or supported by produced membranous endotheca.

Taxonomic state. The genital character state combination together with the heavily sclerotized structure of the aedeagus accompanied by the highly abbreviated paramere ground the generic status of *Glyphopsyche*.

***Glyphopsyche irrorata* (Fabricius, 1781)**

(Figure 130)

Material examined. **Canada**, Quebec, Lac Mondor, Ste. Flore, P.Q. 8.V.1951, leg. E.G. Munroe (1 male, OPC).

***Grensia* Ross, 1944**

(Figure 131)

Original differential diagnosis. Monobasic genus without formal delineation.

Relation. Wing characters relate to *Chilostigma* but male genital characters are highly specialised (Schmid 1955)

Genital character state combinations. (1) Presence (apomorphic) of spinulose protuberance with a neof ormation of deep mesal excision on tergite VIII; (2) Reduced (apomorphic) state of tergite IX; (3) Strongly sclerotized (apomorphic) state of cerci; (4) Produced (plesiomorphic) state of the dorsal branch of paraproct; (5) Fused to each-other (apomorphic) state of the dorsal branch of paraproct; (6) Separate free-from-cerci (plesiomorphic) state of the dorsal branch of paraproct; (7) Produced (plesiomorphic) state of the ventral branch of paraproct; (8) Separate free-from-cerci (plesiomorphic) state of the dorsal branch of paraproct;

Paramere. Paramere simplified into a slender spiniform slim structure with patterned tip. Equally thin along the entire length.

Taxonomic state. Combination of body and genital characters together with the slender thin spiniform highly simplified parameres with patterned tip grounds the generic status of *Grensia*

***Grensia praeterita* (Walker, 1852)**

(Figure 131)

Material examined. **Canada**, Northwest Territories, Padley, 13.VII.1950, leg. R.A. Hennigar (1 male, OPC).

***Homophylax* Banks, 1900**

Original differential diagnosis. Formal delineation is given as simply as “Easily distinguished from all our other Limnophilids by the position of the anterior anastomosis” (Banks 1900).

Relations. Schmid 1955:114: “Le genre *Homophylax* est très isolé. La nervulation et les néoformations des ailes sont très particulières.” “... à cause des néoformations des ailes et de la disposition des appendices inférieurs du ♂ je place provisoirement *Homophylax* parmi les Pseudosténophylacines.” Enlarged second and third segments of the male maxillary palpi are similar to those of *Chyranda*. According to Denning (1963) it may be necessary to propose a new subfamily for *Homophylax*.

Character state combination. (1) Presence (apomorphic) of neof ormation, a smooth sclerotized process on tergite VIII; (2) Reduced (apomorphic) state of tergite IX; (3) Setose inerm (plesiomorphic) state of cerci; (4) Produced (plesiomorphic) state of the dorsal branch of paraproct; (5) Separate free from each-other (plesiomorphic) state of the dorsal branch of paraproct; (6) Separate free-from-cerci (plesiomorphic) state of the dorsal branch of paraproct; (7) Produced (plesiomorphic) state of the ventral branch of paraproct; (8) Separate free from each-other (plesiomorphic) state of the ventral branches of paraproct.

Parameres. Schmid 1955:113: “Il n’y a pas de titillateurs.” Schmid 1998:132: “Paramere lost.” Examining the available four species we have detected the presence of the parameres in all of the four examined species. The simple setaless and spineless spiniform ancestral paramere of the Chilostigmini tribe has highly modified into a short sclerotized paramere with independent rooting of membranous endothecal tissue positioned dorsad of the short sclerotized aedeagus that has its independent membranous endothecal rooting; the aedeagus is clearly indicated by the position of rather enlarged and partially sclerotized ejaculatory duct.

Remarks. These large or medium-sized light-yellowish species inhabit streams and lakes in the mountains of western Nearctic region of the United States and Canada. Poorly known and rarely collected species; always rare and local. Based on the present discovery of two new species just from a few available specimens determined earlier as *H. andax*, it seems that *Homophylax* is liable to contemporary divergences in allopatric isolation with small effective population size. Several cryptic species could be detected by the probable speciation traits of the progs on the tip of the dorsal and ventral arms of the dorsal branch of paraproct. Genus revision is required by fine phenomics.

***Homophylax andax* Ross, 1941**

(Figures 134–138)

Material examined. **USA**, Oregon, Klamath County, Crater Lake Nat. Park. headquarters, 24.VII.1985, leg. R. W. Wisseman (1 male, ROM; 1 male OPC). Washington, Jefferson County, Fawn Lake nr. Port Angeles, 3.VIII.1987, leg. J.F.K., B.L.T (1 male, ROM). **Canada**, British Columbia, Robertson Creek, Spawning Channel, Can. Dep. Fish., Port Albemi, Vancouver Isl., 25.VI.1969, UVL 690131, leg. ROM Field Party (1 male, ROM). British Columbia, Pitt Meadow, VII.1923, leg. W. A. Salter (1 male, CNC).

Remarks. Differential diagnosis to delineate *H. andax* both from *H. beges* sp. nov. is restricted

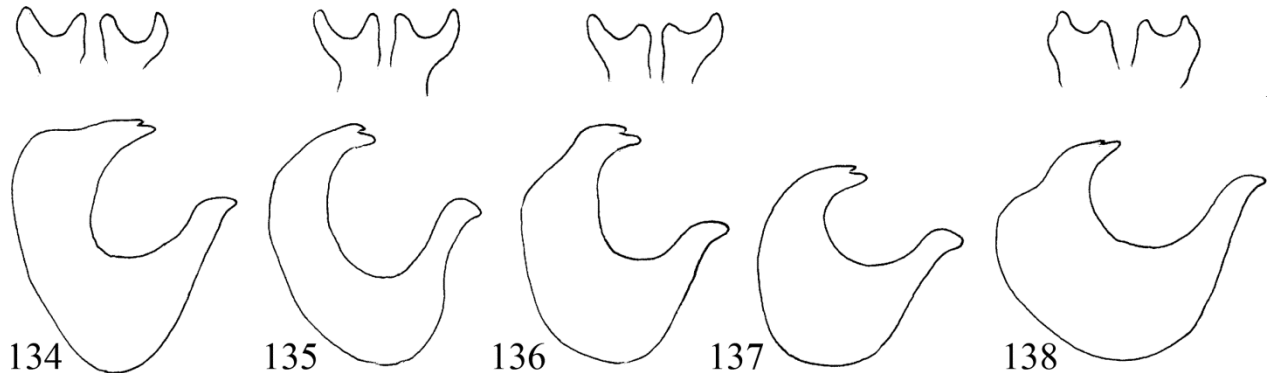
here to the lateral and dorsal profiles of the heavily sclerotized tips of the dorsal and ventral arms of the dorsal branch of the paraproct. The prong neck of the dorsal profile of the dorsal arm is broad at *H. andax* and narrow at *H. beges* sp. nov. This character seems stable in the few specimens examined from Washington and Oregon states of USA and from Vancouver Island and British Columbia of Canada. One specimen from Crater Lake NP, Clamath County, Oregon has dorsal profile completely different, probably represents an unknown sibling species. The lateral profile of the ventral arm of the dorsal branch of the paraproct of *H. andax* is without subapical hump or “craw”. This nominate character present at the examined holotype and four paratypes of *H. beges* sp. nov.

***Homophylax beges* Oláh, sp. nov.**

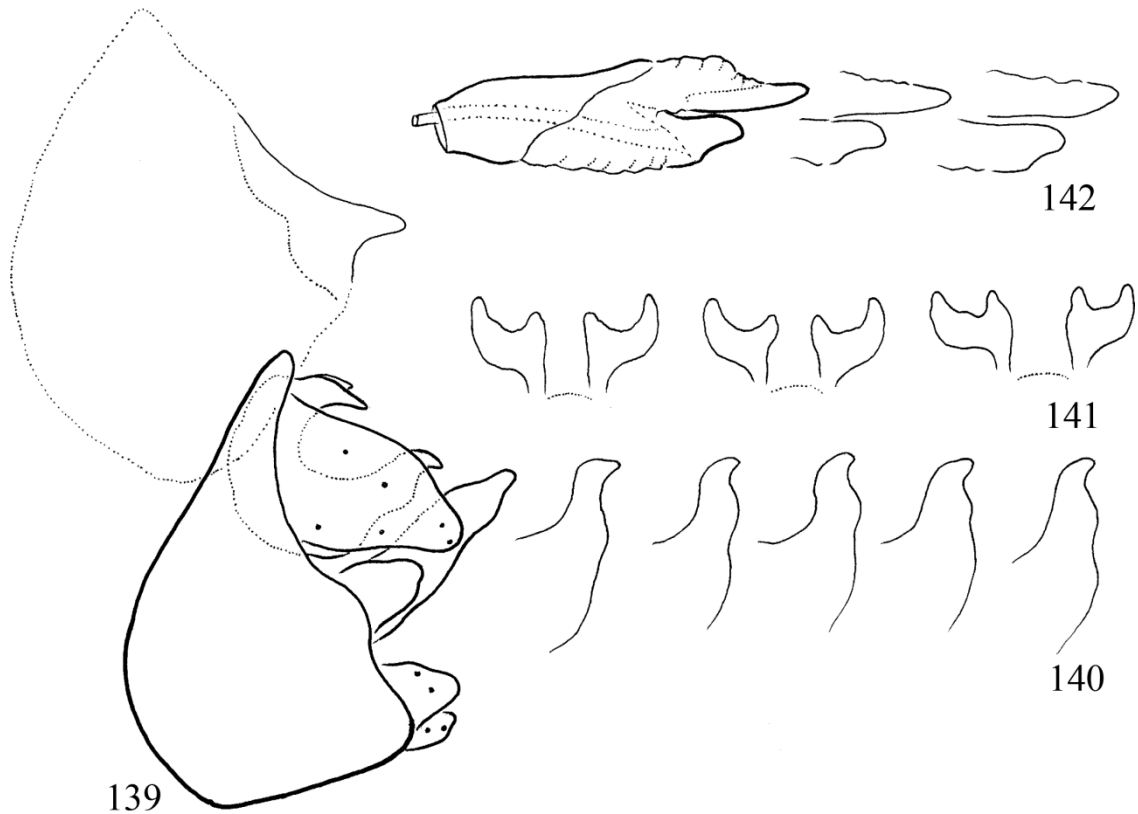
(Figures 139–142)

Material examined. Holotype: **Canada**, British Columbia, Squamish, Diamond Head Trail, 3200 ft. 26.VIII.1953, leg. E. Mason, genitalia in permanent slide (1 male, CNC). Paratypes: British Columbia, Haney, Univ. of B. C. Res. Forest at Loon Lake, 7.-10.VII.1969, UVL 690187. ROM Field Pty (1 male, ROM). British Columbia, Squamish, Diamond Head Trail, 3200 ft. 28.VIII.1953, leg. E. Mason (1 male, OPC). British Columbia, Squamish, Diamond Head Trail, 3200 ft. 26.VIII.1953, leg. E. Mason, CNC279952, genitalia in permanent slide (1 male, CNC). British Columbia, Squamish, Diamond Head Trail, 3200 ft. 30.VIII.1953, leg. W.R.M. Mason, genitalia in permanent slide (1 male, CNC).

Diagnosis. The heavily sclerotized prong-like terminals both of the dorsal and ventral arms of the dorsal branch of paraproct seems rather stable at the examined specimens of these rare animals. The sclerotized tips with specific pattern may function as a stimulatory structure in cryptic female choice during copulation and produced as an adaptive structure during sexual integrative organisation. The prong neck of the dorsal profile



Figures 134–138. *Homophylax andax* Ross, 1941. Lateral profile of the dorsal branch of the paraproct composed of the dorsal and ventral arms as well as the dorsal profile of progs on the tip of the dorsal arms in specimens collected from various regions: 134 = USA, Washington, Jefferson County, Fawn Lake, 135 = Canada, Vancouver Isl. Port Albemi, 136 = USA, Oregon, Klamath County, Crater lake N. P., 137 = Canada, British Columbia, Pttt Meadow, 138 = USA, Oregon Klamath County, Crater Lake N. P.



Figures 139–142. *Homophylax beges* Oláh, *sp. nov.* Holotype male: 139 = genitalia in left lateral view, 140 = lateral profile of the ventral arm of the dorsal branch of the paraproct: holotype and four paratypes, 141 = dorsal profile of the progs on the tip of the dorsal arms with narrow neck, 142 = phallic organ in lateral view.

of the dorsal arm is narrow at *H. beges* sp. nov. and broad at *H. andax*. This character seems stable in the examined five specimens. The lateral profile of the ventral arm of the dorsal branch of the paraproct is armed with subapical hump or “craw”. This name-bearing character is present at the examined holotype and four paratypes of *H. beges* sp. nov., but absent at all of the examined specimens of *H. andax* both from Washington and Oregon states of USA and from Vancouver Island and British Columbia of Canada.

Description. Yellow species with large wings. *Male genitalia.* Tergite VIII with a neoformation/innovation of medium-long smooth sclerotized protrusive process, emerging mesoapical from a surrounding depression. Tergite IX narrowed to a strap. Cerci large foliform and setose. Dorsal branch of paraproct strongly sclerotized and composed of closely appressed, but not fused pairs of dorsal and ventral arms both terminating in specific prongs; ventral branch of paraproct heavily sclerotized longer than the dorsal branch. Gonopods short. Both the sclerotized aedeagus and parameres short.

Etymology. *beges* from “begyes” craw in Hungarian, refers to the bird-craw shape of the dorsal arm of the dorsal branch of the paraproct.

***Homophylax coros* Oláh, sp. nov.**

(Figures 143–146)

Material examined. Holotype: **Canada**, British Columbia, Mt Revelstoke, 5400', 17.VIII.1952, leg. G.J. Spencer (1 male, CNC). Paratype: British Columbia, Mt Revelstoke, 5400', 9.VIII.1952, leg. G.J. Spencer (1 male, OPC).

Diagnosis. *Homophylax coros* new sibling species from British Columbia of Canada differs from *H. andax* by having completely differently diverged dorsal prong profile of the dorsal arm of the dorsal branch of the paraproct; the excision creating the bifid apices is very shallow, not deep and the prong neck or collar is broader than the head that is the very tips. The lateral profile is

more slender and bird-beak shaped with a deep subapical concavity on the ventrum.

Description. Yellow species with large wings. *Male genitalia.* Tergite VIII with a neoformation/innovation of short smooth sclerotized protrusive process, emerging mesoapical from a surrounding depression. Tergite IX narrowed to a strap. Cerci large foliform and setose. Dorsal branch of paraproct strongly sclerotized and composed of closely appressed, but not fused pairs of dorsal and ventral arms both terminating in specific prongs; ventral branch of paraproct heavily sclerotized longer than the dorsal branch. Gonopods short. Both the sclerotized aedeagus and parameres short.

Etymology. *coros* from “csörös” beak in Hungarian, refers to the lateral profile of the dorsal arm of the dorsal branch of the paraproct that is bird-beak shaped.

***Homophylax flavipennis* Banks, 1900**

Material examined. **USA**, Colorado, Chaffee County, Cottonwood Pass, 11900', 29. VII.1961, leg. B. H. Poole, CNC279950 genitalia in permanent slide (1 male, CNC).

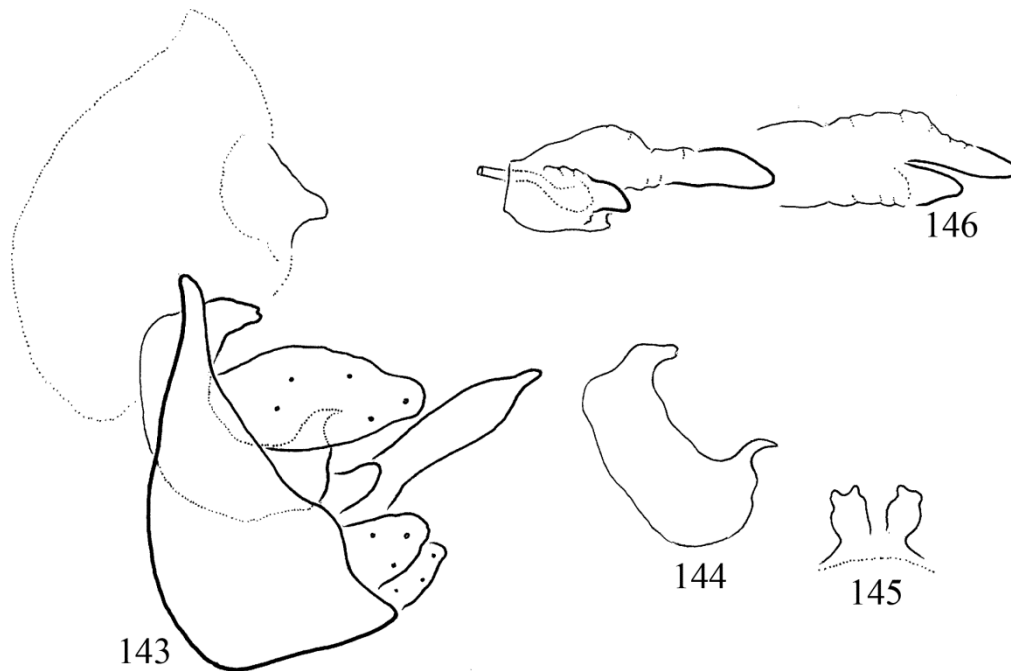
***Phanocelia* Banks, 1943**

(Figure 132)

Original differential diagnosis. No formal generic delineation is given, but emphasised that the new genus has no close relation to *Glyphopsyche*.

Relation. This is a very isolated genus in the Chlostimini tribe (Schmid 1955).

Genital character state combinations. (1) Presence (apomorphic) of spinulose protuberance on tergite VIII; (2) Produced (plesiomorphic) state of tergite IX; (3) Setose inerm (plesiomorphic) state of cerci; (4) Produced (plesiomorphic) state of the dorsal branch of paraproct; (5) Separate free from each-other (plesiomorphic) state of the



Figures 143–146. *Homophylax coros* Oláh, sp. nov. Holotype male: 143 = genitalia in left lateral view, 144 = lateral profile of the dorsal branch of the paraproct; paratype, 145 = dorsal profile of the progs on the tip of the dorsal arms: holotype
146 = phallic organ in lateral view: holotype and paratype.

dorsal branch of paraproct; (6) Separate free-from-cerci (plesiomorphic) state of the dorsal branch of paraproct; (7) Reduced (apomorphic) state of the ventral branch of paraproct; (8) Separate free from each-other (plesiomorphic) state of the ventral branches of paraproct.

Paramere. Paramere simplified into a slender spiniform slim structure. Equally thin along the entire length.

Taxonomic state. Combination of body and genital characters together with the slender thin spiniform highly simplified parameres grounds the generic status of *Phanocia*.

***Phanocelia canadensis* (Banks, 1924)**

(Figure 132)

Material examined. No specimen was available for examination. Paramere drawing was prepared from Nimmo (1971) drawings.

***Psychoglypha* Ross, 1944**

(Figure 133)

Original differential diagnosis. General body and wing venation characters are given without formal delineation.

Relation. This genus contains most of the species which have previously been placed in *Glyphopsyche*. Most specialised genus in the tribe (Schmid 1955).

Genital character state combinations. (1) Presence (apomorphic) of spinulose protuberance on tergite VIII; (2) Reduced (apomorphic) state of tergite IX; (3) Setose inerm (plesiomorphic) state of cerci; (4) Reduced (apomorphic) state of the dorsal branch of paraproct; (5) Fused to each-other (apomorphic) state of the dorsal branch of paraproct; (6) Fused-to-cerci (apomorphic) state of the dorsal branch of paraproct; (7) Produced (plesiomorphic) state of the ventral branch of

paraproct; (8) Separate free from each-other (plesiomorphic) state of the ventral branches of paraproct.

Paramere. The parameres are simplified into slender spiniform slim structure. At the examined species the very tip of the parameres represents a vestigial seta attached to the shaft-end with alveolar remnants of sutures preceded by tiny cuticular spinules.

Taxonomic state. Apomorphic states dominate the genital character combination together with the plesiomorphic produced state of the ventral branch of the paraproct and accompanied with the slender thin spiniform highly simplified parameres all these together grounds the generic status of *Psychoglypha*.

***Psychoglypha bella* Banks, 1903**

(Figures 133)

Material examined. USA, California, Orange county, Santa Ana Mts, Trabuco Canyon, Trabuco Creek 11.I.2012, 420m, N33°40.397' W117°32.484' leg. B. C. Kondratieff, D. Murányi, C.R. Nelson & J.B. Sandberg (2 males, 1 female; OPC). California, Riverside county, San Jacinto Mts, Strawberry Creek along the road No.74, 10.I.2012, 900m, N33°42.657' W116°46.157', leg. B.C. Kondratieff, D. Murányi, C.R. Nelson & J.B. Sandberg (1 male, OPC). California, San Bernardino county, San Bernardino Mts, Snow Fork along the road No.18, 9.I.2012, 2185m, N34°14.690' W117°01.663', leg. B.C. Kondratieff, D. Murányi, C.R. Nelson & J. B. Sandberg (1 male, OPC).

Chaetopterygini tribe

Following the principle of “complex is ancestral” (organised earlier: Oláh et al. 2018a) the probable ancestral structure of paramere in the Chaetopterygini tribe, like in all the other limnephiline tribes, is the rod-shaped shaft with various structures of setal origin. The authentic organisation of spiny forewing in this cool-adapted tribe is accompanied by a similar authentic organisation. This is the integration of the dominance of paramere loss in all lineages of the tribe. The

stimulatory function of the lost paramere is compensated by the enforcement of different structures on the aedeagus. Various dorsal, lateral or apical substructures have been heavily sclerotized or thick-walled on the aedeagus.

The putative ancestral lineage with spines both on the membrane and on the vein of the forewing has also the most ancestral state of paramere with sensory type of setae (*Chaetopteryx*) or with stimulatory spine-like setae (*Chaetopteroides*). There is a tendency even in these ancestral lines for the reduction of the number and size of the setal structures. In the small *Rizeiella* genus the parameres are getting more vestigial and all the other genera of this lineage with spiny membrane and veins have lost the parameres and the enforced heavily sclerotized structures on the aedeagus dominates the copulatory function (*Kelgena*, *Badukiella*, *Chaetopterygopsis*, *Annitella*).

The derived lineage with spines only on the veins of the forewing is represented only by the *Psilopteryx* and the monobasic *Pseudopsilopteryx* genera. The paramere organisation processes is realised by the same genetic arsenal like in the ancestral lineages, but with a more robust and rapid integration. The tendency for the reduction of the number and size of the setal structures is well documented in the *Psilopteryx psorosa* species group (Oláh et al. 2015). In other representatives of the *Psiloptera* genus there is a transformation series of the paramere loss. *P. curvica-vatus* and *P. bosniacus* still function with an almost intact parameres and there is reduced number of apical setal structures (spinules). *P. montanus* still retained massive but very much abbreviated parameres and *P. turcicus*, *Pseudopsilopteryx zimmeri* have lost the parameres completely.

***Annitella* Klapálek, 1907**

(Figures 152)

Original differential diagnosis. No formal delineation is given, similarity to *Chaetopterygopsis* is mentioned.

Relation. Relation to *Chaetopterygopsis* has been confirmed (Schmid 1955).

Genital character state combinations. (1) Presence (apomorphic) of spinulose protuberance and particular neoformation on tergite VIII; (2) Reduced (apomorphic) state of tergite IX; (3) Setose inerm (plesiomorphic) state of cerci; (4) Produced (plesiomorphic) state of the dorsal branch of paraproct; (5) Separate free from each-other (plesiomorphic) state of the dorsal branch of paraproct; (6) Separate free-from-cerci (plesiomorphic) state of the dorsal branch of paraproct; (7) Reduced (apomorphic) state of the ventral branch of paraproct; (8)) Separate free from each-other (plesiomorphic) state of the ventral branches of paraproct.

Paramere. The parameres have been lost.

***Annitella kosciuszki* Klapálek, 1907**

(Figure 152)

Material examined. **Romania**, Maramures county, Rodna Mts. Borsa-Statiunea Borsa, stream along the road towards Prislop Pass, 1014 m, N47°37'34.0'' E24°49'13.0'', 26.IX.2006 leg. L. Dányi, J. Kotschán, D. Murányi, (1♂ HNHM). Rodna Mts. small spring streamlets on the Bistrita Aurie spring area, N47°34'23.8'' E24°48'43.9'', 1654m, 28. IX. 2014, leg. J. Oláh & Cs. Balogh (1 male, OPC). Rodna Mts. Complex Borsa, small side spring stream of Fantana Stream, 29. IX. 2014, leg. J. Oláh & Cs. Balogh (1 male, 1 female; OPC). **Ukraine**, original label: "Chomiak, Blotek, 13.X.1907, leg. Lesmitz" (1 male, Klapalek's Collection in NMPC: No. 14).

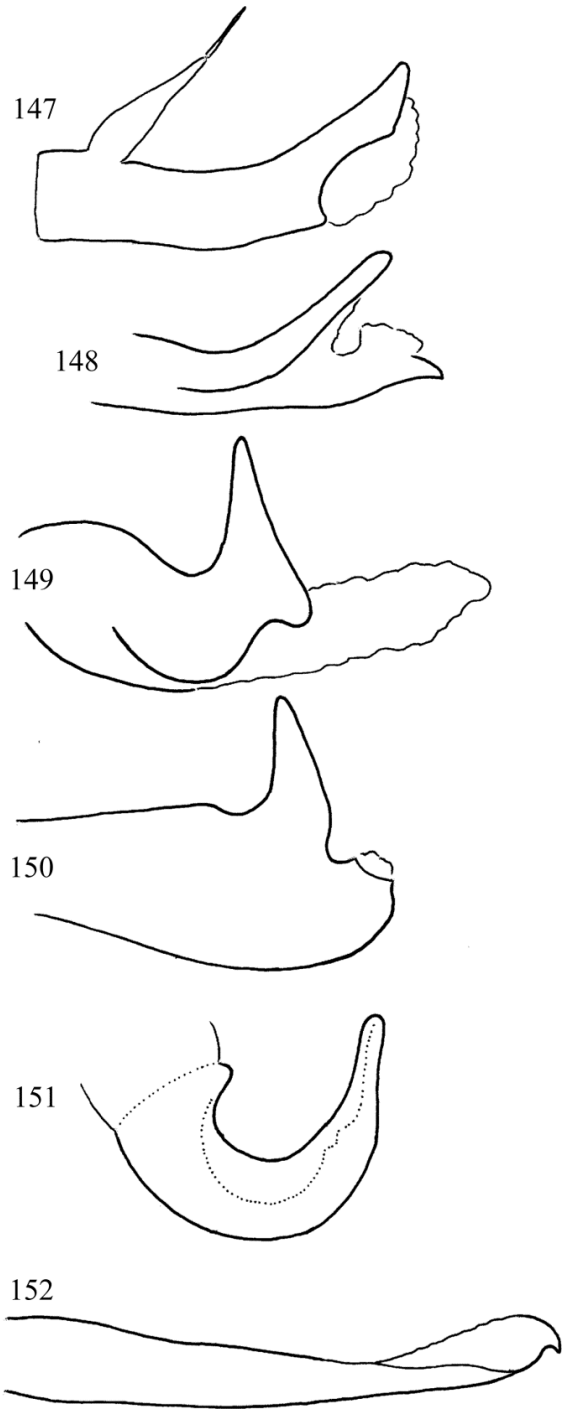
***Badukiella* Mey & Müller, 1979**

(Figure 149–150)

Original differential diagnosis. No formal delineation is given.

Relation. Relation to the unknown male of *Psilopterna* Martynov has to be examined (Mey & Müller 1979).

Genital character state combinations. (1) Absence (plesiomorphic) of spinulose protuberance and particular neoformation on tergite VIII; (2) Reduced (apomorphic) state of tergite IX; (3)



Figures 147–152. Parameres of *Rizeiella*, *Kelgena*, *Badukiella*, *Chaetopterygopsis* and *Annitella* genera. 147 = *Rizeiella anatolica*, 148 = *Kelgena minima*, 149 = *Badukiella prohibita*, 150 = *Badukiella subnigra*, 151 = *Chaetopterygopsis mclachlani*, 152 = *Annitella kosciuszki*.

Setose inerm (plesiomorphic) state of cerci; (4) Produced (plesiomorphic) state of the dorsal branch of paraproct; (5) Separate free from each-other (plesiomorphic) state of the dorsal branch of paraproct; (6) Separate free-from-cerci (plesiomorphic) state of the dorsal branch of paraproct; (7) Reduced (apomorphic) state of the ventral branch of paraproct; (8)) Separate free from each-other (plesiomorphic) state of the ventral branches of paraproct.

Paramere. The parameres have been lost.

***Badukiella prohibita* Mey & Müller, 1979**

(Figure 149)

Material examined. Paratype: Baduk, Teberda, West Caucasus, 13.X.1978, leg. W. Mey & A. Müller (1 male, MNG).

***Badukiella subnigra* Oláh, 1985 stat. restit.**

(Figure 150)

Badukiella subnigra Oláh, 1985:150–151, “This species is very close to the only known species of this genus *B. prohibita* Mey et Müller. There are, however, well-defined differences in the structure of the genitalia. The parameres have no heel-like ventral corner which is so visible on the drawing by Mey and Müller. The aedeagus is very short and not so membranous, retractable and long as in *B. prohibita*. In apical aspect the upward directed parameres are robust not tapering and not curving outwards so much as the more slender parameres in *B. prohibita*. Inferior appendages produce only one well-defined apex.”

Badukiella prohibita Mey & Müller, 1979: Malicky 2005:572, synonymised *B. subnigra* with *B. prohibita* without any justification or explanation.

Material examined. Holotype: **Georgia**, Caucasus, Yugo-Osetinskaya A.O., Vaneli Mountain with a peak of 3196 m, northwest of the capital Tbilisi and south of the chains of Great Caucasus, valey of River Liahvi, 23.X.1956, leg. Gorodkov (1 male, ZIL).

Remarks. We have re-examined and compared the aedeagus and its speciation trait component of

the strongly enlarged and heavily sclerotized pairs of dorsal process and it was clearly diverged. Here we reinstate its species status.

***Chaetopteroides* Kumanski, 1987**

Original differential diagnosis. No formal delineation is given.

Relation. Relation both to the Chaetopterygini and Stenophilacini tribes is discussed by Kumanski (1987).

Genital character state combinations. (1) Presence (apomorphic) of spinulose protuberance on tergite VIII; (2) Reduced (apomorphic) state of tergite IX; (3) Setose inerm (plesiomorphic) state of cerci; (4) Produced (plesiomorphic) state of the dorsal branch of paraproct; (5) Separate free from each-other (plesiomorphic) state of the dorsal branch of paraproct; (6) Separate free-from-cerci (plesiomorphic) state of the dorsal branch of paraproct; (7) Reduced (apomorphic) state of the ventral branch of paraproct; (8) Fused to each-other (apomorphic) state of the ventral branches of paraproct.

Paramere. The parameres form a simple digitiform structure with variously developed and patterned short spine-like modified apical setae.

Taxonomic state. A unique state is characterized by the reduced ventral branches of paraproct fused ventrally forming an almost complete sclerotized ring around the anal opening.

Species delineation. This small genus of rather rare or uncommon and difficult to collect autumn flying caddisflies has attracted our attention due to their contemporary speciation processes producing ongoing segregations in sky islands of the isolated mountain ranges. Our revision (Oláh et al. 2013) was based on a limited number of specimens, but we have detected even without population samples of larger number of specimens subtle, but stable divergences in the fine structure of the stimulatory/titillating organ of parameres. Following the genus revision, we have carried out very significant collecting program during six years between 2013 and 2018 in order to have

population samples with higher number of both the male and females specimens (see the collectors in the examined materials!). Examining the newly collected samples we have delineated two more new species based on the divergences in the setose pattern of the paramere as well as on the fine structure divergences of the female sensory area on the ventrum of the anal tube. There seems to be present a parallel direct/indirect sexual integration between the male stimulatory parameres and the female sensory setose area. Examining the available samples we have recorded these adaptive fine structures more stable than the neutral, non-adaptive periphallallic organs of cerci, paraproct and gonopods.

Distribution. During our intensive sampling program carried out by a large team of collectors we have monitored also the negative collecting effort to outline the distributional area of this small genus. In spite of the intensive and repeated sampling activities there was not any specimens collected in several mountain ranges in Montenegro and in Albania. We have recorded *Chaetopteroides* specimens in the following area: *Chaetopteroides maximus* (Kumanski, 1968): Vitosha Mt., Bulgaria; *C. bulgaricus* (Kumanski, 1969): Pirin Mts., Bulgaria; *C. kosovarorum* Ibrahimi & Oláh, 2013: described from the Kosovo territory of the Kopaonik Mts., Kosovo; *C. plackovicensis* Oláh & Ibrahimi sp. nov.: Plackovica Mts., Macedonia; *C. rilaensis* Oláh sp. nov.: Rila Mts., Bulgaria; *C. tunik* Oláh, 2013: Kožuf Mts. Macedonia; *C. veges* Oláh, 2013: Osogovska Mts., Bulgaria.

Lineage ancestry. Based upon the commonality, generality and locality ranking principles *Chaetopteroides kosovarorum* seems to have the most probable ancestral state in the genus. It has the largest distributional area covering several mountain ranges in Serbia, Kosovo and Macedonia. The distribution of the other six species is very isolated. They are restricted to a single mountain range. The locality character state of *C. kosovarorum* is accompanied with the character combination of the sexually adapted speciation traits of slender paramere with serrated apex and

of the fused, not divided sensory area on the ventrum of the female anal tube. The probable divergences of these traits are produced in the direction of paramere thickening and of the subdivision of the sensory area. Interestingly, the paramere tree and the sensory area tree are incongruent with our species tree. However, this is not surprising, and no way an exception, but rather a rule due to the principal functioning pattern of speciation processes through the chimeric working nature of the integrative organisation.

***Chaetopteroides bulgaricus* (Kumanski, 1969)**

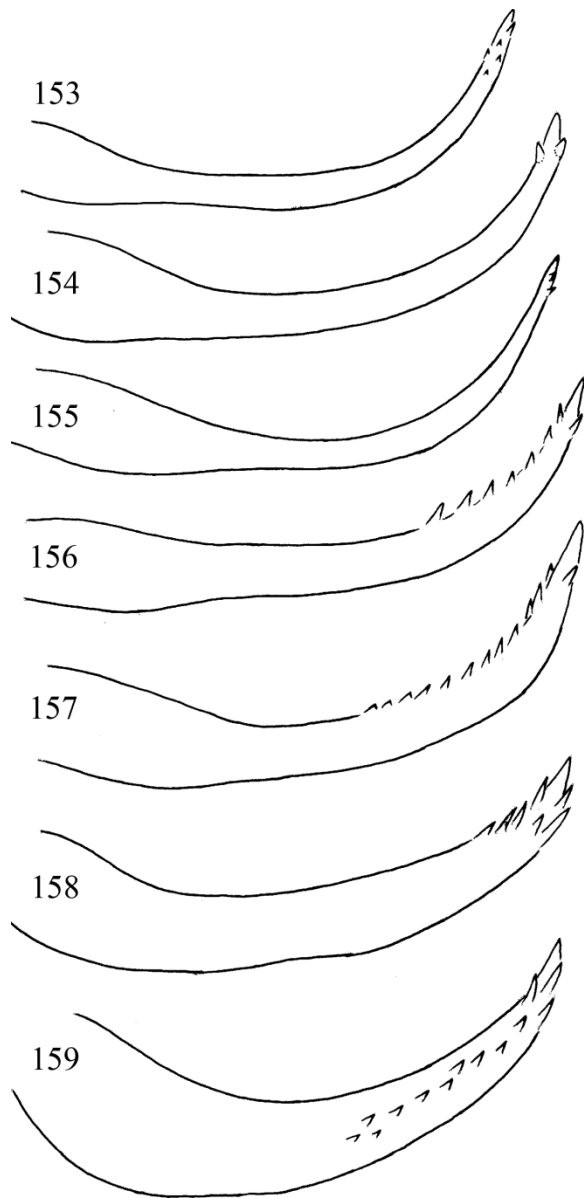
(Figures 158, 164)

Material examined. Paratypes: **Bulgaria**, Pirin Mts., Banderitza Valley, outflow of Muratowi lake (glacial environment), 2200 m, 10.X.1967, leg. K. Kumanski (1male, 2 females; NMNHS). Pirin Mts. 950 m S of Demianitsa hut, left side brook of Valyavitsa stream, N41°44'02.6" E23°28'03.1", 2020 m, 07.10.2011, leg. Á. Ecsedi, T. Kovács & G. Puskás, (1♂, 6♀, OPC). Pirin Mts. 1.5 km E of Begovitsa hut, Begovitsa stream, N41°40'32.6" E23°26'38.8", 1930 m, 08.10.2011, leg. Á. Ecsedi, T. Kovács & G. Puskás (1♂, OPC). Blagoevgrad province, Pirin Mts, Bansko, stream in pine shrub above the Vihren hut, N41°45.293' E23°24.933', 1995m, 24.X.2013, leg. J. Kontschán, D. Murányi & T. Szederjesi, (1 male, HNHM).

***Chaetopteroides kosovarorum* Ibrahimi & Oláh, 2013**

(Figures 153, 160)

Material examined. Pratype: **Kosovo**, Mitrovicë Municipality, Bajgorë area, entrance into the Kaçandoll village from Mitrovicë side, sidespring of the Kaçandoll River by the main road, N42.979° E21.0509°, 1262 m, 25.X.2013 leg. H. Ibrahimi (1 male, OPC). Dëbëlldëh, N42.25454°, E21.40008°, 982m, 22.X.2014, UV light, leg. H. Ibrahimi, A. Bilalli, M. Musliu (2 males, OPC). Bajgorë, N42.979° E21.0509°, 1262 m, 21.X.2018, leg. H. Ibrahimi (4 males, OPC). Bajgorë, N42.979° E21.0509°, 1262 m, 11.X.2016, leg. H.



Figures 153–159. Parameres of *Chaetopteroides* species. 153 = *Chaetopteroides kosovarorum*, 154 = *C. veges*, 155 = *C. tunik*, 156 = *C. maximus*, 157 = *C. plackovicensis* sp. nov., 158 = *C. bulgaricus*, 159 = *C. rilaensis* sp. nov.

Ibrahimi (1 female, OPC). **Macedonia**, Brodec III, N42.160165°, E21.448974°, 1400 m, 15.X.2017, UV light, (3 males, OPC). Macedonia, Tanushë, N42.23356°, E21.42733°, 1358 m, 21.IX.2016, netting, leg. H. Ibrahimi, A. Bilalli, M. Musliu (1 female, OPC). Tanushë, N42.23356°, E21.42733°, 1358 m, 25.IX.2016, netting, leg. H. Ibrahimi, A. Bilalli, M. Musliu (2 males, 2 females; OPC).

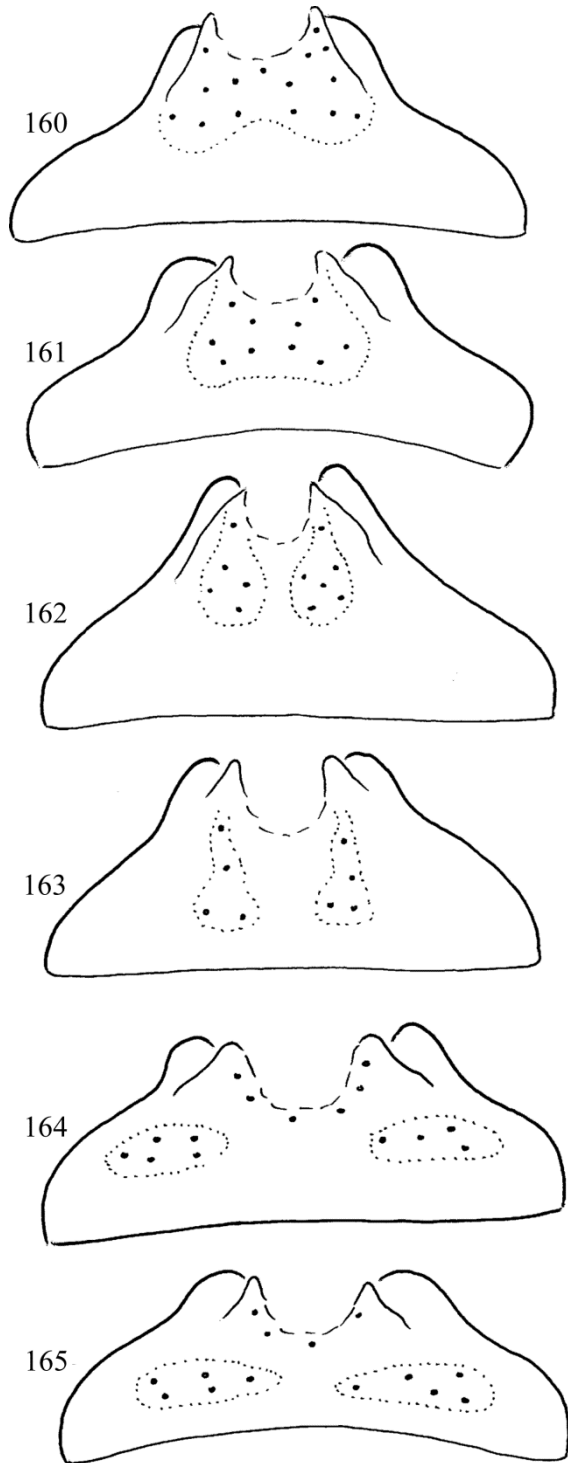
Macedonia, Tanushë, N42.23356°, E21.42733°, 1358 m, 15.X.2017, UV lightg (4 males, OPC). Tanushë, N42.23356°, E21.42733°, 1358 m, 15.X.2017, leg. H. Ibrahimi, A. Bilalli, M. Musliu (2 males, OPC). **Serbia**, Metodje Kopaonik, N43.293670°, E20.854149°, 25.X.2016, leg. A. Bilalli, M. Musliu (1 male, OPC). Metodje Kopaonik, N43.293670°, E20.854149°, 25.X.2018, leg. A. Bilalli, M. Musliu (3 males, OPC). Vlasina Reka, N43.40256°, E21.38337°, 842 m, 13.XI.2016, leg. A. Bilalli, M. Musliu (1 male, OPC). Vlasina Reka, N43.40256°, E21.38337°, 842 m, 8.XI.2016, leg. A. Bilalli, M. Musliu (1 male, OPC). Majorova Cesma, Jastrebac, 21.XI.2016, leg. A. Bilalli (2 males, OPC). Majorova Cesma, Jastrebac, 15.IX.2016, leg. A. Bilalli (6 males, 1 female; OPC).

Female description. Female (in alcohol). Forewing 16 mm. Body and wing colour yellowish stramineous in the alcohol. Forewing broad slightly abbreviated without discernible spots; forewing veins strong, erect spines present both on forewing membrane and veins. Anal tube with distinct dorsolateral setose lobe. Ventral sensory setose surface wide, undivided. Slerite IX with rounded apical margin. Vulvar scale hooked in lateral view and the median lobe short triangular in ventral view.

***Chaetopteroides maximus* (Kumanski, 1968)**

(Figures 156, 162)

Material examined. **Bulgaria**, Vitosha Mt. Zlatni mostove, tourist home Rodina, 1300–1600 m, 19.X.1968, leg. K. Kumanski (2 males, NMNHS). Vitosha Mt. Zlatni mostove, tourist home Rodina, 1300–1600 m, 9.X.1974, leg. K. Kumanski (1 female, NMNHS). Vitosha Mt. Zlatni mostove, tourist home Rodina, 1300–1600 m, 8.X.1981, leg. K. Kumanski (2 males, NMNHS). Vitosha Mts. spring and brook 200 m E of Rodina hut, N42°37'09.6", E23°15'32.3", 1600 m, 3.X.2011, light leg. Á. Ecsedi, T. Kovács, G. Puskás, (4♀, OPC). Vitosha Mts. Lavchemo, Boyanska Reka, N42°34'34.6" E23°16'57.7", 2050 m, 4.X.2011, leg. Á. Ecsedi, T. Kovács, G. Puskás, (2♂, 4♀, OPC).



Figures 160–165. Shape organisation of female sensory area on the ventrum of the anal tube of *Chaetopteroides* species. 160 = *Chaetopteroides kosovarorum*, 161 = *C. plackovicensis* sp. nov., 162 = *C. maximus*, 163 = *C. veges*, 164 = *C. bulgaricus*, 165 = *C. rilaensis* sp. nov.

***Chaetopteroides plackovicensis* Oláh & Ibrahimi, sp. nov.**

(Figures 157, 161, 166–168)

Material examined. Holotype: **Macedonia**, Plachkovitza Mts between Beli Kamen Hotel and Lisec Village, N41°44'41", E022°30'20", 1328m, 24.IX.2018, lamps, light traps. leg. S. Beshkov & A. Nahirnic (1male, OPC). Allotype: same as holotype (1 female, OPC). Paratypes: same as holotype (17 males, 1 female; OPC). Macedonia, Eastern region, Vinica municipality, Plačkovica Mts, Lumen (Lomija) Stream beneath Mt. Lisec, N41°45.858' E22°30.995', 1170 m, 5.X.2017, leg. P. Juhász, T. Kovács & D. Murányi (1 female, OPC). Macedonia, Southeastern region, Radoviš municipality, Plačkovica Mts, forest brook beneath Beli Kamen resorts, N41°44.672' E22°30.356', 1335 m, 5.X.2017, leg. P. Juhász, T. Kovács & D. Murányi (1 female, OPC).

Diagnosis. This large sized species with narrow and long male forewing and with brachypterous female forewing having a combination of broad-based triangular gonopods, downward directed cerci and robust parameres is more similar to *C. maximus*, but differs by having male with spine-like modified paramere setae present in almost doubled number occupying the apical half of the dorsum of paramere shaft. Differs in female by having the setal sensory surface on the ventrum of the anal tube fused, not subdivided by a bare mesal region.

Description. Male (in alcohol). Forewing 22 mm. Body and wing colour faded stramineous. Forewing narrow and long with erected setae present both on veins and membrane, pattern is irregular light-spotted. Similarly to *C. maximus* cerci downward directed, accessory process on the ventral branch of paraproct long, gonopods broad-based triangular. Parameres robust, apical half of the dorsum with short peg-like modified setae.

Female (in alcohol). Forewing 14 mm. Body and wing colour stramineous. Forewing broad and abbreviated, less discernible spots irregularly fused. Anal tube with long dorsolateral setose

lobe, ventral setose surface undivided. Slerite IX subquadratic. Vulvar scale hooked in lateral view and the median lobe broad triangular.

Etymology. Named for the mountain range of type locality.

***Chaetopteroides rilaensis* Oláh, sp. nov.**

(Figures 159, 165, 169–171)

Material examined. Holotype: **Bulgaria**, Rila Mts, Belmeken Diistr, Kazanishka, Reka River, N42.113379°, E23.611974°, 2157 m, 22.IX.2018, leg. J. Kecskés (1 male, OPC). Allotype: Bulgaria, Rila Mts. Borovets, Zavrachitsa hut, Prava Maritsa, N42°10'04.9", E23°38'28.1", 2200 m, 5.X.2011, leg. Á. Ecsedi, T. Kovács & G. Puskás, (1♀, OPC). Paratypes: Rila Mts. Beli Iskar, 1900 m, 23. VIII. 1971, leg. Braasch, (1 male, 1 female; OPC).

Diagnosis. This large sized species with narrow and long male forewing and with brachypterous female forewing having a combination of broad-based elongated tapering gonopods, stalked and rounded cerci and robust parameres is more similar to *C. bulgaricus*, but differs by having (1) male with spine-like modified paramere setae present in almost tripled number occupying the apical lateral half of paramere shaft; (2) the small setose lobe of cerci shifted mesad to paraproct basement present, that is lacking in *C. bulgaricus*. Differs in female by having the subdivided setal sensory surface on the ventrum of the anal tube more close mesad.

Description. Male (in alcohol). Forewing 24 mm. Body and wing colour brown. Forewing narrow and long with erected setae present both on veins and membrane, pattern is clearly light-spotted on the freshly collected holotype. Similarly to *C. bulgaricus* cerci rounded, accessory process on the ventral branch of paraproct medium-sized, gonopods long and tapering. Parameres robust, apical lateral half of the shaft with short peg-like modified setae.

Female (in alcohol). Forewing 14 mm. Body and wing brown. Forewing broad and abbreviated,

with less discernible spots. Anal tube with long dorsolateral setose lobe, ventral setose surface subdivided. Slerite IX subtriangular. Vulvar scale hooked in lateral view and the median lobe broad lobe.

Etymology. Named for the mountain range of type locality.

***Chaetopteroides tunik* Oláh & Kovács, 2013**

(Figure 155)

Material examined. Holotype: **Macedonia**, Vardar region, Kožuf Mts, lake and open brook in alpine grassland towards Ski Kožuf, N41°12.560' E22°13.170', 1670m, 4.X.2013 leg. T. Kovács, D. Murányi, (1 male, OPC).

***Chaetopteroides veges* Oláh, 2013**

(Figures 154, 163)

Material examined. Holotype: **Bulgaria**, Kyustendil province, Osogovska planina, spruce forest, forest brook below Trite buki hut, 1520m, N42°10.463' E22°38.066', 23.X.2013 leg. J. Kontschán, D. Murányi, T. Szederjesi, (1 male, HNHM). Allotype: same as holotype (1 female, HNHM). Paratypes: Same as holotype (1 female, HNHM). Kyustendil province, Osogovska planina, beech forest and forest brook at Igljika hut, 1325m, N42°13.783' E22°38.842', 23.X.2013, leg. J. Kontschán, D. Murányi, T. Szederjesi, (1 female, HNHM).

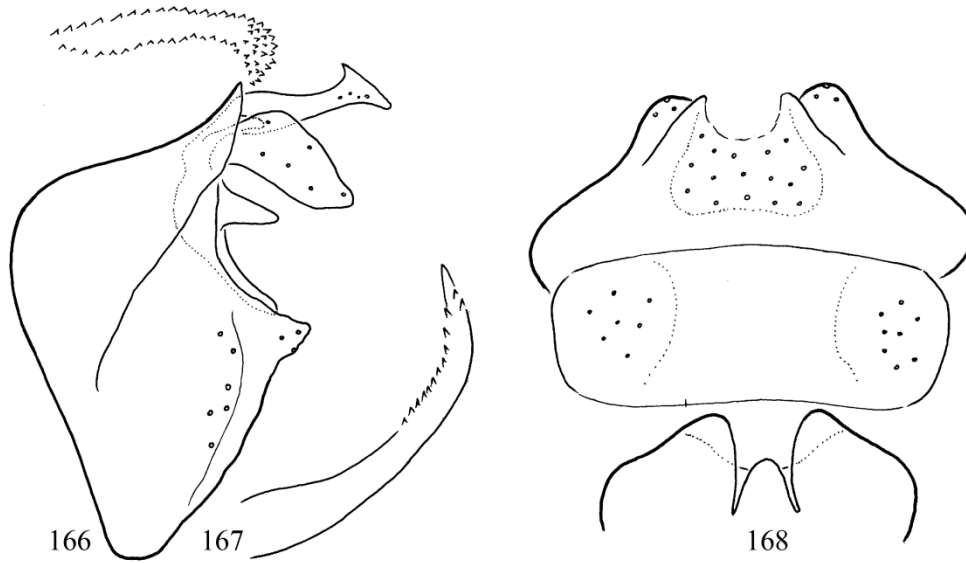
New material. Bulgaria, Ossogovo Mts below Ruen (=Autotransport) chalet, above Kyustendil town 1505m., N42°10'28", E022°37'56.5", 23.IX. 2018, at lamps, light traps, leg. S. Beshkov & A. Nahirnic (9 males, 1 female; OPC).

***Chaetopterygopsis* Stein, 1874**

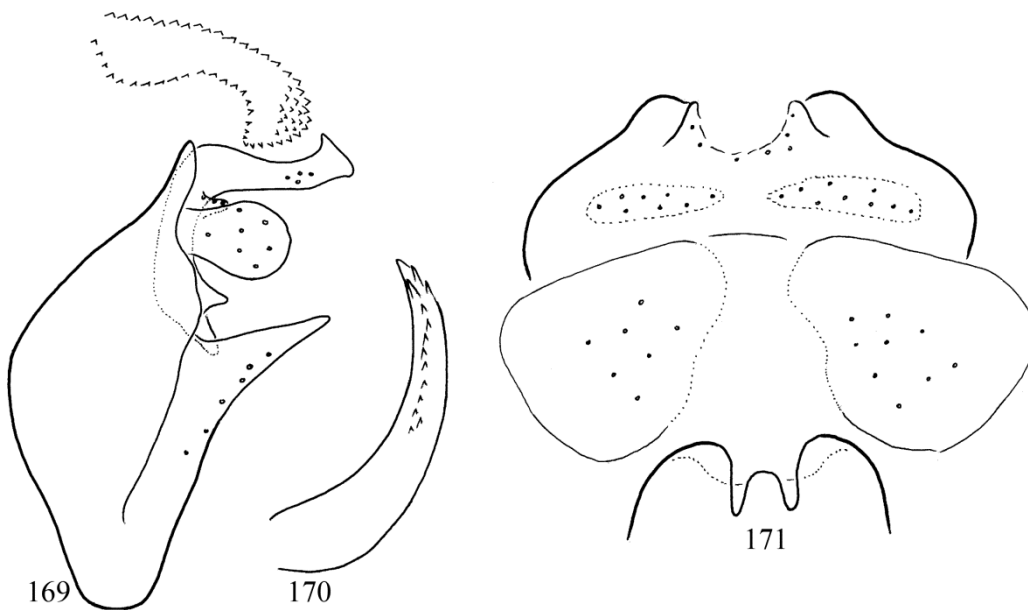
(Figure 151)

Original differential diagnosis. No formal delineation is given.

Relation. Intermediate between *Chaetopteryx* and *Annitella* (Schmid, 1955).



Figures 166–168. *Chaetopteroides plackovicensis* Oláh & Ibrahim, sp. nov. Holotype male: 166 = genitalia in left lateral view, 167 = paramere in lateral view, 168 = female genitalia in ventral view.



Figures 169–171. *Chaetopteroides rilaensis* Oláh, sp. nov. Holotype male: 169 = genitalia in left lateral view, 170 = paramere in lateral view, 171 = female genitalia in ventral view.

Genital character state combinations. (1) Presence (apomorphic) of spinulose protuberance and particular neof ormation on tergite VIII; (2) Reduced (apomorphic) state of tergite IX; (3) Setose inerm (plesiomorphic) state of cerci; (4) Produced (plesiomorphic) state of the dorsal branch of

paraproct; (5) Separate free from each-other (plesiomorphic) state of the dorsal branch of paraproct; (6) Separate free-from-cerci (plesiomorphic) state of the dorsal branch of paraproct; (7) Reduced (apomorphic) state of the ventral branch of paraproct; (8) Separate free from each-other

(plesiomorphic) state of the ventral branches of paraproct.

Paramere. The parameres have been lost.

***Chaetopterygopsis maclachlani* Stein, 1874**

(Figure 151)

Material examined. **Romania:** Apuseni Mts, Padis, open stream near pine forested sphagnum bog, N46°35'20.632" E22°45'54.857", 5.XI. 2011, leg. Gy. Monori, J. Oláh & L. Szél (6♂,5♀, OPC). Apuseni Mts, Stâna de Vale, open small stream, N46° 41'20.004" E22°37'29.2627", 6.XI. 2011, leg. Gy. Monori, J. Oláh & L. Szél (2♂, OPC).

***Chaetopteryx* Stephens, 1837**

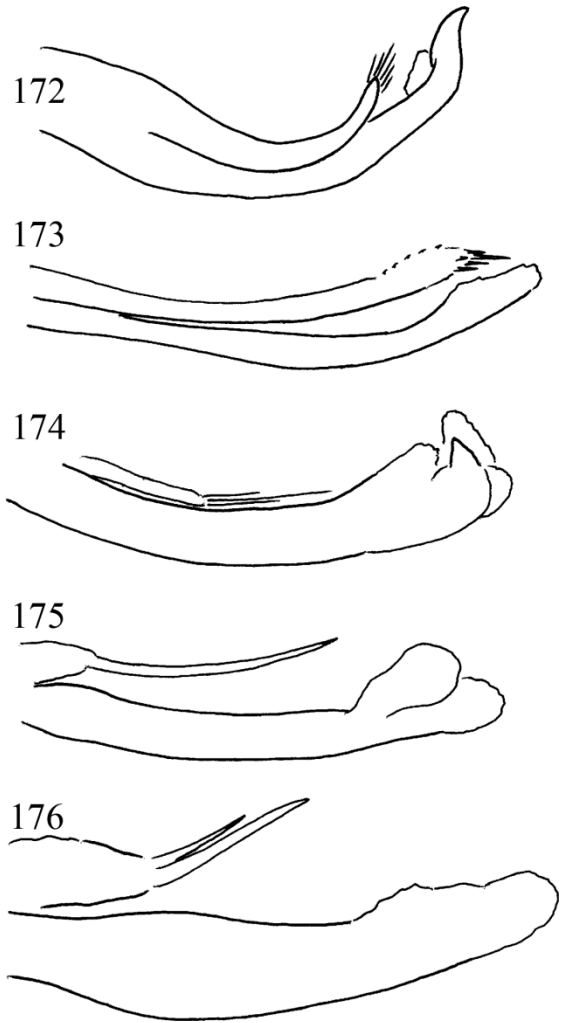
(Figures 172–176)

Original differential diagnosis. No formal delineation is given.

Relation. A central genus in the Chaetopterygini tribe (Schmid 1955).

Genital character state combinations. (1) Presence (apomorphic) of spinulose protuberance on tergite VIII; (2) Reduced (apomorphic) state of tergite IX; (3) Setose inerm (plesiomorphic) state of cerci; (4) Produced (plesiomorphic) state of the dorsal branch of paraproct; (5) Separate free from each-other (plesiomorphic) state of the dorsal branch of paraproct; (6) Separate free-from-cerci (plesiomorphic) state of the dorsal branch of paraproct; (7) Reduced (apomorphic) state of the ventral branch of paraproct; (8) Separate free from each-other (plesiomorphic) state of the ventral branches of paraproct.

Paramere. The parameres form a simple structure with variously long paramere shaft and with variously developed and patterned subapical and apical setae. *Chaetopteryx moretii* has lost its paramere.



Figures 172–176. Parameres of *Chaetopteryx* species. 172 = *Chaetopteryx lusitanica*, 173 = *C. biloba*, 174 = *C. aproka*, 175 = *C. goricensis*, 176 = *C. balcanica*.

***Chaetopteryx aproka* Oláh, 2011**

(Figure 174)

Material examined. Holotype: **Romania**, Maramures county, Muntii Ignis, Desesti, Statiunea Izvoare, open brook with spring bog on the Valhani Plateau, 1020m, N47°43'01.0" E23°44'32.1", 24.09.2005, leg. J. Kotschán, D. Murányi, J. Nédli (1♂ NHMB).

***Chaetopteryx balcanica* Oláh, 2015**

(Figure 176)

Material examined. Holotype: **Serbia**, Derdap Mts. Donji Milanovac, Grgeci spring and its outlet in a beech forest, 500 m, N44°28' E22°02', 13.X.2006, leg. L. Dányi, J. Kontschán & D. Murányi (1 male, in copula with the allotype, HNHM).

***Chaetopteryx biloba* Botosaneanu, 1960**

(Figure 173)

Material examined. **Romania**, Apuseni Mts, Padis N. P. Varasoia, open stream, N46° 36' 31.122 E22° 42' 48.294, 5.XI.2011, leg. Gy. Monori, J. Oláh & L. Szél (1♂, OPC).

***Chaetopteryx goricensis* Malicky & Krusnik, 1986**

(Figure 175)

Material examined. **Slovenia**, Ajdovscina, Predmeja, one spring of Lokavscek stream, 695m, N45°56'21.8", E13°52'17.8", 06.XII.2009, leg. A. Déry & I. Szivák (10♂, OPC).

***Chaetopteryx lusitanica* Malicky, 1974**

(Figure 172)

Material examined. **Portugal**, Albergaria do Gerês, Serra do Gerês, Portugal, 20.XII.1977 leg. L. Terra (3 males, present from Marcos A. Gonzalez, OPC).

***Kelgena* Mey, 1979**

(Figures 148)

Original differential diagnosis. No formal delineation is given.

Relation. Based on paramere organisation this genus has a most probable relation to the *Chaetopteryx* genus (Mey 1979).

Genital character state combinations. (1) Presence (apomorphic) of spinulose protuberance on tergite VIII; (2) Reduced (apomorphic) state of tergite IX; (3) Setose inerm (plesiomorphic) state of cerci; (4) Produced (plesiomorphic) state of the dorsal branch of paraproct; (5) Fused to each-other (apomorphic) state of the dorsal branch of paraproct; (6) Free-from-cerci (plesiomorphic) state of the dorsal branch of paraproct; (7) Reduced (apomorphic) state of the ventral branch of paraproct; (8) Separate free from each-other (plesiomorphic) state of the ventral branches of paraproct.

Paramere. The parameres have been lost.

***Kelgena minima* Mey & Müller, 1979**

(Figure 148)

Material examined. Paratype: West Caucasus, Teberda, Small Baduk Lake, 13.X.1978, leg. W. Mey & A. Müller (1 male, MNG).

***Rizeiella* Sipahiler, 1986**

(Figures 147)

Material examined. No specimen was available for direct examination. However, detailed well presented and interpreted drawings permitted the presentation of the character state combination of this genus.

Original differential diagnosis. No formal delineation is given.

Relation. Has relation to *Chaetopteryx*, *Kelgena* and *Psilopteryx* (Sipahiler 1986).

Genital character state combinations. (1) Presence (apomorphic) of spinulose protuberance on tergite VIII; (2) Reduced (apomorphic) state of tergite IX; (3) Inerm setose (plesiomorphic) state of cerci; (4) Produced (plesiomorphic) state of the dorsal branch of paraproct; (5) Separate free from each-other (plesiomorphic) state of the dorsal branch of paraproct; (6) Free-from-cerci (ple-

omorph) state of the dorsal branch of paraproct; (7) Reduced (apomorphic) state of the ventral branch of paraproct; (8) Separate free from each-other (plesiomorphic) state of the ventral branches of paraproct.

Paramere. The parameres are abbreviated, narrowing apicad and tipped with a bristle of setal origin.

***Pseudopsilopteryx* Stephens, 1837**

(Figure 181)

Original differential diagnosis. No formal delineation is given.

Relation. An aberrant in the tribe without parents (Schmid, 1955).

Genital character state combinations. (1) Absence (plesiomorphic) of spinulose protuberance on tergite VIII; (2) Reduced (apomorphic) state of tergite IX; (3) More sclerotized (apomorphic) state of cerci; (4) Produced (plesiomorphic) state of the dorsal branch of paraproct; (5) Separate free from each-other (plesiomorphic) state of the dorsal branch of paraproct; (6) Free-from-cerci (plesiomorphic) state of the dorsal branch of paraproct; (7) Produced (apomorphic) state of the ventral branch of paraproct; (8) Separate free from each-other (plesiomorphic) state of the ventral branches of paraproct.

Paramere. The parameres have been lost.

***Pseudopsilopteryx zimmeri* McLachlan, 1876**

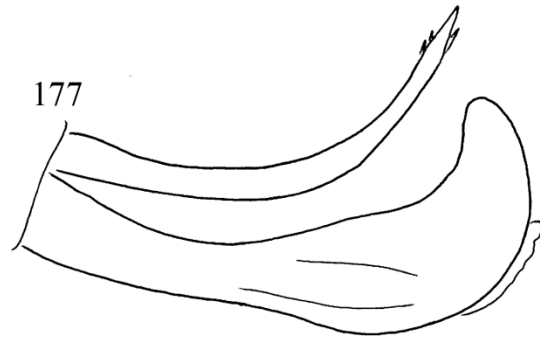
(Figure 181)

Material examined. **Slovenia**, Pohorje Mt, below Pesek, spring area of river Oplotnica, 1345m, 46°28'24,8'' 15°20'55,9'', 8.XI.2012, leg. T. Kovács, & G. Magos, (1♂,1♀, OPC).

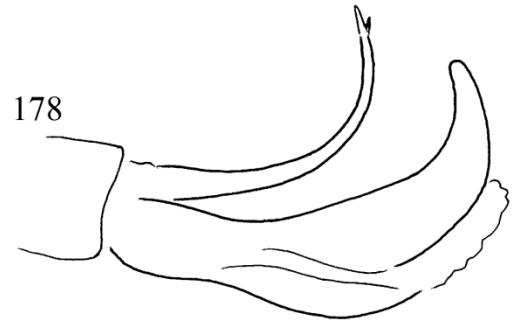
***Psilopteryx* Stein, 1874**

(Figures 177–180, 182–189)

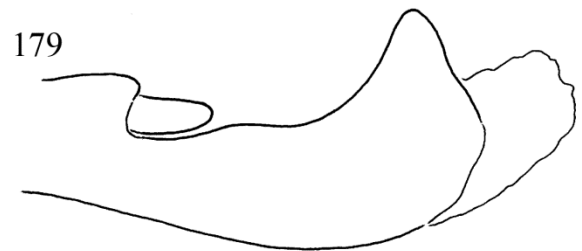
Original differential diagnosis. No formal delineation is given.



177



178



179



180



Figures 177–181. Parameres of *Psilopteryx* and *Pseudopsilopteryx* genera. 177 = *Psilopteryx curvicolavatus*, 178 = *P. bosniacus*, 179 = *P. montanus*, 180 = *P. turcicus*, 181 = *Pseudopsilopteryx zimmeri*.

Relation. No relations have been discussed (Schmid 1955).

Genital character state combinations. (1) Absence (plesiomorphic) of spinulose protuberance on tergite VIII; (2) Produced with neoformation (plesiomorphic) state of tergite IX; (3) More sclerotized (apomorphic) state of cerci; (4) Produced (plesiomorphic) state of the dorsal branch of paraproct; (5) Separate free from each-other (plesiomorphic) state of the dorsal branch of paraproct; (6) Free-from-cerci (plesiomorphic) state of the dorsal branch of paraproct; (7) Reduced (apomorphic) state of the ventral branch of paraproct; (8) Separate free from each-other (plesiomorphic) state of the ventral branches of paraproct.

Paramere. The parameres form digitiform or abbreviated structures with or without variously patterned apical and subapical short modified setae.

***Psilopteryx bosniacus* Marinkovic-Gospodnetic, 1971**

(Figure 178)

Material examined. **Bosnia**, Vares, ex ovo V. 1989, leg Malicky (1♂, 1♀; OPC present from MPC).

***Psilopteryx curvoclavatus* Botosaneanu, 1957**

(Figure 177)

Material examined. **Romania**, Apuseni Mts, Padis, small stream in pine forested sphagnum bog, N46°35'36.528" E22°45'54.751", 5.XI.2011, leg. Gy. Monori, J. Oláh & L. Szél (2♂, OPC).

***Psilopteryx montanus* Kumanski, 1968**

(Figure 179)

Material examined. **Albania**, Dibër district, Korab Mts, brook beneath Fushë Korabit, N41°49.209' E20°30.745', 1770 m, 07.10.2012, leg. P. Juhász, T. Kovács, D. Murányi, G. Puskás (12 males, 7 females; OPC).

***Psilopteryx turcicus* Sipahiler, 1983**

(Figure 180)

Material examined. No specimen was available for direct examination. However, detailed

well presented and interpreted drawings permitted the presentation of the paramere.

***Psilopteryx psorosa* species group**

(Figures 182–189)

The unique apomorphic trait of the *Psilopteryx psorosa* species group is the posterad elongated dorsal keel of segment IX. The paraproct of the superanal genitalic complex is also modified into the apomorphic state of a huge elongated and lanceolated structure. This enlarged and heavily sclerotized structure with particularly patterned surface must have a dominant copulatory function of barriers in reproductive isolation. The parameres are retained in the form of strong digitiform structure with specific curvature and apical spine pattern (Oláh et al. 2015). In gross phenomics these specific paramere divergences are usually treated as usual variations; only fine phenomics discovered their stability or complementarity. If apical spine pattern are less diverged like at *P. javorensis* and *P. carpathica* the paraproct divergences may contribute to reproductive isolation.

***Psilopteryx bohemosaxonica* Mey & Botosaneanu, 1985**

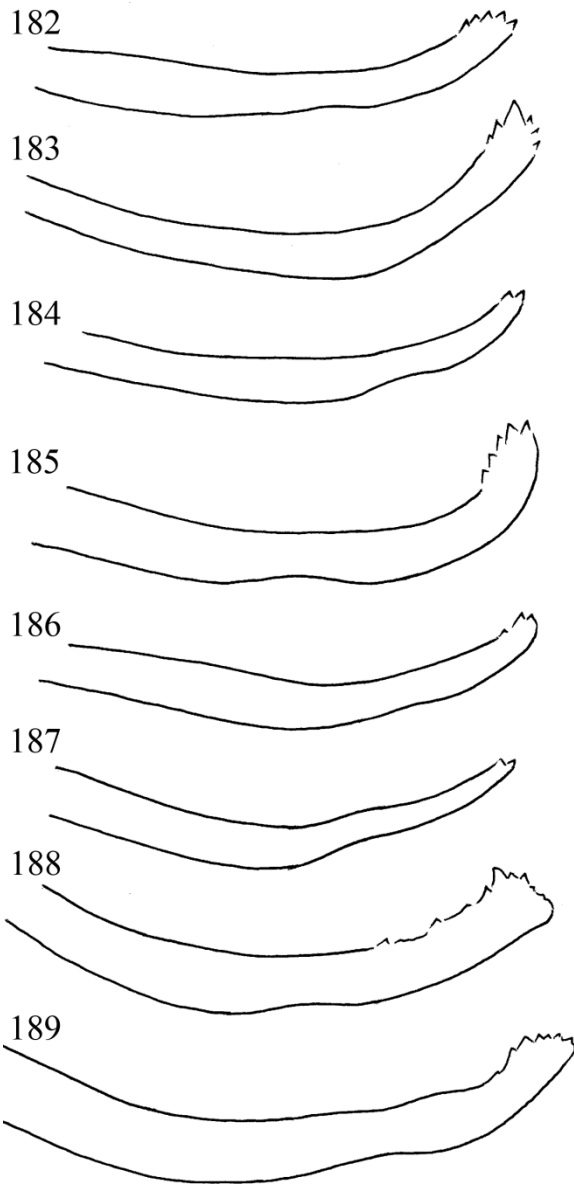
(Figure 182)

Material examined. **Slovakia**, Banskobystrický region, Poľana Mts, Hriňová, Bystré, spring brook of Bystrý Stream, N48°37.569' E19°29.261', 1025m 8.X.2013, singled leg. J. Oláh & L. Szél (1 male, 1 female; OPC).

***Psilopteryx carpathica* Schmid, 1952**

(Figure 187)

Material examined. **Romania**, Borsa, 26.IX. 1992, leg J. Oláh, (1 male, OPC). Rodnei Mts. numerous spring streamlets on the spring area of Cailor waterfall, Piatra Rea, N47°35'1.9" E24°47'49.4", 1564m, 28. IX. 2014, leg. J. Oláh & Cs. Balogh (1 male, OPC). Rodnei Mts. small spring below Lake Izvorul Bistritei, N47°34'46.4" E24°48'49.34", 1586m, 28. IX. 2014, leg. J. Oláh & Cs. Balogh (1 male, 1 female; OPC).



Figures 182–189. Parameres of *Psilopteryx psorosa* species group. 182 = *Psilopteryx bohemosaxonica*, 183 = *P. gutinensis*, 184 = *P. javorensis*, 185 = *P. harmas*, 186 = *psorosa*, 187 = *P. carpathica*, 188 = *P. retezatica*, 189 = *P. transylvanica*.

***Psilopteryx gutinensis* Mey & Botosaneanu, 1985**

(Figure 183)

Material examined. **Romania**, Maramureş County, Munţii Ignis, Deseşti-Staţiunea Izvoare,

open spring brook at settlement, 920m, N47° 45.167' E23°43.013', 22.X.2010 leg. Á. Ecsedi, J. Oláh & I. Szivák, (3 males, 1 female, OPC).

***Psilopteryx harmas* Oláh & Chvojka, 2015**

(Figure 185)

Material examined. Holotype: **Poland**, East Carpathians, Bieszczady Mts. at Wolosatka brook, 900m, 28.X.2010, leg B. Szczesny (1 male, OPC).

***Psilopteryx javorensis* Oláh & Chvojka, 2015**

(Figure 184)

Material examined. **Slovakia**, Banskobystrický region, Poľana Mts, Hriňová, sidebrook of Slatina Stream, N48°37.210' E19°31.582', 514m 8.X.2013, singled leg. J. Oláh & L. Szél (1 male, OPC).

***Psilopteryx psorosa* (Kolenati, 1860)**

(Figure 186)

Material examined. **Poland**, Right tributary of the Olczycki Potok, (Olczycki Spring), the Tatra Mts., 12.XI.1986, leg. B. Szczęsny (16 males, 5 females, OPC).

***Psilopteryx retezatica* Mey & Botosaneanu, 1985**

(Figure 188)

Material examined. **Romania**, Caraş-Severin County, Ţarcu Mts. spring and its outlet at Cuntu Meteorological Station, N45°18'00.2", E22°30' 04.3", 1465 m, 14.10.2011, leg. Á. Ecsedi, T. Kovács, G. Puskás, (19♂, 8♀, OPC).

***Psilopteryx transylvanica* Mey & Botosaneanu, 1985**

(Figure 189)

Material examined. **Romania**, Harghita Mts. Filio stream side spring, N: 46°27' 14.53" E: 25°33' 53.04", 1415m, 31.X.2014 leg. Z. Baczó, Cs. Balogh, J. Kecskés & J. Oláh. (12 males, 6 females; OPC).

Stenophylacini tribe

The basic pattern of parameres is the spiniform shaft without apical branches, lobes and without ancestral primordial sensory setae, but with variously developed or vestigial spine-like modified structures of setal origin. Spine-like structures develop in various basal, apical and between positions along the paramere shaft. The reduction of setal structures frequently occurs inside the same genus. The paramere shaft may undergo enlarging, thickening, abbreviation or could be almost lost as vestigial thread-like structure (*Hydatophylax*).

Acrophylax Brauer, 1867

(Figures 190–192)

Original differential diagnosis. Formal delineation is not given.

Relation. In the original genus description it was related to *Chaetopteryx* (Brauer 1867). This position was regarded by McLachlan (1875) as doubtful. Schmid (1951) first related it to *Stenophylax*, later (Schmid 1955) to *Potamophylax*, especially to *P. millenii*.

Genital character state combinations. (1) Presence (apomorphic) of spinulose protuberance on tergite VIII; (2) Reduced (apomorphic) state of tergite IX; (3) Setose inerm (plesiomorphic) state of cerci; (4) Produced (plesiomorphic) state of the dorsal branch of paraproct; (5) Separate free from each-other (plesiomorphic) state of the dorsal branch of paraproct; (6) Separate free-from-cerci (plesiomorphic) state of the dorsal branch of paraproct; (7) Reduced (apomorphic) state of the ventral branch of paraproct; (8) Separate free from each-other (plesiomorphic) state of the ventral branches of paraproct.

Parameres. A pair of simple spine-like spiniform rods with mesad turning apical portion; paramere apices armed with additional single or double small subapical spinules.

Remarks. We have found decisive and stable shape divergences in the organisation of the examined three species. The three species differs also by pronounced shape divergences in the lateral

and dorsal shape of the aedeagus. The variability of the periphalllic structure of the cerci, paraproct and gonopods was not examined, however the rounded head of gonopods as visible in caudal view at *A. sowai* and *A. vernalis* seems differs from the truncate gonopod head of *A. zerberus*.

Acrophylax sowai Szczesny, 2007

(Figure 190)

Material examined. **Poland**, High Tatra, Koscieliska Valley, V.–VI. leg B. Szczesny (2 males, 1 female, OPC). Poland, Babia Gora, V. 1965, leg. B. Szczesny (3 males, OPC). Poland, Gorce Mts., Komienica stream, VI-VII.1966, leg. B. Szczesny (2 male, 2 females; OPC).

Acrophylax vernalis Dzieziewicz, 1912

(Figure 191)

Material examined. **Romania**, Rodnei Mts., Lala, 6.V.2006. leg M. Bálint (2 males, OPC). Romania, Rodnei Mts., Lala, 6.V.2012. leg J. Olah (2 males, OPC).

Acrophylax zerberus Brauer, 1867

(Figure 192)

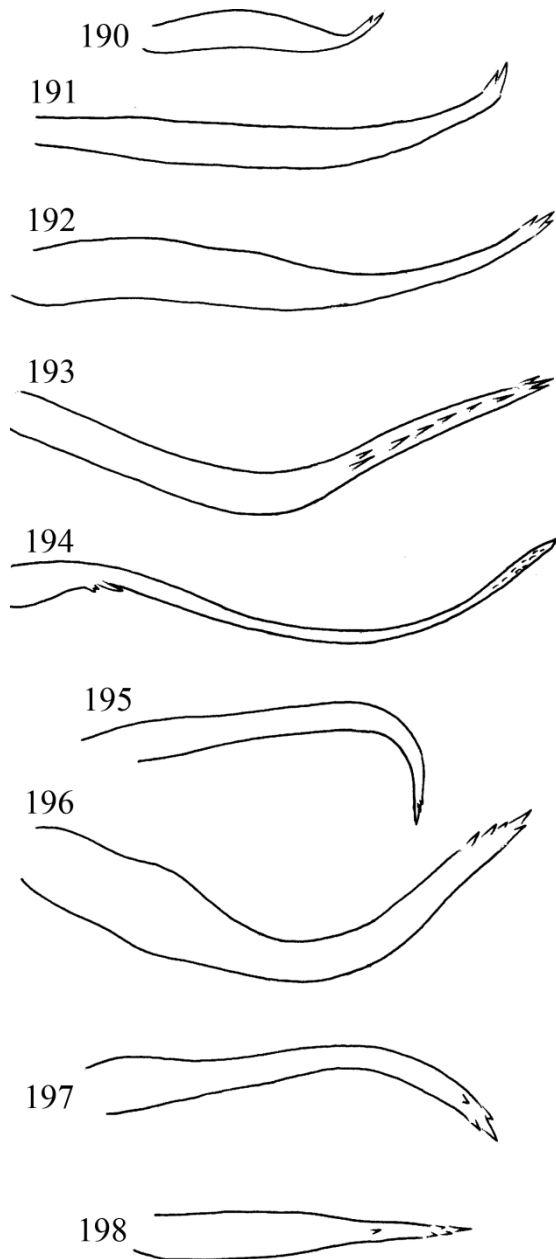
Material examined. **Poland**, Babia Gora, V. 1965, leg. B. Szczesny (6 males, 4 females; OPC). Poland. High Tatra, Chocholowska Valley, 22.VIII.1986 leg J. Oláh (8 males, OPC). Poland. High Tatra, Chocholowska Valley, Wywierzysko karstic spring, 21.VIII.2009 leg J. Oláh (5 males, OPC). **Slovakia**, Lower Tatra, Mlynica stream, 21.VII.1966, leg. J. Oláh (1 male, OPC).

Allogamus Schmid, 1955

(Figures 199–201, 202–205)

Original differential diagnosis. Formal delineation is not given.

Relation. Schmid, 1955:195, “évolué dans la même direction que *Hydatophylax* mais qui, étant moins spécialisé que ce dernier, à conservé des caractères communs avec *Potamophylax*.”



Figures 190–198. Parameres of *Acrophylax*, *Alpopsyche*, *Anisogamus* and *Chionophylax* genera. 190 = *Acrophylax so-wai*, 191 = *A. vernalis*, 192 = *A. zerberus*, 193 = *Alpopsyche ucenorum*, 194 = *Anisogamus difformis*, 195 = *Chionophylax bulgaricus*, 196 = *C. czarnohoricus*, 197 = *C. mindszentyi*, 198 = *C. monteryla*.

Genital character state combinations. (1) Presence (apomorphic) of spinulose protuberance on tergite VIII; (2) Reduced (apomorphic) state of

tergite IX; (3) Setose inerm (plesiomorphic) state of cerci; (4) Produced (plesiomorphic) state of the dorsal branch of paraproct; (5) Separate free from each-other (plesiomorphic) state of the dorsal branch of paraproct; (6) Separate free-from-cerci (plesiomorphic) state of the dorsal branch of paraproct; (7) Reduced (apomorphic) state of the ventral branch of paraproct; (8) Separate free from each-other (plesiomorphic) state of the ventral branches of paraproct.

Parameres. Oláh et al. 2014: 42: “The ancestral plesiomorphic state of the parameres is represented by a pair of rod-shaped shaft nested separately in the membranous endotheca and armed with variously developed spine-like setae. Paramere fusion is an apomorphic state of the phallic organ accompanied by a pair of apico-ventral sclerites of varying complexity on the aedeagus. This paramere evolution together with complexity evolution of aedeagus helps us to establish species groups inside the *Allogamus* genus.

The plesiomorphic state of the separated, unfused parameres characterizes the ancestral *Allogamus auricollis* species group. Further lineages inside this group have been distinguished by the location of setae on the paramere shaft and by the presence and development of the sclerites on the aedeagus. In *auricollis* group we have distinguished four species subgroups based on setal distribution on the parameres: *Allogamus ligonifer* subgroup with subequal apical spines, *A. antennatus* and *A. auricollis* subgroups with a heavily enforced single primary spinelike seta accompanied by smaller secondary spine-like setae dorsoapicad at *A. antennatus* and ventromesad at *A. auricollis* subgroups. *A. hilaris* subgroup has been separated by paramere with ventral row of setae. *Allogamus mortoni* new species complex has been distinguished in the *ligonifer* subgroup based upon the diversified apomorphic neofor-mation of the paraproctal accessory process.

In the small *Allogamus corsicus* new species group the paired parameres fused along the basal third and diverted, widely on the apical two thirds.

The *Allogamus uncatus* rediagnosed species group has basally fused and apically adhering parameres and evolved the highest complexity of aedeagus with a pair of heavily sclerotized dorsal rod-shaped processes.”

Remarks. We have tried earlier (Oláh et al. 2014) to separate siblings of incipient species among the examined populations of *Allogamus ligonifer*. Significant, currently segregating standing variations have been detected without fixation among and inside the examined populations in the shape of dorsal sclerite of the aedeagus, and of the accessory paraproctal process. Recently we have discovered populations in the Gredros Mts. of Spain with a new segregating character state of these traits. Based on this new finding here we have re-examined all of the available populations from the entire distributional area and distinguished three traits that is three character states of the dorsal sclerite and of the accessory paraproctal process, but with significant standing variations. With this high infra- and interpopulational variabilities that is without trait fixations these peripatric populations do not represent still siblings of incipient species.

***Allogamus ligonifer* (McLachlan, 1876)**

(Figures 199–201)

Material examined. Vosges (North) Region with “vosgesensis” trait. France, Vosges Department, Xonrupt Longemer, Lac de Retourner, 16.IX.2011, leg. G. Coppa (1 male, 1 female; CPC). Vosges Department, Le valtin, La meurthe en Amont de l’Etang, 4.X.2010, leg. G. Coppa (1 male, OPC). Vosges, 1883, in Klapalek’s collection (1 male, K379, NMPC). No data, in Klapalek’s collection, (1 male, K381, NMPC). Vosges, 1886, in Klapalek’s collection (1 female, K380, NMPC). Morbihan Department, Inguiniel, Sur le Sebrevet le Porz, 22.IV.20106, leg. G. Coppa (1 male, CPC).

Massif Central Region with “ligonifer” trait. France, Correze Department, Chenaillers Mascheix, Le Chambariol, 28.IX.2010, leg. G. Coppa, (1♂, 1♀, CPC). Corrèze Department, Monceau sur Dordogne, D12 le Gand Dordogne,

16.XI.1997, leg. G. Coppa (2 males, 1 female; OPC). Corrèze Department, Argentat, D5 Moulin bas Dordogne, 15.X.1995, leg. G. Coppa (5 males, OPC). Corrèze Department, Argentat, Aveyron, 31.X.2007, leg. G. Coppa (2 males, 2 females; OPC). Corrèze Department, Argentat, D9 Rive Gauche, 6.X.2012, leg. G. Coppa (1 male, 1 female; OPC). Corrèze Department, Bassignac le Bas, D21 Port de Vours, 16.X.2001, leg. G. Coppa (4 males, CPC). Corrèze Department, Bassignac le Bas, D21 Port de Vours, 11.X.2010, leg. G. Coppa (1 male, CPC). Corrèze Department, Monceaux sur Dordogne, Le Chambon, 12.XII.2010, leg. G. Coppa (1 female, CPC). Corrèze Department, Argentat, D5 Moulin bas Dordogne, 7.X.2000, leg. G. Coppa (3 males, 1 female; CPC). Corrèze Department, Argentat, D5 Moulin bas Dordogne, 29.X.1999, leg. G. Coppa (1 male, OPC). Corrèze Department, Bassignac, D24 Recoudier Dordogne, 30.X.2012, leg. G. Coppa (2 males, OPC). Corrèze Department, Argentat, Confluence de la Dordogne D9 confluence Maronne, 10.IX.2008, leg. G. Coppa (1 female, CPC). Corrèze Department, Beaulieu sur Dordogne, Dordogne Sortie Beaulieu D41 vers Milliagne, 21.X.2008, leg. G. Coppa (2 males, 2 females, CPC). Cantal Department, Murat, Sur l’Alagnon Pont du Camping, 26.X.2005, leg. G. Coppa (1 male, CPC). Puy-de-Dome Department, Besse et Saint Anastaise, Lac de Bourdouze, 7.X.2007, leg. G. Coppa (1 male, CPC). Puy-de-Dome Department, Besse et Saint Anastaise, Lac de Montcineyre, 7.IX.2007, leg. G. Coppa (1 male, 1 female; OPC). Puy-de-Dome Department, Saint Germain Lembron, Couse d’Ardes pont D909, 28.X.2005, leg. G. Coppa (1 male, CPC). Lozere Department, Meyrueis, Ru de Bethuzon, 27.X.2010, leg. G. Coppa (1 male, CPC). Lozere Department, Saint Bonnet de Chirac, Les Bories ru Romardies, 25.X.2010, leg. G. Coppa (1 male, CPC). Lozere Department, Saint Bonnet de Chirac, Les Bories Lot, 25.X.2010, leg. G. Coppa (1 female, CPC). Lozere Department, Saint Chely d’Apcher, Sur le Chapouillet Confluence avec la Truyere, 18.VIII.2011, leg. G. Coppa (1 male, CPC). Lozere Department, Altier, Cascade sur l’oultre au Niveau du Moulin, 20.VII.2003, leg. G. Coppa (1 male, OPC). Lozere Department, Co-

cures, Tarn Rive gauche Aval Confluence ru Vallongue, 2.X.2017, leg. G. Coppa (5 males, OPC). Lozere Department, Langogne, Aval Pont D392 sur l'Allier, 3.VII.2017, leg. G. Coppa (3 males, CPC). Aveyron Department, Entraygues sur Truyere, La Truyere, 1.XI.2007, leg. G. Coppa (1 female, CPC).

Pyrenean Region. France, Hérault Department, Languedoc-Roussillon, Saint-Pons-de-Thomières, around camping place, hard leaved forest, at housewalls and in grassland, 285 m, N43,49037° E2,78524°, 18.X.2009, leg. A. Schönhofer (3♂; CNSMB). Aude Department, Alet, 28.X.1989, leg. G. Coppa (4 males, OPC). Haut-Garonne Department, Galie, pas de précision, 30.IX.2006, leg. G. Coppa (1 male, CPC). Haut-Garonne Department, Galie, pas de précision, 13.X.2006, leg. G. Coppa (1 female, CPC). Pyrénées Orientales Department, Cattlar, La Tet Pont D616, 28.X.2008, leg. G. Coppa (5 males, 1 female; CPC). Pyrénées-Atlantiques Department, Montaner, pas de precision, 27.II.2006, leg. G. Coppa (1 male, CPC).

Sierra de Gredos Region with “gredosensis” trait. Spain, Sierra de Gredos, Cáceres Province, Garganta Jaranda, 614m, Tajo river basin, Tiétar river, Jarandilla de la Vera, 1.XI.2018, leg. A. Ruiz Garcia (5 males, 2 females; OPC). San Martín del Pimpollar, Ávila Province, Rio Alberche, 25.X.2017, leg. G. Coppa (1 male, 1 female; CPC).

Remarks. *Allogamus ligonifer* is characterized by unfused parameres of *Allogamus auricollis* species group, by subequal secondary apical setae on the parameres of *A. ligonifer* species subgroup and specified by upward curving subequal apical setae.

Based on the generality and distribution principles of character ranking we have distinguished three phenotypic traits of characters of the dorsal sclerite on the aedeagus. The shape of the dorsal sclerite is drawn in strict ventroperpendicular view; the dorsal sclerite is arching upward as a function of copulation history, any small deviation from this view may create confusion. Specific traits (expression of allel complex of quantitative trait loci) of the dorsal sclerite:

(1) deep and wide “ligonifer” ancestral trait of the dorsal sclerite on the aedeagus, as drawn from South France by Schmid (1951),

(2) shallow and wide “vosgesensis” derived trait of the dorsal sclerite on the aedeagus and

(3) deep and narrow “gredosensis” derived trait of the dorsal sclerite on the aedeagus.

However, besides populations with stable diverged fine structure at least in the “ligonifer” trait, there are variations detectable also inside populations. This suggests ongoing diversification in sexual integration processes both on phallic structures and on the paraproctal accessory process. There is a real possibility also for reinforcement processes in contact populations under the influence of gene flow by immigrants. In this case there are pure populations, not discovered yet, with “vosgensis” and “gredosensis” traits representing siblings of incipient species.

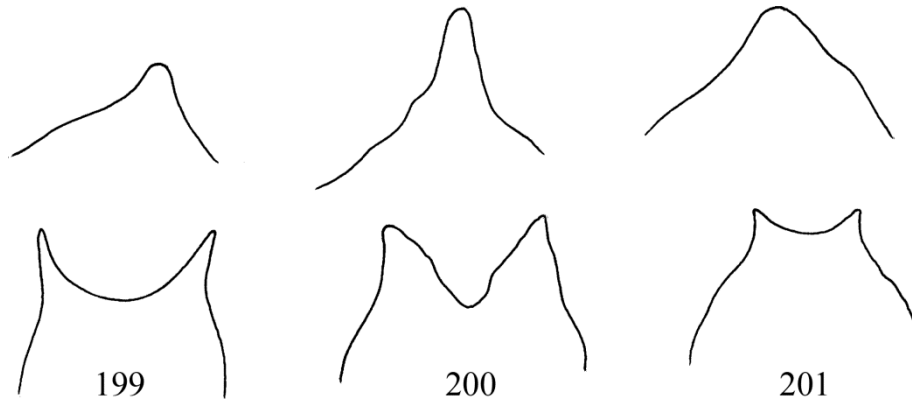
A more detailed study on the structure matrices is required with more specimens in order to quantify the extent of diverged or diverging state of the populations on the entire distributional area of *Allogamus ligonifer* species or species complex. However, this study has no actual reality in the present devastated state of the western taxonomy.

Allogamus ketpar Oláh & Coppa, sp. nov.

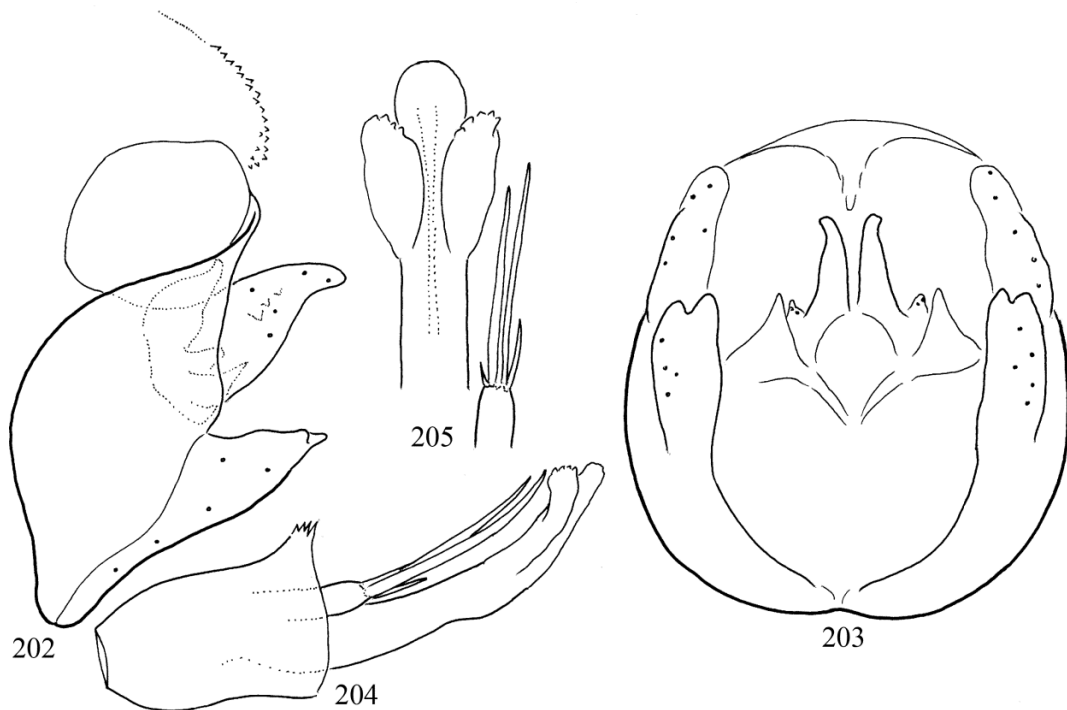
(Figures 202–205)

Material examined. Holotype: Spain, Cabañas del Castillo, Cáceres Province. Affluent Rio Almonte, 30.XI.2017, leg. G. Coppa (1 male, CPC).

Diagnosis. This new *Allogamus* species is a typical model taxon for chimeric integration. The structure of aedeagus with subapical membranous, not sclerotized dentate wings was integrated from the *Allogamus corsicus* species group, but the unfused parameres are character of the *A. auricollis* species group. Based upon the setal pattern and location *A. ketpar* sp. nov. belongs to the *A. ligonifer* species subgroup. Most close to the *A. pertuli* species described from Greece, but



Figures 199–201. The distinguished three phenotypic traits of characters of the dorsal sclerite on the aedeagus and the variously triangular accessory process on the paraproct in *Allogamus ligonifer* populations. 199 = “ligonifer”, 200 = “gredosensis”, 201 = “vosgesensis”.



Figures 202–205. *Allogamus ketpar* Oláh & Coppa, sp. nov. Holotype male: 202 = genitalia in left lateral view, 203 = genitalia in caudal view, 204 = phallic organ in lateral view, 205 = phallic organ in dorsal view.

differs by the reduced number of primary spines on the paramere and by the different shape of the periphallic organs of cerci and gonopods.

Description. This is a light yellow, brownish animal. The single male specimen stored in alcohol. The forewing length is 15 mm.

Male genitalia. Tergite VIII with spinulose protuberance. Segment IX reduced in size, very short both dorsad and ventrad; the demarcation line between segment IX and gonopods well discernible. Cavity of segment X, lined by cerci and subdivided by a dorsomesal inner ridge, is very pronounced. The cerci are large, subtri-

angular with digitate upper lobe. The paraproct is triangular in lateral more digitate in apical view; there is a small setose process on the basoventrum of the dorsal branches and there is a pointed triangular accessory paraproctal process on the ventral branches. Gonopods bilobed, more discernible in apical view. Phallic organ composed of phallosome (phallobase), endotheca, aedeagus, endophallus and parameres. The parameres are characterized by short sclerotized shaft and by two long primary spine-like setae accompanied by two small basal setae. Aedeagus armed with a pair of lateral subapical wings, almost fully membranous with dentate apical pattern.

Etymology. *ketpar* from *két pár* two pairs in Hungarian, refers to paramere character transformation of the doubled primary spines on each paramere shaft. A unique state of having two primary spines on a short paramere shaft (refers to *pair*) and there are two, unfused such a parameres.

***Alpopsyche* Botosaneanu & Giudicelli, 2004**

(Figure 193)

Original differential diagnosis. The main differences between *Alpopsyche* and *Rhadicoleptus* is listed.

Relation. *Alpopsyche* is more related to *Hydatophylax* than to *Rhadicoleptus* (Botosaneanu & Giudicelli 2004).

Genital character state combinations. (1) Presence (apomorphic) of spinulose protuberance on tergite VIII; (2) Reduced (apomorphic) state of tergite IX; (3) Setose inerm (plesiomorphic) state of cerci; (4) Produced (plesiomorphic) state of the dorsal branch of paraproct; (5) Separate free from each-other (plesiomorphic) state of the dorsal branch of paraproct; (6) Separate free-from-cerci (plesiomorphic) state of the dorsal branch of paraproct; (7) Reduced (apomorphic) state of the ventral branch of paraproct; (8) Separate free from each-other (plesiomorphic) state of the ventral branches of paraproct.

Parameres. Paramere is a single robust rod, more sinuous in lateral view, distal third slightly

spatulate armed marginally with strong rigid spines of setal origin with alveoli.

Remarks. *Alpopsyche ucenorum* described originally as *Stenophylax* (McLachlan 1876); listed later among *Rhadicoleptus* (Schmid 1955); suggested to describe as a new genus (Malicky 2001); described as *Alpopsyche* gen. nov. (Botosaneanu & Giudicelli 2004). The new genus status has been questioned in order to ensure stability in nomenclature (Malicky 2005). However, the morphology of the two taxa is clearly different therefore here we retain the genus *Alpopsyche* Botosaneanu & Giudicelli, 2004.

***Alpopsyche ucenorum* (McLachlan, 1876)**

(Figure 193)

Material examined. **France**, Alpes de Hautes Provence, Allos, torrent Medouille, 15.VII.2008, leg. G. Coppa (2 male, 2 females; OPC).

***Anisogamus* McLachlan, 1875**

(Figure 194)

Original differential diagnosis. Formal delimitation is not given.

Relation. In the original genus description it was related to *Stenophylax* (McLachlan, 1875). Schmid (1955) related it to *Potamophylax*.

Genital character state combinations. (1) Presence (apomorphic) of spinulose protuberance on tergite VIII; (2) Reduced (apomorphic) state of tergite IX; (3) Setose inerm (plesiomorphic) state of cerci; (4) Produced (plesiomorphic) state of the dorsal branch of paraproct; (5) Separate free from each-other (plesiomorphic) state of the dorsal branch of paraproct; (6) Separate free-from-cerci (plesiomorphic) state of the dorsal branch of paraproct; (7) Reduced (apomorphic) state of the ventral branch of paraproct; (8) Separate free from each-other (plesiomorphic) state of the ventral branches of paraproct.

Paramere organisation. A pair of simple spine-like, spiniform rods with upward turning apical portion; paramere surface is glabrous; the

subapical region has corrugated-striated surface; the very tip of the paramere glabrous again without corrugations.

Remarks. The type species *A. difformis* prefers to populate creanal and epirhithral alpine habitats and distributed in the Alps. A sibling species, *A. waringeri* Graf & Vitecek, 2015 was described recently (Graf et al. 2015) from the Pyrenees with well-defined divergences in the paramere organisation. The paramere of *A. waringeri* is shorter and supplied with dorsomesal tine on the apical ending of the basal bulbous part lacking at *A. difformis*. The variability/stability of paramere divergences was however, not examined. We have found stable fine structures on the parameres at the examined four specimens of *A. difformis*.

***Anisogamus difformis* (McLachlan, 1867)**

(Figure 194)

Material examined. Austria, Carinthia, Sau-alpe, Ladinger Hütte, 25.VI.2007, leg. W. Graf, (4 males, OPC).

***Chionophylax* Schmid, 1951**

(Figures 195–198)

Original differential diagnosis. Schmid 1951: 55: “Le genre *Chionophylax* est curieux; il est extrêmement voisin de *Acrophylax* par tous les caractères fournis par les pattes et les ailes; mais, au contraire, l’armature génitale est des plus caractéristiques et des plus étranges; je n’ai jamais vu, chez les Limnophilides, de semblable conformation” 56: “Les principaux caractères génériques résident dans la conformation des genitales.”

Relation. In the original genus description it was related, like *Acrophylax*, to *Stenophylax*, especially to *S. wineguthi* Klapálek (Schmid 1951).

Genital character state combinations. (1) Presence (apomorphic) of spinulose protuberance on tergite VIII; (2) Reduced (apomorphic) state of

tergite IX; (3) More sclerotized (apomorphic) state of cerci; (4) Produced (plesiomorphic) state of the dorsal branch of paraproct; (5) Separate free from each-other (plesiomorphic) state of the dorsal branch of paraproct; (6) Separate free-from-cerci (plesiomorphic) state of the dorsal branch of paraproct; (7) Reduced (apomorphic) state of the ventral branch of paraproct; (8) Separate free from each-other (plesiomorphic) state of the ventral branches of paraproct.

Parameres. Various developed spiniform structure with specific curvatures and apical spinule patterns.

***Chionophylax bulgaricus* Kumanski, 1973 stat. nov.**

(Figure 195)

Chionophylax mindszentyi bulgaricus Kumanski, 1973: 196.

Material examined. Holotype: Bulgaria, Stara Planina, Mt. Botev, 26.IV.1968, 2100–2200 m, collected on snow covering stream below Botev, leg. P. Beron (1 male, 1 female; NMNHS).

Remarks. In the original subspecies description there was stable divergences recorded and documented in the periphallidic organs of cerci, paraproct and gonopods (Kumanski 1973). Paramere divergence between the two taxa was detected and confirmed here. Based upon these structural divergences and our theoretical presentation (Oláh et al. 2018a) we conclude that *Chionophylax bulgaricus* stat. nov. is a sibling species of *C. mindszentyi* evolved in allopatry in the Stara Planina.

***Chionophylax czarnohoricus* (Dziedzielewicz, 1911)**

(Figure 196)

Material examined. Romania, Munții Maramuresului, Borsa-Baile Borsa, brook and alpine grassland above the Balacini Pass, N47°40.934' E24°52.774', 1573 m, 22.V.2007, leg. Cs. Csuzdi, L. Dányi, J. Kotschán & D. Murányi (1 male, HNHM).

***Chionophylax mindszentyi* Schmid, 1951**

(Figure 197)

Material examined. Holotype: **Romania**, Vurfu Mare, Szeben, 11.VI.1910, leg. Csiki (1 male, HNHM). Fagaras Mts. Bilea Valley, 45.610 24.618, 1894 m, 4.VI.2007, leg. M. Bálint (14 males, OPC). Romania, Sibiului Mts. Paltinis, NW, 12–13.V.2007, leg. Székely, Kiss, Dénes, Bálint (9 males, OPC).

***Chionophylax monteryla* Botosaneanu, 1957**

(Figure 198)

Material examined. **Bulgaria**, Rila Mts., Seven Rila Lakes, 8.VI.1973, leg. K. Kumanski (1 male, 1 female; OPC).

***Chyranda* Ross, 1944**

(Figure 206)

Original differential diagnosis. Ross, 1944: 283: “The very long palpi distinguish this genus from *Limnephilus* and others to which it is related.”

Relation. In the original genus description it was related to *Limnephilus* (Ross 1944). According to Schmid (1951) male palpi relate *Chyranda* to *Notopsyche*, female segment IX to *Parachiona*, several neurination and male genital characters to between *Enoicyla* and *Stenophylax*. Later Schmid (1955) placed *Chyranda* in the Stenophylacini tribe between *Parachiona* and *Stenophylax* by male genital structure and between *Hydatophylax* and *Pycnopsyche* by the vulvar scale and vaginal structure of the female. Evidences indicate again that characters are integrated with some channelled stochastic independences against the permanent flux of internal and external environmental effects.

Genital character state combinations. (1) Absence (plesiomorphic) of spinulose protuberance or any neoformation on tergite VIII (2) Reduced (apomorphic) state of tergite IX; (3) More sclerotized (apomorphic) state of cerci; (4) Produced

(plesiomorphic) state of the dorsal branch of paraproct; (5) Separate free from each-other (plesiomorphic) state of the dorsal branch of paraproct; (6) Fused to-cerci (apomorphic) state of the dorsal branch of paraproct; (7) Produced (plesiomorphic) state of the ventral branch of paraproct; (8) Fused to each-other (apomorphic) state of the ventral branches of paraproct.

Parameres. Variously developed spiniform structure without any apical spinules; usually asymmetric.

Remark. The produced state of the ventral branch of the paraproct is unique in the Stenophylacini tribe.

***Chyranda centralis* (Banks, 1900)**

(Figure 206)

Material examined. **USA**, Colorado, Clear Creek County, Hoop Creek springs and seeps from gage to headwaters, 11200–11440 feet, 8.VIII.2009, leg D. Ruiter (1 male, 1 female; OPC). Pennsylvania Mts. summer 1980, leg. D.K. Colorado, 79KSB F85 (1 male, CNC). Utah, Utah county, Wasatch Mts, Mt. Timpanogos Trailhead Spring at Timpooneke Campground, N40°25.826' W111°38.313' 2230m 14.IX.2011 leg. R. Baumann, S. Clark & D.Murányi (2 males, 2 females; OPC).

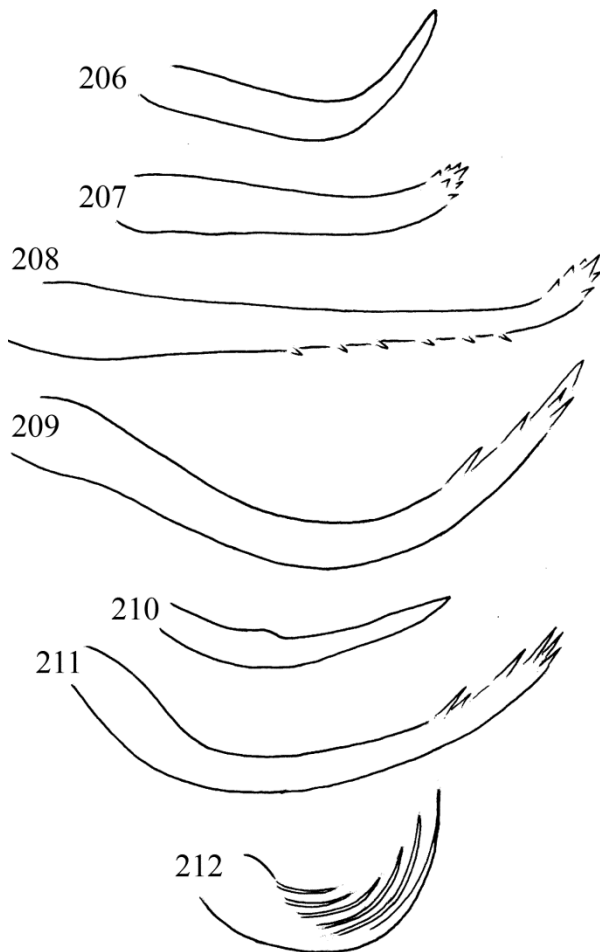
***Clostoeca* Banks, 1943**

(Figures 207–208)

Original differential diagnosis. Formal delineation is not given.

Relation. In the original description this small genus was related to *Anisogamus* (Banks 1943). According to the general habitus it is similar to *Rhadicoleptus alpestris*, but the genital structure relates *Clostoeca* close to *Hydatophylax* and *Pycnopsyche* but specialization of several genital structures indicates a lineage with isolated status (Schmid 1955).

Genital character state combinations. (1) Absence (plesiomorphic) of spinulose protuberance or any neoformation on tergite VIII; (2)



Figures 206–212. Parameres of *Chyranda*, *Clostoecca*, *Con-sorophylax*, *Enoicyla*, genera and *Fogophylax* gen nov. 206 = *Chyranda centralis*, 207 = *Clostoecca disjuncta*, 208 = *C. sperryae*, 209 = *Con-sorophylax consors*, 210 = *Enoicyla costae*, 211 = *E. reichenbachii*, 212 = *Fogophylax lineatus*.

Produced although membranous (plesiomorphic) state of tergite IX; (3) Setose inerm (plesiomorphic) state of cerci; (4) Produced (plesiomorphic) state of the dorsal branch of paraproct; (5) Fused to each-other (apomorphic) state of the dorsal branch of paraproct; (6) Separate free-from-cerci (plesiomorphic) state of the dorsal branch of paraproct; (7) Produced (plesiomorphic) state of the ventral branch of paraproct; (8) Fused to each-other (apomorphic) state of the ventral branches of paraproct.

Parameres. Spiniform parameres with small apical and/or ventral spines.

Remark. The produced state of the ventral branch of the paraproct and the fused state of the dorsal and ventral branches of paraproct are unique in the Stenophylacini tribe.

***Clostoecca disjuncta* (Banks, 1914)**

(Figure 207)

Material examined. USA, Oregon, Douglas County, Muir Cr. Cprgd., Rogue R. Nat. Forest, 1.VII.1961, u.v.l. leg. G.B. Wiggins, (1 male, ROM). Oregon, Benton County, Finley Wildlife Refuge, temp. pool nr. Gray Cr. Swamp, 8.IV.1983, leg. Furnish, (1 male, 2 females; OPC). Oregon, Lincoln County, Flynn Cr., Gate str. rd. ditch, 19.V.1982, leg. R. W. Wisseman (1 male, ROM).

***Clostoecca sperryae* Banks, 1943 stat. restit.**

(Figure 208)

Material examined. USA, California, San Bernardino County, Crab Flats Cprgd., 8.VII.1967, Bl.Lt. leg. C.W. Baler, (1 male, ROM). California, Napa County, Milliken Creek at Circle S Ranch entrance, 38.4163 122.2491, 24.IV.2010, at light, leg. D. E. Ruitter (1 male, 1 female; OPC).

Remarks. *Clostoecca sperryae*, described from California as the type species of the genus was synonymised with *C. disjuncta* described from British Columbia (Flint 1966). A careful comparative hermeneutics of the old original drawings of Banks (1914, 1943), although not of the quality of his contemporary Martynov, clearly indicates that he has described two different species. On the two drawings the differences are very clearly detectable in the shape of parameres. We have examined specimens of *C. disjuncta* from Oregon and specimens of *C. sperryae* from California and the message of the original drawings was confirmed. *C. disjuncta* has paramere short, stout with apical spines only, while *C. sperryae* has paramere much longer, slender, tapering apicad and besides the apical spines supplied with small, scattered spines on the ventrum. However, there are remarkable

shape divergences also in all of the periphallallic structures: cerci, paraproct, and gonopods. There are shape divergences also in the female genital structures. Here we reinstate the species status of *Clostoecca sperryae* Banks.

***ConSOROPHYLAX* Schmid, 1955**

(Figure 209)

Original differential diagnosis. Formal delineation is not given.

Relation. Schmid 1955:197, “Par l’armature génitale du ♂, *ConSOROPHYLAX* est intermédiaire entre *POTAMOPHYLAX* et *ALLOGAMUS*.”

Genital character state combinations. (1) Presence (apomorphic) of spinulose protuberance on tergite VIII; (2) Reduced (apomorphic) state of tergite IX; (3) Setose inerm (plesiomorphic) state of cerci; (4) Produced (plesiomorphic) state of the dorsal branch of paraproct; (5) Separate free from each-other (plesiomorphic) state of the dorsal branch of paraproct; (6) Separate free-from-cerci (plesiomorphic) state of the dorsal branch of paraproct; (7) Reduced (apomorphic) state of the ventral branch of paraproct; (8) Separate free from each-other (plesiomorphic) state of the ventral branches of paraproct.

Parameres. Spiniform structure having shaft of various shape and curvature and specified by apical spine pattern.

***ConSOROPHYLAX CONSORS* (McLachlan, 1880)**

(Figure 209)

Material examined. **Switzerland**, Furkapass, 13.X.2006, leg. W. Graf (1 male, 1 female; OPC).

***ENOICYLA* Rambur, 1842**

(Figures 210–211)

Original differential diagnosis. Formal delineation is not given.

Relation. Schmid 1955:188: “*ENOICYLA* est voisin de *PARACHIONA* par sa nervulation et l’armature génitale du ♂.”

Genital character state combinations. (1) Presence (apomorphic) of spinulose protuberance on tergite VIII; (2) Reduced (apomorphic) state of tergite IX; (3) Setose inerm (plesiomorphic) state of cerci; (4) Produced (plesiomorphic) state of the dorsal branch of paraproct; (5) Separate free from each-other (plesiomorphic) state of the dorsal branch of paraproct; (6) Separate free-from-cerci (plesiomorphic) state of the dorsal branch of paraproct; (7) Reduced (apomorphic) state of the ventral branch of paraproct; (8) Separate free from each-other (plesiomorphic) state of the ventral branches of paraproct.

Parameres. Spiniform structure with shorter or longer shaft and without apical spines at *E. costae* and *E. pusila*, but with 2–3 apical and 1–2 dorso-mesal subapical spines at *E. reichenbachi*.

***ENOICYLA COSTAE* McLachlan, 1876**

(Figure 210)

Material examined. **Albania**, Kolonjë district, Grammos Mts, Rehovë, brook at forest edge, mountain pasture E of the village, N40°20.111' E20°43.467', 1445m, 15.X.2013, P. Juhász, T. Kovács, D. Murányi, G. Puskás, (1 male, OPC).

***ENOICYLA REICHENBACHI* (Kolenati, 1848)**

(Figure 211)

Material examined. **Italy**, Garessio (CN) 650 m, affl. fiume Tanaro c/o Trapna, 10.X.2001, leg. Museo Caffi BG (1 male, OPC).

***ENOICYLOPSIS* Navas, 1917**

Original differential diagnosis. Navas, 1917: 16: “Il est très voisin d’*ENOICYLA* Ramb., mais il s’en sépare par la présence d’un éperon au tibia antérieur du ♂...”

Relation. Navas 1917:15: “*Similis Enoicylae Ramb.*”

Genital character state combinations. (1) ?; (2) ?; (3) Setose inerm (plesiomorphic) state of cerci; (4) Produced (plesiomorphic) state of the dorsal branch of paraproct; (5) Separate free from each-other (plesiomorphic) state of the dorsal branch of paraproct; (6) Separate free-from-cerci (plesiomorphic) state of the dorsal branch of paraproct; (7) Reduced (apomorphic) state of the ventral branch of paraproct; (8) Separate free from each-other (plesiomorphic) state of the ventral branches of paraproct.

Parameres. Spiniform upward curving structure.

Remarks. There is no information about the type that was collected in a *Quercus ilex* forest of Massif du Djurdjura (Algérie) with brachypterous female. This material is probably lost. The original description and drawings were somewhat improved by Lestage (1921). The character state combination and paramere structure were reconstructed from these drawings with somewhat more details.

***Fogophylax* Oláh, gen. nov.**

(Figure 212)

Taxonomic history. *Anisogamus lineatus* was described by Klapálek (1903a, 1903b) stated from the Austrian Alp (Styria) erroneously. It was never collected there, despite many years of systematic search. But it was found very common in the Fogaras Mountain ranges of the South Carpathians. This confusion was probably resulted by mistakes in the original labelling (Mallicky 2005), as it frequently happened in those times with profit-oriented insect dealers (Oláh et al. 2015).

The small *Anisogamus* genus with 5 known taxa (*aequalis aequalis*, *a. czarnohorensis*, *difformis*, *lineatus*, *noricanus*) was split and the new genus *Isogamus* was created for the taxa of *A. aequalis aequalis* and *A. a. czarnohorensis*

(Schmid 1955). Later *A. noricanus* was synonymised with *A. difformis* (Botosaneanu & Mallicky 1978) and *A. lineatus* was transferred to the genus *Isogamus* (Botosaneanu 1967).

However, as was documented before (Oláh et al. 2015) “*Isogamus lineatus* forms possibly an independent genus having completely different genital architecture, gross structure and fine structure, representing both neutral and non-neutral adaptive traits, probably evolved in different divergence ages or splitting times. At this time we haven't got any theoretical model to estimate phylogenetic age for architectural gross and fine structural divergences. A more sophisticated model for elaboration of trait divergence ages and a comprehensive comparative examination of relevant genera are required to revise the Stenophylacini tribe.”

Diagnosis. The character state combination of the basic structural units of the genitalia suggests an independent genus rank status for the unique species of *Isogamus lineatus*. The presence of apomorphic spinulose protuberance on tergite VIII is further organised into a unique bipartite spinulose structure deeply invaginated mesad forming a bilobed spinulose neoformation unique in the Stenophylacini tribe, as was recognised already by Klapálek (1903a). The fused to-cerci apomorphic state of the dorsal branch of paraproct is accompanied by the almost entire loss of the ventral arm of the dorsal branch of paraproct. *Isogamus* genus has a separate free-from-cerci (plesiomorphic) state of the dorsal branch of paraproct. The genus rank state is further supported by the paramere organisation. The highly abbreviated stout paramere shaft with upward arching tuft of strong spines is far from the parameres of the *Isogamus* genus. Female genital structure has entirely different organisation.

Type species. *Anisogamus lineatus* Klapálek, 1903. The genus is monobasic.

Genital character state combinations. (1) Presence (apomorphic) of spinulose protuberance on

tergite VIII; (2) Reduced (apomorphic) state of tergite IX; (3) Setose inerm (plesiomorphic) state of cerci; (4) Produced (plesiomorphic) state of the dorsal branch of paraproct; (5) Separate free from each-other (plesiomorphic) state of the dorsal branch of paraproct; (6) Fused to-cerci (apomorphic) state of the dorsal branch of paraproct; (7) Reduced (apomorphic) state of the ventral branch of paraproct; (8) Separate free from each-other (plesiomorphic) state of the ventral branches of paraproct.

Parameres. Highly abbreviated stout paramere shaft with upward arching tuft of strong spines.

Distribution. Romania: South Carpathians. Very common in the Fagaras Mts., but 3 males and 1 female have been recorded also from the Cibin Mts. (Botosaneanu & Schneider 1978).

Etimology. *Fogophylax* from “*fogor*” a local name of “*fogoly*” the grey partridge (*Perdix perdix*) in Hungarian, also known as the Hungarian partridge, or hun, and from „*phylax*” guard in Greek. *Fogor* gives the name of City Fogaras and Mountain Fogaras, the home of *Fogophylax lineatus*.

Fogophylax lineatus (Klapálek, 1903)

(Figure 212)

Anisogamus lineatus Klapálek, 1903a:1–2. „Ein ♂, (Scheibleregger Hochalpe, 3/6 98, Strobl) Ist sicher von beiden bisher bekannten Arten durch die form des VIII. Hinterleibsringes und der Genitalfüsse verschieden. Durch die Flügelform und die halb-abstehenden Börstchen auf den Längsadern erinnert das Stück an *Acrophylax* aber die Spornzahl, das lange 1. Fussglied des ♂ und die Form der Analsegmente bi’den wesentliche Unterschiede.”

Anisogamus lineatus Klapálek, 1903b:1–2. „Mam pred sebou jediny kus ♂ ze Scheiblereger Hochalpe (3./6.98, Strobl)”.

Isogamus lineatus (Klapálek, 1903): Botosaneanu 1967:99–106. Transferred to genus *Isogamus*.

Isogamus lineatus (Klapálek, 1903): Botosaneanu 1967:103. „L’exemplaire type (que nous designons ici comme lectotype ♂; conservé a sec; abdomen en préparation au baume du Canada, attachée a l’épingle supportant la reste de l’insecte), provient

de Styrie, Scheibleregger Hochalpe, 3. VI. 1898 (Strobl). Nous ne savons rien du milieu ou se développent les larves. Notre material comprend 38 ♂ des Mts. de Fagarash (Carpatés Méridionales de Roumanie). Ces insectes furent capturés le 7. VI. 1961, le 8. VIII. 1960, entre les 7.–9. VIII. 1962, ainsi que le 16. IX. 1964. Il s’agit donc d’une espèce „on the wing” durant le printemps, l’été et au moins la première moitié de l’automne alpine. Les stations sont des sources, des ruisseaux et des torrents, dans la zone alpine, dans celle subalpine et a la limite superieure de la forêt de conifères, eaux appartenant aussi bien a des bassins du versant N. que du versant S. du massif (Podu Giurguiului – Buda, Podrag – Arpas, Bilea – Cirtzisoara, Simbata). Les altitudes varient de 1500 a 2300 m.

Isogamus lineatus (Klapálek, 1901): Malicky 2005: 576. „Nach Angabe in der Beschreibung stammt der Holotypus von der Scheibleregger Hochalpe bei Admont (Steiermark). Diese Art ist sonst nie mehr in den Alpen, sondern immer nur in Südkarpaten gefunden worden. Ich habe mehrere Jahre hindurch wiederholt die Scheibleregger Hochalpe besucht und dort zu allen Jahreszeiten gesammelt, auch viele Larven aus einzigen dort fliessenden Bach mitgenommen und im Labor zu Adulten gezüchtet. Dabei ich niemals einen *Isogamus* gefunden. Offenbar ist entweder Klapálek oder dem Sammler Strobl eine Etikettenverwechslung unterlaufen. Beide haben auch in der Karpaten gesammelt. Die Art kommt in Alpen nicht vor.”

Material examined. **Romania**, Argeş county, Făgăraş Mts, Căpătânenii Ungureni, small springlake by the Capra Stream along road No.7C, N45°34.605’ E24°37.060’, 1405m, 29.VIII.2012 leg. T. Kovács, D. Murányi, J. Oláh (2 males, 5 females; OPC). Argeş county, Făgăraş Mts, Căpătânenii Ungureni, sidebrook of Capra Stream along road No.7C, N45°35.185’ E24°37.691’, 1705m, 29.VIII.2012 leg. T. Kovács, D. Murányi, J. Oláh (8 males, 7 females, 1 copula; OPC). Sibiu county, Făgăraş Mts, Cârțișoara, forest seep along road No.7C, N45°38.742’ E24°36.464’, 1325m, 29.VIII.2012 leg. T. Kovács, D. Murányi, J. Oláh (3 females, OPC). Braşov county, Făgăraş Mts, Dejani, forest sidebrook of Dejani stream, N45°36.408’ E24°56.466’, 1310m, 30.VIII.2012 leg. T. Kovács, D. Murányi, J. Oláh (8 males, 5 females, OPC). Braşov county, Făgăraş Mts, Dejani, right side-

brook of Dejeni stream, N45°35.446' E24° 56.348', 1755m, 30.VIII.2012 leg. T. Kovács, D. Murányi, J. Oláh (1 male, 1 female, OPC). Braşov county, Făgăraş Mts, Dejeni, forest sidestream of Dejeni stream, N45°36.720' E24°56.533', 1250m, 30.VIII.2012 leg. T. Kovács, D. Murányi, J. Oláh (5 males, 3 females, OPC)."

Halesus Stephens, 1836

(Figure 213)

Original differential diagnosis. Formal delineation is not given.

Relation. Schmid 1955:180, "Halesus est un genre isolé. Avec Potamophylax, il présente en commun le dessin des ailes antérieures et les grandes lignes de l'appareil vaginal, caractère qu'il partage aussi avec Allogamus et Acrophylax. La conformation de la pièce tubulaire et la partie ventrale du IX^e segment si volumineuse, le rapproche de Allogamus et de Melampophylax. Par contre, l'armature génitale du ♂ isole le genre de tous les autres."

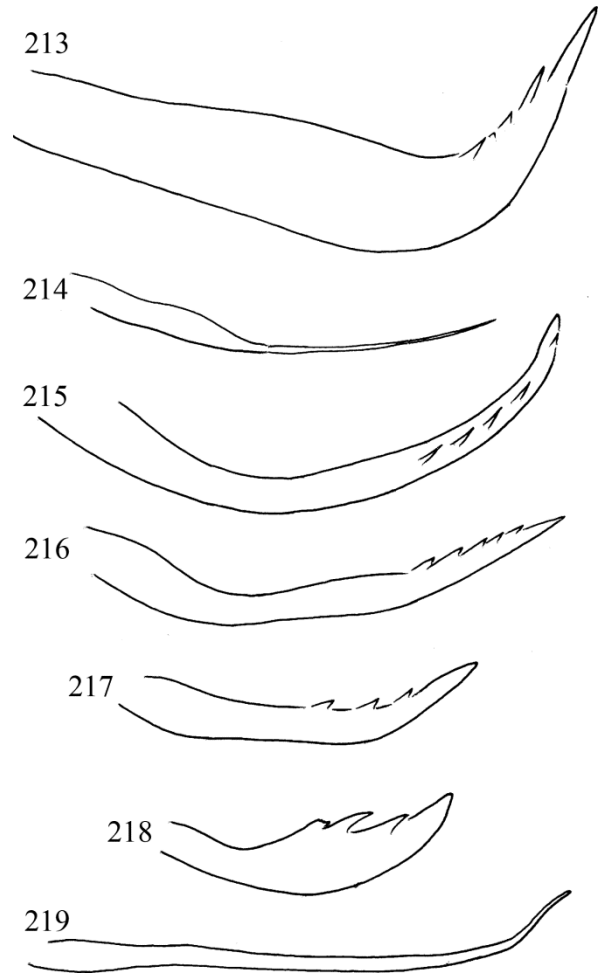
Genital character state combinations. (1) Presence (apomorphic) of spinulose protuberance on tergite VIII; (2) Reduced (apomorphic) state of tergite IX; (3) Setose inerm (plesiomorphic) state of cerci; (4) Produced (plesiomorphic) state of the dorsal branch of paraproct; (5) Separate free from each-other (plesiomorphic) state of the dorsal branch of paraproct; (6) Separate free-from-cerci (plesiomorphic) state of the dorsal branch of paraproct; (7) Reduced (apomorphic) state of the ventral branch of paraproct; (8) Separate free from each-other (plesiomorphic) state of the ventral branches of paraproct.

Parameres. Enforced spiniform paramere with various curvatures, and varying apical spine pattern.

Halesus radiatus (Curtis, 1834)

(Figure 213)

Material examined. Germany, without collection details (1 male, OPC).



Figures 213–219. Parameres of *Halesus*, *Hydatophylax*, *Iso-gamus*, *Melampophylax*, and *Leptotaulius* genera. 213 = *Halesus radiatus*, 214 = *Hydatophylax infumatus*, 215 = *Iso-gamus aequalis*, 216 = *Melampophylax melampus*, 217 = *M. scalcioi*, 218 = *M. vestinorum*, 219 = *Leptotaulius gracilis*.

Hydatophylax Wallengren, 1891

(Figure 214)

Original differential diagnosis. Formal delineation is not given.

Relation. Schmid 1955:180, "Hydatophylax et Pycnopsyche sont très voisins – ils ont en commun la majorité des caractères des armatures genitales - et comptent parmi les genres les plus évolués de la tribu."

Genital character state combinations. (1) Presence (apomorphic) of spinulose protuberance on tergite VIII; (2) Reduced (apomorphic) state of tergite IX; (3) More sclerotized variously dentate (apomorphic) state of cerci; (4) Produced (plesiomorphic) state of the dorsal branch of paraproct; (5) Separate free from each-other (plesiomorphic) state of the dorsal branch of paraproct; (6) Separate free-from-cerci (plesiomorphic) state of the dorsal branch of paraproct; (7) Produced (plesiomorphic) state of the ventral branch of paraproct; (8) Fused to each-other (apomorphic) state of the ventral branches of paraproct.

Parameres. Paramere structure is highly reduced to a thread-like process originates from a membranous basement.

Remarks. The apomorphic fused state of the ventral branches of paraproct (lateral sclerite of segment X at Schmid) forms a complete ring around the anal opening together with the dorsal branches of the paraproct. However, this fused state is variously present at the different species.

***Hydatophylax infumatus* (McLachlan, 1865)**

(Figure 214)

Material examined. **Bosnia & Herzegovina**, Una-Sana Canton, Rudenice, Sana River, N44°30.999', E16°48.556', 260 m, 27.V.2012, leg. T. Kovács & G. Puskás (3 males, OPC).

***Isogamus* Schmid, 1955**

(Figure 215)

Original differential diagnosis. Formal delineation is not given.

Relation. Schmid 1955:184, “*Isogamus* est probablement un genre dérivé du complexe de *Potamophylax* et spécialisé à partir de celui-ci. Il occupe une position isolée.”

Genital character state combinations. (1) Presence (apomorphic) of spinulose protuberance on tergite VIII; (2) Reduced (apomorphic) state of tergite IX; (3) Setose inerm (plesiomorphic) state

of cerci; (4) Produced (plesiomorphic) state of the dorsal branch of paraproct; (5) Separate free from each-other (plesiomorphic) state of the dorsal branch of paraproct; (6) Separate free-from-cerci (plesiomorphic) state of the dorsal branch of paraproct; (7) Reduced (apomorphic) state of the ventral branch of paraproct; (8) Separate free from each-other (plesiomorphic) state of the ventral branches of paraproct.

Parameres. Spiniform paramere shaft with specific upward directed curvature and apical-subapical spine patterns.

***Isogamus aequalis* (Klapálek, 1907)**

(Figure 215)

Material examined. **Poland**, Bieszczady Mts. leg. B. Szczesny (2 males, 2 females; OPC). **Slovakia**, Vihorlat Mts. Zempl Hamre, 700 m, 15. IX. 1962, leg. P. Chvojka (3 males, 4 females, aedeagus and parameres on slide No. 13, 14, NMPC; 3 males, 2 females, OPC). Vihorlat Mts. prameniste pot.-Morska eko, 15.IX.1962, leg. P. Chvojka, (4 males, aedeagus and parameres on slide No. 16, NMPC). Vihorlat, 16.IX.1962, leg. P. Chvojka (2 males, aedeagus and parameres on slide No. 1, 2, NMPC). Vihorlat Mts. prm. N. Zempl. Hamre, 740 m, 12.X.1990, leg. P. Chvojka (1 male, aedeagus and parameres on slide No. 18, NMPC). Vihorlat Mts. prm. N. Zempl. Hamre, 740 m, 12.X.1990, leg. P. Chvojka (1 male, aedeagus and parameres on slide No. 18, NMPC). Vihorlat Mts. potucek severne, N Sedlice, 10.X.1990, leg. P. Chvojka (1 male, aedeagus and parameres on slide No. 17, NMPC). Vihorlat Mts. levostr. Pritok Bystre, 5-700 m, 9.X.1990, le. P. Chvojka (4 males, aedeagus and parameres on slide No. 16, NMPC). **Ukraine**, Klapálek Collection: No. 21, Worochtensky, 7.IX.1908, leg. Dziedzielewicz (1 female, NMPC). Klapálek Collection: No. 5, Chomiak (Blotek), 22.IX.1906, leg. Dziedzielewicz (1 male, aedeagus and parameres on slide No K5, NMPC). No. 6, Chomiak, 5.IX.1908, leg. Dziedzielewicz (1 male, aedeagus and parameres on slide No K6, NMPC). No. 7, Chomiak, 5.IX.1908, leg. Dziedzielewicz (1 male, aedeagus and parameres on slide No. K7, NMPC). No. 8, Chomiak,

5.IX.1908, leg. Dziędzielewicz (1 male, aedeagus and parameres on slide No K8, NMPC). No. 9, Chomiak, 5.IX.1908, leg. Dziędzielewicz (1 male, aedeagus and parameres on slide No K9, NMPC). No. 10, Chomiak, 5.IX.1908, leg. Dziędzielewicz (1 male, aedeagus and parameres on slide No K10, NMPC). No. 20, Chomiak (Blotek), 22.IX.1906, leg. Dziędzielewicz (1 female, NMPC). Bieszczady Mts (Besszádok), Ung National Park, below Lubnya (Kiesvölgy), N49°00'54,81" E22°43'23,82", 478 m, singled, 20. IX. 2013, leg. J. Oláh, Cs. Balogh, Cs. Deák & I. Meszesán (1 female, OPC).

***Melampophylax* Schmid, 1955**

(Figures 216–218)

Original differential diagnosis. Formal delimitation is not given.

Relation. Schmid 1955:182–183, “*Melampophylax* est un genre issu du groupe *Potamophylax-Allogamus-Consorophylax* mais qui est isolé surtout par la conformation de l’armature génitale du ♂ et l’appareil vaginal de la ♀.”

Genital character state combinations. (1) Absence (plesiomorphic) of spinulose protuberance or any neof ormation on tergite VIII; (2) Reduced (apomorphic) state of tergite IX; (3) Setose inerm (plesiomorphic) state of cerci; (4) Produced (plesiomorphic) state of the dorsal branch of paraproct; (5) Separate free from each-other (plesiomorphic) state of the dorsal branch of paraproct; (6) Separate free-from-cerci (plesiomorphic) state of the dorsal branch of paraproct; (7) Reduced (apomorphic) state of the ventral branch of paraproct; (8) Separate free from each-other (plesiomorphic) state of the ventral branches of paraproct.

Parameres. Highly enforced stout paramere shaft with strong dorsolateral spines.

***Melampophylax melampus* (McLachlan, 1876)**

(Figure 216)

Halesus melampus McLachlan, 1876:158–159.

Melampophylax melampus (McLachlan, 1876): New genus erected by Schmid (1955)

Material examined. **Italy**, Sasso Nero, 14.X.2006 leg. O. Lodovici (1 male, OPC). Lombardia, Mezzoldo, (BG), fiume Brembo, 1100m, 3.X.1995 leg. Albrici & Valle (47 males, 12 females, CNSMB; 10 males, 3 females, OPC). Lombardia, Parzanica, (BG), Valle dei Foppi, 550m, 13.XI.1996 leg. Cornali Gozzini (15 males, 4 females, CNSMB). Lombardia, Valcanale, (BG), 1000m, 30.XI.2007 leg. W. Zocchelli (5 males, CNSMB; 3 males, 1 female, OPC). Emilia Romagna, S. Sofia, La Stretta, Fosso Abetio, 43.878°N 11.732°E 1200m, 13.X.1989 leg. G. Campadelli (2 males, CNSMB). Emilia Romagna, S. Sofia, La Stretta, Fosso Abetio, 43.878°N 11.732°E 1200m, 30.X.1989 leg. G. Campadelli (1 female, CNSMB). Toscana, Marradi, (FI), Mte. Bruno Rio Canneto, 700m, 15.IX.2003 leg. A. Usvelli (11 males, 2 females, CNSMB; 6 males, 2 females, OPC).

***Melampophylax scalarcioi* Valle & Lodovici, 2018**

(Figure 217)

Melampophylax scalarcioi Valle & Lodovici, 2018:167–170.

Material examined. Paratype: **Italy**, Calabria, Samo (RC), Torrente loc. Giardini, 38.142°N, 15.928°E, 1570 m, 14.X.2014, light trap, leg. O. Lodovici, F. Manti & M. Valle (1 male, 1 female; OPC). Calabria, Spezzano della Sila (CS), Vivaio Sbanditi, 39.388°N, 16.6028°E, 1350 m, 20.X.2014, light trap, leg. S. Scalercio (1 male, OPC). Calabria–Scilla (RC) m 1260, P. te S. Antonio, torr. Favazzina 38,187°N 15,846°E, 10. XI. 2013, light trap leg. E. Castiglione, F. Manti & P. Pantini, (2 females, CNSMB; 2 females, OPC).

***Melampophylax vestinorum* Moretti, 1991**

(Figure 218)

Material examined. **Italy**, Lorenzo Bellizzi (CS), torr. Vascello, 30. XI. 1994, tr. lum. leg. Pantini & Valle (1 male, CNSMB). Lorenzo Bellizzi (CS), torr. Vascello, m 1000, 30. X. 1994, tr. lum. leg. Pantini & Valle (1 male, OPC). Abruzzo P.N.A., Lago di Caronte, Val Fondillo (AQ) Racc, 12.X.1955, leg. Consiglio (1 male, 1 female; OPC).

Remarks. The single males from Calabria and Abruzzo available for this study probably represent two independent sibling species according to the divergences in aedeagus and paramere structures, but requires population samples to establish their sibling species status.

***Leptotaulius* Schmid, 1955**

(Figure 219)

Original differential diagnosis. Formal delineation is not given.

Relation. Schmid 1955:179–180: “Voyant l’armature génitale seule, je considérerais sans hésitation *L. gracilis* comme un *Acrophylax* très voisin de *vernalis*. Mais tous les autres caractères s’opposent formellement à une telle classification. Cette espèce est aussi fine et grêle que les *Acrophylax* sont courts, lourds et trapus.”

Genital character state combinations. (1) Absence (plesiomorphic) of spinulose protuberance or any neoformation on tergite VIII; (2) Reduced (apomorphic) state of tergite IX; (3) Setose inerm (plesiomorphic) state of cerci; (4) Produced (plesiomorphic) state of the dorsal branch of paraproct; (5) Separate free from each-other (plesiomorphic) state of the dorsal branch of paraproct; (6) Separate free-from-cerci (plesiomorphic) state of the dorsal branch of paraproct; (7) Reduced (apomorphic) state of the ventral branch of paraproct; (8) Separate free from each-other (plesiomorphic) state of the ventral branches of paraproct.

Parameres. Spiniform slender paramere shaft with slightly upward curving apices without any additional spines.

***Leptotaulius gracilis* Schmid, 1955**

(Figure 219)

Material examined. Austria, Carinthia, Sau-alm, Offener Hütte, 16.VI.2006, leg. W. Graf (2 males, OPC).

***Simaphylax* Oláh, gen nov.**

(Figure 220)

Taxonomic history. *Melampophylax* genus is composed of two groups: *M. melampus* group and *M. mucoreus* group (Oláh et al. 2015). Malicky (1990) has emphasized that the two groups differ much and a revision is required. Based on the present surveys on genitalic character state and paramere organisation here we split and create a new genus *Simaphylax* gen. nov. from the *Melampophylax* genus. This is a long awaited nomenclatorial act. *Melampophylax melampus* and *M. vestinorum* were subject to treat as a separate genus compared to all the other species of the genus *Melampophylax* s.l (Oláh et al. 2015). The discovery of the third species *M. scalercioi* Valle & Lodovici (2018) confirms the separate genus status of the *M. melampus* group. *Melampophylax melampus* is the type species of the *Melampophylax* genus therefore here we establish the new genus, *Simaphylax* for all the other members of the genus: *altuspyrenaicus* Botosaneanu, 1994; *austriacus* Malicky, 1990; *banaticus* Botosaneanu, 1995; *cantalicus* Botosaneanu, 1994; *gutinicus* Botosaneanu, 1995; *keses* Coppa & Oláh, 2015; *mucoreus* Hagen, 1861; *nepos* McLachlan, 1880; *orientalopyrenaicus* Coppa, 2016; *polonicus* Malicky, 1990; *szczesnyorum* Oláh & Chvojka, 2015; *triangulifera* Botosaneanu, 1957

Diagnosis. The character state combination of the basic structural units of the genitalia suggests an independent genus ranking status for this taxon. The apomorphic presence of the spinulose protuberance on tergite VIII of the *Simaphylax* is contrasted with the plesiomorphic absence of the spinulose protuberance of the *Melampophylax* genus. The paraproct is complex in *Melampophylax* and simple in *Simaphylax*. The phallic organ, both the aedeagus and the paramere is highly diverged in the two genera. Aedeagus with variously produced spine-shaped processes in *Melampophylax* and the aedeagus is simple without any spine-like processes in *Simaphylax*,

only lateral flange present to house the parameres. Parameres abbreviated stout with several spine-like modified setae in *Melampophylax* and paramere elongated, slender without any spine-like setae in *Simaphylax*. Co-organisation of female genitalia is detectable in the generic divergences. Vaginal dorsal sclerite complex not elongated, but accompanied with a unique ventral vaginal sclerite giving ventral support to the membranous and flexible vaginal chamber in *Melampophylax* and the vaginal dorsal sclerite complex is very much elongated to receive the parameres and the vaginal chamber is without any ventral sclerite in *Simaphylax*.

Type species. Melampophylax nepos triangulifera Botosaneanu, 1957

Etymology. *Simaphylax* from *sima*, smooth or plane in Hungarian refers to the simple paramere having no any spines or other additional structures of setal origin as well as to the simple paraproct and from the „*phylax*” guard in Greek.

Genital character state combinations. (1) Presence (apomorphic) of spinulose protuberance on tergite VIII; (2) Reduced (apomorphic) state of tergite IX; (3) Setose inerm (plesiomorphic) state of cerci; (4) Produced (plesiomorphic) state of the dorsal branch of paraproct; (5) Separate free from each-other (plesiomorphic) state of the dorsal branch of paraproct; (6) Separate free-from-cerci (plesiomorphic) state of the dorsal branch of paraproct; (7) Reduced (apomorphic) state of the ventral branch of paraproct; (8) Separate free from each-other (plesiomorphic) state of the ventral branches of paraproct.

Parameres. Slender elongated structure without any spine-like modified setae co-organised with the elongated dorsal vaginal sclerite complex. Very characteristic and species specific terminal blade evolved on the apical region of paramere in each species. This peculiar terminal configuration is a product of sexual coevolution. The pair of the internal tubes inside the elongated vaginal sclerite complex receives the elongated rod-shaped parameres during copulation. The terminal blade has crucial function during copulation

by guiding to introduce the paramere shafts into the internal tubes inside the elongated vaginal sclerite complex.

Simaphylax triangulifera (Botosaneanu, 1957)

(Figure 220)

Material examined. **Romania**, Eastern Carpathians, Harghita Mts., springs and streamlets between Baile Harghita and Cabana Madaras, 1650–1700 m, 14. X. 1970 leg. L. Botosaneanu (6 males, OPC). Gurghiu Mts. near Bucin Pass, Tárnava Mica springs and stream, N46°39'16,63" E25°16'42,46", 1290m, 30.X.2014, leg. Z. Baczó, Cs. Balogh, J. Kecskés & J. Oláh. (49 males, 6 females; OPC). Gurghiu Mts. near Bucin Pass, Gainasa springs and stream, N46°40'11,35" E25°17'39,06", 1400m, 30.X.2014, leg. Z. Baczó, Cs. Balogh, J. Kecskés & J. Oláh (1 male, 1 female; OPC). Harghita Mts. Filio stream side spring, N46°27'03,90" E25°33'29,29", 1350m, 31.X.2014 leg. Z. Baczó, Cs. Balogh, J. Kecskés & J. Oláh. (1 male, 3 females; OPC). Caliman Mts. Fantanele stream, N 46°59'04,00" E25°05'52,56", 776m, 1.XI.2014, leg. Z. Baczó, Cs. Balogh, J. Kecskés & J. Oláh. (3 females; OPC).

Mesophylax McLachlan, 1882

(Figure 221)

Original differential diagnosis. “Very closely allied to *Stenophylax*; differs especially in the spur of the anterior tibiae of ♂ being so much reduced as to be microscopic”.

Relation. Schmid 1955:193, “Ce genre est voisin de *Stenophylax* et de *Micropterna*.”

Genital character state combinations. (1) Presence (apomorphic) of spinulose protuberance on tergite VIII; (2) Reduced (apomorphic) state of tergite IX; (3) Sclerotized variously dentate (apomorphic) state of cerci; (4) Produced (plesiomorphic) state of the dorsal branch of paraproct; (5) Separate free from each-other (plesiomorphic) state of the dorsal branch of paraproct; (6) Separate free-from-cerci (plesiomorphic) state of the

dorsal branch of paraproct; (7) Reduced (apomorphic) state of the ventral branch of paraproct; (8) Separate free from each-other (plesiomorphic) state of the ventral branches of paraproct.

Parameres. Stout spiniform paramere shaft with roundly upward curving apical half. Paramere tip simple, bifid-trifid or the apical region armed with several spine-like setae.

***Mesophylax aspersus* (Rambur, 1842)**

(Figure 221)

Material examined. **Bulgaria**, Eastern Rhodopi, Byala Reka River, Zhultichalskoto dere near Meden Buk Village, Ivaylovgrad District, 111m, N41°22'48" E26°01'39", 3.V.2013, at lamps, light traps leg. S. Beshkov & B. Beshkovi, (1 male, OPC).

Parachiona Thomson, 1891

(Figure 222)

Original differential diagnosis. Formal delineation is not given.

Relation. Schmid 1955:187, "Le genre *Parachiona* est très voisin de *Enoicyla*, mais se révèle moins spécialisé par son faible dimorphisme sexuel. Par beaucoup de caractères de l'armature génitale du ♂, il se révèle voisin de *Stenophylax* et *Anisogamus*."

Genital character state combinations. (1) Presence (apomorphic) of spinulose protuberance on tergite VIII; (2) Reduced (apomorphic) state of tergite IX; (3) Setose inerm (plesiomorphic) state of cerci; (4) Produced (plesiomorphic) state of the dorsal branch of paraproct; (5) Separate free from each-other (plesiomorphic) state of the dorsal branch of paraproct; (6) Separate free-from-cerci (plesiomorphic) state of the dorsal branch of paraproct; (7) Reduced (apomorphic) state of the ventral branch of paraproct; (8) Separate free from each-other (plesiomorphic) state of the ventral branches of paraproct.

Parameres. Spiniform structure roundedly arching upward along the entire shaft without any spines. Apex is blunt pointed.

***Parachiona picicornis* (Pictet, 1834)**

(Figure 222)

Material examined. **Romania**, Apuseni Mts. Muntii Gilaului, Caps, stream Iara, N46°35.688' E23°15.067', 979m, 27.V.2013, singled leg. J. Oláh, E. Bajka, Cs. Balogh, & G. Borics (1 male, OPC).

Philocasca Ross, 1941

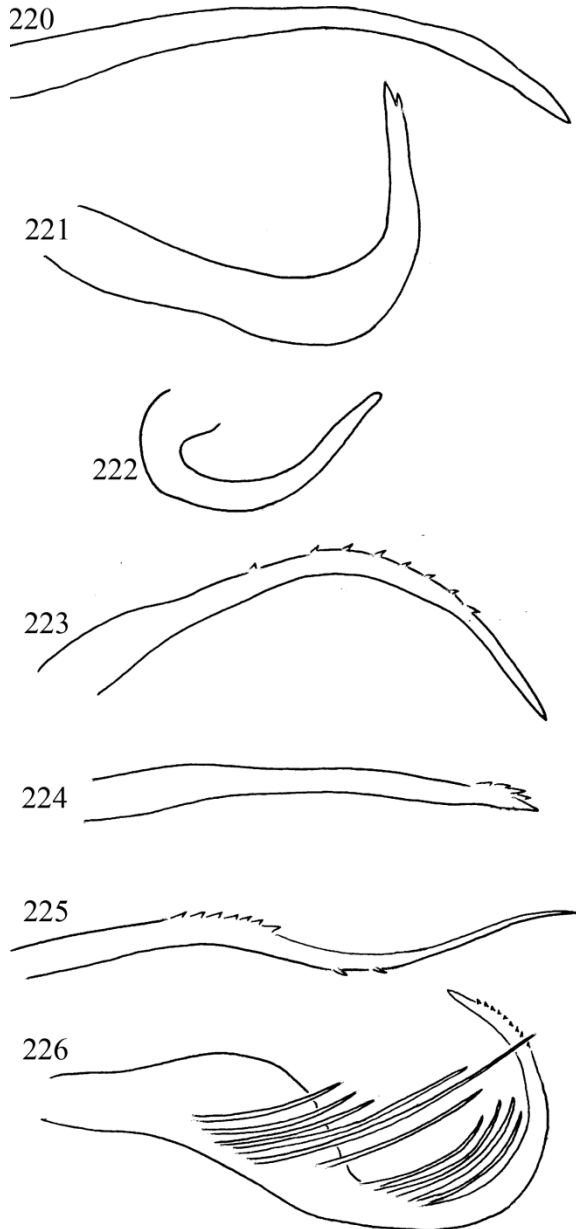
(Figure 223)

Original differential diagnosis. "This genus is apparently most closely related to *Anisogamus* but may be distinguished from it by the fused condition of Sc and R1 in the hind wing."

Relation. This genus is close to *Hydatophylax* (Schmid 1955).

Genital character state combinations. (1) Absence (plesiomorphic) of spinulose protuberance on tergite VIII; (2) Reduced (apomorphic) state of tergite IX; (3) Setose inerm (plesiomorphic) state of cerci; (4) Produced (plesiomorphic) state of the dorsal branch of paraproct; (5) Separate free from each-other (plesiomorphic) state of the dorsal branch of paraproct; (6) Separate free-from-cerci (plesiomorphic) state of the dorsal branch of paraproct; (7) Reduced (apomorphic) state of the ventral branch of paraproct; (8)) Separate free from each-other (plesiomorphic) state of the ventral branches of paraproct.

Paramere. Parameres form highly sclerotized spines of various lengths. *P. demita* has the longest spine-like paramere that is downward curving and has some very small setae, minute spines or alveoli on the dorsum. The parameres are getting abbreviated in the sequence of *demita-rivularis-oron-banksi-antennata-alba-thor*.



Figures 220–226. Parameres of *Simaphylax*, *Mesophylax*, *Parachiona*, *Philocasca*, *Platyphylax* and *Potamophylax* genera. 220 = *Simaphylax triangulifera*, 221 = *Mesophylax aspersus*, 222 = *Parachiona picicornis*, 223 = *Philocasca demita*, 224 = *Platyphylax frauenfeldi*, 225 = *Potamophylax fesus*, 226 = *P. seprus*.

***Philocasca demita* Ross, 1941**

(Figure 223)

Material examined. USA, Oregon, Lincoln Co. Flynn Cr., gate area to Cliff strm. trib. in

Salmon-berry bushes, 22.III.1982, leg B. Wisseman (2 males, ROM; 2 males OPC).

***Platyphylax* McLachlan, 1871**

(Figures 224, 227–234)

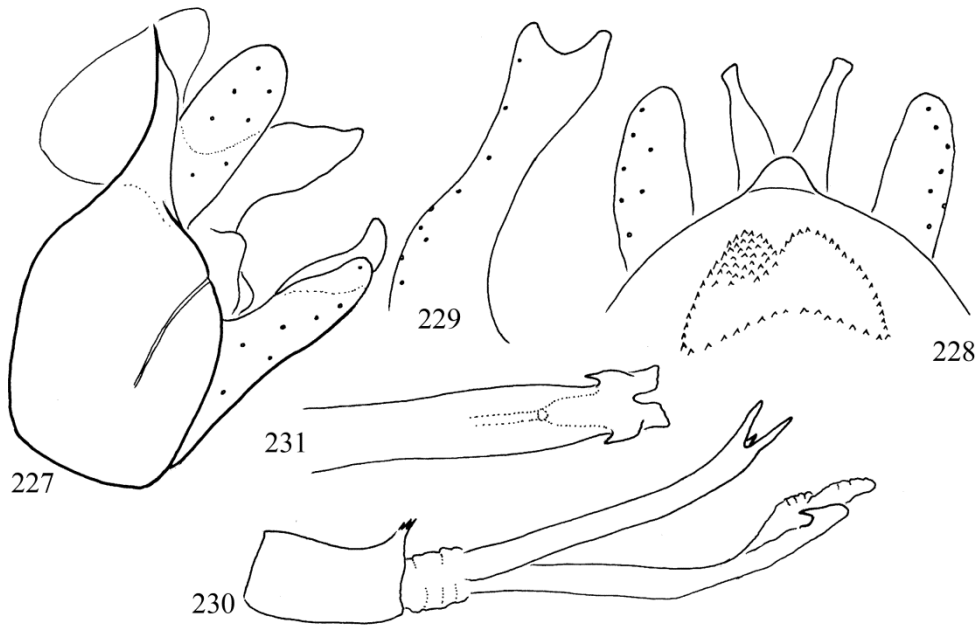
Original differential diagnosis. McLachlan 1871:109–110, “Agreeing in almost every respect with the typical forms of *Stenophylax* (e.g. *hieroglyphicus*, *striatus* &c.), but with only 1,2,2 spurs instead of 1,3,4.”

Relation. Schmid 1955: 182, “*Platyphylax* est très voisin de *Halesus* par les grandes lignes de l’armature génitale des deux sexes et surtout par la structure de l’appareil vaginal”

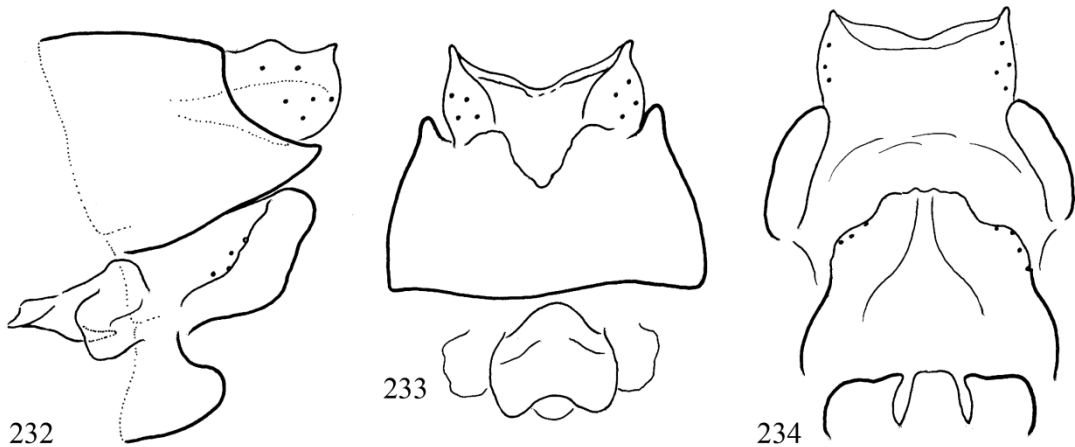
Genital character state combinations. (1) Presence (apomorphic) of spinulose protuberance on tergite VIII; (2) Reduced (apomorphic) state of tergite IX; (3) Setose inerm (plesiomorphic) state of cerci; (4) Produced (plesiomorphic) state of the dorsal branch of paraproct; (5) Separate free from each-other (plesiomorphic) state of the dorsal branch of paraproct; (6) Separate free-from-cerci (plesiomorphic) state of the dorsal branch of paraproct; (7) Reduced (apomorphic) state of the ventral branch of paraproct; (8)) Separate free from each-other (plesiomorphic) state of the ventral branches of paraproct.

Paramere. The parameres form a simple digitiform structure with variously patterned bifid or multifid apices formed by spine-like modified setae.

Taxonomic state. This genus originally contained four known species, but Schmid (1955) has removed with justification three species and *Platyphylax* became a monobasic genus. We have found the second species of the genus in the Balkan Mountains and describe here as *Platyphylax beshkovi* sp. nov. Like many other limnephiline taxa the *Platyphylax* genus has the mostly neutral periphallic structures and their character combination very similar to many other limnephiline genera, notably close to *Agaphylax balcanicus*, and distinguished only by the specific structure of the phallic organ.



Figures 227–231. *Platyphylax beshkovi* Oláh, sp. nov. Holotype male: 227 = genitalia in left lateral view, 228 = genitalia in dorsal view, 229 = gonopod in ventro-perpendicular view, 230 = phallic organ in lateral view, 231 = paramere in dorsal view.



Figures 232–234. *Platyphylax beshkovi* Oláh, sp. nov. Allotype female: 232 = genitalia with the vaginal sclerite complex in left lateral view, 233 = genitalia with the vaginal sclerite complex in dorsal view, 234 = genitalia in ventral view.

***Platyphylax beshkovi* Oláh, sp. nov.**

(Figures 227–234)

Material examined. Holotype: **Albania**, Delvina Region, Syri i Kaltër near Bistrice Village, 155 m, N39°55'23"; E020°11'30" 23.X.2017, leg. S. Beshkov & A. Nahirnic (1 male, OPC). Allotype: Albania, Gjirokastër county Finiq mu-

nicipality, Syri i Kaltër spring, N39°55'23", E020°11'30", 155 m, 3.XI.2018, leg. S. Beshkov & A. Nahirnic (1 female, OPC). Paratype: same as holotype (1 male, OPC). Albania, Gjirokastër county, Finiq municipality, Syri i Kaltër spring, N39°55'23", E020°11'30", 155 m, 3.XI.2018, leg. S. Beshkov & A. Nahirnic (17 males, 23 females; OPC)

Diagnosis. This new species is close to *Platyphylax frauenfeldi*, but differs by having apices of gonopods bilobed, not pointed, cerci elongated, not subtriangular, paraproct elongated, not short. The paramere tip bifid, not multifid.

Description. Male (in alcohol). Large-sized taxon. Yellowish light brown-coloured animal; forewing light-brown-coloured with speckled darker brown spots dominating on the apical half of the forewing of the male, indiscernible at females. Spurs: male:133. female:134. Forewing length 25 mm.

Male genitalia. Tergite VIII with spinulose protuberance, with anchoring strong setae, short spines or pegs, that is with setate or spinate area. Segment IX long almost subovoid in lateral view with short dorsal strap. Cavity of segment X lined by cerci and subdivided by a dorsomesal inner ridge, very pronounced. Cerci robust, elongated. Paraproct as long as cerci. Gonopod bilobed. Phallic organ with aedeagus supplied with a pair of backward curving hook-like spines and with paramere of simple rod with bifid apex; there is an additional very small spine in the basement of the bifid apex.

Female genitalia. There is a closed “anal tube” formed by the complex of the fused tergite IX and segment X; this tube that is more or less closed at many limnephilid females. Tergite IX with narrowing, almost pointed apicolateral processes in lateral view and with a triangular apicomeresal excision in dorsal view. Sternite IX represented by setose surface, not very pronounced in lateral and ventral view; the mesal plate constricted posterad, widened anterad; this glabrous ventral surface of sternite IX functions like the upper vaginal lip present as a free supragenital plate. Segment X represented by a closed ring heavily setose laterad and with a small pointed process dorsoapical. The lower vaginal lip, the vulvar scale visible somewhat separated from sternite VIII by its more sclerotized structure; the mesal lobe as long as the lateral lobes. Vaginal sclerite complex short.

Etymology. Named after the collector, Stoyan Beshkov, devoted lepidopterologist, sophisticated and very efficient field collector of caddisflies on the Balkan Peninsula.

***Platyphylax frauenfeldi* Brauer, 1857**

(Figure 224)

Material examined. **Hungary**, Szentborbás, River Dráva, 25.X.1981, light leg. Á. Uherkovich (3 males, 1 female; OPC). **Hungary**, Órtilos, River Dráva, 22.X.1991, light leg. Á. Uherkovich (2 males, OPC). **Hungary**, Órtilos, River Dráva, 21.X.1996, light leg. Á. Uherkovich (2 females, OPC). **Hungary**, Vízvár, Dráva part, N46°05'13" E17°13'27", leg. S. Nógrádi & Á. Uherkovich (1 male, OPC)

***Potamophylax* Wallengren, 1891**

(Figures 225–226)

Original differential diagnosis. Formal delineation is not given.

Relation. Schmid 1955:175, “Peut-être le genre *Potamophylax* est-il le plus primitive de la tribu?”

Genital character state combinations. (1) Presence (apomorphic) of spinulose protuberance on tergite VIII; (2) Reduced (apomorphic) state of tergite IX; (3) Setose inerm (plesiomorphic) state of cerci; (4) Produced (plesiomorphic) state of the dorsal branch of paraproct; (5) Separate free from each-other (plesiomorphic) state of the dorsal branch of paraproct; (6) Separate free-from-cerci (plesiomorphic) state of the dorsal branch of paraproct; (7) Reduced (apomorphic) state of the ventral branch of paraproct; (8) Separate free from each-other (plesiomorphic) state of the ventral branches of paraproct.

Parameres. Spiniform structure armed with various numbers of spine-like modified setae on various regions of the shaft.

***Potamophylax cingulatus* species group**

***Potamophylax fesus* Oláh, 2018**

(Figure 225)

Material examined. Holotype: **Macedonia**, Pe-lister Mts. Planinarski Dom “Shiroka”, 1955 m,

N41°00'17" E21°10'07", 6.VIII.2016, leg. S. Beshkov & A. Nahirnic (1 male, OPC).

***Potamophylax seprus* Oláh, Lodovici & Valle, 2011**

(Figure 226)

Material examined. Holotype. **Albania**, Skrapar County, Tomor Mts, Kulmak Pass, mountain grassland near the bektashi teqe, N40°37.116' E20°11.945', 1485m, 23.VIII.2006, leg. Z. Fehér, A. Hunyadi, T. Huszár & D. Murányi, (1 male, HNHM).

***Psilopterna* Martynov, 1914**

(Figure 235)

Original differential diagnosis. Formal delineation is not given.

Relation. Martynov 1914b:422, "This genus belongs to the group of *Drusus* and is allied to *Psilopteryx* Stein." Schmid 1959:787, "Il est voisin et probablement issu de *Mesophylax* en commun avec lequel il présente les caractères de la nervulation. Par les formules calcariennes et les genitalia, il est beaucoup plus spécialisé."

Genital character state combinations. (1) Presence (apomorphic) of spinulose protuberance on tergite VIII; (2) Reduced (apomorphic) state of tergite IX; (3) Setose inerm (plesiomorphic) state of cerci; (4) Produced (plesiomorphic) state of the dorsal branch of paraproct; (5) Separate free from each-other (plesiomorphic) state of the dorsal branch of paraproct; (6) Separate free-from-cerci (plesiomorphic) state of the dorsal branch of paraproct; (7) Reduced (apomorphic) state of the ventral branch of paraproct; (8) Separate free from each-other (plesiomorphic) state of the ventral branches of paraproct.

Parameres. Extremely enforced structure produced into a pair of heavily sclerotized enlarged process.

Remarks. This small Middle Asian genus with only four known species is very interesting and

unique in having three genital transformation series preserved in this small lineage. (1) Transformation series with the absence (plesiomorphic) or the presence (apomorphic) of spinulose protuberance on tergite VIII is represented from the absence at *P. pezvovi*, through initiation at *P. alageza*, presence at *P. hirsuta*, to the very pronounced development of the spinulose protuberance at *P. eukratida*. (2) Transformation series with the produced (plesiomorphic) or reduced (apomorphic) state of the dorsal branch of paraproct is represented from very produced at *P. alageza*, produced at *P. eukratida*, slightly produced at *P. hirsuta* and reduced at *P. pezvovi*. (3) Transformation series with separate free-from-cerci (plesiomorphic) or fused to-cerci (apomorphic) state of the dorsal branch of paraproct is represented by slightly fused at *P. pezvovi* to more fused at *P. eukratida*, *P. hirsuta* and most fused at *P. alageza*.

***Psilopterna alageza* Oláh, 1981**

(Figure 235)

Material examined. Holotype: **Armenia**, Alagez, 2–3.VI.19551, leg. Zaguljajev (1 male, OPC). **Turkey**, Van Province, Yuksekova Mts., 2.5 km E of Guseldere Pass, 38°11'N 43°56'E, 2600 m, 2.VII.2002, leg. B. Benedek & T. Csövári (3 males, OPC). Van Province, Yuksekova Mts., 2.5 km E of Guseldere Pass, 38°11'N 43°56'E, 2600 m, 5.VII.2002, leg. B. Benedek & T. Csövári (1 male, OPC).

***Psilopterna eukratida* Schmid, 1961**

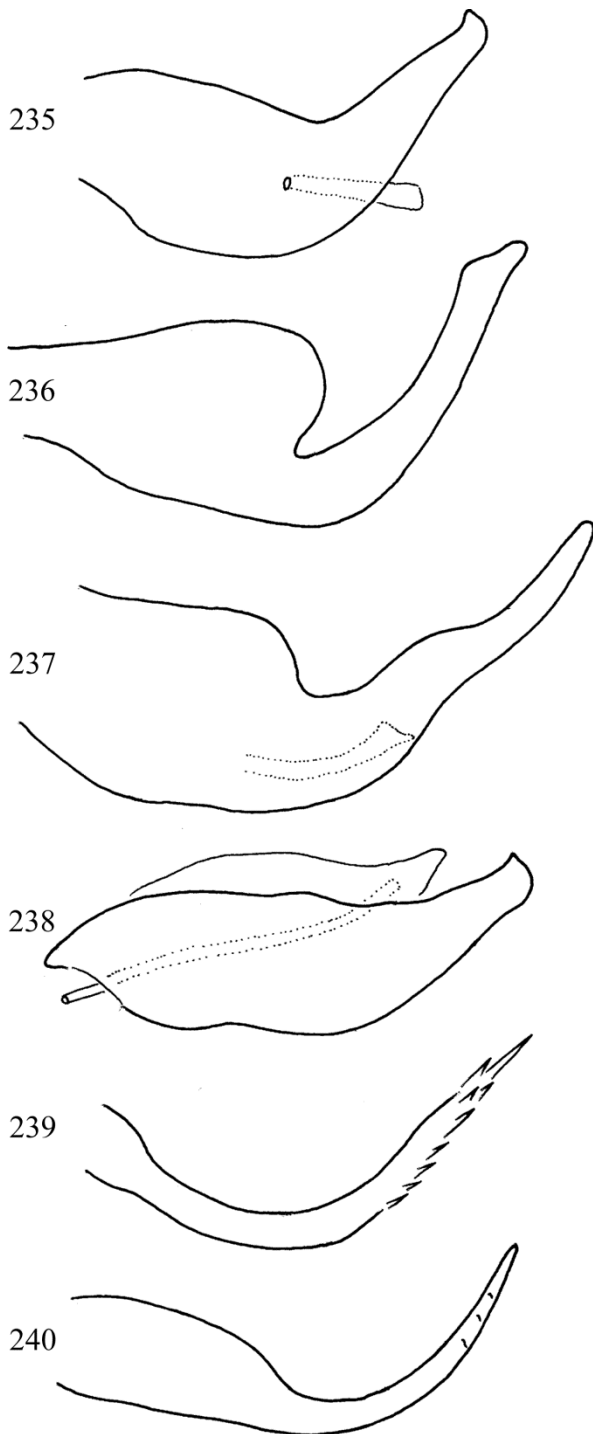
(Figure 236)

Material examined. **Pakistan**, Hindukush Mts. 5 km E. of Shandur Pass, 3750 m, 21.VIII.2001, leg. B. Benedek & G. Ronkay (2 males, HNHM).

***Psilopterna hirsuta* Martynov, 1928**

(Figure 237)

Material examined. **Uzbekistan**, Fergansk, Jordan, 26–27.IX.1985, light leg. Z. Varga (1 male, OPC).



Figures 235-240. Parameres of *Psilopterna*, *Rhadicoleptus* and *Stenophylax* genera. 235 = *Psilopterna alageza*, 236 = *P. eukratida*, 237 = *P. hirsuta*, 238 = *P. pezvovi*, 239 = *Rhadicoleptus meridiocarpaticus*, 240 = *Stenophylax permistus*.

***Psilopterna pezvovi* Martynov, 1914**

(Figure 238)

Material examined. **Armenia**, Jerevan, Zoo-park, 16.V.1955, light leg. Zaguljavev (1 male, 1 female; OPC). **Armenia**, Jerevan, 15-16.VI.1955, light leg. Zaguljavev (1 male, OPC). **Turkmenistan**, Kopet-Dagh Mts., Ipay-Kala, 26.VI.1992, light leg. Gy. Fábian, B. Herczig, A. Podlussány & Z. Varga (1 male, OPC).

***Pycnopsyche* Banks, 1905**

Original differential diagnosis. Banks, 1905:9, Formal delineation is not given.

Relation. Banks, 1905:9, "Hagen put it in *Halesus*, Walker described it as a *Neuronia*; I have kept in *Stenophylax*, but it is better in a new genus." According to Schmid (1955) *Pycnopsyche* is very close to *Hydatophylax*.

Genital character state combinations. (1) Presence (apomorphic) of spinulose protuberance or neoformations on tergite VIII; (2) Reduced (apomorphic) state of tergite IX; (3) Setose inerm (plesiomorphic) state of cerci; (4) Produced (plesiomorphic) state of the dorsal branch of paraproct; (5) Separate free from each-other (plesiomorphic) state of the dorsal branch of paraproct; (6) Separate free-from-cerci (plesiomorphic) state of the dorsal branch of paraproct; (7) Reduced (apomorphic) state of the ventral branch of paraproct; (8) Separate free from each-other (plesiomorphic) state of the ventral branches of paraproct.

Paramere organisation. Possessing membranous bases and four modified paramere shaft or stylet of Wojtowicz (1982): (1) single slender and elongate, (2) multiple slender and elongate, (3) stout with spinous apical region, (4) broadly bladelike.

Variability or limited knowledge? This genus, like many Nearctic limnephiline genera was found or thought to be represented by highly varying species (Wojtowicz 1982). This is a well-known position of limited knowledge. The recorded ap

parent variations could be products of various epistemic/epistemological shortages faced during analysis of microstructures. We have listed 11 types of error possibilities from the endless sources of our limited capacity and skill (Oláh et al. 2015). On the other hand, the variations could be real existing ontic/ontological inherent modalities (Oláh 2018). Neutral, non-adaptive traits are exposed to stochastic population effects and could be highly variable, but adaptive, non-neutral speciation traits under elaborated network of protective mechanisms are stable (Oláh & Oláh, 2017).

There is still no targeted research carried out on population samples of the Nearctic limnephilines including *Pycnopsyche* to distinguish between neutral and adaptive traits. There is no systemic research on variability and stability ranges of genitalic traits. Wojtowicz (1982) has discussed and listed the useful diagnostic characters of the genus: (1) wing coloration and pattern, (2) tibial spur formula, (3) spinulose protuberance and shape innovations of tergite VIII, (4) lateral (cerci) and mesal (paraproct) of segment X, (4) tips of gonopods, (5) paramere morphology. According to his final conclusion wing coloration and pattern, tibial spurs, tergite VIII are the most variable traits and certain genitalic structures are less variable.

During material exchanges, by courtesy of O. S. Flint, Jr. and J. C. Morse we have got nine species and a few population samples of specimens of *Pynopsyche* genus in order to examine the organisation of their parameres. When preparing and examining the parameres we were surprised to discover sibling species in that few population samples both under the name of *P. gentilis* and *P. flavata*. Examining the population samples of *P. letova* sp. nov. we have found the paramere and gonopod tips as well as the paramere structure subtly but stably diverged with very narrow range of variation.

***Pycnopsyche aglona* Ross, 1941**

(Figure 141)

Material examined. **Canada**, Ontario, Nipissing Dist., Algonquin Park, Mud Creek, 27.VIII.1985, leg. R. Hall (2 males, 1 female; OPC). Ontario, Oro Station, 15.VIII.1952, leg. G. B. Wiggins, det. G.B. Wiggins, 1962 (1 male, ROM). Ontario, Kearney, Parry Sound Dist., at U. V. light, 2.–10.IX.1981, leg. G.B. Wiggins (4 males, ROM).

***Pycnopsyche antica* (Walker, 1852)**

(Figure 142)

Material examined. **USA**, South Carolina, Salem, Burgess Creek, 12.IX.1969, leg. J. Morse. Det. J. Morse (3 males, OPC).

***Pycnopsyche flavata* (Banks, 1914)**

(Figures 248–250)

Material examined. **USA**, Virginia, Grayson County, Grayson Highlands S. P. picnic area, E. of homestead display, 36.2895°N, 81.4786°W, 3910ft. 24.IX.2014, leg. S. M. Roble (1 male, 2 females; OPC).

***Pycnopsyche gentilis* (McLachlan, 1871)**

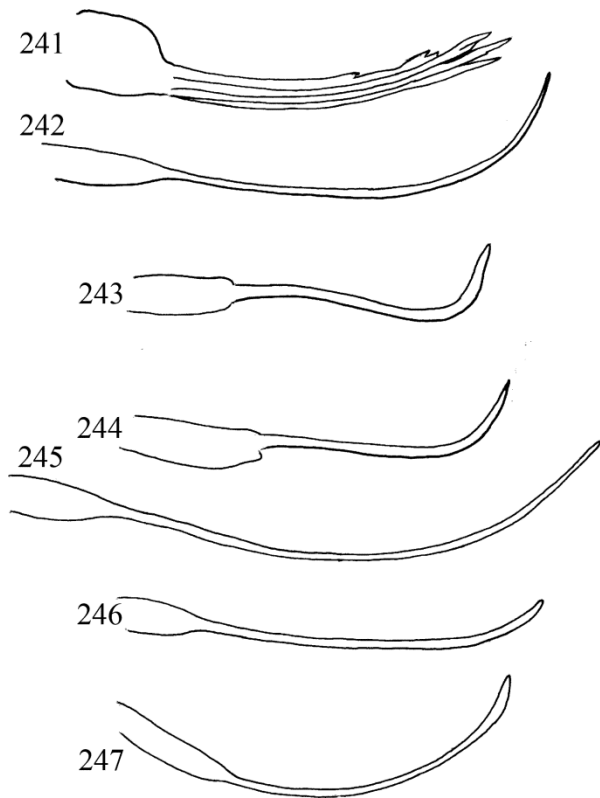
(Figures 251–253)

Material examined. **USA**, Virginia, Grayson County, Grayson Highlands S. P. picnic area, E. of homestead display, 36.2895°N, 81.4786°W, 3910ft. 24.IX.2014, leg. S. M. Roble (10 males, 1 female; OPC).

***Pycnopsyche indiana* (Ross, 1938)**

(Figure 143)

Material examined. **USA**, South Carolina, Aiken County, Upper Three Runs Creek, @ Road



Figures 241–247. Parameres of *Pycnopsyche* species. 241 = *Pycnopsyche aglona*, 242 = *P. antica*, 243 = *P. indiana*, 244 = *P. lepida*, 245 = *P. luculenta*, 246 = *P. scrabripennis*, 247 = *P. sonso*.

C br. crossing, Savannah River Site, 4.X.1990, leg. M. A. Floyd (3 males, OPC).

***Pycnopsyche lepida* (Hage, 1861)**

(Figure 144)

Material examined. USA, South Carolina, Aiken County, Savannah R Plant Upper Three Runs Cr, SRP 8-1, 19.–20.XI.1976, leg. Herlong, Prichard (5 males, OPC).

***Pycnopsyche letova* Oláh, sp. nov.**

(Figures 254–256)

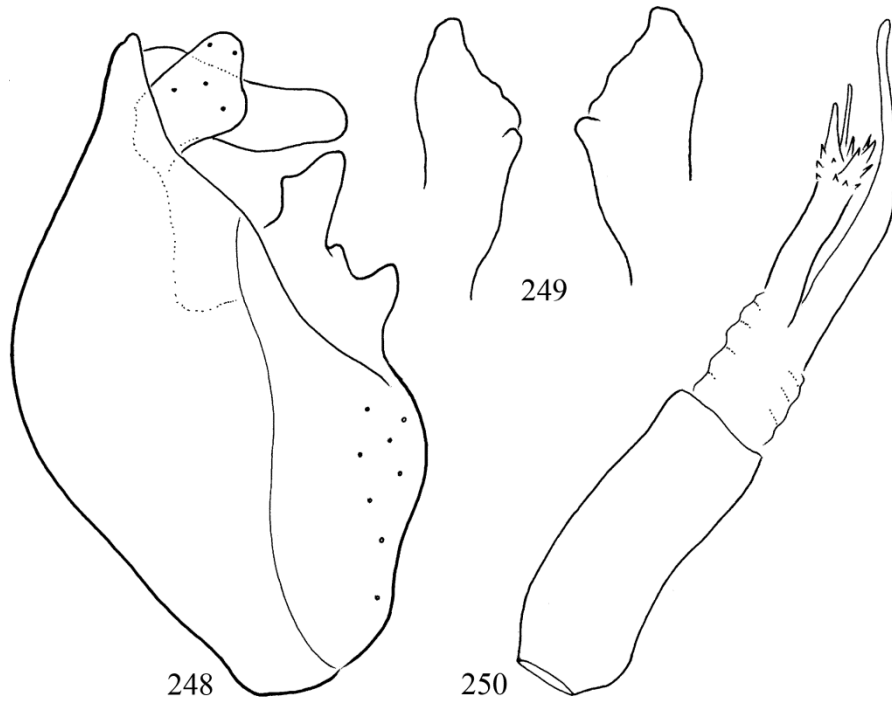
Material examined. Holotype: USA, Virginia, Fauquier County, Bull Run Mtn., Shurberg Home, 4566, Hopewell Rd., upper, 38.8678°N, 77.7035°W, 29.VIII–23.IX.2013, malaise trap, leg. D. R. Smith (male, NMNH). Paratypes: same as holo-

type (4 males, 2 females; NMNH). Virginia, Fauquier County, Bull Run Mtn., Shurberg Home, 4566, Hopewell Rd., lower, 38.86665°N, 77.70392°W, 18.IX–27.X.2014, malaise trap, leg. D. R. Smith (5 males, 1 female; OPC). Virginia, Fauquier County, Bull Run Mtn., Shurberg Home, 4566, Hopewell Rd., upper, 38.86786°N, 77.70338°W, 7.IX–7.X.2015, malaise trap, leg. D. R. Smith (12 males, 2 females; OPC).

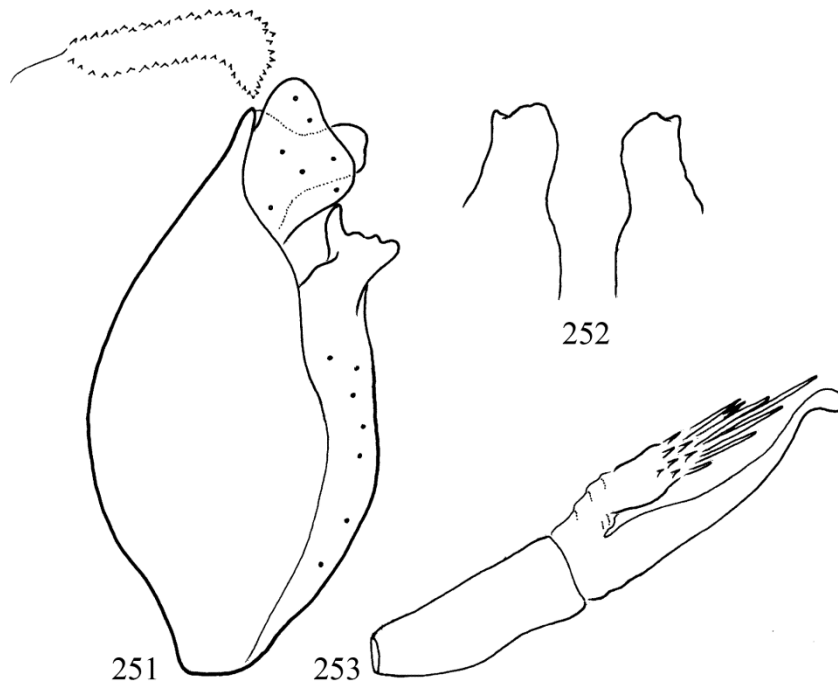
Diagnosis. Just demonstrating the fine phenomics of the speciation trait in the *Pycnopsyche* genus, as a test trial based on the available limited specimens, it seems that the lateral profile of the paramere, paraproct and probably the free tip of the gonopods exhibit stable divergences compared to his sibling species of *P. gentilis* McLachlan. Although as in the case of neutral traits there are significant variation in the shape and magnitude of the spinulose protuberance on tergite VIII, but the spinulose area of *P. letova* is much smaller compared to *P. gentilis*. The gonopod apices of the new species are short and pointed, not long and blunt. The shape divergence of the paraproct is very stable and we have given the name of the new species according to the shape divergence of the dorsal branch of the paraproct: it is low and downward arching, not high and straight and slightly produced upward. The shape divergence of paraproct is also remarkable: the robust sclerotized shaft is elongated almost triple and the apical spine brush is composed of short spines compared to *P. gentilis*.

Description. Male genitalia. Tergite VIII with medium-large spinulose protuberance on mesal position of dorsoapical margin. Segment IX long almost subovoid in lateral view with low and short dorsal strap. Cerci rounded setose without pronounced sclerotization. Paraprocts slightly shorter than cerci. Gonopod apices short with pointed configuration in apical view. Parameres of the phallic organ with long stout sclerotized shaft, the apical spine brush much shorter than the paramere shaft.

Etymology. *letova* from “le és tova ” downward and further spill in Hungarian, refers to the lateral profile of the dorsal branch of paraproct arching further downward.



Figures 248–250. *Pycnopsyche flavata* (Banks) 1914. 248 = genitalia in left lateral view, 249 = gonopods in ventro-perpendicular view, 250 = phallic organ in lateral view.



Figures 251–253. *Pycnopsyche gentilis* (McLachlan) 1871. 251 = genitalia in left lateral view, 252 = gonopods in ventro-perpendicular view, 253 = phallic organ in lateral view.

***Pycnopsyche luculenta* (Betten, 1934)**

(Figure 245)

Material examined. USA, South Carolina, Barnwell County, Savannah R Plant, Lower Three Runs Cr, nr. SRP roads 8&8-8, 12.-13.X.1979, leg. L. Kelley & E. McEwan (3 males, 1 female; OPC).

***Pycnopsyche scabripennis* (Rambur, 1842)**

(Figure 246)

Material examined. USA, Georgia, Crawford County, Spring Creek above pond at Camp Eunice, 5 min SSE of Roberta, 20.X.1983, leg. R. W. Holzenthal & S. W. Hamilton (3 males, OPC).

***Pycnopsyche sonso* (Milne, 1935)**

(Figure 247)

Material examined. USA, South Carolina, Oconee County, n.fk. Limberpole Cr., SC hwy 130, 1960 alt., 16.-17.IX.1997, leg. Hoffman, English. Det. M. A. Floyd, 1995 (3 males, OPC).

***Pycnopsyche telea* Oláh, sp. nov.**

(Figures 257–259)

Material examined. Holotype: USA, South Carolina, Oconee County, Howard Creek, (right fork) off hwy S-413, 2420' alt., Duke loc. 577.0, 18.-19.VI.1987, leg. Hamilton, Det. M.A. Floyd, 1994 (1 male, CUAC). Paratypes: same as holotype (2 males, OPC).

Diagnosis. The reliability of morphological divergence estimated on the small population sample of the three male specimens of *P. telea* sp. nov. is supported by those of the 22 male paratypes of *P. letova* sp. nov. *P. telea* sp. nov. is a sibling species of *P. flavata* Banks but diverged by the shape of gonopod tip, paraproct and paramere. The new species has the tip of gonopod blunt, not pointed in caudal view, paraproct elongated, not short and the paramere has apical spine pattern fully and regularly packed with gradually elongating spines; in contrary *P. flavata* has the apical spine pattern on the paramere organised in bilobed pattern.

Description. Male genitalia. Tergite VIII without any spinulose protuberance. Segment IX long almost subovoid in lateral view with low and short dorsal strap. Cerci with truncate apical margin without pronounced sclerotization. Paraprocts are only slightly longer than cerci. Gonopod free apices with blunt configuration in apical view. Parameres of the phallic organ with long stout sclerotized shaft, the apical spine brush starts from the middle and fully and densely packed with gradually elongating spines.

Etymology. *telea* from “*telea*” full of something in Hungarian, refers to the apical spine brush pattern fully packed by gradually elongating spines.

***Rhadicoleptus* Wallengren, 1891**

(Figure 239)

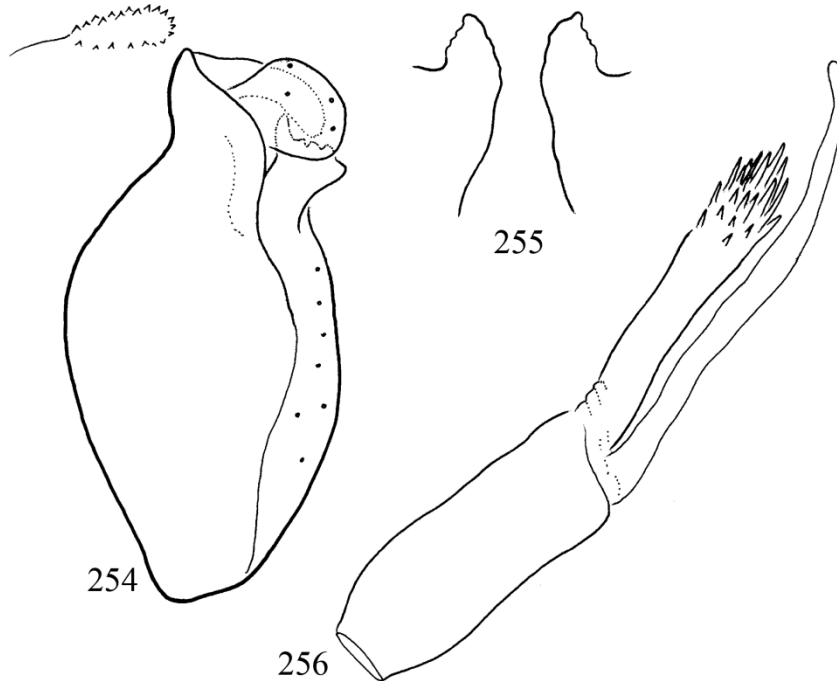
Original differential diagnosis. Formal delineation is not given.

Relation. Schmid 1955:167, “Le genre *Rhadicoleptus* est assez éloigné de *Limnophilus*... La coloration des ailes antérieures de *alpestris* se rapproche fort de celle des *Asynarchus*.”

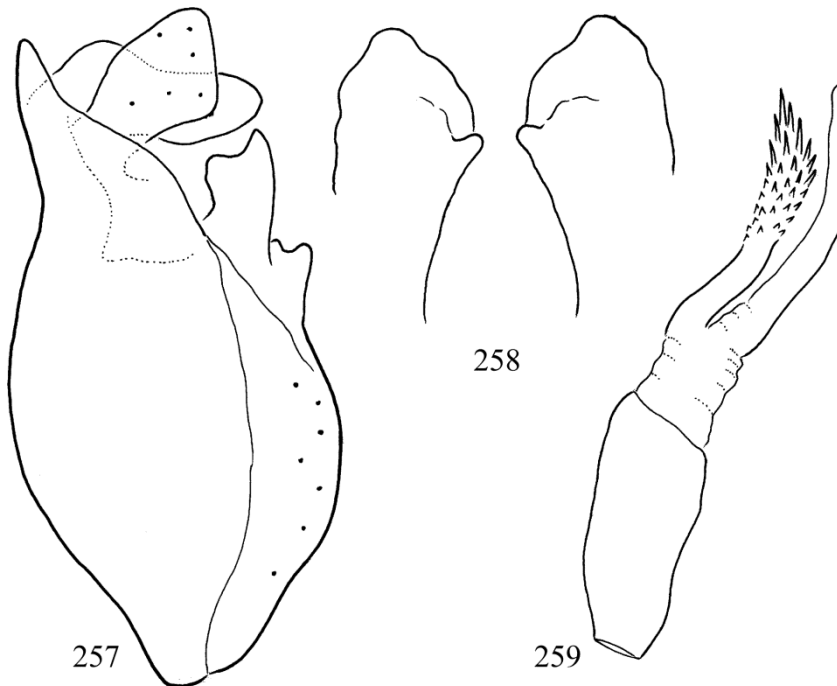
Genital character state combinations. (1) Presence (apomorphic) of spinulose protuberance on tergite VIII; (2) Reduced (apomorphic) state of tergite IX; (3) Setose inerm (plesiomorphic) state of cerci; (4) Produced (plesiomorphic) state of the dorsal branch of paraproct; (5) Separate free from each-other (plesiomorphic) state of the dorsal branch of paraproct; (6) Separate free-from-cerci (plesiomorphic) state of the dorsal branch of paraproct; (7) Reduced (apomorphic) state of the ventral branch of paraproct; (8) Separate free from each-other (plesiomorphic) state of the ventral branches of paraproct.

Parameres. Spiniform structure armed with various numbers of spine-like modified setae on various regions of the shaft.

Taxonomic status. Schmid (1955) has placed the genus *Rhadicoleptus* in his newly created tribe *Limnophilini* with some uncertainty. The *Rhadi*



Figures 254–256. *Pycnopsyche letova* Oláh, sp. nov. Holotype male: 254 = genitalia in left lateral view, 255 = gonopods in ventro-perpendicular view, 256 = phallic organ in lateral view.



Figures 257–259. *Pycnopsyche telea* Oláh sp. nov. Holotype male: 254 = genitalia in left lateral view, 255 = gonopods in ventro-perpendicular view, 256 = phallic organ in lateral view.

coleptus genus was removed from the Limnephilini tribe and placed into the Stenophylacini tribe by its particular paramere organisation (Oláh et al. 2015).

***Rhadicoleptus meridiocarpaticus* Botosaneanu & Riedel, 1965**

(Figure 239)

Material examined. **Romania**, Apuseni Mts. Muntii Gilaului, Statiunea Muntele Baisorii, La Mocirle, spring stream, N46°30.241' E23°15.550', 1552m, 19-20.VI.2015, singled leg. J. Oláh, Cs. Balogh, & P. Juhász (3 males, 1 female; OPC).

***Stenophylax* Wallengren, 1891**

(Figure 240)

Original differential diagnosis. Formal delineation is not given.

Relation. Schmid 1955:191, “Il est extrêmement semblable – et même identique – à *Micropterna*, présente de nombreux caractères communs avec *Mesophylax* et partage certaines particularités avec *Anisogamus* et le groupe de *Enoicyla*.”

Genital character state combinations. (1) Presence (apomorphic) of spinulose protuberance on tergite VIII; (2) Reduced (apomorphic) state of tergite IX; (3) Setose inerm (plesiomorphic) state of cerci; (4) Produced (plesiomorphic) state of the dorsal branch of paraproct; (5) Separate free from each-other (plesiomorphic) state of the dorsal branch of paraproct; (6) Separate free-from-cerci (plesiomorphic) state of the dorsal branch of paraproct; (7) Reduced (apomorphic) state of the ventral branch of paraproct; (8) Separate free from each-other (plesiomorphic) state of the ventral branches of paraproct.

Parameres. Simple digitiform, variously arching rod with or without short apical spine-like outgrowths.

Taxonomical status. *Micropterna* cannot be considered as a really distinct genus from *Stenophylax*.

nophylax. This is clearly confirmed by their similar phallic organ with similar parameres.

***Stenophylax permistus* McLachlan, 1895**

(Figure 240)

Material examined. **Bosnia & Herzegovina**, Banja Luka region, Kozara Mts, Kozarac, Zofik Stream, N44°59.968', E16°52.946', 450 m, 25.V. 2012, leg. T. Kovács & G. Puskás (4 males, OPC).

***Thermophylax* Nimmo, 1995**

Material examined. No specimen was available for direct examination.

Original differential diagnosis. Formal delineation is not given.

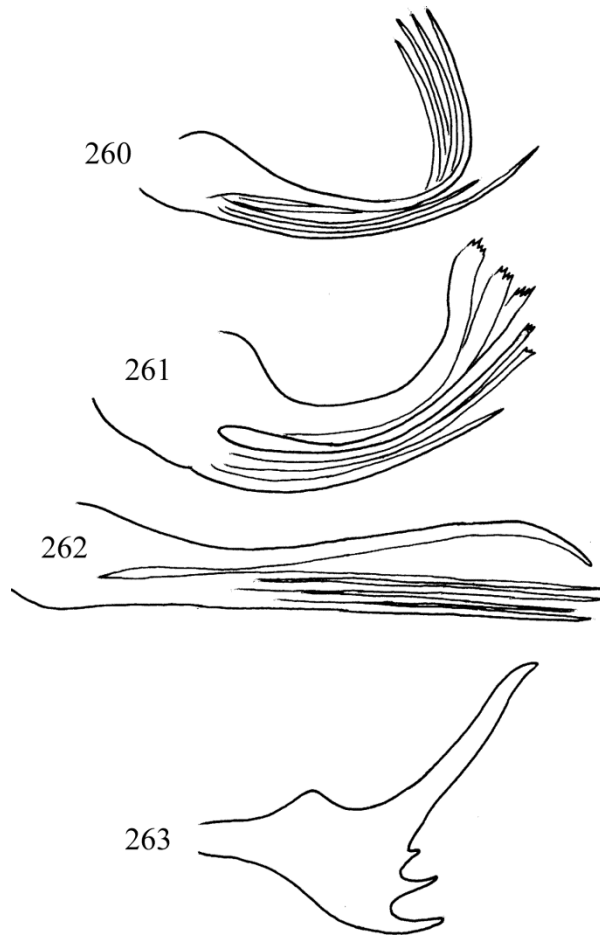
Relation. Nimmo 1995:5–6, “General habitus typically limnephiline. I cannot relate this genus more closely at this time.”

Genital character state combinations. Drawing details are not sufficient enough to determine the character state combination of this genus

Parameres. Simple digitiform, with some apical setae.

Hesperophylacini tribe

The ancestor of this unique small tribe is organised by integration of drastic interactive external and internal perturbations. The basic pattern of parameres in this small tribe with three small genera is only characterized by short shaft followed apically with broom-like burst of strongly sclerotized and variously recurved or curving long spines. This paramere architecture is highly differs from the basic patterns of simple setose rod type in the Limnephilini tribe, of the slender spine type of the Chilostigmini tribe, of the simple setose rod with heavy enforcement type in the Chaetopterygini tribe and of the simple spiny rod type in the Stenophylacini tribe.



Figures 260–263. Parameres of *Crenophylax*, *Hesperophylax*, *Psychoronia* and *Agaphylax* genera. 260 = *Crenophylax sperryi*, 261 = *Hesperophylax designatus*, 262 = *Psychoronia brooksi*, 263 = *Agaphylax balcanicus*.

***Crenophylax* Ruiter & Nishimoto, 2007**

(Figure 260)

Original differential diagnosis. Formal delineation is presented and discussed in details.

Relation. Ruiter & Nishimoto, 2007:321, “belongs to a group very closely related with *Hesperophylax* and *Psychoronia*.”

Genital character state combinations. (1) Presence (apomorphic) of spinulose protuberance on tergite VIII; (2) Reduced (apomorphic) state of tergite IX; (3) Setose inerm (plesiomorphic) state of cerci; (4) Produced (plesiomorphic) state of the

dorsal branch of paraproct; (5) Separate free from each-other (plesiomorphic) state of the dorsal branch of paraproct; (6) Separate free-from-cerci (plesiomorphic) state of the dorsal branch of paraproct; (7) Produced (plesiomorphic) state of the ventral branch of paraproct; (8) Separate free from each-other (plesiomorphic) state of the ventral branches of paraproct.

Parameres. Paramere shaft short and stout with up and laterad turning long 4-5 dorsal spines running along independtly and accompanied with 2-3 ventral spines only slightly arching upward, but not turning laterad.

***Crenophylax sperryi* (Banks, 1943)**

(Figure 260)

Material examined. USA, New Mexico, Lincoln County, tributary to North Fork Rio Ruidoso, N33.39906°, W105.78890°, 3.VI.2010, at light, leg. D. Ruiter (4 males, 1 female; OPC).

***Hesperophylax* Banks, 1916**

(Figure 261)

Original differential diagnosis. Formal delineation is not given.

Relation. Schmid 1955: 169, “*Hesperophylax* est un genre intermédiaire entre les Limnephilini et les Stenophylacini.”

Genital character state combinations. (1) Presence (apomorphic) of spinulose protuberance on tergite VIII; (2) Reduced (apomorphic) state of tergite IX; (3) Setose inerm (plesiomorphic) state of cerci; (4) Produced (plesiomorphic) state of the dorsal branch of paraproct; (5) Fused to each-other (apomorphic) state of the dorsal branch of paraproct; (6) Separate free-from-cerci (plesiomorphic) state of the dorsal branch of paraproct; (7) Reduced (apomorphic) state of the ventral branch of paraproct; (8) Fused to each-other (apomorphic) state of the ventral branches of paraproct.

Parameres. Paramere shaft stout, the dorsal part is longer. There are two partially separated bundles of long spines with various curvatures

and apical pattern; spines of dorsal bundle stronger.

Remarks. We have examined the lateral profile of cerci, paraprocts and parameres of several specimens in four species. It seems that their species status is rather uncertain. Both the old identifications and the old drawings are frequently contradicting. Unfortunately in the most update publication (sic!) there are no paramere drawings for the species (Parker & Wiggins 1985). The published paraproct drawings from several locations under the same species name are treated as variations. Most probably they represent independent species. Examination, with fine phenomics on population samples, at least the lateral profiles of the paraproct and the lateral profile of the paramere is essential to delineate species.

***Hesperophylax alaskensis* (Banks, 1908)**

Material examined. USA, Utah, Cache county, Wasatch Mts, Logan Canyon, Spring Hollow Creek at Spring Hollow Camping, 7.IX.2011, 1550m, N41°45.153' W111°42.948' leg. R. Baumann, S. Clark, & D. Murányi (1 male, OPC). Utah, Cache county, Wasatch Mts, Logan Canyon, Rick's Spring and its outlet, 7.IX.2011, 1780m, N41°50.383' W111°35.334' leg. R. Baumann, S. Clark & D. Murányi (2 males, 1 female; OPC).

***Hesperophylax designatus* (Walker, 1852)**

(Figure 261)

Material examined. USA, California, Modoc County, Warner Mts., Cedar Pass, 6000', 6.VIII.1965, black light leg. E. & I. Munroe (1 male, CNC). California, Modoc County, Warner Mts., Cedar Pass, 6000', 10.VIII.1965, black light leg. E. & I. Munroe (1 male, CNC). USA, Colorado, 10 mi. East of Mancos, Hwy, 160, 3' wide rocky cool str., 2.VII.1960, leg. A. G. Edmund (1 male, 1 female; OPC). Canada, British Columbia, Alaska Hwy. km 359, Prophet R. Prov. Pk., 9.VIII.1979, u.v.light ROM 791199, leg. ROM Field Party (2 males, ROM). Alberta, Banff National Park, Alta, Johnston Canyon Cpgrd.,

30.VII.–4.VIII.1969, ROM690278, UVL leg. ROM Field Party (1 male, ROM). Alberta, Banff National Park, Alta, roadside spr. on rd to Sundance Canyon, 22.VII.1962, leg. G.B. Wiggins (1 female, ROM). Alberta, Alta, Elkwater County, Reesor L. Cpgrd., Drinking Water Spring, ½ mi. up hill from cpgrd, 19.VIII.1981, leg. C. R. Parker (1 female, ROM).

***Hesperophylax magnus* (Banks, 1908)**

Material examined. USA, Arizona, Cochise County, Huachuca Mts., Miller Creek Canyon, Miller Creek, 0.5 mile west of Trailhead parking, at light leg. C.W. Melton (6 males, 2 females; OPC). Utah, Washington county, Beaver Dam Mts, Lytle Ranch Reserve, Beaver Dam Wash, streamshore soil and grass roots 1–2.XI.2011, 845m, N37°08.645' W114°01.462' leg. Sz. Czigány & D. Murányi (1 male, OPC). Utah, Washington county, Pine Valley Mts, Leeds-Silver Reef, Leeds Creek and its gorge 22.IX. 2011, 1200m, N37°15.990' W113°22.120' leg. S. Clark, D. Murányi, R. Nelson (1 male, 1 female; OPC).

***Hesperophylax occidentalis* Banks, 1918**

Material examined. USA, Arizona, Greer, White Mts., Apache County, 8500', 3.VIII.1962, black light leg. E. & I. Munroe, *Hesperophylax occidentalis* (Banks) ♂, det. Parker, 1982 (1 male, CNC). USA, Arizona, Greer, White Mts., Apache County, 8500', 4.VIII.1962, black light leg. E. & I. Munroe, *Hesperophylax occidentalis* (Banks) ♂, det. Parker, 1982 (1 male, CNC). USA, Utah, Wasatch county, Wasatch Mts, upper boggy springs of Cascade Springs, 18.IX.2011, 1920m, N40°27.505' W111°33.094' leg. Sz. Czigány & D. Murányi (1 male, 1 female; OPC).

***Psychoronia* Banks, 1916**

(Figure 262)

Original differential diagnosis. Formal delineation is not given.

Relation. Related to the *Crenophylax* and *Hesperophylax* genera.

Genital character state combinations. (1) Presence (apomorphic) of spinulose protuberance on tergite VIII; (2) Reduced (apomorphic) state of tergite IX; (3) Setose inerm (plesiomorphic) state of cerci; (4) Produced (plesiomorphic) state of the dorsal branch of paraproct; (5) Fused to each-other (apomorphic) state of the dorsal branch of paraproct; (6) Separate free-from-cerci (plesiomorphic) state of the dorsal branch of paraproct; (7) Reduced (apomorphic) state of the ventral branch of paraproct; (8) Fused to each-other (apomorphic) state of the ventral branches of paraproct.

Parameres. Paramere shaft short and stout with apicodorsal and ventrodorsal branch of strong and stout spines.

***Psychoronia brooksi* Ruiter, 1999**

(Figure 262)

Material examined. No specimen was available for direct examination. However, detailed well presented and properly interpreted drawings permitted the presentation of the parameres and character state combination.

***Psychoronia costalis* (Banks, 1901)**

Material examined. No specimen was available for direct examination. However, detailed well presented and properly interpreted drawings permitted the presentation of the paramere and character state combination.

Agaphylacini Oláh, tribe nov.

This unique monobasic tribe is organised by integration of drastic interactive external and internal perturbations. The basic pattern of parameres is characterized by strong, heavily sclerotized vertical plate with apical branching arms. This paramere architecture is highly differs from the basic patterns of simple setose rod type in the Limnephilini tribe, of the slender spine type in the Chilostigmini tribe, of the simple setose rod with heavy enforcement type in the Chaetopterygini tribe, of the simple spiny rod type in the Steno-

phylacini tribe, and of the many spine type in the Hesperophylacini tribe.

Type genus: *Agaphylax* Oláh, Kovács & Ibrahimi, 2018

***Agaphylax* Oláh, Kovács & Ibrahimi, 2018**

(Figure 263)

Original differential diagnosis. The unique upright directed ramose paramere is delineated from the *Mesophylax* parameres.

Relation. This highly diverged genus has general body and genitalic character combination related to all of the other five limnephiline tribes.

Genital character state combinations. (1) Presence (apomorphic) of spinulose protuberance on tergite VIII; (2) Reduced (apomorphic) state of tergite IX; (3) Setose inerm (plesiomorphic) state of cerci; (4) Produced (plesiomorphic) state of the dorsal branch of paraproct; (5) Separate free from each-other (plesiomorphic) state of the dorsal branch of paraproct; (6) Separate free-from-cerci (plesiomorphic) state of the dorsal branch of paraproct; (7) Reduced (apomorphic) state of the ventral branch of paraproct; (8) Separate free from each-other (plesiomorphic) state of the ventral branches of paraproct.

Parameres. Strong heavily sclerotized vertical plate with upright directed ramose and with apical branching arms.

***Agaphylax balcanicus* Oláh, Kovács & Ibrahimi, 2018**

(Figure 263)

Material examined. Holotype: **Macedonia**, Pelagonia region, Pelister Mts, Capari, springs area of Caparska Reka, 41°00'14.0", 21°10'4.6", 1952 m, 13. IX. 2016, leg. P. Juhász, T. Kovács & G. Szilágyi (1 male, OPC).

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