

# New Neotropical Trichoptera: *Banyallarga* and *Phylloicus* species delineation by revisited paraproct (Calamoceratidae)

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**Abstract.** We have revised the theory of the condensed complexity of the simple by incremental subtraction to understand the apparently vestigial character state of the simplified paraproct, especially pronounced at the *Banyallarga* and *Phylloicus* genera in the Calamoceratidae family. We have recorded *Leptonema album* Mosely, 1933 and *Leptonema intermedium* Mosely, 1933 from Ecuador, and *Leptonema spirillum* Flint, McAlpine & Ross, 1987 from Colombia, as well as described six new species: *Banyallarga (Histricoverpa) isidra* sp. nov., *Banyallarga (Histricoverpa) taraja* sp. nov., *Banyallarga (Histricoverpa) tinalandia* sp. nov., *Phylloicus sarlos* sp. nov., *Oecetis tina* sp. nov. in the *Oecetis avara* species group and *Helicopsyche (Cochliopsyche) nyurga* sp. nov.

**Keywords.** Condensed complexity, incremental subtraction, Neotropis, new caddisflies

## INTRODUCTION

This paper is a continuation of papers (Oláh & Johanson 2011, 2012, Oláh & Oláh 2017) based partly on the material collected by the second author in Ecuador and Colombia in the years between 2010 and 2017 (Appendix 1).

Besides describing new species of caddisflies we had to review the theory of condensed complexity of the simple by the incremental subtraction. Describing new Neotropical calamoceratid species in the genus of *Banyallarga* and *Phylloicus* we are faced the problem of the simplification of paraproct structure of somite origin, as a possible complexity by incremental subtraction as compared to the organs of extreme perfection built up by incremental addition with increasingly functional intermediate stages. Complexity could arise also by incremental subtraction of the spontaneous internal-variance (McShea & Hordijk 2013). The initial complexity is built up by the zero-force evolutionary law in the tendency for parts to differentiate. The produced structure is

more complex than they need to be and complexity is reduced by incremental subtraction. Ancestral, more complex structures could be less fit and early excessive complexity is followed by adaptive reduction to create condensed complexity of simple (CCS). The idea of incremental subtraction (McShea & Hordijk 2013) could be a possible explanation for Williston's law of simplification. (Williston 1914).

## Paraproct terminology revisited

Long ago we have argued for an appendicular and functional genital terminology and against the use of neutral, meaningless, blind and blinding directional terms of preanal, superior (upper), external (outer), internal (inner) or intermediate (in-between) and inferior (lower) appendages (Oláh & Johanson 2008). According to an important revision of high value, the genitalia of the calamoceratid *Phylloicus* genus lack superior and intermediate appendages (Prather 2003). This is a misleading statement. According to the appendicular genital terminology the cerci (superior,

preanal appendages and external branches) and the paraprocts (intermediate appendages) are present or its vestiges are detectable in all of the caddisfly superfamilies, although less obviously in Leptoceroidea. However, structures of primitive somite and podite origin disappear seldom without vestigial traces!

In caddisfly taxonomy, when describing genital structural elements, we are staggering among unjustified, meaningless directional terms. They are the surrogates or substitutes of the reality, how the genital structures developed and represent the primordial somite and podite of the primitive segments on the analogy of the head structures. In our reasoning of an appendicular and functional caddisfly genital terminology, we have synonymised the superior appendages with preanal appendages as well as with the outer or external branches of segment X present in some limnephilids. We simplify that these highly setose structures are the cerci, the appendicular sensory organ, and the debated podite remnant of the primitive limb appendages on abdominal segment XI. The superior appendages as differing from preanal appendages and the external branches of segment X are those of Schmid's few misconceptions he has developed for limnephilid taxa, as was established in specialised studies: the setose ear-like lateral process has wrongly been termed superior appendages (Nielsen 1957).

### **Trials**

According to the appendicular genital terminology, still obscured by incomplete homologies, most of the genital appendages, similarly to the head appendages, are vestigial limb podites or somite remnants and not neoformations of sternal evagination (Oláh & Johanson 2008). Old findings of comparative structural and functional empiricism (Ross 1938, Nielsen 1957, Schmid 1970) give some perspective and orientation. Until having more knowledge we argue for a simplified practice to homologize the gonopods with the ninth, the phallic organ with the tenth and the cerci with the eleventh abdominal segmental appendages of the primitive limb podites. In

contrary the paraprocts and epiproct are vestigial organs of the eleventh abdominal segment. They are somite origin that is the remnants of the segment body itself. In our reasoning (Oláh & Johanson 2008) we have tried to support and recall the appendicular ideas of Ross (1938), Nielsen (1957) and Schmid (1970), but the old neutral directional terminology, first adopted by McLachlan (1874–1880), further applied (Martynov 1934, Betten 1934), distributed (Mosely 1939), and slightly modified (Mosely & Kimmins 1953), remained firmly frozen into the present day practice of species descriptions (Prather 2003). Nielsen (1957) comparative anatomical study was the first and the last real and detailed trial to elaborate fine phenomics of genital architecture with a perspective to incorporate it into character ranking of cladistics. In 1974 at the First International Trichoptera Symposium there was a unanimous voting to adopt Nielsen's appendicular terminology in species descriptions (Vshivkova 2006). Sixty years after Nielsen, there is no real progress in understanding the morphogenetic history of speciation traits. Without sound comparative studies there is no perspective visible on the horizon to adopt and apply the appendicular and functional terminology! Without real novelty we are firmly stuck in the swamp of the old and empty directional terms of superior, intermediate and inferior appendages.

### **Practical attempts**

There is some hope at least for a practical perspective of appendicular terminology created mostly (1) by sporadic comparative observations, (2) by functional speculations and (3) by the reconstructed genital ground plan of the primordial Trichoptera. This fossil evidence was reconstructed from *Amphiesmenoptera* (Ivanov 2005) integrating the clasping function of gonopods, the intromittent function of the phallic organ, the sensory function of the cerci and the stimulatory function of paraproct. Moreover caddisfly taxonomy has realised quite a significant number of attempts to detect somehow the morphogenetic of paraproct, although with unsettled homologies, and made some effort to understand the paraproct

function applying it for species descriptions and character ranking in various caddisfly taxa:

(1) Ross (1956) has recorded the epiproct and paraproct of segment XI in *Rhyacophila* genus, as an unpaired anal sclerite bearing an internal root and as a band apical of U-shaped or wishbone-shaped structure.

(2) According to Nielsen (1957) the segment XI is well developed in the Rhyacophilidae family with distinct epiproct and paraproct. In most other taxa traces of segment XI can be found: well-developed paraprocts are found in families of Polycentropididae, Psychomyiidae; in Integripalpia the epiproct and paraproct have united with the sclerite of segment X forming a tripartite structure; especially clearly shown by Apataniidae and Goeridae; variously reduced similar structures are detectable in Sericostomatidae and Hydroptilidae families.

(3) Schmid (1958, 1970) has adopted and integrated the paraproct concept formulated by Ross (1956) and Nielsen (1956) as the epiproct and paraproct, the somite remnants of segment XI.

(4) In his detailed anatomical studies Nielsen (1957) has recognised the paraproct in *Orthotrichia tetensii*, as a semiannular sclerite with two spine-like asymmetric processes. We have also found this structure in many, but not in all *Orthotrichia* species, present in the capsule of segment IX, freely suspended alongside the phallic organ without sclerotic connection to any structures (Oláh 2012). It has a striking shape of a long protruding spine united basally by a variously formed semiannular sclerite to a shorter curved spine and producing frequently a long thin filament. The basal short curved spine and/or the thin filament are the vestigial component of the paired paraproct. They are frequently indistinct or variously developed.

(5) In Hydroptilidae family the paraproct is highly diverse and modified, but present in most of the examined taxa, under various terminologies (Oláh & Ito 2013): ventral part of segment X, process above claspers, apophyses supérieure, semiannular sclerite with two spine-like asym-

metric processes, paramere, appendices supérieure, venral plate of segment X, aedeagal sheath, pair of spines arising basoventrally on segment X, subgenital appendages, intermediate appendages, lateral penis sheath, lower penis cover.

(6) The paraproct is present as a dominating structure in *Chimarra* genus (Oláh & Malicky 2010). We have adopted Schmid's principles (1998) in separating the usually small, semi-membranous or fully membranous segment X without specific shape from the well-developed and usually more sclerotized paraproct of specifically characteristic shape. On cleared genitalia the membranous segment X is frequently almost indiscernible.

(7) The paraproctal complex is variously formed in Ecnomidae family, but we have detected it present in all genera at basomesad position of the cerci, sometimes in vestigial forms (Oláh 2014).

(8) In the Arctopsychidae family the segment X is highly reduced or almost lost and segment XI is strongly developed inserting cerci and the anal sclerites (Schmid 1968). The mesal less sclerotized structure and the lateral more sclerotized processes together represent the body of segment XI and the cerci represent the primitive limb podites.

(9) In family of Hydropsychidae the segment X either membranous, highly reduced or fused with segment XI (Oláh & Johanson 2012). Borders between the segments X and XI are poorly visible, although *Y* or variously shaped sutures are frequently present. Segment XI is represented by cercus and paraproct and associated with periphery of segment X and always located together or nearby. Cerci of podite origin always covered with numerous sensillae and the segmental plates of paraproct having somite origin may have setose sensory, as well as less setose stimulatory or setaless brace elements.

(10) In *Leptonema* up to three pairs of setose warts are present on the combined segments X and XI highly varying in size, shape, reduction, duplication and fragmentation (Oláh & Johanson 2012). Flint *et al.* (1987) has homologised the

wart *a*, located in a sublateral, dorsal position near the anterior margin of segment X, with the cerci (superior appendages of Nielsen (1957) or preanal appendages of Schmid (1968)). We have treated all the three warts (*a*, *b*, *c*), frequently petiolated and located along the apical margin of mesal sinus, as setose paraproctal processes (dorsoapical and ventroapical setose lobes in several hydropsychid genera) and homologise the setose area present permanently on the lateral lobes with the cerci (superior or preanal appendages). Usually these warts and the ventrolateral sclerotized straps constitute the paraproct in hydropsychids. The variously developed and sclerotized ventrolateral straps of the paraproct, function like a phallic guides forming the dorsolateral sheath of the phallocrypt or fused membranously to the basis or dorsum of the phallosome serving a supplementary role during intromittent movements of the phallic apparatus.

(11) According to Kumanski (1968, 1969, 1987) in the *Chaetopteroides* genus the ventral branch of paraproct (intermediate appendages) forms a complete heavily sclerotized ring around anus and the entire paraproct complex, except the dorsal (internal, apical, horizontal) branches, represents the vestigial segment X.

(12) In limnephilids (Oláh *et al.* 2014) the *paraproct complex* is a paired structure with variously developed branches named in four different directional nomenclatures: (1) apparent dorsal and ventral branches of Vshivkova (2007), (2) internal (plus plesiomorphic external) and inferior branches of Schmid (1955), (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 nomenclatures of the paraproctal branches we may summarize that the dorsal branch is bilobed in plesiomorphy (internal and external), apical and horizontal; the ventral branch is inferior, basal and vertical. Branches could be partially or completely fused in various shapes and forming a completely or partially sclerotized ring around anus.

(13) In limnephilids the paraproct complex is variously fused with dorsum IX, segment X and with cerci forming together the *superanal genitalic complex* of Vshivkova (2007). Structures of the superanal genital complex are separated from each other by membranes or by sutures. According to Schmid (1968, 1970) the body of segment X is frequently reduced and even the paraproct as well as the cerci are somite and podite remains of the vestigial segment XI. A plesiomorphic condition, in insect generally, is the separation of segment IX from segment X by discernible sutures. In many insects the limits of segment X often difficult to determine due to the frequent union between the segments X and XI. Probably the superanal genital complex of Limnephilidae represents the amalgamated segments X and XI. We may conclude that in limnephilids an apomorphic condition developed by the variously fused dorsum of segments IX, X and XI.

(14) In limnephilids the paraproctal complex is strongly sclerotized, mostly devoid of setae, muscled and movable (Oláh *et al.* 2014). The ventral branches, representing probably the reduced somite of segment X and XI (Kumanski 1968, 1969, 1987), form a pair of triangle with various sclerotizations. The pair of triangles encircles the anal opening with mesal edges less sclerotized or completely membranous. These triangles enlarge the total surface of the ventral branches embedded into the soft tissue around the anal region and below the genital cavities. The triangles are formed (1) by the lateral angle, frequently enlarged and housing various accessory processes; (2) by the dorsal angle connecting into the dorsal branches; and (3) by the mesal angle. The mesal angles of the two ventral branches are frequently fused to complete the sclerotized ring around the anal opening. The mesal edge of the triangle is less sclerotized, frequently obscure or even indiscernible. The lateral angle or corner is the lateral sclerite of segment X (Schmid 1998). The ventral edges of the triangles are called sometimes as the ventral sclerites.

(15) The enlarged triangles of the ventral (inferior, basal, vertical) branch of the paraproctal

complex serve as a supporting, pivoting fulcrum for the muscled movable dorsal branch of the paraprot (Oláh *et al.* 2014). The dorsal branches function as grabbing tool and/or as stimulating courtship or harm device delivering internal signals to the females. It seems that the *Allogamus mortoni* species group has an effective additional apomorphic tool evolved to produce stimulating and titillating signals to the females during copulation. This is the pair of the extremely enlarged accessory processes developed, diversified and stabilized on the lateral corner of the basal triangles of the paraproctal complex. Diversification was driven probably by intense sexual selection processes. Postcopulatory sexual selection can lead to rapid divergences in reproductive traits related to the very complex mating and copulating processes. These accessory processes are also present on the paraproctal complex of the *Allogamus ligonifer* species.

(16) For generic ranking in the Drusinae subfamily we have recognised the importance of the ancestral architectural divergences in the adaptive paraprot structures (Oláh *et al.* 2017). The *Drusus* genus has retained the variously shaped, but complete structure of paraprot with full stimulatory function. The heavily sclerotized head on the dorsal branch of the paraprot roughened with densely spaced short peglike setae serves as stimulatory organ in copulatory processes. In contrary the paraprot of *Ecclisopteryx*, both its ventral and dorsal branches, have almost completely disappeared, rather vestigial, reduced to a pair of narrow sclerotized bands shifted ventrad and sunken and hidden deep between the enlarged cercal complex and the phallobase. The stimulatory function of paraprot has been taken over by the gonopods. There is gradualism in the character state transformation of paraprot reduction. (1) The unique species of *Ecclisopteryx malickyi* is still characterized with mixed character states of the *Drusus* and *Ecclisopteryx* genera. Its compact, not reduced, non-vestigial paraprot relates this species to *Drusus* genus but its gonopod with peg packed roughened surface relates it already to the *Ecclisopteryx* genus. (2) The dorsal branches of the paraprot

are already lost, but the ventral branches of the paraprot are still present at *Ecclisopteryx madida*. (3) All the other species of the *Ecclisopteryx* genus have only vestigial paraprot in the form of narrow stripes or bands.

(17) In Drusinae subfamily species complex ranking of incipient siblings are detectable mostly by ancestral divergences in the architecture of basal shape formation of the entire paraprot (Oláh *et al.* 2017). Apparent architectural shape formation of paraprot is realised by reduction, enlargement, pattern alteration or fusion of the dorsal and ventral branches, detectable both in lateral, dorsal and caudal profiles. Species complexes could be specific for particular paraprot profiles having the most pronounced divergences. Species complexes could be also specific for what are the most indicative paraprot profiles offering the most stable and reliable detection and demonstration.

(18) In Drusinae subfamily species ranking is based on the contemporary subtle divergences in the shape of the paraprot head (Oláh *et al.* 2017). This roughened surface of peg-armed structure is most exposed and most intimately involved in the direct stimulatory contact with the female during the various processes of the cryptic female choice. Confirming this sexual communication we have detected that the rapid, subtle and stable divergences are usually localised on the very top of the dorsal branch of the paraprot.

(19) In Leptoceridae family understanding the real state of paraprot especially needs a systematic survey. The so called segment X frequently represents a complex structure integrating remnants of segments X and XI. In some Vietnamese members of *Oecetis* genus we have detected the paraprot present as the lower part of segment X; usually membranous, unpigmented, difficult to recognise on the cleared genitalia (Oláh 2013). In several Australasian members of *Triaenodes* genus the segment X is composed of the filiform mesal process (upper process of segment X) and the paraprot (lower process of segment X) frequently with a less sclerotized long mesal process. (Oláh 2016a).

### Condensed complexity of the simple

In character ranking procedures we are faced to answer the simple question still unresolved in the evolution of genital complexity. Do genital structures evolve from simple to complex or the opposite (Oláh *et al.* 2014)? In order to understand what is simple and complex and which character state is ancestral plesiomorphic or derived apomorphic we need to outline some basic relations in complexity theories. This brief survey oversimplifies the ever-changing and complicated understandings and speculations about entities and their interactions forming together the self-organising complexity. Here we try to review some orientation mostly for alpha taxonomy.

#### Williston's law of simplification

According to the Williston's law the structures tend toward reduction: the numbers of scull bones are reduced by loss and fusion (Williston 1914). A general evolutionary pattern of reduction in structural parts was also demonstrated by Gregory (1935). Similarly, an ancestor must be constituted by the integration of the largest possible number of characters (Schmid 1979). Based on this simplification's law we have selected the structurally most complex parameres for the ancestral plesiomorphic state in the *Potamophylax nigricornis* species group (Oláh *et al.* 2013b), and in the *Allogamus* genus (Oláh *et al.* 2014). Our decision is justified and confirmed by the locality principle; the fact that the ancestral species with the most complex paramere has the largest distributional area, compared to large series of newly described peripatric sibling species with reduced complexity of parameres and having small distributional area (Oláh *et al.* 2017). But, we have to consider that the terms simple, complex, primitive, generalized, specialized, are all disputable construct of human hubris and strictly comparative (Ross 1956, Schmid 1958). The simplification trend in evolution seems to be associated with a decrease in complexity. Complexity-increase through evolution has become a contentious issue. There is apparent simplification

with increasing complexity, noticeable and considerable only by fine structure analysis!

#### Complexity without natural selection

Organisms accumulate variations spontaneously and there is a theory to manifest this internal variance (internal degree of differentiation) as an evolutionary vector toward increasing complexity with or without reinforcement by natural selection (McShea 2005). The complexity is understood as (1) amount of differentiation among parts where variation is continuous or as (2) number of part types, where variation is discrete. This vector is a complexity generative mechanism without any consideration of natural selection. Parts become differentiated along an internal-variance-vector and the selection could reinforce, act neutrally or oppose it. The product of complexity is not a passive mechanism, but driven by pervasive spontaneous constraints detectable by mathematical or statistical formalism, rather than driven by natural selection. This spontaneous internal-variance principle is predated (1) by Herbert Spencer's (1900, 1904) metaphysics and by his notion of "instability of the homogeneous"; (2) by Gregory's (1935) and Weiss's (1990) duplication and differentiation of parts; (3) by morphological evolution as a diffusive process (Raup 1977), and (4) by the spontaneously increasing morphological differentiation or disparity (Foote 1997, Ciamaglio *et al.* 2001).

#### Complexity by incremental subtraction

In contrary to the irreducible complexity theory of the creationists, the evolution of complex structures, that is the organs of extreme perfection are built up by incremental addition with increasingly functional intermediate stages. Complexity could arise also by incremental subtraction of the spontaneous internal-variance (McShea & Hordijk 2013). The initial complexity is built up by the zero-force evolutionary law in the tendency for parts to differentiate. The produced structure is more complex than they need to be and complexity is reduced by incremental subtraction.

Ancestral more complex structures could be less fit than the less complex derived ones and early excessive complexity is followed by adaptive reduction to create condensed complexity of simple (CCS).

### **Zero-force evolutionary law**

A mechanism for reduction, simplification or specialization during evolution of complexity was speculated in debate with the concept of irreducible complexity (McShea & Hordijk 2013). Unfortunately their oversimplified complexity concept was unreasonably reduced to the number of parts (skull bones). Their complexity by subtraction suggests that complexity could arise, not by incremental addition but by incremental subtraction. Early complexity is followed by later reduction to CCS, but this is a kind of Williston's law. To account for this early complexity liable to subtract, McShea & Brandon (2010) have developed and introduced the zero-force evolutionary law, as an analogy of the law of inertia in Newtonian mechanics. This theory explains the evolution of complexity without natural selection. They say that in any evolutionary system in which there is variation and heredity, there is a tendency for diversity and complexity increase. This may be opposed by natural selection, other forces, or constraints acting on diversity or complexity. Organisms are expected to accumulate random variations spontaneously along entropy increase (McShea 2005). Evolutionary zero-force law states what will happen if no forces impinge on the system and moving into the direction of decomposing variation. A recent criticism says that diversity and complexity do not change when there are no evolutionary causes (Barett *et al.* 2012).

### **Complexity, entropy and negentropy**

The second law of statistical thermodynamics, the stochastic average energy behaviours of large groups of individual particles (Boltzmann 1886), viewed nature as decaying toward a certain death of random disorder by equilibrium seeking, to-

ward the entropy, a measure of disorder, a state measure of microscopic configurations. This pessimistic view opposed Darwin's paradigm that is based on increasing complexity, specialization and organisation of biological systems through time. This dilemma was solved by the nonequilibrium thermodynamics of Schrödinger (1944). He observed that the gene generates order from order (negentropy from negentropy) during reproduction that is the progeny inherits the traits of the parents. To sustain this process the living systems defy of the second law of thermodynamics and move away from disorder into highly organised structures far from equilibrium, and create order from disorder. Living systems build complexity in energy and material fluxes, as constrained gradient dissipaters, while importing energy (negentropy) from outside at the expense of producing entropy in the environment and maintaining its local level of organisation at the expense of global entropy budget. Like the emergence of convection (Bénard cells) as an emergent coherent self-organisation by external energy input (Schneider & Kay 1995).

More entropic macrostate is characterised by the greater number of microstates. Complexity is negentropy governed through macrostate probabilities and adjusted stochastically by the greater number of microstates, by the combined, often opposite effects of the entropy increasing "temperature-entropy", when more kinetic energy is distributed in more ways and the entropy decreasing "constraint-entropy". Entropy decreases when more constraints and thus less freedom of motion are produced, for instance: (1) decreasing number of entities (structures); (2) fusion of entities (structures); (3) decreasing volume (abbreviation, miniaturization); (4) phase changing when entities condense into a more organised form. Complexity is the result of exergy, the energy that is available to use, that is the capacity of an energy system to perform useful work processing to equilibrium with the environment. How this permanent increase in complexity during evaluation supports Williston's finding of the experienced reduction or simplification?

### **Simplification with complexity**

Williston's law has been revisited recently by network theory (Esteve-Altava *et al.* 2013). It was found that reduction in the number of structural parts could be associated with increasing complexity yielding CCS. Complexity increased with complementary qualities associated to the decrease of structural units. Reduction of elements was compensated (1) by anisomerism, that is by specialization of the structures (measured by dissimilarity of connectivity heterogeneity); (2) by the number of unpaired structures as a side-measure of anisomerism (fusion of two or more pre-existing structures, representing the most modified, specialized ones); (3) by density of connections (more connected is more complex); (4) by characteristic path length (speed of information flow), (5) by cluster development (loops of connections, integration, modularity).

As a result the reduction in skull bones correlates with an increase in complexity. Specialization by simplification could be an inherent complexity increase. Parts tend toward reduction in number, with the fewer parts greatly specialized in function. In already complex systems, sometimes more complex than they need to be, selection (natural or sexual) may favour a reduction in the structural pattern of complexity. Ancestral more complex structures were less fit than the less-complex derived ones. Early excessive complexity followed by adaptive reduction is a possible route to adaptation. More advanced structures can have fewer parts.

### **Genomic complexity**

Complex organisms cannot adapt as quickly as simpler ones (Orr 2000). A random mutation of particular size is more likely to disrupt a complex than a simple organism (Fischer 1930). Genome complexity is correlated with biological complexity and is driven mostly by non-adaptive stochastic forces, rather than by adaptive evolution (Lynch & Conery 2003). Selective effect of mutations is reduced at organisms with small effective population size and the neutral mutations

can passively accumulate increasing genome complexity. This reduced selection efficiency in small populations can lead also to intron accumulation further increasing the biological complexity (Yi 2006).

We need more rigorously defined and measurable traits to study the evolution of complexity. Genomic complexity expressed in morphological and functional diversity can be measured directly by the number of base pairs in a sequence (Adami *et al.* 2000). However, equating genomic complexity with genome length in base pairs produced several conundrums. G-value paradox refers to the lack of correspondence between gene number and organismal complexity. C-value paradox disconnect between genome size and morphological complexity (Gregory 2004).

### **Adaptive complexity by integration**

Adaptive complexity, especially the very complex structures like eyes and brains, are definitely not the products of McShae's entropic spontaneous variation produced by the zero-force evolutionary law and not even of its version improved by natural selection. In contrary, these disintegrative processes of increasing entropy are ever manifested in the permanent load of the external and internal environment causing or rather provoking a response that is resulted in the balancing power of the adequate counteractive mechanisms organised by integrative negentropy. This spontaneous internal-variation of increasing entropy triggers and induces various mechanisms and processes of environmental mutations, permutations, transmutations and perturbations. The permanent flux of these adverse, neutral or advantageous external and internal effects generates and gives rise to responsive and balancing integrative mechanisms of comparative magnitude and multitude with a trend to produce CCS. This permanently balancing integrative organisation process develops and drives, with negentropy, a large number of interactions along various patterns of supervenient emergent mechanisms in order to integrate them into an oscillating autonomy to overcome the increasing entropy (Oláh *et al.*



2017). This integrative response to increasing entropy represent the real power of the life reality, the adaptive organic complexity, created and supported by negentropy.

## MATERIALS AND METHODS

All of the specimens have been collected by János Oláh jr. during his birdwatching trips in Colombia and Ecuador with light traps applying the BioQuip pocket light, the smallest self-contained light source available. All the specimens reported here are deposited in the Oláh Private Collection, Debrecen, Hungary, under national protection by the Hungarian Natural History Museum, Budapest (OPC).

## TAXONOMY

### Hydropsychidae Curtis, 1835

#### *Leptonema album* Mosely, 1933

*Material examined.* **Ecuador**, West Andean foothills, Tinalandia Nature Reserve, Rio Toachi, 85 km from Quito, 600 m, 6. XI. 2014, light trap, leg J. Oláh jr. (1 male, OPC).

#### *Leptonema intermedium* Mosely, 1933

*Material examined.* **Ecuador**, West Andean foothills, Tinalandia Nature Reserve, Rio Toachi, 85 km from Quito, 600 m, 6. XI. 2014, light trap, leg J. Oláh jr. (6 males, OPC).

#### *Leptonema spirillum* Flint, McAlpine & Ross, 1987

*Material examined.* **Colombia**, West Andes, West Slope, Tatama National Park, Montezuma, 8.III.2015, light trap, leg J. Oláh jr. (1 male, 1 female; OPC).

### Calamoceratidae Ulmer, 1905

#### Genus *Banyallarga* Navas, 1916

*Banyallarga* species are quite uniform with drab brown and gold colouring, compared to the

*Phylloicus* genus with contrasting wing patterns of colourful stripes or bands. The species of *Histicoverpa* subgenus are usually more uniformly coloured than species of the *Banyallarga* subgenus. The fused complex of tergite IX and segments X-XI, functioning as the dorsal hood of the phallocrypt is more simplified than at genus *Phylloicus*, representing the most advanced state for the theory of the condensed complexity of the simple (see below at the *Phylloicus* genus and at the theoretical part!). Specialised anatomical and histological studies will help to homologise the composition of this highly simplified and fused dorsal structure.

#### *Banyallarga (Histicoverpa) isidra* sp. nov.

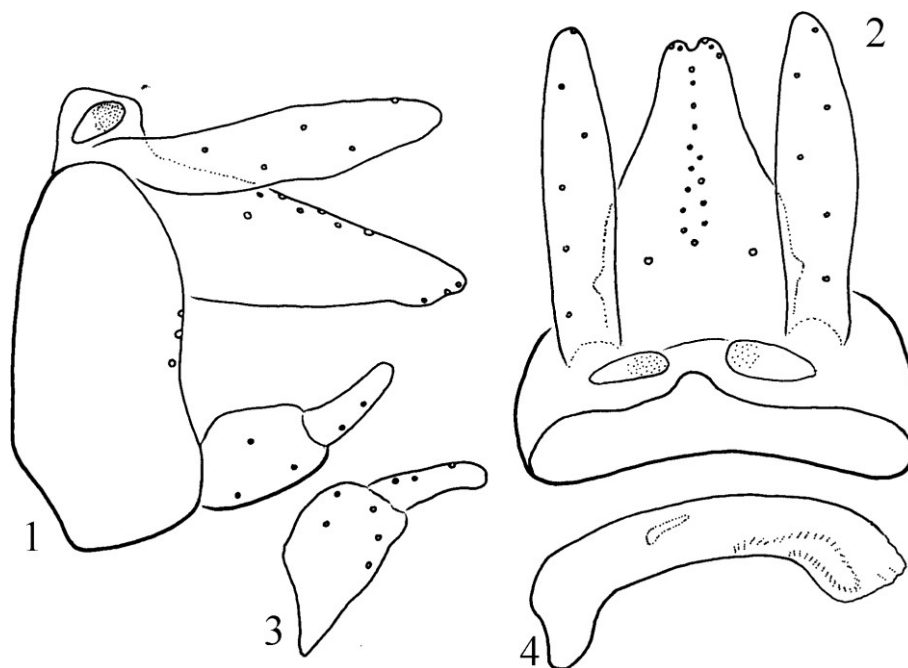
(Figures 1–4)

*Material examined.* Holotype: **Ecuador**, Eastern Andean Slope, San Isidro, 1800m, 15.VIII.2011, light trap leg. J. Oláh jr. (1 male, OPC).

*Diagnosis.* This new species is a member of the *Histicoverpa* subgenus and close to *B. loxana* Navas, but differs by having short segment IX in lateral view; anterior margin of segment IX straight vertical, not triangular; lateral shape of the dorsal complex very low; cerci parallel-sided, not with lateral elbow in dorsal view; harpago almost as long as the coxopodite, not short; phallic organ with elongated basolateral lobes.

*Description.* Wings (in alcohol) dark brown with few indefinite lighter dots scattered mostly along apical region; forewing length 11 mm; fork 1 present on hindwing; antennae twice forewing length, Maxillary palp formula I-(IV,V)-II-III. Tibial spur formula 2,4,4. Head, thoracic sclerites and legs lighter than wing.

*Male genitalia.* Segment IX with short almost straight vertical anterior margin in lateral view; posterior marginal ridge of pleuron IX without triangular lobe, the margin itself is almost straight vertical; the dorsal hood over the phallocrypt, the fused complex of tergite IX and segments X–XI, the segment X in the directional terminology of Prather (2004), is a simple hood, tapering both in



Figures 1–4. *Banyallarga (Histicoverpa) isidra* sp. nov. Holotype male: 1 = genitalia in left lateral view; 2 = genitalia in dorsal view; 3 = gonopods in ventral view; 4 = phallic organ in left lateral view.

lateral and dorsal view with bifid apex; the anterior part of the complex, the tergite IX short enclosing a pair of drop-shaped lateral structures densely packed with pointed micro-pegs or rather by granulated texture. Cerci stout, parallel sided, as long as the dorsal hood. Gonopods less produced; coxopodite short and wide, harpago long. Phallus is slender having horseshoe-shaped phallotremal sclerite; endothelial membrane with indefinite, not black setal cluster.

*Etymology.* Named after the locus typicus.

***Banyallarga (Histicoverpa) taraja* sp. nov.**

(Figures 5–8)

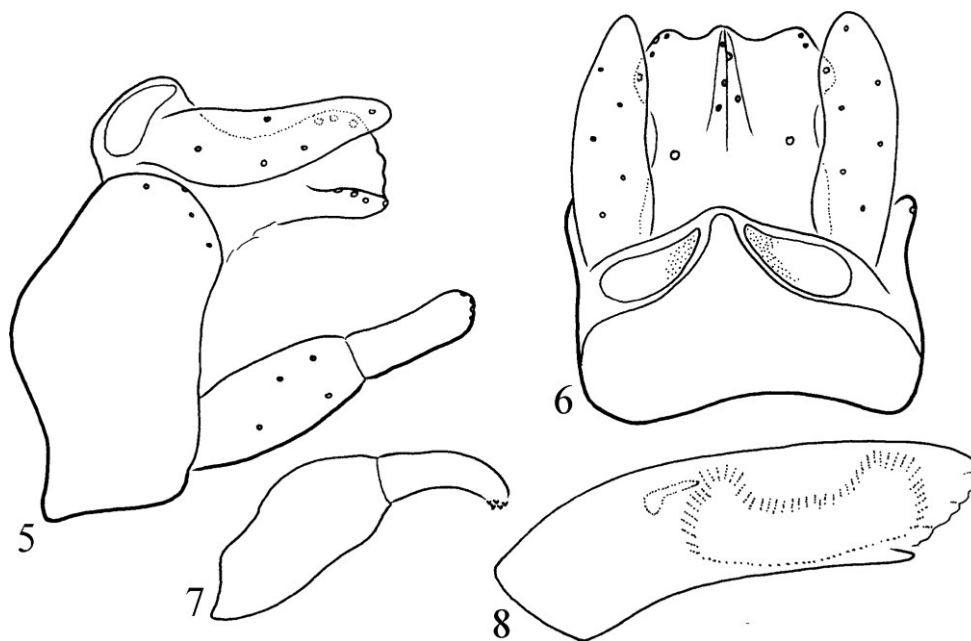
*Material examined.* Holotype: **Ecuador**, Eastern Andean Slope, Amazonia, Archidona, 800m, 9.VIII.2011, light trap, leg J. Oláh jr. (1 male, OPC).

*Diagnosis.* This new species is a member of the *Histicoverpa* subgenus and close to *B. molliscula* (McLachlan, 1871) but differs by the lateral

and dorsal shape of the dorsal complex and by the very stout phallic organ.

*Description.* Wings (in alcohol) dark brown with few indefinite lighter dots scattered mostly along apical region; forewing length 11 mm; fork 1 present on hindwing; antennae twice forewing length, Maxillary palp formula I-(IV,V)-II-III. Tibial spur formula 2,4,4. Head, thoracic sclerites and legs lighter than wing.

*Male genitalia.* Segment IX with short triangular anterior margin in lateral view; posterior marginal ridge of pleuron IX without triangular lobe; the dorsal hood over the phallocrypt, the fused complex of tergite IX and segments X–XI, the segment X in the directional terminology of Prather (2004), is a simple hood, quadrangular in dorsal view with apical lateral obliquely truncate lobes; the anterior part of the complex, the tergite IX reduced to a pattern of dorsal sutures, surrounding a pair of drop-shaped lateral structures densely packed with pointed micro-pegs or rather by granulated texture. Cerci stout, as long as the dorsal hood. Gonopods, especially the harpago, long. Phallus short, very stout with horseshoe-



Figures 5–8. *Banyallarga (Histicoverpa) taraja* sp. nov. Holotype male: 5 = genitalia in left lateral view; 6 = genitalia in dorsal view; 7 = gonopods in ventral view; 8 = phallic organ in left lateral view.

shaped phallostremal sclerite, endothelial membrane fully packed with black spine-like setae.

*Etymology.* *taraja*, from „taraj, tarajos”, crest in Hungarian, refers to the pronounced mesal crest on the dorsal hood of the genitalia.

***Banyallarga (Histicoverpa) tinalandia* sp. nov.**

(Figures 9–15)

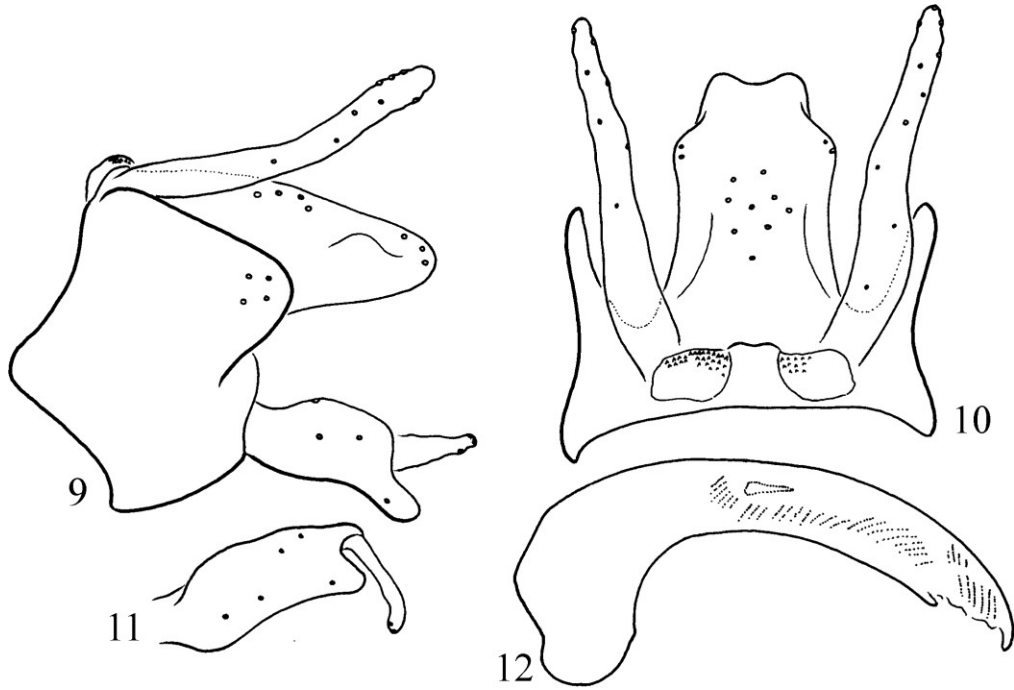
*Material examined.* Holotype: **Ecuador**, West Andean foothills, Tinalandia Nature Reserve, Rio Toachi, 85 km from Quito, 600m, 6.XI.2014, light trap, leg J. Oláh jr. (male, OPC). Allotype: same as holotype (female, OPC). Paratypes: same as holotype (1 female, OPC). West Andean foothills, Tinalandia Nature Reserve, Rio Toachi, 85 km from Quito, 600m, 19.VIII.2011, light trap, leg J. Oláh jr. (2 females, OPC).

*Diagnosis.* According to the structure of the dorsal hood, the reduced complex of tergite IX and segments X–XI this new species is most close to *B. sylvana* Prather, 2004, but differs by its

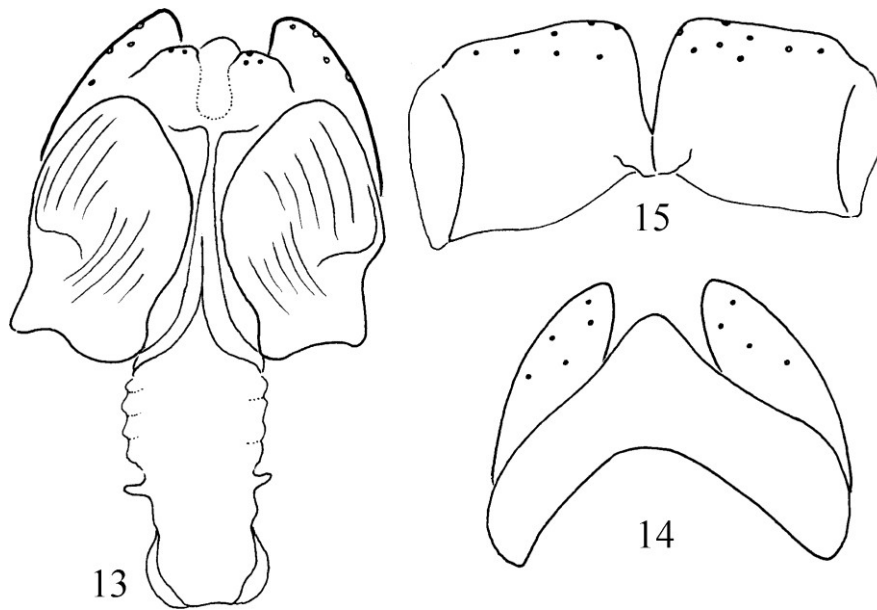
unique gonopod’s structure and by the fine structure of the dorsal hood.

*Description.* Wings (in alcohol) dark brown with few indefinite lighter dots scattered mostly along apical region; forewing length 12 mm; fork 1 present on hindwing; antennae twice forewing length, Maxillary palp formula (V,IV)-( I,II)-III. Tibial spur formula 2,4,4. Head, thoracic sclerites and legs lighter than wing.

*Male genitalia.* Segment IX with triangular anterior margin in lateral view; posterior marginal ridge of pleuron IX produced into a triangular lobe with setae; the dorsal hood over the phallocrypt, the fused complex of tergite IX and segments X–XI, the segment X in the directional terminology of Prather (2004), is a simple hood, quadrangular in dorsal view with subapical lateral lobes; the anterior part of the complex, the tergite IX short with a small mesal elongation, laterad to this mesal elongation of tergite IX there is a lateral pair of subquadrangular surfaces well-delineated (by suture?) and densely packed with pointed micro-pegs, sharply demarcating from the rest of tergite IX. Cerci slender, longer than the



Figures 9–12. *Banyallarga (Histicoverpa) tinalandia* sp. nov. Holotype male: 9 = genitalia in left lateral view; 10 = genitalia in dorsal view; 11 = gonopods in ventral view; 12 = phallic organ in left lateral view.



Figures 13–15. *Banyallarga (Histicoverpa) tinalandia* sp. nov. Allotype female: 13 = sterna IX, X and vaginal apparatus, ventral view; 14 = terga IX and X, dorsal view; 15 = sternum VIII, ventral view.

dorsal hood, apical half seem flexible. Gonopods short, coxopodite with unique ventroapical lobe, harpago slender in ventral view. Phallus with horseshoe-shaped phallotremal sclerite, endothelial membrane fully packed with black spine-like setae.

*Female genitalia.* Tergite IX short, protruding into a triangular mesal lobe, sternite IX somewhat flattened and depressed ventrally with indistinct longitudinal mesal suture; surfaces with specific striated pattern. Segment X fused with segment IX terminating apically with a pair of setose lobes discernible in ventral view. Vaginal sclerite complex supplied with small lateral digitiform lobes middle; rounded anterior terminal flanked by rounded lateral lobes.

*Etymology.* *tinalandia*, from the name of the type locality: Tinalandia Nature Reserve with nature lodge, one of the first ecotourism adventure in Ecuador and South America.

#### **Genus *Phylloicus* Müller, 1880**

*Phylloicus paraproct.* The cercus (preanal appendages, superior appendages) is present in each caddisfly taxa and it is the dominating structure in calamoceratid taxa as well, including *Phylloicus*. Contrary to Prather (2003) the paraproct or its variously discernible vestiges are also present in most caddisfly taxa or at least its traces are detectable in all caddisflies. In leptoceroids the paraproct is easily detectable in most taxa, but less studied and considered less distinct in calamoceratids. However, we believe that the dorsoapical complex dominating on the entire genitalia is composed mostly by the paraproct (see theoretical part!).

Calamoceratids are excellent models for future studies on the theory of condensed complexity of the simple (CCS). Here, in our species description we use the appendicular genital terminology and clearly distinguish the paraproct as the dominating structure of the fused complex of segment X and XI. This complex is also fused, frequently with well visible suture, to tergum IX. The sutures fragments between the remnant structures of seg-

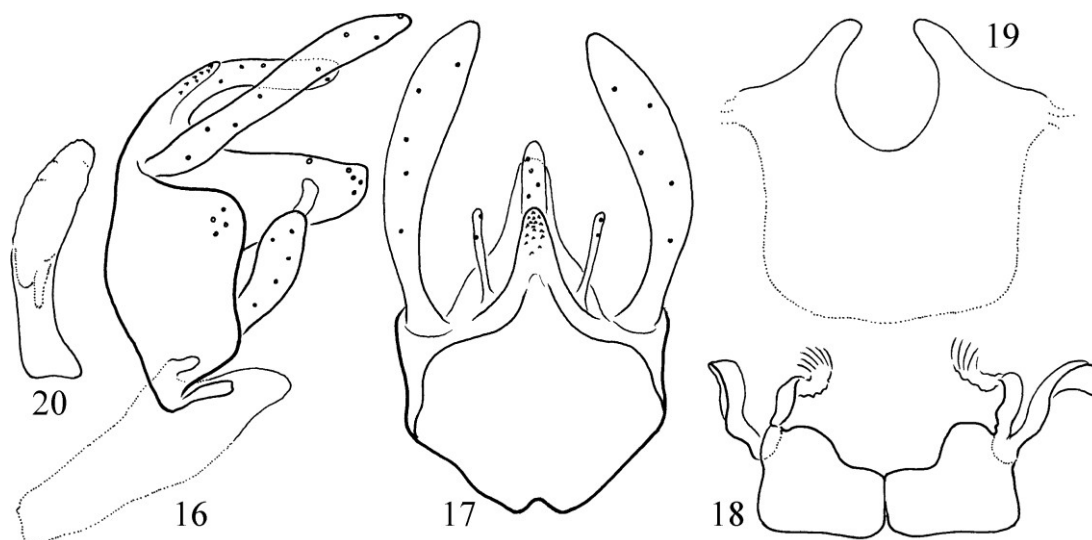
ments X and XI is difficult to detect. Sometimes discernible in the contour of contrasting surface textures, specific micro sculptures, differentiations in setal field patterns or its traces detectable as furrows, grooves or notches. This dorsoapical fused complex of tergite IX, segments X and XI delineates the dorsum of the phallocrypt and functions as a dorsal plate while channelling the movement of the phallic organ dorsally.

This three-segmental complex being variously amalgamated, rather simplified and compact may well represent the CCS principle; this complex structure is composed of the following structures starting from anterior to posterior: (1) The short transverse or V-shaped band-like tergite IX frequently delineated posteriorly by suture; its dorsum may be covered with well differentiated surface texture of cuticular surface processes of microspines or micropegs. (2) Segment X starts after the suture and represented by the variously setose basement with vertical or horizontal configuration. (3) The basement of segment X frequently produced into a setose basodorsal process, short or long, bifid or digitate, sometimes shifted from the basement to the dorsum of the paraproct. (4) Basolateral pair of processes, mostly setaless or supplied with a few microsetae, frequently asymmetrical and frequently very small or reduced. (5) Cercus of podite origin, the sensory appendages of segment XI. (6) The larger part of the three-segmental complex is the paraproct itself, forming the variously shaped large hood supplied with a few apical or dorsal microsetae; these stout, short and pointed small spike-like structures are characterized by large alveoli. These mini spikes are arranged in some pattern or at least exhibit some regularity in spacing and may have a combined sensory and stimulatory function.

#### ***Phylloicus sarlos* sp. nov.**

(Figures 16–20)

*Material examined.* Holotype: **Colombia**, Central Andes, Antioquia Department, Medellín, Municipality Anori, La vereda El Roble, Arrierito Antioqueno Bird Reserve, 6°59'19.6"N 75°07'12.8"W, 1700 m, 10.VII.2002, light trap, leg. J. Oláh jr. (1 male, OPC).



**Figures 16–20.** *Phylloicus sarlos* sp. nov. Holotype male: 16 = genitalia with partially dotted sternum in lateral view; 17 = genitalia in dorsal view; 18 = segment VI, dorsal view; 19 = partially dotted sternum VIII, ventral view; 20 = phallic organ in lateral view.

**Diagnosis.** This new species is similar to *P. hansonii* Denning, 1983, and *P. quitacalzon* Prather, 2003, but differs from both by having corematic structure more complex, as well as basodorsal setose lobe and setaless pair of digitate processes, representing segment X are more produced. Its corematic structure is most close to *P. spectabilis* Martynov, 1912, but *P. sarlos* sp. nov. has posteromesal process which is lacking at *P. spectabilis*; moreover, the fused complex of the tergite IX and segments X–XI is entirely different in all of its components.

**Description.** Wings (in alcohol) dark brown with few indefinite lighter dots scattered mostly along radial region; forewing length 14 mm; fork 1 lacking on hindwing; hind wing basal brush present, dark; stem of Cu1 on hindwing extremely dilated bearing elongated brown setae, compact pencil-like together in resting position, this is possibly an additional alar androconial structure to the basal brush. Antennae twice of forewing length, Maxillary palp formula IV-I-II-(III,V). Tibial spur formula 2,4,4. Head, thoracic sclerites and legs lighter than wing.

**Male genitalia.** Corematic structure present and elaborated on tergite IV; paired subquadratic posterior processes and paired spatulate lateral

sclerites present; in lateral view the heavily sclerotized lateral sclerite with two longitudinal transparent lines. Tergum V with modified smaller subquadratic posterolateral processes. In ventral view sternum VIII with posteromesal processes forming mesad turning slender digitate lobes enclosing sinus shaped mesal excision; small digitate lobes joining dorsolaterad on both sides visible in lateral view. Dorsum of tergite IX long V-shaped, protruding posterad; its surface fully and densely packed with pointed microspines, sharply demarcating from the setae covered long basodorsal process; there is no distinct lateral ridge anteriorly on segment IX, ventral to the base of cerci, just usual posterior margin; dorsal pleural setae 8 both on left and right side, ventral pleural setae lacking; a ventral additional flanking plate present. Segment X is represented by long setose basodorsal mesal lobe; this very produced mesal process is accompanied both sides by thin less setose lateral process, usually present on many *Phylloicus* species as very short digitate lateral process or rather as budding gemma. Paraproct forming a long triangular hood over the phallocrypt; apical margin armed with a few stout short spines with enlarged alveolus; a pair of similarly short and stout spines presents dorsally subapicad. Cerci are falcate in lateral view elongated and

densely packed with long setae. Gonopods simple, both coxopodite and harpago short. Phallobase forming a simple curved tube with terminal membranous endotheca; sclerotized phallosclerite just discernible.

*Etymology.* *sarlos*, from „sarló, sarlós” falcate in Hungarian, refers to the falcated pattern of the elongated cerci in dorsal view.

## Leptoceridae Brewster, 1815

### *Oecetis avara* species group

*Oecetis avara* species group, present in the Nearctic and Neotropical regions, belongs to *Oecetis* (*Pseudosetodes*), one of the four subgenus established by Chen (1993) in the *Oecetis* genus. The monophyly of the subgenus is based on males having symmetrical phallic organ without parameres (internal spines). The *O. avara* species group inside the *Pseudosetodes* subgenus is characterized by the shape of the gonopods with mitten-like form of the large dorsal and smaller ventral arms. Despite the relatively minor differences that seem to separate these closely related species they have really subtle, but rather stable divergences. The *O. avara*, *O. inconspicua* (Blahnik & Holzenthal 2014) and *O. amazonica* (Oláh 2016b) species complexes exhibit the same speciation pattern of closely related species. There are differences between species in coloration, forewing spotting, and wing venation as well as in the shape of gonopod, but phallobase shape is the single most stable and useful character to detect and separate the closely related incipient species in these *Oecetis* species complexes (Blahnik & Holzenthal 2014).

They are easily detectable by the subtle, but stable shape divergences in the speciation traits of the phallobase (phallosclerite). These really super traits are organised in allopatric isolation by integrative processes under the primary influence of sexual processes and realised by building reproductive barriers in the fine structure of reproductive organs (Oláh *et al.* 2017). The speciation trait of the phallobase seems stable even in species

having rather extensive distributions or occurring together in sympatric populations (Blahnik & Holzenthal 2014). Nevertheless, in the traditional taxonomic treatments, limited mostly to gross morphological characters, these subtle but stable divergences in the fine structures of speciation traits was considered as minor morphological variations of widely distributed and highly variable species. However, in the last few years various speciation traits of the reproductive structures have been detected in several caddisfly taxa:

(1) Lateral process on the head of aedeagus: *Chaetopteryx rugulosa* species group (Oláh *et al.* 2012).

(2) Paramere tip: *Chaetopteroides* genus (Oláh *et al.* 2013a).

(3) Structure of paramere split: *Oxyethira flavicornis* species group (Oláh & Ito 2013).

(4) Paramere and aedeagus fine structure: *Potamophylax nigricornis* species group (Oláh *et al.* 2013b).

(5) Paramere and aedeagus fine structure of phallic organ as well as the coevolved elongation of the modified common duct of accessory glands with single internal tube to accommodate the fused single paramere: *Allogamus* genus (Oláh *et al.* 2014).

(6) Clasp complex of mesal lobe of gonopod with the movable harpago: *Triplectides* (Oláh 2014).

(7) Speciation fine structure of the phallic organ: *Hydropsyche* (Oláh & Kiss 2015).

(8) Endothecal sclerite of the aedeagus: *Polycentropus sinuosus* species complex (Oláh 2015).

(9) Phallobase (phallosclerite) and harpago: *Lepidostoma japonensis* species complex (Oláh 2015).

(10) Paramere and aedeagus tips: *Potamophylax tagas* species cluster (Oláh & Kovács 2015).

(11) Head of the dorsal branches of paraproct: *Drusus bolivari* species complex (Oláh *et al.* 2015), *Drusus discolour* species complex (Oláh *et al.* 2016), entire revised *Drusus* genus (Oláh *et al.* 2017).

(12) Dorsal branch of paraproct: *Psilopteryx psorosa* species group (Oláh *et al.* 2015).

(13) Superanal genital complex: *Annitella kosciuszki* species complex (Oláh *et al.* 2015).

(14) Paramere: *Isogamus* and *Melampophylax* genera (Oláh *et al.* 2015).

(15) Paramere and apical tip of gonopod: *Rhadicoleptus* genus (Oláh *et al.* 2015).

(16) Fine setal spine microstructure pattern on the phallic head and on the mesal surface of the gonopods: *Hyalopsyche* (Oláh 2016c).

(17) Fine structure of the apex of paramere: *Hydroptila* (Oláh 2016c).

(18) Dorsal process of the phallosome and tripartite aedeagus: *Rhyacophila* (Oláh & Beshkov 2016).

(19) Pegged apical lobes on the gonopods: *Ecclisopteryx* genus (Oláh *et al.* 2017).

***Oecetis tina* sp. nov.**

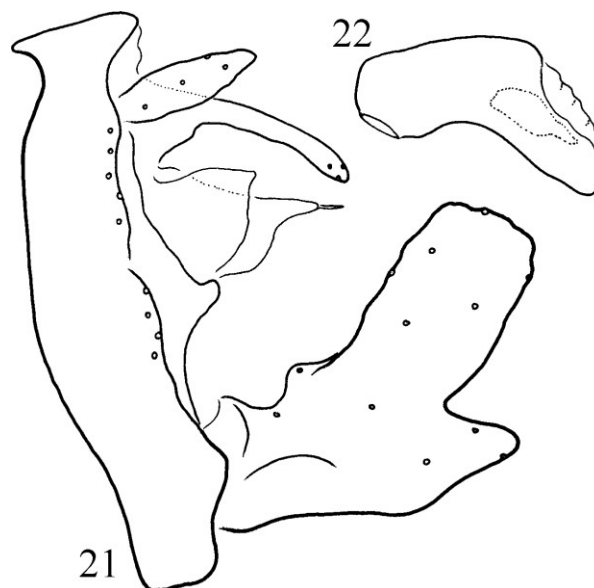
(Figures 21–22)

*Material examined.* Holotype, **Ecuador**, West Andean foothills, Tinalandia Nature Reserve, Rio Toachi, 85 km from Quito, 600 m, 24.XI.2007, light trap, leg. J. Oláh (1male, OPC). Paratypes: same as holotype (2 associated females, OPC).

*Diagnosis.* This remarkable species with pronounced forewing spotting belongs to the *Oecetis avara* species group and its gonopod and phallobase shapes are most close to *O. protrusa* Blahnik & Holzenthal, 2014 described from Costa Rica. Its gonopods differs by quadratic dorsal arms and by the more pointed ventral arms as well as the lateral profile of the phallobase differs.

*Description.* Male (in alcohol). Light yellow animal. Male forewing length 8 mm, female forewing length 7 mm. Wing membrane pale with pronounced spotting pattern on veins.

*Male genitalia.* Segment IX fused, very short annular, with slightly longer dorsum; elongate setae present along posterolateral margin. Segment X forming a long mesal digitiform process, uniform in width, apex with short sensilla and basement is high. Cerci elongated. Segment X continuous basoventrally with the paraproct, a pair of asymmetrical membranous lobes. Gonopods with mitten-like form, its large dorsal arm



**Figures 21–22.** *Oecetis tina* sp. nov. Holotype male: 21 = genitalia in left lateral view; 22 = phallic organ in left lateral view.

quadrangular, its small ventral arm pointed. Lateral profile of the phallobase elongated, ventral margin with shorter basal and longer apical half, phallosomal sclerite prominent.

*Etymology.* *tina*, from the name of the type locality: Tinalandia Nature Reserve to remember this first ecotourism adventure in Ecuador with plenty of hummingbird species attracted to feeders.

**Helicopsychidae Ulmer, 1912**

***Helicopsyche (Cochliopsyche) napoa* Johanson, 2003**

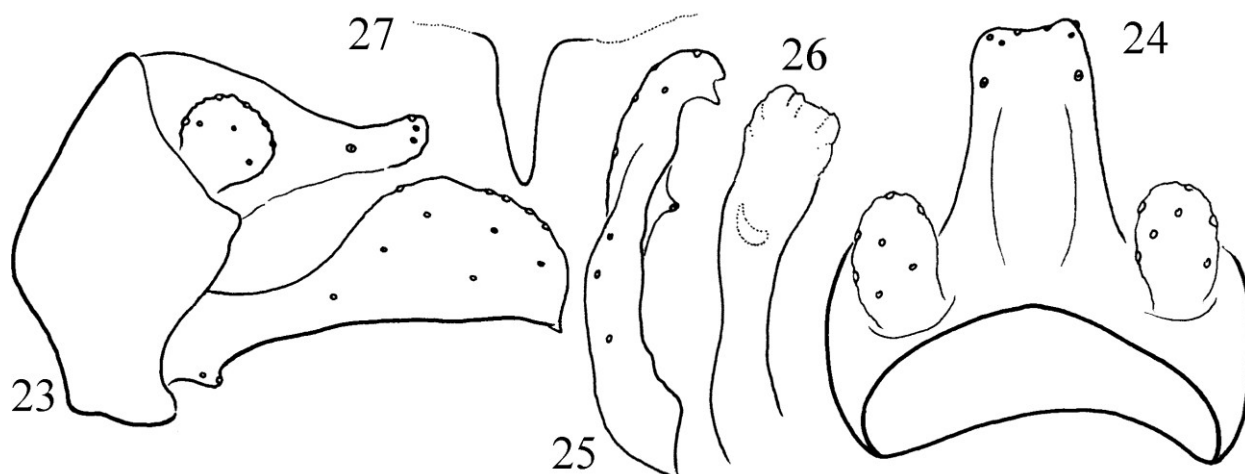
*Material examined.* **Ecuador**, Amazonian Lowland, Terra Firme, Gareno lodge, Near Puerto Napo, 400 m, 13-14. VIII.2011, light trap, leg. J. Oláh (2 males, OPC).

***Helicopsyche (Cochliopsyche) nyurga* sp. nov.**

(Figures 23–27)

*Material examined.* Holotype, **Ecuador**, Amazonian Lowland, Terra Firme, Gareno lodge, near Puerto Napo, 400 m, 13-14. VIII.2011, light trap,





**Figures 23–27.** *Helicopsyche (Cochliopsyche) nyurga* sp. nov. Holotype male: 23 = genitalia in left lateral view; 24 = genitalia in dorsal view; 25 = left gonopod in ventral view; 26 = phallic organ in left lateral view; 27 = digitate process on sternum VI.

leg. J. Oláh (1 male, OPC). Paratypes: same as holotype (20 males, OPC).

**Diagnosis.** Species in the long-horned *Helicopsyche (Cochliopsyche)* subgenus are difficult to distinguish from each other (Johanson 2003). Not any divergences have been yet recognised in the fine structure of the intromittent organ. Gonopods seem to be diverged most significantly and produced subtle, but stable shape modifications in the basic forms of the proximal shaft and the distal lobe as well as in the number, forms and positions of various gonopod processes. This new species is most similar *H. opalescens* (Flint, 1972), but differs by having significantly elongated distal lobes on the gonopods, not short.

**Description.** Wings (in alcohol) dark brown; forewing length 5 mm; antennae long, 14 mm. Spur formula 1,2,2. Pointed sternal process on segment present, directed ventrally.

**Male genitalia.** Segment IX rhomboid in lateral view. Segment X (dorsal hood) narrowing apicad in lateral view; in dorsal view its apical margin slightly concave; few short setae with pronounced alveoli present on apical margin; one pair of stronger setae present subapicad. Cerci circular in lateral view densely packed with long setae with enlarged alveoli giving an undulating margin. Gonopods are simple, proximal shaft is

short and low, distal lobe is elongated with a pointed ventroapical downward directed ending. Phallobase forming a simple curved tube with terminal membranous endotheca; sclerotized phal-lotremal sclerite just discernible.

**Etymology.** *nyurga*, elongated in Hungarian, refers to the elongated distal lobe of the gonopod.

## REFERENCES

- ADAMI, C., OFRIA, C. & COLLIER, T.C.(2000): Evolution of biological complexity. *Proceedings of the National Academy of Sciences of the United State of America*, 97(9): 4463–4468. doi: [10.1073/pnas.97.9.4463](https://doi.org/10.1073/pnas.97.9.4463)
- BARETT, M., CLATTERBUCK, H., GOLDSBY, M., HELGESON, C., MCLOONE, B., PEARCE, T., SOBER, E., STERN, R. & WEINBERGER, N. (2012): Puzzles for ZFEL, McShea and Brandon's zero force evolutionary law. *Biology and Philosophy*, 27: 723–735. doi: [10.1007/s10539-012-9321-7](https://doi.org/10.1007/s10539-012-9321-7)
- BETTEN, C. (1934): The caddis flies or Trichoptera of New York state. *New York State Museum Bulletin*, 292: 1–576.
- BLAHNIK, R.J. & HOLZENTHAL, R.W.(2014): Review and redescription of species in the *Oecetis avara* group, with the description of 15 new species (Trichoptera, Leptoceridae). *ZooKeys*, 376: 1–83. doi: [10.3897/zookeys.376.6047](https://doi.org/10.3897/zookeys.376.6047)

- BOLTZMANN, L. (1886): *The second law of thermodynamics*. In: B. MCGINNES (Ed.) Ludwig Boltzmann, theoretical physics and philosophical problems. Springer Nature, (1974). p. 13–32. doi: [10.1007/978-94-010-2091-6\\_2](https://doi.org/10.1007/978-94-010-2091-6_2).
- CHEN, Y. (1993): *Revision of the Oecetis (Trichoptera: Leptoceridae) of the world*. Unpublished Ph.D. Dissertation. Clemson University, Clemson, South Carolina, 704 pp.
- CIAMPAGLIO, C.N., KEMP, M. & MCSHEA, D.W. (2001): Detecting changes in morphospace occupation pattern in the fossil record: characterization and analysis of measures of disparity. *Paleobiology*, 27: 695–715. doi: [10.1666/0094-8373\(2001\)0272.0.CO;2](https://doi.org/10.1666/0094-8373(2001)0272.0.CO;2)
- ESTEVE-ALTAVA, B., MARUGÁN-LOBÓN, J., BOTELLA, H., & RASSKIN-GUTMAN, D. (2013): Structural constraints in the evolution of the tetrapod skull complexity: Williston's law revisited using network models. *Evolutionary Biology*, 40: 209–219. doi: [10.1007/s11692-012-9200-9](https://doi.org/10.1007/s11692-012-9200-9)
- FISCHER, R.A. (1930): *The genetical theory of natural selection*. Clarendon Press, Oxford, U. K. 272 pp. doi: [10.5962/bhl.title.27468](https://doi.org/10.5962/bhl.title.27468)
- FLINT, O.S. JR., MCALPINE J.F. & ROSS, H.H. (1987): A revision of the genus *Leptonema* GUÉRIN (Trichoptera: Hydropsychidae: Macronematinae). *Smithsonian Contributions to Zoology*, 450: 1–193. doi: [10.5479/si.00810282.450](https://doi.org/10.5479/si.00810282.450)
- FOOTE, M. (1997): The evolution of morphological diversity. *Annual Review of Ecology and Systematics*, 28: 129–152. doi: [10.1146/annurev.ecolsys.28.1.129](https://doi.org/10.1146/annurev.ecolsys.28.1.129)
- GREGORY, W.K.(1935): Reduplication in evolution. *Quarterly Review of Biology*, 10: 272–290. doi: [10.1086/394485](https://doi.org/10.1086/394485)
- IVANOV, V.D. (2005): *Ground plan and basic evolutionary trends of male terminal segments in Trichoptera*. In: TANIDA, K. & ROSSITER, A. (Eds.) Proceedings of the XIth International Symposium on Trichoptera. Tokai University Press, Kanagawa, Japan. p. 207–218.
- JOHANSON, K.A. (2003): Revision of the Neotropical caddisfly subgenus *Helicopsyche* (*Cochliopsyche*) (Trichoptera, Helicopsychidae), with descriptions of twelve new species. *Insect Systematics & Evolution*, 34: 381–414. doi: [10.1163/187631203X00036](https://doi.org/10.1163/187631203X00036)
- KUMANSKI, K.P. (1968): *Chaetopteryx maximus* n. sp. aus Bulgarien (Trichoptera, Limnephilidae). *Comptes rendus de l'Académie bulgare des Sciences*, 21(1): 59–61.
- KUMANSKI, K.P. (1969): *Chaetopteryx bulgaricus* – ein neue Art aus der maximus-Gruppe (Trichoptera, Limnephilidae). *Reichenbachia*, 12(3): 21–27.
- KUMANSKI, K.P. (1987): A new genus of the Chaetopterygini-tribe (Trichoptera: Limnephilidae). *Trichoptera Newsletter (Lunz, Austria)*, 14: 17–19.
- LYNCH, M. & CONERY, J. S. (2003): The origins of genome complexity. *Science*, 302: 1401–1404. doi: [10.1126/science.108937](https://doi.org/10.1126/science.108937)
- MARTYNOV, A.B. (1934): *Trichoptera, Annulipalpia*. Tableaux analytiques de la Fauna de l'URSS, publiés par l'Institut zoologique de l'Académie des Sciences, Science Press, Leningrad, 343 pp.
- MCLACHLAN, R. (1874–1880): *A monographic revision and synopsis of the Trichoptera of the European fauna*. Reprinted 1968, E.W.Classey Ltd. 353 Hanworth Road, Hampton, Middlesex, 523 pp. + 59 plts. doi: [10.5962/bhl.title.28556](https://doi.org/10.5962/bhl.title.28556)
- MCSHEA, D.W.( 2005): The evolution of complexity without natural selection, a possible large-scale trend of the fourt kind. *Paleobiology*, 31( Supplement 5): 146–156. doi: [10.1666/0094-8373\(2005\)031\[0146:TEOCWN\]2.0.CO;2](https://doi.org/10.1666/0094-8373(2005)031[0146:TEOCWN]2.0.CO;2)
- MCSHEA, D.W. & BRANDON, R. (2010): *Biology's first law*. University of Chicago Press, Chicago, 184 pp. doi: [10.7208/9780226562278](https://doi.org/10.7208/9780226562278)
- MCSHEA, D.W. & HORDIJK, W. (2013): Complexity by substruction. *Evolutionary Biology*, 40: 504–520. doi: [10.1007/s11692-013-9227-6](https://doi.org/10.1007/s11692-013-9227-6)
- MOSELY, M.E. (1939): *The British Caddis Flies (Trichoptera)*. George Routledge & Sons, Ltd, London, 320 pp.
- MOSELY, M.E. & KIMMINS, D.E. (1953): *The Trichoptera (caddis-flies) of Australia and New Zealand*. British Museum (Natura History), London, 550 pp. doi: [10.5962/bhl.title.118696](https://doi.org/10.5962/bhl.title.118696)
- NIELSEN, A. (1957): A comparative study of the genital segments and their appendages in male Trichoptera. *Biologiske Skrifter Udgivet af det Kongelige Danske Videnskabernes Selskab*, 8(5): 1–159.
- OLÁH, J. (2012): New species and records of Trichoptera from Batanta and Waigeo Islands (Indonesia,

- Raja Empat Archipelago, Papua [Irian Jaya]). *Braueria* (Lunz am See, Austria), 39: 39–57.
- OLÁH, J. (2014): On the Trichoptera of Batanta Island (Indonesia, Papua, Raja Ampat Archipelago), III. *Folia Entomologica Hungarica*, 75: 91–131.
- OLÁH, J. (2015): On the Trichoptera of New Guinea II. *Folia Entomologica Hungarica*, 76: 119–166.
- OLÁH, J. (2016): On the Trichoptera of Batanta Island (Indonesia, West Papua, Raja Ampat Archipelago) V. *Folia Historico-Naturalia Musei Matraensis*, 40: 95–135.
- OLÁH J. & JOHANSON, K.A. (2008): Reasoning an appendicular and functional caddisfly genital terminology. *Braueria* (Lunz am See, Austria), 35: 29–40.
- OLÁH J. & MALICKY, H. (2010): New species and new species records of Trichoptera from Vietnam. *Braueria* (Lunz am See, Austria), 37: 13–42.
- OLÁH, J. & JOHANSON, K.A. (2011): Description of a new endemic genus of Trichoptera from Madagascar (Odontoceridae). *Acta Zoologica Academiae Scientiarum Hungaricae*, 57(2): 117–129.
- OLÁH J. & JOHANSON, K.A. (2012): New species and records of Neotropical Macronematinae and Smicrideinae (Trichoptera: Hydropsychidae). *Annales Historico-Naturales Musei Nationalis Hungarici*, 104: 215–297.
- OLÁH, J. & ITO, T. (2013): Synopsis of the *Oxyethira flavicornis* species group with new Japanese *Oxyethira* species (Trichoptera, Hydroptilidae). *Opuscula Zoologica, Budapest*, 44(1): 23–46.
- OLÁH, J., IBRAHIMI, H. & KOVÁCS, T. (2013a): The *Chaetopteroidea* genus (Trichoptera, Limnephilidae) revised by fine structure analysis of parameres. *Folia Historico Naturalia Musei Matraensis*, 37: 93–108.
- OLÁH, J., ANDERSEN, T., CHVOJKA, P., COPPA, G., GRAF, W., IBRAHIMI, H., LODOVICI, O., PREVIŠIĆ, A. & VALLE, M. (2013b): The *Potamophylax nigricornis* group (Trichoptera, Limnephilidae): resolution of phylogenetic species by fine structure analysis. *Opuscula Zoologica, Budapest*, 44(2): 167–200.
- OLÁH, J., CHVOJKA, P., COPPA, G., GRAF, W., IBRAHIMI, H., LODOVICI, O., RUIZ GARCIA, A., SÁINZ-BARIÁIN, M., VALLE, M. & ZAMORA-MUÑOZ, C. (2014): The genus *Allogamus* Schmid, 1955 (Trichoptera, Limnephilidae): revised by sexual selection-driven adaptive, non-neutral traits of the phallic organ. *Opuscula Zoologica, Budapest*, 45(1): 33–82.
- OLÁH, J. & KISS, O. (2015): New species and records of Trichoptera from Turkey. *Folia Historico-Naturalia Musei Matraensis*, 39: 99–104.
- OLÁH, J. & T. KOVÁCS 2015. New species and records of Balkan Trichoptera III. *Folia Historico-Naturalia Musei Matraensis* 38:97-131.
- OLÁH, J., CHVOJKA, P., COPPA, G., GODUNKO, R. J., LODOVICI, O., MAJECKA, K., MAJECKI, J., SZCZĘSŃNY, B., URBANIC, G. & VALLE, M. (2015): Limnephilid taxa revised by speciation traits: *Rhadicoleptus*, *Isogamus*, *Melampophylax* genera, *Chaetopteryx rugulosa*, *Psiloptyx psorosa* species groups, *Drusus bolivari*, *Annitella kosciuszki* species complexes (Trichoptera, Limnephilidae). *Opuscula Zoologica, Budapest*, 46(1): 3–117. doi: [10.18348/opzool.2015.1.3](https://doi.org/10.18348/opzool.2015.1.3)
- OLÁH, J. & BESHKOV, S. (2016): New records of Trichoptera in the Balkan Peninsula and Romania, with the description of new *Rhyacophila* sibling species by speciation traits. *Folia Entomologica Hungarica*, 77: 87–104.
- OLÁH, J., BESHKOV, S., CHVOJKA, P., CIUBUC, C., COPPA, G., IBRAHIMI, H., KOVÁCS, T., MEY, W. & OLÁH, J. JR. (2017): Revision of Drusinae subfamily (Trichoptera, Limnephilidae): divergence by paraproct and paramere, speciation in isolation by integration. *Opuscula Zoologica, Budapest*, 48 (Supplementum 1): 3–228. doi: [10.18348/opzool.2017.S1.3](https://doi.org/10.18348/opzool.2017.S1.3)
- ORR, H. A. (2000): Adaptation and the cost of complexity. *Evolution*, 54(1): 13–20. doi: [10.1111/j.0014-3820.2000.tb00002.x](https://doi.org/10.1111/j.0014-3820.2000.tb00002.x)
- PRATHER, A.L. (2003): Revision of the Neotropical caddisfly genus *Phylloicus* (Trichoptera: Calamoceratidae). *Zootaxa*, 275: 1–214. doi: [10.11646/zootaxa.275.1.1](https://doi.org/10.11646/zootaxa.275.1.1)
- PRATHER, A.L. (2004): Revision of the Neotropical caddisfly genus *Banyallarga* (Trichoptera: Calamoceratidae). *Zootaxa*, 435: 1–76. doi: [10.11646/zootaxa.435.1.1](https://doi.org/10.11646/zootaxa.435.1.1)
- RAUP, D.M. (1977): *Stochastic models in evolutionary paleobiology*. In: HALLAM, A. (Ed.) Patterns of evolution as illustrated by the fossil record. Elsevier, Amsterdam, p. 59–78.

- ROSS, H.H. (1938): Description of Nearctic caddis flies (Trichoptera) with special reference to the Illinois species. *Illinois Natural History Survey Bulletin*, 21(4): 101–183.
- ROSS, H.H. (1956): *Evolution and classification of the mountain caddisflies*. The University of Illinois Press, Urbana, 213 pp. doi: [10.1093/aesa/50.3.312](https://doi.org/10.1093/aesa/50.3.312)
- SCHMID, F. (1955): Contribution à l'étude des Limnophilidae (Trichoptera). *Mitteilungen der Schweizerischen Entomologischen Gesellschaft*, 28: 1–245.
- SCHMID, F. (1958): A propos de deux récents ouvrages sur la phylogénie et la zoogéographie des Trichopteres. *Miscellania Zoologica Barcelona*, 1(5): 1–27.
- SCHMID, F. (1968): La famille des Arctopsychides (Trichoptera). *Mémoires de la Société Entomologique du Québec*, 1: 1–84.
- SCHMID, F. (1970): Le genre *Rhyacophila* et la famille des Rhyacophilidae (Trichoptera). *Mémoires de la Société Entomologique du Canada*, 102(Supplement 66): 5–334. doi: [10.4039/entm10266fv](https://doi.org/10.4039/entm10266fv)
- SCHMID, F. (1979): On some new trends in Trichopterozoology. *Bulletin of the Entomological Society of Canada*, 11: 48–57.
- SCHNEIDER, E.D. & KAY, J.J. (1995): *Order from disorder: the thermodynamics of complexity in biology*. In: MURPHY, M.P. & O'NEILL L.A.J. (Eds.) *What is life: the next fifty years. Reflections on the future of biology*. Cambridge University Press, pp. 161–172. doi: [10.1017/CBO9780511623295.013](https://doi.org/10.1017/CBO9780511623295.013)
- SCHRÖDINGER, E. (1944): *What is life? The physical aspect of the living cell*. Cambridge. The University Press, 91 pp.
- SPENCER, H. (1900). *The principles of biology*. Appleton, New York, 676 pp.
- SPENCER, H. (1904): *First principles*. J. A. Hill, New York, 576 pp.
- VSHIVKOVA, T.S. (2006): *Phylogeny of family Limnophilidae (Insects: Trichoptera) with emphasis on tribe Limnephilini (subfamily Limnephilinae)*. PhD Thesis, UMI Dissertation Services, i-xxiii + 686 pp.
- WEISS, K.M. (1990): Duplication with variation: metameric logic in evolution from genes to morphology. *Yearbook of Physical Anthropology*, 33: 1–23. doi: [10.1002/ajpa.1330330503](https://doi.org/10.1002/ajpa.1330330503)
- WILLISTON, S.W. (1914): *Water Reptiles of the past and present*. University of Chicago Press, Chicago, 251 pp. doi: [10.5962/bhl.title.27909](https://doi.org/10.5962/bhl.title.27909)
- YI, S.V. (2006): Non-adaptive evolution of genome complexity. *BioEssays*, 28: 979–982. doi: [10.1002/bies.20478](https://doi.org/10.1002/bies.20478)

## Appendix

List of newly described species and species records collected by J. Oláh jr. in Colombia and Ecuador and published by Oláh & Johanson (2011, 2012) and by Oláh & Oláh, 2017

<b>Hydropsychidae</b> (Oláh & Johanson, 2012)	
<i>Leptonema album</i> Mosely, 1933	Ecuador: Tinalandia
<i>L. enikolah</i> Oláh & Johanson, 2012	Colombia: Minca
<i>L. intermedium</i> Mosely, 1933	Ecuador: Tinalandia
<i>L. janolah</i> Oláh & Johanson, 2012	Ecuador: Alambi
<i>L. mastigion</i> Flint, McAlpine & Ross, 1987	Ecuador: Tinalandia
<i>L. rosenbergi</i> Mosely, 1933	Ecuador: Lita
<i>L. spirillum</i> Flint, McAlpine & Ross, 1987	Colombia: Otun Quinbaya
<i>L. viridianum</i> Navas, 1916	Ecuador: Gareno
<i>Smicridea (Rhyacophylax) begorba</i> Oláh & Johanson, 2012	Ecuador: Gareno
<i>Smicridea (R.) begorba</i> Oláh & Johanson, 2012	Ecuador: Gareno
<i>Smicridea (Smicridea) bivittata</i> (Hagen, 1861)	Ecuador: Archidonia, Tinalandia
<i>Smicridea (R.) felsa</i> Oláh & Johanson, 2012	Ecuador: Gareno
<i>Smicridea (R.) fogasa</i> Oláh & Johanson, 2012	Ecuador: Wild Sumaco
<i>Smicridea (R.) furesa</i> Oláh & Johanson, 2012	Ecuador: Archidonia
<i>Smicridea (R.) hajla</i> Oláh & Johanson, 2012	Ecuador: Gareno
<i>Smicridea (R.) homora</i> Oláh & Johanson, 2012	Ecuador: Gareno
<i>Smicridea (R.) horga</i> Oláh & Johanson, 2012	Ecuador: Tinalandia
<i>Smicridea (R.) medena</i> Oláh & Johanson, 2012	Colombia: Otun Quinbaya
<i>Smicridea (S.) mincana</i> Oláh & Johanson, 2012	Colombia: Minca
<i>Smicridea (R.) murina</i> McLachlan, 1871	Colombia: Jarden; Ecuador: Alambi
<i>Smicridea (R.) nemtompa</i> Oláh & Johanson, 2012	Ecuador: Gareno
<i>Smicridea (R.) sarkoska</i> Oláh & Johanson, 2012	Colombia, Ecuador
<i>Smicridea (R.) sudara</i> Oláh & Johanson, 2012	Ecuador: Alambi, Tinalandia
<i>Smicridea (R.) tavola</i> Oláh & Johanson, 2012	Ecuador: Gareno
<i>Smicridea (R.) tina</i> Oláh & Johanson, 2012	Ecuador: Tinalandia
<i>Smicridea (R.) ventridenticulata</i> Flint, 1991	Colombia, Ecuador
<b>Hydroptilidae</b> (Oláh & Johanson, 2011)	
<i>Hydroptila grenadensis</i> Flint, 1968	Ecuador: Gareno
<i>Hydroptila venezuelensis</i> Flint, 1981	Ecuador: Gareno
<i>Oxyethira simanka</i> Oláh & Johanson, 2011	Ecuador: Wild Sumaco
<i>Rhyacopsyche bunkotala</i> Oláh & Johanson, 2011	Ecuador: Wild Sumaco
<i>Rhyacopsyche hajtoka</i> Oláh & Johanson, 2011	Ecuador: Alambi
<i>Bredinia venezuelensis</i> Harris, Holzenthal & Flint 2002	Ecuador: Gareno
<b>Leptoceridae</b> (Oláh & Oláh, 2017)	
<i>Nectopsyche flinti</i> Oláh & Oláh, 2017	Surinam
<i>Nectopsyche garenosa</i> Oláh & Oláh, 2017	Ecuador: Gareno
<i>Nectopsyche lenula</i> Oláh & Oláh, 2017	Bolivia, Guayamerin
<i>Nectopsyche oliveri</i> Oláh & Oláh, 2017	Surinam
<i>Nectopsyche sima</i> Oláh & Oláh, 2017	Ecuador, Gareno
<i>Nectopsyche padka</i> Oláh & Oláh, 2017	Ecuador, Tinalandia
<i>Nectopsyche bunka</i> Oláh & Oláh, 2017	Colombia, Tatama
<i>Nectopsyche eltera</i> Oláh & Oláh, 2017	Colombia, Urrao
<i>Nectopsyche flintorum</i> Oláh & Oláh, 2017	Colombia
<i>Nectopsyche taga</i> Oláh & Oláh, 2017	Ecuador, Gareno