

The genus *Allogamus* Schmid, 1955 (Trichoptera, Limnephilidae): revised by sexual selection-driven adaptive, non-neutral traits of the phallic organ

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Abstract. Based upon our previous reviews on the phylogenetic species concept, initial split criteria and fine structure analysis here we summarize population and model thinking as support to our diverged structure matrix procedure to test simply visually or, if required, by geometric morphometrics the stability of sexual selection-driven adaptive, non-neutral traits of the phallic organ. Complexity review helped us to establish plesiomorphic and apomorphic states of parameres of the phallic organ. Fine structure diversity of the adaptive traits of paramere and the apical portion of aedeagus has been applied to revise the *Allogamus* genus. All the known 22 taxa, 19 species and 3 subspecies, have been revised. Apomorphic fusion of parameres and complexity evolution of aedeagus directed us to erect 2 rediagnosed species groups, 1 new species group, 4 new species subgroups, 1 new species complex, 10 new species and 4 new or revised species status as follows: *Allogamus auricollis* species group, rediagnosed. *Allogamus antennatus* new subgroup: *A. antennatus* (McLachlan, 1876), *A. ausoniae* Moretti, 1991, stat. rev., *A. morettii* DePietro & Cianficconi, 2001, stat. rev., *A. silanus* Moretti 1991, stat. nov. *Allogamus auricollis* new subgroup: *A. alpenensis* Oláh, Lodovici & Valle sp. nov., *A. auricollis* (Pictet, 1834), *A. despaxi* Decamps, 1967, *A. zomok* Oláh & Coppa sp. nov. *Allogamus hilaris* new subgroup: *A. hilaris* (McLachlan, 1876). *Allogamus ligonifer* new subgroup: *A. gibraltarius* Gonzalez & Ruiz, 2001, *A. kefes* Coppa & Oláh sp. nov., *A. laureatus* (Navas, 1918), *A. ligonifer* (McLachlan, 1876), *A. pertuli* Malicky, 1974, *A. pupos* Coppa & Oláh sp. nov. *Allogamus mortoni* new species complex: *A. kamos* Oláh & Ruiz sp. nov., *A. kettos* Oláh & Ruiz sp. nov., *A. kurtas* Oláh & Zamora-Muñoz sp. nov., *A. mortoni* (Navas, 1907), *A. pohos* Oláh & Zamora-Muñoz sp. nov., *A. tuskes* Oláh & Sáinz-Bariáin sp. nov. *Allogamus corsicus* new species group: *A. corsicus* (Ris, 1897). *A. illiesorum* Botosaneanu, 1980 stat. rev. *Allogamus uncatatus* species group, rediagnosed: *A. botosaneanui* Moretti, 1991, *A. dacicus* (Schmid, 1951), *A. fuesunae* Malicky, 2004, *A. mendax* (McLachlan, 1876), *A. pantinii* Oláh, Lodovici & Valle sp. nov., *A. periphetes* Malicky, 2004, *A. stadleri* (Schmid, 1951), *A. starmachi* Szczesny, 1967, *A. tomor* Oláh, 2012, *A. uncatatus* (Brauer 1857).

Keywords. *Allogamus*, Trichoptera, shape analysis, complexity evolution, non-neutral structural traits, new species.

INTRODUCTION

The species of the autumn flying genus *Allogamus* Schmid, 1955 populate the European triangle of England-Pyrénées-Greece and inhabit mountain streams and springs. Nine species of the genus *Allogamus* have previously been listed in the *uncatus* group of the genus *Halesus* (Schmid 1951a): *Halesus mendax* McLachlan, *H. uncatus* Brauer, *H. liganifer* McLachlan, *H. hilaris* McLachlan, *H. mortoni* Navas, *H. laureatus* Navas, *H. auricollis* Pictet, *H. antennatus* McLachlan, and *H. corsicus* Ris. Two new *Halesus* species were described by Schmid (1951b): *H. stadleri* from France and Germany and *H. dacicus* from Romania. The genus *Allogamus* has been erected for these eleven *Halesus* species (Schmid 1955).

Eleven new *Allogamus* taxa have been described in the last half century: *Allogamus starmachi*, *A. lazarei* and *A. tatricus* from the High Tatras (Szczeny 1967), but *A. lazarei* and *A. tatricus* were synonymised with *A. starmachi* by Botosaneanu & Malicky (1978). *A. despaxi* was described from the French Pyrénées by Décamps (1967), *A. pertuli* from Greece by Malicky (1974), *A. illiesorum* from Sardinia by Botosaneanu (1980), however this latter was reduced to subspecies status by Malicky (2005) as *A. corsicus illiesorum*. *A. ausoniae* was described from Italy by Moretti (1991), but reduced to subspecies status by Malicky (2005) as *A. antennatus ausoniae*. *A. botosaneanui* was described from Italy by Moretti (1991). *A. hilaris silanus* described also from Italy by Moretti (1991) was later transferred by Malicky (2005) to *A. antennatus* as subspecies *silanus*. *A. morettii* was described from Sicily by De Pietro & Cianficconi (2001), but synonymized with *Allogamus antennatus silanus* Moretti, 1991 by Malicky (2005). *A. gibraltarius* was described from Spain by González & Ruiz (2001), *A. periphetes* from Italy and Switzerland as well as *A. fuesunae* from Spain, Pyrénées by Malicky (2004). *A. tomor* was described from Albania by Oláh in Oláh & Kovács (2012). In the present state of knowledge the genus *Allogamus* contains 22 taxa: 19 species and 3 subspecies.

Based on the phylogenetic species concept (Oláh *et al.* 2012), on the initial split criteria and on the fine structure analysis (Oláh *et al.* 2013a) here we revise the taxonomy of the genus *Allogamus* applying the sexual selection-driven, non-neutral adaptive traits of the phallic organ: the parameres and the head of the aedeagus. In order to visualize the stability of these adaptive traits we have applied here the diverged structural trait matrix, by reviewing population and model thinking, shape analysis and complexity alternatives of adaptive parameres.

THEORETICAL PART

Working on closely related species complexes exhibiting morphological signs of recent speciation processes it may be necessary to enrich our routine alpha taxonomy with more population and model thinking and to apply the growing arsenal of shape analysis. Here we introduce a simple practice of producing graphical matrices of recently diverged fine structures. In the everyday practice of species determination and description such a visual presentation is sufficient. The drawings of diverged structural matrices indicate clearly the stability or variability of the diverged structural traits without need of statistics and morphometrics. If later is required, the published population matrices of diverged fine structures offer future possibility to analyse and compare them by various procedures of geometric morphometrics. The interpretation of the discovered stable fine structure of the diverged incipient species requires to understand and to evaluate its complexity, whether plesiomorphic or apomorphic. Here we review briefly the population and model thinking and the application of our diverged structure matrix as well as the principles of shape analysis and the complexity interpretation of the investigated shape.

Diverged structure matrix and population thinking

Darwin's innovation, the population thinking opposes the Platonic doctrine of "essentialism" or "typological thinking" (Ariew 2008). Type (eidos)

is real and variation is an illusion or type (average) is an abstraction and the variation is real (Mayr 1959). Aristotle's natural-state model with interfering forces unites the type and expressing variations (Sorber 1994). The reality is dual: particles and interacting forces. This is why every particle differs from each others. Natural states and interfering forces illustrate best also the theory of heredity. This is why the population thinking developed into the growing universe of population genetics.

Our goal in alpha taxonomy is to distinguish the incipient species with initial split criteria. In practice we examine structural diversifications nearby the structural diverging point. We search the first morphological product of speciation with unknown ranges of ubiquitous variation. Searching such fine structures we need to study many specimens from many populations to discover the first, although delicate structural trait already diverged. Its mere existence indicates that it is probably stable enough to provide early barriers to gene flow. If discovered we start a detailed research on its stability by preparing the graphical diverged structure matrix for each population.

Visual empiricism and model thinking

In alpha taxonomy we are studying the phenotypes, the morphological expression of genomic processes. We rely upon mostly on the visual empiricism, while molecular genetics applies almost exclusively models. Model thinking gives us a powerful tool to understand the realistic processes. This is further fortified by progress in statistical methodology for detecting molecular adaptation and positive selection (Nei *et al.* 2010). However statistics are measuring something and the reality could be far more complex than our interpretations. Moreover several distinct causal mechanisms can yield the same statistical pattern (Pigliucci 2006). We have to acknowledge if visual empiricism is available and applicable to separate incipient species without molecular genetical models. Visualized structure matrix is a graphical copy of the reality. Model is our idea, a human created limited thinking about reality.

However it could be far from the real environmental situation. For instance in contrast to the Wright-Fisher population model widely applied in molecular genetics: (1) most of the population has two sexes; (2) mating is non-random due assortative mating and sexual selection; (3) reproductive success is non-random; (4) population size vary in time; (5) population is subdivided into demes of local populations; and deterministic forces of (6) selection and stochastic forces of (7) recombination, (8) genetic drift and (9) gene flow are all variously present (Charlesworth 2009).

Shape analysis

Comparing shapes of anatomical structures forms our work in the classification of organisms and helps us to understand and to quantify the diversity of life. At the same time we do not realize that shapes are fundamental genetic traits as well competing with molecular traits. It is tempting to believe that genomic complexity is mirrored in phenotypic morphological and functional complexity and vice versa with obvious difficulty of matching genes with structure or function (Adami *et al.* 2000). New genes are the sources of functional and phenotypic diversity and recent progress has been made in understanding the evolution and phenotypic effects of genomes acquiring novel genetic elements (Chen *et al.* 2013). Combining fine structures of shape with principles of molecular traits yields synthetic insights into understanding of biological diversity at refined resolution.

Morphometrics is the study of shape variation and covariation. Analysis of shape developed to multivariate morphometrics. Quantitative variables of length, width, height, sometimes counts, ratios, and angles are compared among populations and species applying several statistic procedures: statistical analyses of principal component analysis, factor analysis, canonical variates analysis, and discriminant function analysis.

Difficulties while working in traditional morphometrics appear in size correction, linear homology, shape-independent distance as well as the

lack of graphical representation. These limits forced scientists to explore alternative methods to capture the geometry of shape. The newly developed approach has revolutionized our shape research with the geometric morphometrics (Rohlf & Marcus 1993). Outline methods were the first method developed by digitized points along outline and fitting the points with mathematical function, usually by Fourier analysis. Landmarks methods are based on the collection of two- or three-dimensional coordinates of biologically definable landmarks on shapes. Superimposition methods eliminated non-shape variation in landmark configuration and produced reliable shape information from primary landmark data.

The future of geometric morphometrics was discussed by Adams *et al.* (2004). There are potential for (1) the use of three-dimensional data, (2) combining landmarks and surfaces using sliding semilandmarks, (3) use imputation methods for missing data and absent structures, (4) estimating landmark covariance structure, (5) solving difficulties to combine morphometrics and phylogenetics.

Evolution of paramere complexity

Genome complexity is correlated with morphological complexity and driven primarily by non-adaptive stochastic forces, rather than by adaptive evolution (Lynch 2006, Yi 2006). There is a need to answer the simple question still unresolved in the evolution of paramere complexity: do parameres evolve from simple to complex or the opposite? This question emerged important for paramere structures, especially nowadays, when their non-neutral, adaptive sexual selection driven evolution become more documented (Oláh *et al.* 2012, Oláh & Ito 2013, Oláh *et al.* 2013a; Oláh *et al.* 2013b). Titillating and/or harming parameres of the phallic organ directly involved in sexual selection processes diverge into variously complex structural patterns fitting to perform their multiple and complex functions in the initial stage of divergence (Oláh *et al.* 2013b). In order to understand what is simple and complex or which character state is ancestral plesiomorphic or de-

rived apomorphic we need to outline some basic relations in complexity theory. This condensed survey oversimplifies the ever-changing and complicated understandings and speculations about entities and interactions inside the self-organising complexity, intending simply to help some orientation in alpha taxonomy.

According to the Williston's law the structures tend toward reduction: in vertebrate evolution the numbers of skull bones are reduced by loss and fusion (Williston 1914). A general evolution pattern of reduction in structural parts was demonstrated by Gregory (1935). An ancestor must be constituted by the integration of the largest possible number of characters (Schmid 1979). Based upon these findings we have selected the structurally most complex parameres for the ancestral plesiomorphic state in the *Potamophylax nigricornis* species group (Oláh *et al.* 2013a), but considered that the terms simple, complex, primitive, generalized, specialized, are all strictly comparative (Ross 1956; Schmid 1958). This experienced simplification trend in evolution is associated to a decrease in complexity or whether or not complexity increases through evolution has become a contentious issue.

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 death of random disorder by equilibrium seeking. 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 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. Life exists and builds complexity in energy and material fluxes, as constrained gradient dissipator, while importing energy (negentropy) from outside at the ex-

pense of producing entropy in the environment (Schneider & Kay 1995). However, how this permanent increase in complexity during evaluation supports Williston's finding of the experienced reduction or simplification?

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, 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 analog of the law of inertia in Newtonian mechanics. This is 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. Their internal parts become differentiated along an internal-variance-vector. Selection could reinforce, act neutrally or oppose it (McShea 2005). Evolutionary zero-force law states what will happen if no forces impinge on the system. However 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 "constraint-entropy" and the entropy decreasing "temperature-entropy". Complexity is the result of exergy, the capacity of an energy system to perform useful work processing to equilibrium with the environment. The zero-force evolutionary law seems to move into an opposite direction with decomposing variation. A recent criticism says that di-

versity and complexity do not change when there are no evolutionary causes (Barett *et al.* 2012).

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. 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.

We need more rigorously defined and measurable traits to study the evolution of complexity in biological evolution. 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). 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).

MORPHOLOGICAL PART

Pointed accessory process on paraproctal complex

Here we briefly review what is the accessory pointed process on the paraproctal complex? Why is it so diverse? In limnephilids the *paraproctal complex* is a paired structure with variously developed branches named in four different directional nomenclature: (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 are partially or completely fused in various shape and forming a completely or partially sclerotized ring around anus.

This paraproctal 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 genitalic 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. At 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 genitalic 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.

According to Kumanski (1968, 1969, 1987) at the *Chaetopteroides* genus the ventral (inferior,

basal, vertical) branch of paraproct forming a complete heavily sclerotized ring around anus and the entire paraproct complex, except the dorsal (internal, apical, horizontal) branches, represents the vestigial segment X.

The paraproctal complex is strongly sclerotized, mostly devoid of setae, muscled and movable. The ventral branches, representing probably the reduced somite of segment X and XI (Kumanski 1968, 1969, 1987), form a pair of triangulum with various sclerotization. The pair of triangulums 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, housing the accessory process; (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 triangulums are called sometimes as the ventral sclerites.

Why the pointed accessory process is so diverse?

The enlarged triangulums of the ventral (inferior, basal, vertical) branch of the paraproctal complex serves as a supporting, pivoting fulcrum for the muscled movable dorsal branch of the paraproct. 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 pro-

bably by intense sexual selection processes. Post-copulatory sexual selection can lead to rapid divergence in reproductive traits related to the very complex mating and copulating processes. These genital structures may have courtship, harm, cleaner and anchor device functions, depending on the dominating actual processes of the sexual selection: cryptic female choice, sperm competition or sexually antagonistic coevolution. Finding stable fine structures in order to establish initial split criterion nearby the structural diverging point, where early barriers to gene flow develops is a promising tool for alpha taxonomy. These childhood stable traits of the incipient phylogenetic species are the targets of selection and the first morphological product of speciation. In incipient species the genetic mosaic of speciation involves only few stable characters of the diverging loci leaving the genom largely homogenised with polymorphisms by ongoing gene flow (Oláh et al. 2013a). In caddisflies we have already discovered stable structures to detect incipient phylogenetic species by fine structure analysis on the intro-mittent organ: parameres and various processes on the aedeagus (Oláh et al. 2012, Oláh & Ito 2013, Oláh et al. 2013a, Oláh et al. 2013b). The accessory processes on the paraproctal complex discovered in the *Allogamus mortoni* species complex and in the *A. ligonifer* species is diversified in sexual selection processes.

Understanding and visualization of the vaginal sclerite complex

Earlier we have distinguished six substructures in the vaginal sclerite complex (Oláh et al. 2013a). As we are examining more limnephilid genera and species we understand more details on this diversified sclerite complex. Here we separate three more substructures for practical taxonomic purposes and listing them together with the previously distinguished six substructures. (1) *Vaginal sclerite plate* itself on the dorsum of the membranous vagina and ventrum of the membranous accessory gland duct; this basal plate integrates all the substructural components of the vaginal sclerite complex. (2) *Dorsal articulation sclerites*, a variously sclerotized internal continu-

ation of the supragenital plate (upper vulvar lip). The internal dorsal articulation sclerites and external supragenital plate together participate to receive the stimulating or harm effect of the male parameres in the processes of sexual selection. Much developed if accessory duct enlarged laterad or elongated anterad and gives additional support to help the function of the junction sclerite. Heavily sclerotized if male parameres function as harm device in the sexually antagonistic coevolution. (3) *Ventral articulation sclerites* attach the sclerite complex to the internal continuation of the lateral processes of the vulvar scales (lower vulvar lip), that is to the paired gonopods of segment IX. (4) *Lateral joints* of the upper and lower lips. Usually not, or less sclerotized, but sometimes enlarged and bloated by proliferation of hard tissue. (5) *Wing sclerites* with stretch function for vagina and with apodemic function anterad to receive vaginal muscles, variously combined with ventral articulation sclerites. (6) Hood-shaped *junction sclerite* holding and stretching the junction where the ducts of accessory gland and ovarium meet as well as separating accessory duct from spermathecal duct. (7) *Spermathecal process* receiving ductus spermathecae and forming frequently a longitudinal keel on the ventrum of the vaginal sclerite. (8) *Bursal sclerite* receiving ductus bursae that opens between the spermathecal process and the common oviduct at the anteriomesal margin of the vaginal sclerite. These substructures and functions constitute the vaginal sclerite complex, but their development and sclerotization are highly varying in the different groups. (9) *Anterior apodemes* appear as the anteriomost lateral extension of the vaginal plate separated by the mesal bursal sclerite. Receive muscles and frames the space for the bursal sclerite ensuring to receive ductus bursae.

Modified duct of the accessory gland

A paired accessory reproductive gland is present in most male and female insects. Its main function in females is to secrete sticky substance that forms either the egg cases or the cement that binds the eggs to a surface. Other name is colleterial gland or glue-secreting organ from Greek

kolla glue. The common unpaired duct of the accessory glands opens on the posteriodorsal wall of the genital chamber. In some species of the *Allogamus* genus this unpaired section of accessory gland is elongated and enforced by strong musculature or hardened tissue. This elongated sheath frequently with various lateral wings is connected to the dorsum of the vaginal or spermathecal sclerite was first mentioned by Schmid (1951a) as a *vestibular apparatus* with equilibrating function. Later Schmid (1955) mentioned as *bursa copulatrix*. However the ductus bursae of bursa copulatrix opens between the processus spermathecae and the common oviduct and not posterad. Posterad opening common duct drains the accessory gland to the vaginal chamber through the brace of vaginal sclerite complex. It seems the modified accessory duct participate in sexual selection and coevolves with male parameres. We have collected *Allogamus tomor* in copula and have found the long tube-like structure of the modified duct of the accessory glands in function as to receive the long fused paramere during copulation.

MATERIAL AND METHODS

It was a great challenge and required sustained effort to bring together all the necessary specimens to revise this genus. We have to emphasize again that collected, sorted and determined materials already incorporate significant scientific work and has high primary value for such surveys. Therefore we invited colleagues who had interest and specimens and agree with our final findings to become a coauthor of the paper and/or of the species automatically.

Clearing, cleaning, and drawing procedures. This study is based on animals preserved in 70–80% alcohol. In order to observe morphological details in the genitalia, the entire or only the terminal segments of abdomen were removed and placed in a small glass beaker of 25 cm³ with 10% KOH solution and boiled during 5–15 minutes for digestion above a spirit burner. The duration of the treatment is adjusted individually to the effectiveness of clearing process which depends on the

species or even on the nutritive state of tissues or on the physiological condition of the specimens. The process of digestion can easily be followed by transparency. The dissolution rate of the soft tissues, the clearing transparency is visible to naked eye. The clearing process and time are so much taxon, size, age, sex, and nutrition state specific that automatic hot plate or bath clearing is not practical. The digested abdomen was subsequently transferred to distilled water and the macerated tissue was removed mechanically in patient cleaning process by fine tipped forceps and needles. The internal vaginal sclerite complex was exposed to clear view by cutting windows into the dorsum and left pleuron with fine scissor. The cleared and cleaned abdomen was transferred to 80% ethylalcohol, and to glycerine for examination under microscope. Different sized pins modified to supporting ring bottom was introduced into the abdomen and used to hold and stabilise the genitalia in lateral, dorsal, and ventral position for drawing. However, the plane of view is never perfect and we made no special procedures of grid, matrix, or reflection to produce absolute mirror symmetry of the drawings. Instead, the genital structures were drawn exactly as seen in the microscope. However, setae are represented only by their alveoli and moreover their density is only symbolic. If essential, the setal length or setal shape are presented by drawing a single or a few setae only. The genital structure was traced by pencil on white paper using a drawing tube mounted on a WILD M3Z microscope at between 260x and 416x magnification. Final illustrations were prepared by enlarging the original pencil drawings and re-drawn on transparent paper by Black India Ink.

Terminology. We used our functional appendicular terminology and not the conventional anatomical directional terminology to describe the genital structures in species description (Oláh & Johanson, 2008). Species descriptions were standardized to ensure consistently formatted and comparable description in general accord with Evenhuis's template principle (Evenhuis 2007). We have standardized also the terminology to describe space extensions of variously formed

structural elements. The following terms were used to qualify the dimensions and extensions of genital structural elements: (1) *short* or *long* for length dimension on the longitudinal direction of coronal plane along the anteroposterior axis; (2) *low* or *high* (traditionally *shallow* or *deep* especially for excisions) for height dimension on the vertical direction of the sagittal plane along the dorsoventral axis and (3) *narrow* or *wide* (broad) on the lateral direction of the transversal plane along the mediolateral or left-right axis. The three dimensional Cartesian coordinate system provides theoretical possibility to quantify by measurements the three physical dimensions of length, width, and height of each structural element. However this quantification is used very seldom in species description. Here we quantify only the length of forewing.

Depositories

Natural History Museum, London (NHML)
Civic Natural Science Museum "E. Caffi", Bergamo, Italy (CNSMB)
Cianficconi Collection, Italy (CC), deposited at the Civic Natural Science Museum "E. Caffi" of Bergamo, Italy
Civic Natural History Museum, Verona, Italy (CNH MV)
Coppa Private Collection, France (CPC)
Departamento de Zoología Facultad de Ciencias. Universidad de Granada, Spain (DZFCUG).
Friuli Museum of Natural History, Udine, Italy (FM NHU)
Moretti Collection, Department of Chemistry, Biology, and Biotechnology, University of Perugia, Italy (MC)
National Museum, Prague, Czech Republic (NMPC)
Oláh Private Collection, under national protection by the Hungarian Natural History Museum (OPC).
The Manchester Museum, University of Manchester, England (MMUE)

TAXONOMY

Allogamus Schmid, 1955

Type species. *Halesus uncatatus* Brauer, 1857 by original designation.

Allogamus genus belongs to the *Stenophylacini* tribe. This tribe has wing and spur characters very homogenous and less diverse. All the new stenophylacini genera erected by Schmid (1955) are based on male genital divergences. Genus *Allo-*

gamus has short segment IX, deep genital cavity (anal cavity of Schmid), small paraproct, as well as long and vertical gonopods. This character combination, especially the presence of genital cavity brings *Allogamus* close to *Hydatophylax* and *Pycnopsyche* genera. *Allogamus* differs from these two related genera by the gonopod apex that is turned to transversal plane and appears like a harpago. However, this is an apparent harpago not a true one. There is no suture discernible between coxopodite and apparent harpago.

In the genus *Allogamus* the periphallalic organs, the cerci, the paraprocts and the gonopods, are very homogenous. Cerci form a lateral located, variously compact, heavily setose plate and supplied with variously developed mesal digitiform process. Only *A. hilaris* has lateral digitate process on the lateral plate of the cerci. Paraproct is small; in some lineages the basal triangle produced a pointed accessory setaless process, possibly in the sexual selection processes. This unique titillating or harming structure much developed in the recently diverging *A. ligonifer* species and in the already diverged *A. mortoni* new species complex. Gonopods directed in sagittal plane are characterised by an apparent harpago turned almost right-angle to the transversal plane. This apparent harpago could be very variable both among and inside populations. The apparent harpago exhibits rather high intraspecific variation in the widely distributed *A. uncatatus* species well discernible in caudal view. Cerci, paraproct, and gonopods, all are characterized by low structural diversity and high infraspecific variability. These structures have no real diagnostic value to distinguish among species. At the same time the intromittent component of the genitalia, that is the phallic organ, directly involved in the copulatory and postcopulatory processes, is very diverse, species specific and stable.

Non-neutral adaptive traits. In the *Allogamus* genus the aedeagus and/or the parameres of the phallic organ are adaptive traits under rapid evolution driven by sexual selection. Their divergences provide diverse fine structures in alpha taxonomy to recognise early stages of recent speci-

ation and can be used as initial split criteria to establish incipient phylogenetic species. The mostly neutral non-adaptive traits of periphallid genital structures of cerci, paraproct, and gonopods evolved slowly, during millions of years, as estimated by neutral molecular markers. At the same time the non-neutral adaptive traits of the phallic organ undergo more rapid evolution with some historical accumulation of branching structure of lineages.

Species grouping. 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 apicoventral sclerites of varying complexity on the aedeagus. This paramere evolution together with complexity evolution of aedeagus helps us to establish species groups inside the genus *Allogamus*.

The plesiomorphic state of the separated 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 ventroapical 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 dorso-apical 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 neof ormation of the paraproctal accessory process.

In the small *Allogamus corsicus* new species group the paired parameres fused basally and diverted apically.

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

The female genitalia are more plesiomorphic in *A. auricollis* group compared to *A. corsicus* and *A. uncatu s* species groups. External structure of female genitalia has anal tube less fused having various lobes of the amalgamated segment IX and X in *auricollis* and more fused without such lobes in *corsicus* and *uncatu s* groups. The vaginal sclerite complex of the internal structure has plesiomorphic state with simple accessory duct and apomorphic state with enlarged, elongated, and enforced duct of the accessory glands. The apomorphic state of the duct is present and variously developed in *A. antennatus* and *A. hilaris* subgroups as well as in the *A. uncatu s* group.

Applying these principles we have grouped all the known and the new species into the following three species groups, four species subgroups and one species complex.

***Allogamus auricollis* species group, rediagnosed**

Schmid (1955) listed three species in his *auricollis* group: *A. auricollis*, *A. antennatus*, and *A. corsicus*. According to the paramere evolution these species belong either to different species groups or to different species subgroups. *Allogamus auricollis* species group is characterized and rediagnosed here by the plesiomorphic state of paramere that is having paramere shafts well separated and embedded individually into the membranous endotheca. Female anal tube complex supplied with various lobes. Modified accessory duct present in *A. antennatus* and *A. hilaris* subgroups, but absent in *A. auricollis* and *A. ligonifer* subgroups.

The *A. auricollis* group developed four lineages according to the position of the paramere setae: *Allogamus ligonifer* subgroup with sub-

equal apical spines, *A. antennatus* subgroup with a strong single primary seta accompanied by smaller secondary setae in dorsoapical position, *A. auricollis* subgroup with a strong single primary seta accompanied by smaller secondary setae in ventromesad position, *A. hilaris* subgroup with ventral row of setae.

***Allogamus antennatus* new species subgroup**

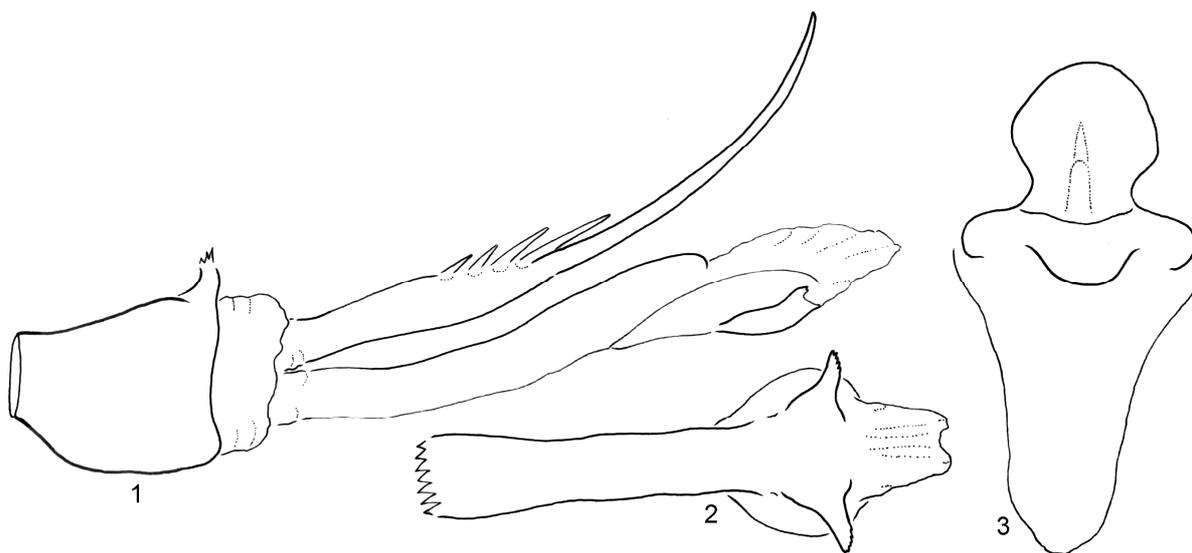
Light species with a strong single primary seta on paramere accompanied by smaller secondary setae in dorsoapical position. Modified accessory duct of female variously modified into an anterad elongated structure.

***Allogamus antennatus* (McLachlan, 1876)**

(Figures 1–3, 11)

Material examined. Italy. Liguria-Savona, Garesio, affluente fiume Tanaro c/o Trappa, N 44.235° E8.1267°, 650 m, 10.X.2001, leg. Museo Caffi BG, (1 male, 1 female; OPC). Liguria-Genova, Montoggio, Acquafredda Superiore, N 44.4878° E9.0162°, 500 m, 12.X.1996, leg. Museo Caffi BG, (10 males, 10 females; OPC). Liguria-Imperia, Triora, rio di Barbone, 1000 m, light trap, N44,0370° E7,7197°, 9.X.2001, leg. Museo Caffi BG (2 males, 4 females; CNSMB). Lombardia - Bergamo, Nembro, Salmezza, 1000

m, light trap, N45,7811° E9,7275°, 30.IX.1989, leg. M. Magoni (1 male; CNSMB). Lombardia-Bergamo, Nembro, Salmezza, 1000 m, light trap, N45,7811° E9,7275°, 4.X.1989, leg. M. Magoni (2 males; CNSMB). Emilia-Romagna-Parma, Bedonia, 600 m, N44,5032° E9,6292°, 25.X.1992, leg. R. Cerbino, M. Valle (2 males; CNSMB). Toscana-Firenze, Marradi, Ponte Valle, N 44.0481° E11.6746°, 500 m, 9.X.2002, leg. A. Usvelli, (12 males, 5 females; OPC). Toscana-Firenze, Marradi, Badia Valle, N44.0481° E 11.6746°, 430 m, 28.X.1999, leg. A. Usvelli, (1 male; FMNHU). Toscana-Arezzo, Pieve Santo Stefano, F. Tevere, Valsavignone, N43.738° E12.029°, 550 m, 25.XI.1992, (1 male; n°251 CC). Toscana-Arezzo, aff. di destra dell'Arno, 27.X.1991, leg. Melai (4 females, n°120 CC). Marche-Ancona, Fabriano, alto corso torr. Giano, N43.28° E12.80°, about 600–700m, 11.XI.1994, leg. S. Capocchia (1 male; n°1064 CC). Piemonte-Torino, Robassomero, Canale Druento, N 45.2095° E7.5519°, 385 m, 30.XI.2005, leg. F. Vaccarino, (3 males, 2 females; OPC). Piemonte-Torino, Robassomero, Canale Druento, N 45.2095° E7.5519°, 385 m, 22.X.2006, leg. F. Vaccarino, (1 male; CNSMB). Piemonte-Cuneo, Revello, La Rocchietta, fiume Po, N44.6340° E7.3714°, 390 m, 1.X.1997, leg. O. Lodovici, (6 males, 11 females; OPC).



Figures 1–3. *Allogamus antennatus* (McLachlan, 1876). 1 = male phallic organ in left lateral view, 2 = aedeagus in ventral view, 3 = female vaginal sclerite complex with the tip of accessory duct, dorsal profile.

Remarks. It is distinguished as an incipient species by the shape of the ventral sclerites on the head of the aedeagus modified into a laterally serrated large tooth, by the pattern of the secondary spines on the parameres and by both the dorsal and lateral pattern of the modified accessory duct of the female vaginal sclerite complex. The dorsolateral pair of semisclerotized plates less produced laterad, subtriangular. Anterior ending of the enlarged modified accessory duct broad, not tapering slender and not capitate.

***Allogamus ausoniae* Moretti, 1991 stat. nov.**

(Figures 4–6, 12)

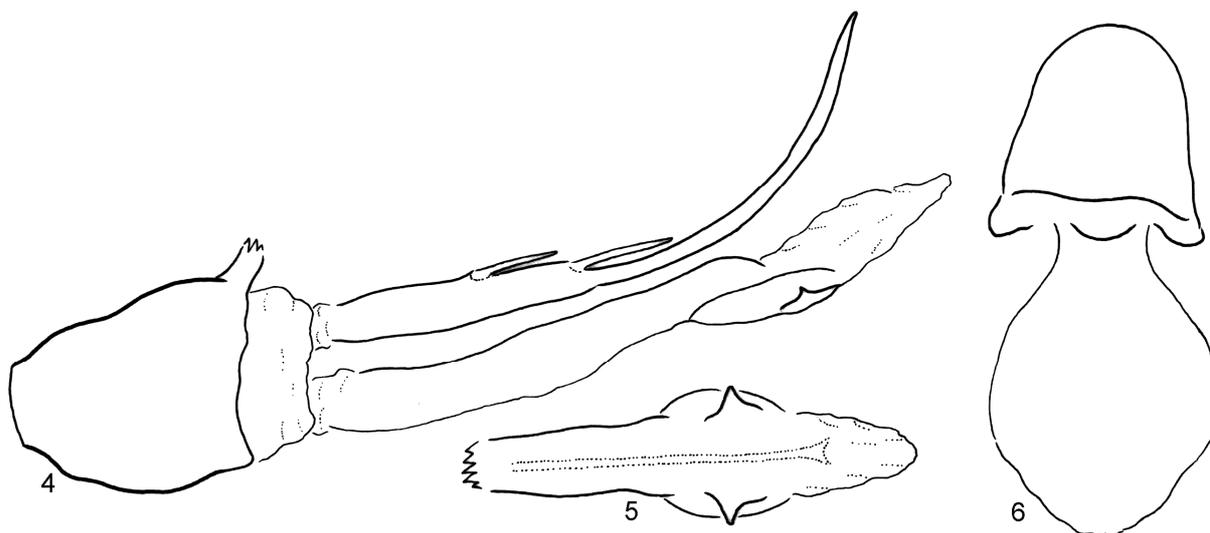
Allogamus ausoniae Moretti, 1991:393,399.

Allogamus antennatus ausoniae Moretti, 1991 reduced to subspecies level by Malicky (2005:574–575).

Material examined. Italy. Marche-Macerata, Visso, torrente Nera, 9.X.1997, leg. F. Cianficconi, (1 male, 4 females; OPC). Marche-Macerata, Visso, fiume Nera c/o stab. Cherubini, 24.X.1977 leg. Santicchia, (8 males, n°243 CC; 4 males, OPC). Abruzzo, Monti della Laga, 18. IX.1996, leg. B. Osella (5 males, 1 female; n°201 CC). Abruzzo-Aquila, Ortona de'Marsi, Cesoli, fiume Giovenco, N42.011° E13.709°, 870 m, 21. X.2000, leg. B. Osella (3 males, 6 females;

n°1594 CC). Molise-Campobasso, Bojano, sorgenti del Biferno, N41.4798° E14.4779°, 480 m, 31.VIII.2000, leg. E. Bertuetti et al. (1 male, 1 female, CNSMB). Molise-Campobasso, Bojano, torr. Calderone aff. Biferno, N41.482° E14.659°, 24.X.1995, leg. M. Baccaro (18 males, n°1010 CC; 10 males, OPC). Molise-Campobasso, Bojano, Fiume Biferno, sorg. Majella, N41.483° E 14.461°, 500 m, 30.X.1995, leg. M. Baccaro (14 females, n°1005 CC). Molise-Campobasso, Bojano, Fiume Biferno, Sorg. Pietre Cadute, N41.479° E14.478°, 488 m, 24.X.1995, leg. M. Baccaro (3 males; n°1013 CC). Lazio-Rieti, Cittareale, Fiume Velino 1 km a valle del paese, loc. Vezzano, N 42.615° E13.156°, 940 m, 17.X.1991, leg. P. Cappocchia (1 male; n°926 CC). Lazio-Rieti, Rieti, Sorgenti del Cantaro, N42.409° E12.889°, 418 m, 25.X.1999, leg. S. Ceccarelli (1 male; n°772 CC).

Remarks. It is distinguished as an incipient species by the shape of the ventral sclerites on the head of the aedeagus with protruding sharp lateral tooth, by the pattern of the secondary spines on the parameres and by both the dorsal and lateral pattern of the modified accessory duct of the female vaginal sclerite complex. The dorsolateral pair of semisclerotized plates less produced laterad, rounded. Anterior ending of the enlarged modified accessory duct is capitate or clavate.



Figures 4–6. *Allogamus ausoniae* Moretti, 1991 stat. nov. 4 = male phallic organ in left lateral view, 5 = aedeagus in ventral view, 6 = female vaginal sclerite complex with the tip of accessory duct, dorsal profile.

***Allogamus morettii* De Pietro & Cianficconi,
2001 stat. nov.**

(Figures 7–8, 13)

Allogamus morettii De Pietro & Cianficconi, 2001:61–66.

Allogamus antennatus silanus Moretti, 1991 synonymized by Malicky (2005:574–575).

Material examined. Italy. Sicilia-Messina, San Teodoro Aff. T. dei 3 Valloni, c. da Lineri, 1220 m, 10.XI.2001, leg. R. DePietro (1 male; OPC). Sicilia-Catania, Randazzo, affluente sorgente Alcantara, N37,8924° E14,9453°, 850 m, 28.XI.1995, light trap, Leg. P. Pantini, M. Valle (1 male; CNSMB). Sicilia-Catania, Maniace, Nebrodi Mountains, torrente Saracena, 1350 m, 23.X.1992, R. DePietro (1 female; OPC). Calabria-Reggio Calabria, Reggio Calabria, Serro Longo, torr. Listi, 1360 m, light trap, N38,145° E15,836°, 10.XI.2013, leg. E. Castiglione, F. Manti, P. Pantini (2 males, 5 females CNSMB; 1 male 3 females, OPC). Calabria-Reggio Calabria, Scilla, P.te S. Antonio, torr. Favazzina, 1260 m, light trap, N38,187° E15,846°, 10.XI.2013, leg. E. Castiglione, F. Manti, P. Pantini (1 male; CNSMB). Calabria-Reggio Calabria, Cardeto, Cendri, rivolo sorgentizio, 1340 m, light trap, N38,105° E 15,845°, 10.XI.2013, leg. E. Castiglione, F. Manti, P. Pantini (1 male; CNSMB). Calabria-Reggio

Calabria, San Lorenzo, Sega di Cufolo, fiume Melito, 1300 m, light trap, N38,097° E15,854°, 10.XI.2013, leg. E. Castiglione, F. Manti, P. Pantini (10 females; CNSMB).

Remarks. Distinguished as an incipient species by the blunt triangular shape of the ventral sclerites on the head of the aedeagus without protruding sharp lateral tooth and by both the dorsal and lateral pattern of the modified accessory duct of the female vaginal sclerite complex. The dorsolateral pair of semisclerotized plates much produced laterad, rounded. Anterior ending of the enlarged accessory duct is tapering, not broad, clavate or capitate; in lateral view S-shaped sigmoid.

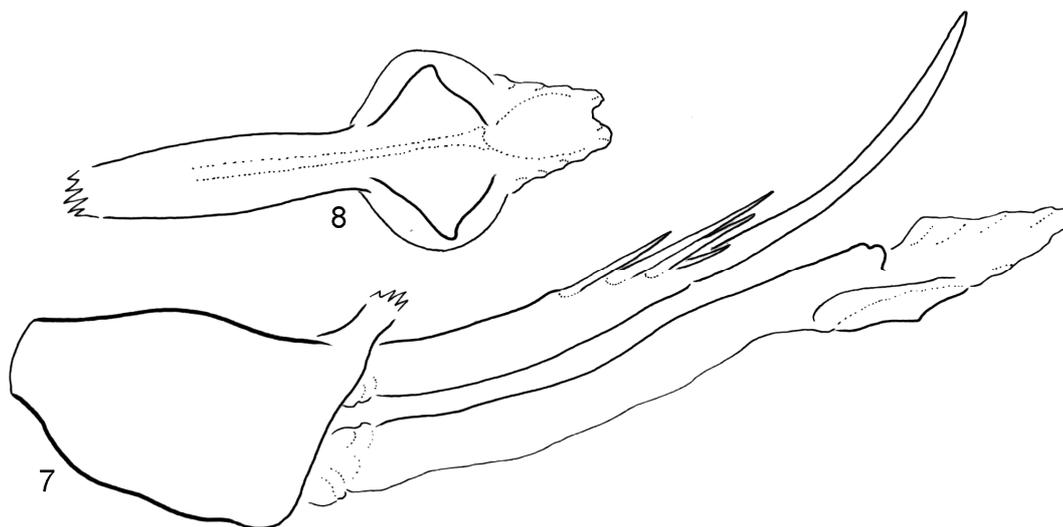
***Allogamus silanus* Moretti, 1991, stat. nov.**

(Figures 9–10)

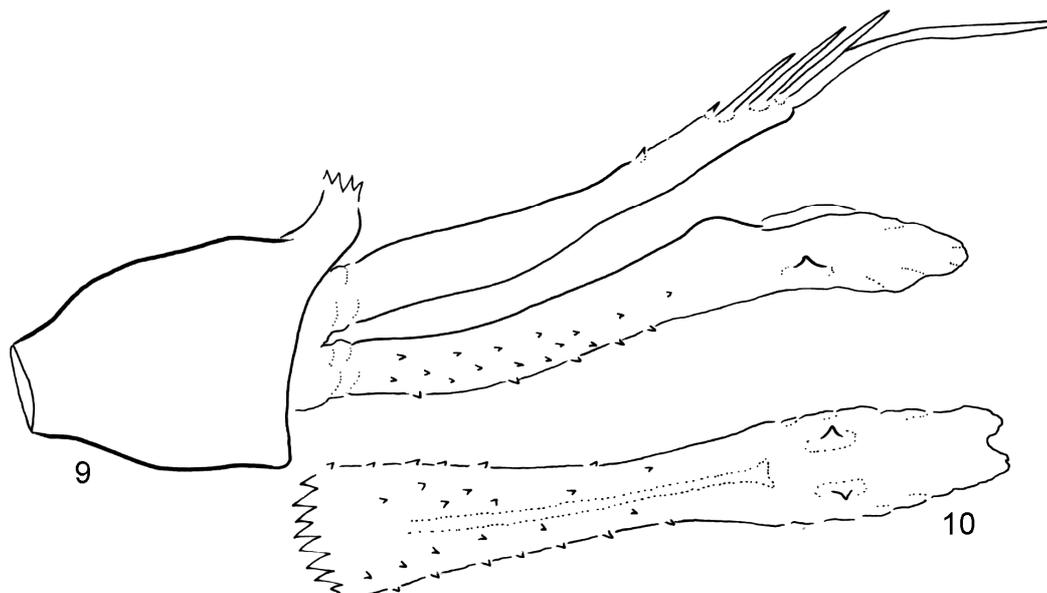
Allogamus hilaris silanus Moretti, 1991:400.

Allogamus antennatus silanus Moretti, 1991. Transferred by Malicky 2005:574–575.

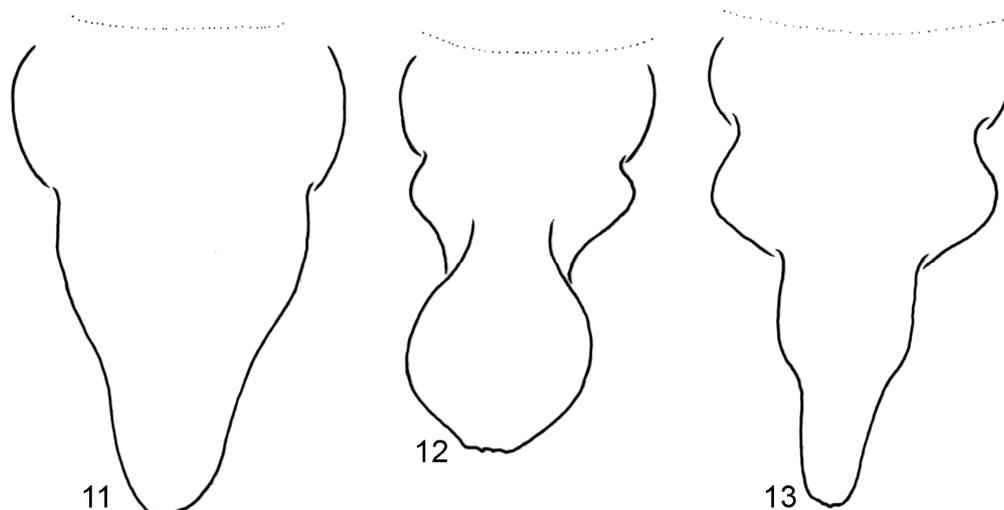
Material examined. Holotype. The collection data have been corrected on the label of the holotype: Calabria, Sorgente, Materazzelli, Aspromonte, 1780 m, 18.IX.1972, leg. A. Michelizzi (1 male, MC).



Figures 7–8. *Allogamus morettii* De Pietro & Cianficconi, 2001 stat. nov. 7 = male phallic organ in left lateral view, 8 = aedeagus in ventral view.



Figures 9–10. *Allogamus silanus* Moretti 1991, stat. nov. 9 = male phallic organ in left lateral view, 10 = aedeagus in ventral view.



Figures 11–13. Dorsal profile of the tip of female accessory duct. 11 = *Allogamus antennatus* (McLachlan, 1876), 12 = *Allogamus ausoniae* Moretti 1991, 13 = *Allogamus morettii* De Pietro & Cianficconi, 2001.

Remarks. The description of this taxon has been based on a single male specimen and no more material was discovered. The re-examination of the carefully cleared genitalia of the holotype confirms its well differentiated divergent state. The ventral pair of sclerotized plates reduced its triangular tooth miniaturized, almost indiscernible. The dorsolateral pair of semisclerotized plates are very narrow, not produced laterad;

aedeagal stem densely covered with small triangular teeth, a unique apomorphic trait. Terminal spine pattern of parameres specific.

Allogamus auricollis new species subgroup

Dark species characterized with a strong single primary seta on paramere accompanied by smaller secondary setae in ventromesal position. Modified accessory duct of female lacking.

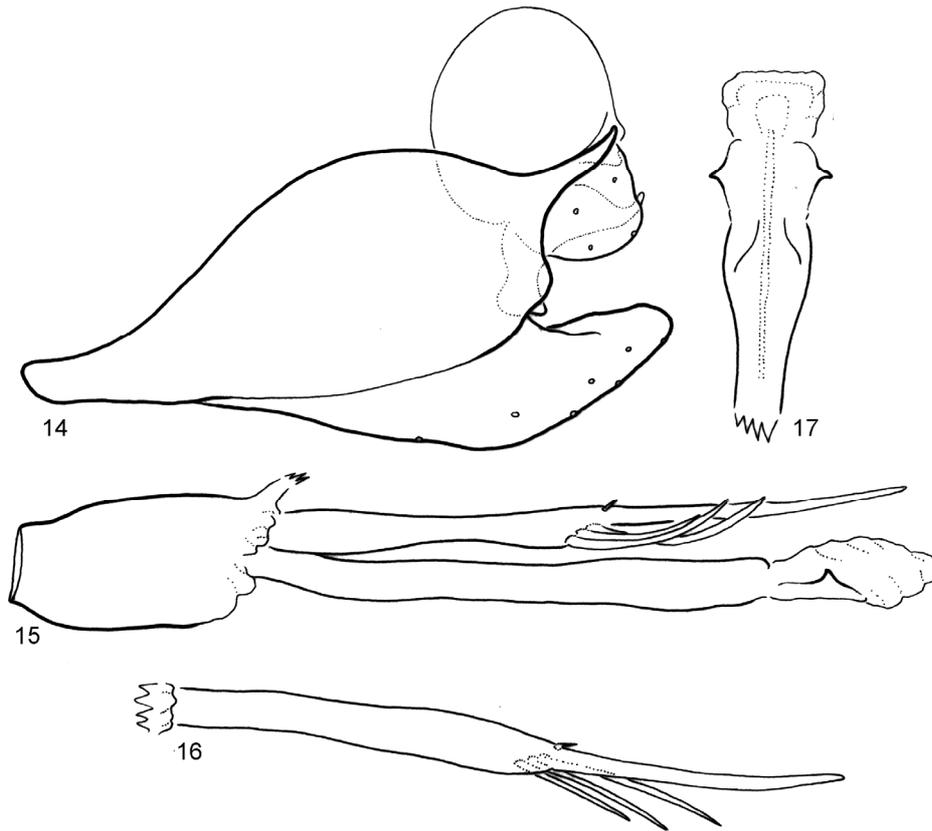
***Allogamus alpensis* Oláh, Lodovici & Valle sp. nov.**

(Figures 14–17, 18–21, 22–46, 47–66)

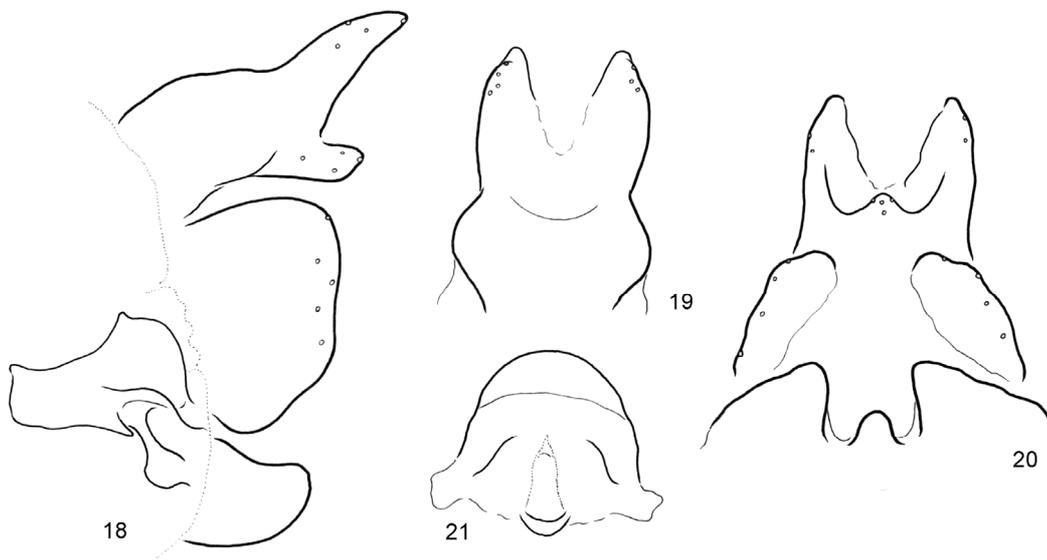
Diagnosis. All specimens revised here from the Central Alps have been determined earlier as *Allogamus auricollis*. Here we split *Allogamus alpensis* sp. nov. from *Allogamus auricollis* as an incipient species inhabiting the Central Alps. This new species is characterized by having very stable non-neutral, selection-driven adaptive diverged traits on the phallic organ evolved in sexual selection processes. The periphallic organs are similar and vary in wide range of the neutral traits. Especially the lateral profile of cerci varies both among and inside populations. In contrary the recently diverged non-neutral fine structures of the parameres and aedeagus are very stable. *Allogamus alpensis* sp. nov. has 3 (2–4) secondary setae on parameres in ventral position, lacking at *A. auricollis*. The pair of ventroapical sclerite on the aedeagus head is characterized by distinct lateral dentate and pointed tip. The ventroapical sclerite on the aedeagus head has oblique apical pointed tip at *A. auricollis*. There are stable divergences also in the structures of the vaginal sclerite complex both in lateral and dorsal profiles. However the fine structure diversifications on vaginal sclerite complex are frequently difficult to recognise clearly because of masking effect of the undigested residues of membranous vaginal chamber and its draining ducts even after careful clearing and cleaning processes. We have examined the diverged structure matrices of the new species from Austria, Italy, Liechtenstein and Switzerland populations (Figures 22–46, 47–66). The comparison of matrices of the new species to diverged structure matrices of *A. auricollis* populations collected from the entire distributional area demonstrates significant and stable divergences in the diverged non-neutral traits of paramere setae and aedeagus sclerites.

Material examined. *Holotype.* Italy, Lombardia Bergamo, Valgoglio, Valsanguigno, torrente, N 45.9669° E9.8853°, 1300 m, 10.X.2009, light trap, leg. S. CEREÀ (1 male, CNSMB). *Allotype*

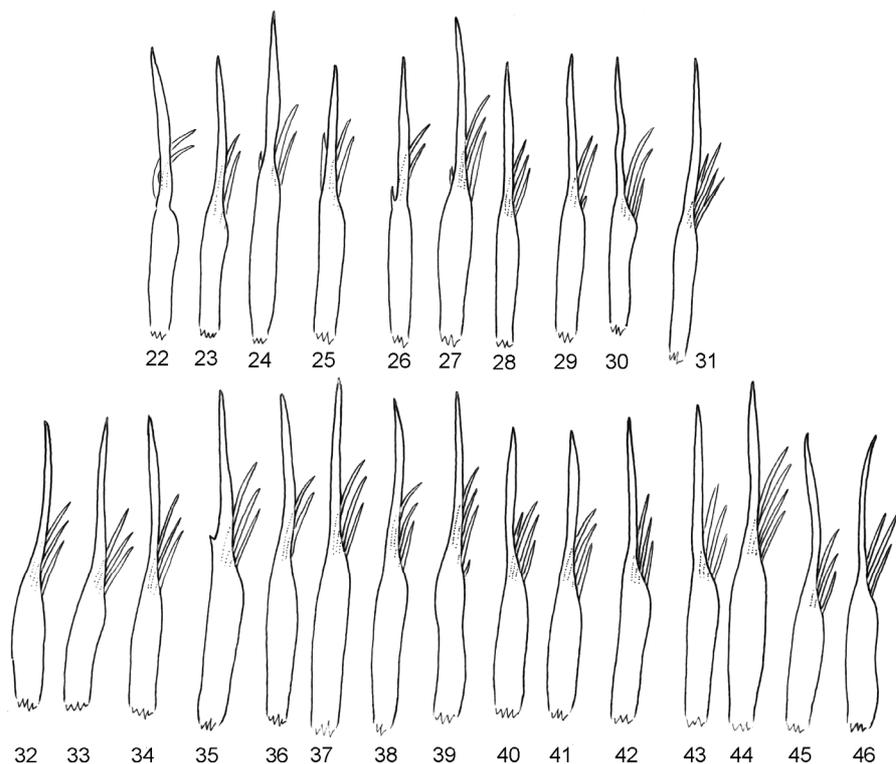
same as holotype (1 female, CNSMB). *Paratypes* same as holotype (1 male, OPC). Lombardia-Bergamo, Valcanale 1000 m, 30.X.2007, leg. W. Zucchelli (1 male, CNSMB). Lombardia-Bergamo, Ardesio, Valcanale, prato stabile, Light trap, N45.949° E9.855°, 1000 m, 15.X.2008, leg. W. Zucchelli (2 males, CNSMB). Lombardia-Bergamo, Carona, N46.0196° E9.7802°, 1100 m, 11.X.2006, leg. M. Valle (1 male, 2 females; CNSMB). Lombardia-Bergamo, Casnigo, 45.8175 9.8695, 520 m, 12.IX.2002, leg. R. Calandrino (2 males, 1 female; CNSMB). Lombardia-Bergamo, Mezzoldo, fiume Brembo, 1100 m, light trap, N46,0236° E 9,6611°, 3.X.1995, leg. F. Albrici, M. Valle (1 male; CNSMB). Lombardia-Bergamo, Gazzaniga, valle Platz, 850 m, light trap, 2.X.1993, leg. Gusmini (38 males, 3 females; CNSMB). Lombardia-Brescia, Vione, Val Canè Rifugio Cortebona, 1800 m, light trap, N46,2765° N10,4521°, 20.IX.1982, leg. Bonacina, M. Valle (21 males; CNSMB). Trentino-Alto Adige-Trento, Rabbi, affluenti torrente Rabbits, N 46.4085° E10.7913°, 1250 m, 8.IX.2004, light trap leg. O. Lodovici & M. Massaro (1 male, CNSMB; 4 males, OPC). Trentino-Alto Adige-Bolzano, Taufers im Münstertal (Tubre), Südtirol, 1300 m, 6.X.2007, leg. F. Pühringer, (9 males, present from MPC, OPC). Trentino-Alto Adige-Bolzano, Bolzano, IX.1978, leg. Osella (1 male; CNHNV). Trentino-Alto Adige-Bolzano, Glorenza, IX.1978, leg. Osella (4 males, 2 females; CNHNV). Trentino-Alto Adige-Bolzano, Bressanone, 28.IX.1986, leg. Campadelli (5 males, 1 female; CNSMB); Piemonte-Cuneo, Crissolo, Pian del Re, fiume Po, N44.7005° E7.0934°, 2020 m, 1.X.1997, light trap leg. O. Lodovici (11 males, 5 females; OPC). Piemonte-Cuneo, Briga Alta, rivolo sorgentizio dopo Viozene, N44.1443° E7.7751°, 1250 m, 10.X.2001, light trap leg. Museo Caffi BG (19 males, 1 female; OPC). Piemonte - Cuneo, Crissolo, Piano della Regina, Monviso sorgenti del Po, 20.IX.1990, leg. Chiappafreddo, Pulcinelli (1 female, n°1254 CC). Piemonte - Cuneo, Sampeyre, Becetto, Meire Ruà, 1550 m, N44.596° E7.201° 6.X.2007, leg. G. Gardini (1 male; CNSMB). Piemonte - Cuneo, Crissolo, Piano della Regina, fiume Po, light trap, N44,7000° E7,1163°, 2.IX.1997 (51 males, 1 fe-



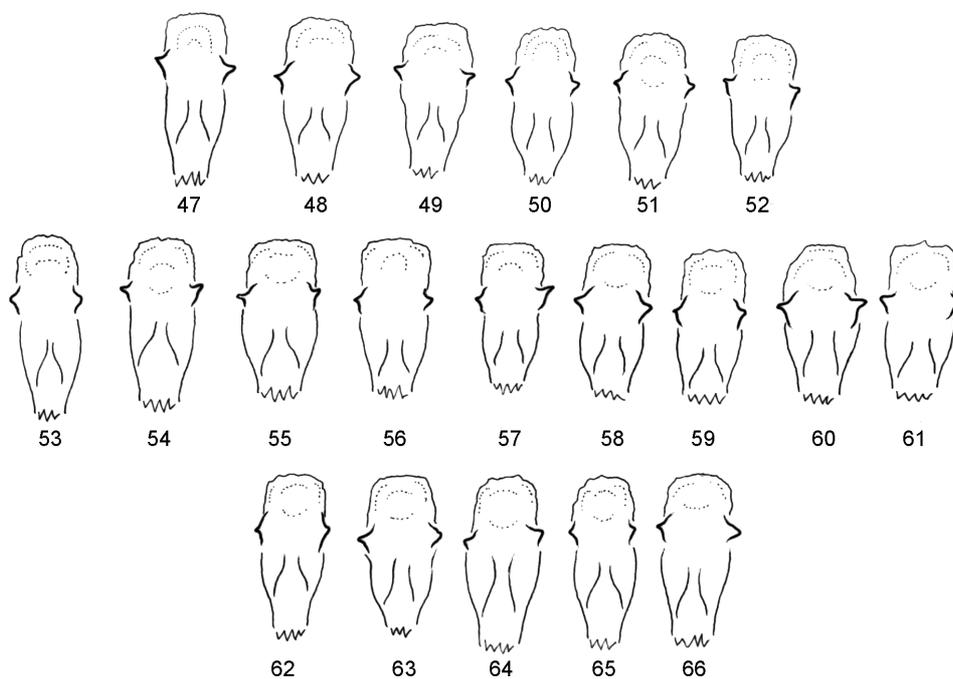
Figures 14–17. *Allogamus alpensis* Oláh, Lodovici & Valle sp. nov. 14 = male genitalia in left lateral view, 15 = phallic organ in left lateral view, 16 = left paramere in dorsal view, 17 = aedeagus head in ventral view.



Figures 18–21. *Allogamus alpensis* Oláh, Lodovici & Valle sp. nov. 18 = female genitalia in left lateral view with vaginal sclerite complex, 19 = female anal tube in dorsal view, 20 = female genitalia in ventral view, 21 = dorsal profile of vaginal sclerite complex.



Figures 22–46. *Allogamus alpensis* Oláh, Lodovici & Valle sp. nov. Diverged structure matrix of left paramere in dorsal view. 22–31 = Italian populations, 32–41 = Switzerland population, 42 = Liechtenstein population, 43–46 = Austrian population.



Figures 47–66. *Allogamus alpensis* Oláh, Lodovici & Valle sp. nov. Diverged structure matrix of aedeagus head in ventral view. 47–52 = Italian population, 53–61 = Switzerland population, 62 = Liechtenstein population, 63–66 = Austrian population.

male; CSNMB). Valle d'Aosta - Aosta, Aosta, 500 m, 26.IX.1980, leg. F. Faraci (1 male, CNHNV). Valle d'Aosta - Aosta, Prè Saint Didier, 1200 m, 27.IX.1980, leg. F. Faraci (2 males; CNHNV Veneto-Belluno, Cesiomaggiore, Val Canzoi, torrente Caorame, N46.1167° E 11.9376°, 590 m, 14.X.2002, light trap leg. O. Lodovici, P. Pantini (2 males, 29 females; CNSMB). Veneto-Belluno, Cesiomaggiore, Val Canzoi, rivolo sorgentizio, N46.1167° E11.9376°, 590 m, 14.X.2002, light trap leg. O. Lodovici, P. Pantini (3 males, 3 females; CNSMB). Veneto-Belluno, Cesiomaggiore, Val Canzoi pozza c/o rivolo sorgentizio, 590 m, light trap, N46,111673° E11,937602°, 14.X.2002, leg. O. Lodovici, P. Pantini (2 males, 3 females; CNSMB). Friuli Venezia Giulia-Udine, Paularo, torr. Chiarsò, 670 m, light trap, N45,5776° E13,1139°, 18.IX.1996, leg. Pantini, Valle (1 male; CNSMB). Friuli Venezia Giulia-Udine, Tarvisio, torr. Slizza, 630 m, light trap, N46,5136° E13,6137°, 19.IX.1996, leg. P. Pantini, M. Valle (1 male; CNSMB). *Austria*. superior, Reichraming, 9.X.1983, leg. H. Malicky (10 males, 6 females; present from MPC, OPC). Voralberg, Ferwall, Zeinisjoch, 1850m, 4. IX.1975, leg. Aistleitner (7 males, present from MPC, OPC). Styria, Ardning, 29.IX.1992, leg. H. Malicky, (9 males, 7 females; present from MPC, OPC). Tirol, Innsbruck, Alpenzoo, 1977, leg. G. Tarmann, (11 males, 8 females; present from MPC, OPC), (PS vary 3-1). Carinthia, Gitschtal, 1984-1990, leg. C. Wieser (25 males, 10 females; present from MPC, OPC). Carinthia, Lendorf, 14.IX.1987, leg. C. Wieser (73 males, 13 females, OPC; 9 males, 3 females MMUE; 9 males, 1 female; NHML). *France*. Isère Department, Saint Christophe en Oisans, D 530 les Pièces du Clot la Berande, 13. IX. 2007 leg. G. Coppa (1 male, CPC). *Liechtenstein*. Schellenberg, 26. IX. 1988, leg. Aistleitner (9 males, 7 females; present from MPC, OPC). *Switzerland*. Wallis, 2.5 km nò Salgesh, N46°19'34" E7° 35'24", 1390 m, 12.X.2001, leg. A. Bischof & G. Bischof, (6 males, present from MPC, OPC). Ticino, Gudo, Mitte X. 1982, leg. L. Rézbányai (7 males, 2 females; present from MPC, NMPC). Uri, Hospental, 1500 m, Ende IX. 1982, leg. L. Rézbányai (6 males, 4 females; present from MPC, OPC).

Description. Male and female (in alcohol). Dark and medium-sized animals. Forewing length 12 mm.

Male genitalia. Genital cavity is very large and deep. Cerci rounded in lateral and harpagones rounded in caudal view. Parameres with 3 secondary setae in ventral position. Scelrites on aedeagus head with lateral tooth.

Female genitalia. External genital structure is similar to the subgroup. Anterior apodemes on the vaginal sclerite complex laterad directed. Accessory duct on the vaginal sclerite simple not enlarged and modified.

Etymology. Named for the region of Central Alps, where this new species is distributed.

Allogamus sp.

Material examined. Molise - Campobasso, Guardiaregia, Piana Perrone, Matese, 1200 m, 27. IX.2000, leg. Marinelli (1 female, CNSMB).

Remarks. A single female lacking modified accessory duct belongs to the *Allogamus auricollis* species subgroup. More specimens including males are required to identify properly. It could be either *A. alpenensis* or *A. auricollis*.

Allogamus auricollis (Pictet, 1834)

(Figures 67–73, 74–117, 118–142)

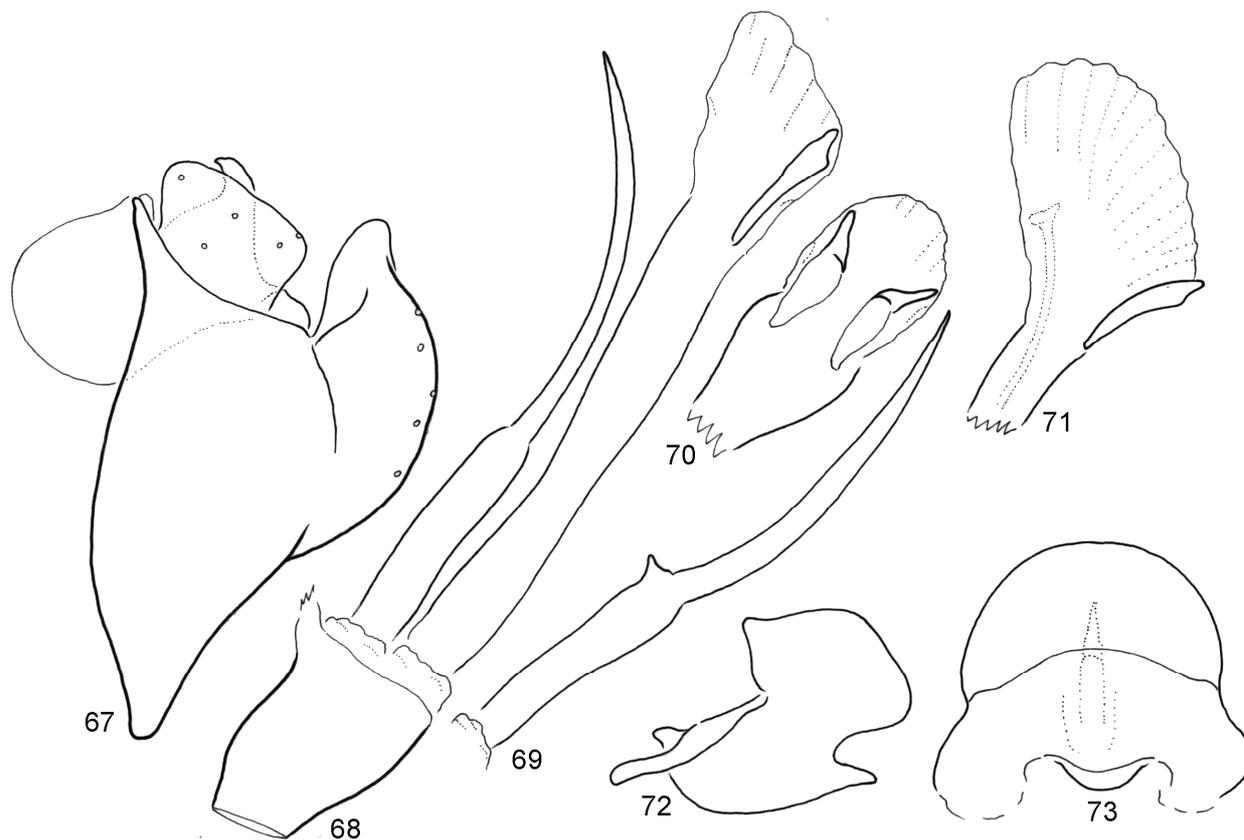
Material examined. *Albania*. Dibër district, Korab Mts, brook beneath Fushë Korabit, N41°49.209' E20°30.745', 1770 m, 07.X.2012, leg. P. Juhász, T. Kovács, D. Murányi, G. Puskás (1 male, OPC). Dibër district, Korab Mts, Radomirë, stream E (above) of the village, N41°49.043' E20°30.013', 1440 m, 7.X.2012, leg. P. Juhász, T. Kovács, D. Murányi, G. Puskás (2 males, 4 females; OPC). Dibër district, Korab Mts, open stream above Fushë Korabit, N41°49.215' E20°32.738', 1945 m, 07.X.2012, leg. P. Juhász, T. Kovács, D. Murányi, G. Puskás (2 females, OPC). Dibër district, Korab Mts, Radomirë, brook E (above) of the village, N41°49.152' E20°30.111', 1495 m, 07.X.2012, leg. P. Juhász, T. Kovács, D. Murányi, G. Puskás

(3 males, 3 females; OPC). *Austria*. Inferior, Lunz, Ybbs bei Weissenbach, 20. VIII. 1969 leg. H. Malicky, (12 males, 7 females; present from MPC, OPC). Inferior, Purgstall, N 48.255 E15.81, 305m, 7.X.2012, leg. E. & J. Hüttinger (19 males, 25 females; present from MPC, OPC). *Czech Republic*. Southern Bohemia, Šumava Mts, Modrava, Weitfallerské slatě, N49°01' E13°25', 3.VIII.2011, leg. A. Pavlicko (4 males, 4 females; present from MPC, OPC). Southern Bohemia, Šumava Mts, Teplá Vltava river above Kvilda, 1050 m, N49°00'38" E13°34'23", 26. VII.1991, leg. P. Chvojka (7 males, 3 females, NMPC). Northern Bohemia, Jizerské hory Mts, Jizerka, 850 m, N50°49'12" E15°20'43", 05.-08.VIII.1997, at light, leg. F. Krampl (15 males, NMPC). Northern Bohemia, Jizerské hory Mts, Příčná voda (tributary of Jizerka stream), 880 m, N50°50'14" E15°18'55", 27.VIII.1991, leg. P. Chvojka (7 females, NMPC). Eastern Bohemia, Broumovské hills, Metuje river below Adršpach, 500 m, N50°36'54" E16°07'22", 08.X.1997, leg. P. Chvojka (1 male, 3 females, NMPC). *England*. River Dove, Derbysire, 4. X. 1913, leg. M. E. Mosely, Mosely Bequest. B.M. 1948-589, Ex. NHM-London (6 males, 4 females; OPC). R. Wharfe, Grass Wood, Grassington, North Yorks, 17. IX. 1925, leg. A. Brindle (6 males, 6 females; present from MMUE; OPC). *France*. Massif-central, Lozère Department, Meyrueis, La Breze, 27. X. 2010 leg. G. Coppa (1 male, 3 females; CPC). Massif-central, Lozère Department, Bassurels, Le Tarnon Pont D19, 28. X. 2010 leg. G. Coppa (6 females; CPC). Massif-central, Lozère Department, Bassurels, Le Trepalou, 26. X. 2010 leg. G. Coppa (4 females; CPC). Massif-central, Puy-de-Dôme Department, La Tour d'Auvergne, La Burande Pont, 28. X. 2011 leg. G. Coppa (1 male; OPC). Massif-central, Puy-de-Dôme Department, Saint Victor la Riviere, Ru en Dessus de Courbanges Ru Malvoissiere/Gr, 24. X. 2013 leg. G. Coppa (1 male; 3 females; OPC). Vosges Department, Le Valtin, La Meurthe en Amont de l'Etang, 4. X. 2012 leg. G. Coppa (1 male, OPC). Pyrénées, Pyrénées-Orientales Department, Porte Puymorens, Ru de l'Orris, 21. VIII. 2011, leg. G. Coppa (6 males, 6 females; OPC). Pyrénées, Pyrénées-Orientales Department, Err, Ru d'Err Aiguanein, 24. VIII. 2011, leg. G. Coppa (2 males, 1 female; CPC). Pyrénées, Aude Department, Saint Martin Lys, Pont Village sur l'Aude, 29. X. 2008, leg. G. Coppa (1 male, 1 female; CPC). Pyrénées, Ariège Department, Belesta, Source Fontes Tarbes, 29. X. 2008, leg. G. Coppa (1 male, CPC). Pyrénées-Atlantiques, Vallée Ossau, 1984, leg. G. Vincon (1 male, OPC). *Kosovo*. Brod River, 6. X. 2013, leg. H. Ibrahim (7 males, 4 females; OPC). *Macedonia*. Polog region, Šar Planina, Vešala (Veshallë), open, rocky stream at the village, N42°03.865' E20°50.866', 1290m, 1.X.2013, leg. T. Kovács, D.Murányi, (2 males, 5 females; OPC). Polog region, Šar Planina, Bozovce, seeps and woody pasture W (above) of the village, N42°03.125' E20°49.377', 1350m, 1.X.2013, leg. T. Kovács, D.Murányi, (2 males, OPC). *Montenegro*. Berane municipality, Bjelasica Mts, Kurikuće, Suvoda Stream, 1170 m, N42°52.781', E19°44.467', 11.X.2008, L. Dányi, Z. Fehér, J. Kontschán & D. Murányi (11 females). Plav municipality, Gusinje, Alipašini Springs, 935 m, N42°33.014', E19°49.486', 4.X.2005, leg. T. Deli, Z. Eröss, Z. Fehér & D. Murányi (2 males, 1 female). Plav municipality, Prokletije Mts, Vusanje, Oko Spring and Grlja Stream, 1035 m, N42°30.704', E19°50.088', 12.X.2008, leg. L. Dányi, Z. Fehér, J. Kontschán & D. Murányi (1 female). Šavnik municipality, Sinjajevina Mts, Boan, Bukavica Stream W of the village, 1005 m, N42°57.042', E19°10.410', 10.X.2008, leg. L. Dányi, Z. Fehér, J. Kontschán & D. Murányi (1 female). Šavnik municipality, Vojnik Mts, Mokro, forest spring and its outlet brook at the village, 1060 m, N42°56.858', E19°05.463', 9.X.2008, leg. L. Dányi, Z. Fehér, J. Kontschán & D. Murányi (3 males, 1 female). Prokletije Mts, Gusinje, Alipašini Izvori, 42°33'01.2", 19°49'30.5", 930 m, 08. XI.2011, leg. Kovács, T., Magos, G. (1 male, 7 females; OPC). *Poland*. High Tatras, Chochołowska valley 22.VIII.1986, leg. J. Oláh, (6 males, 2 females, OPC). High Tatras, Chochołowska valley, potok na Polianie Huciska, 21.VIII.2009 leg. J. Oláh, (1 male, OPC). High Tatras, Bela River, 6.X.1976, ligh trap leg. Nagy (7males, 1 female; OPC). Gorce Mts. 21.IX.1989, leg. H. Malicky (3 males, 3 females; present from MPC,

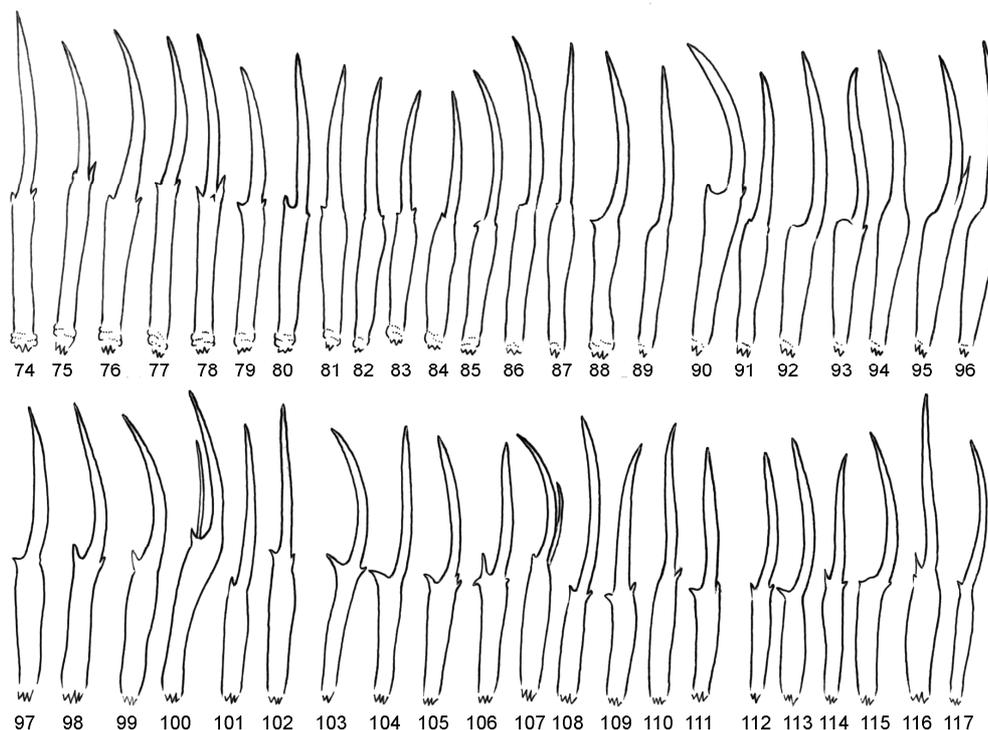
OPC). *Romania*. Arges County, Fagaras Mts. Capatanenii Ungureni, small springlake by the Capra stream along road No. 7C, N45°34.605' E45°34.605', 1405 m, 29.VIII.2012, leg. T. Kovács, D. Murányi & J. Oláh (4 males, 1 female, 13 pupae; OPC). *Slovakia*. Low Tatras, Východná, 17.IX.1999, leg. J. Ortner (4 males, 4 females; present from MPC, OPC). River Ľupčianka Partizánska Ľupča, Low Tatras National Park, 570 m, 5. X. 2008, leg. Richabun team (1 female, OPC). River Ľubochnianka, Ľubochná, Veľká Fatra National Park, 570 m, 5.X.2008, leg. Richabun team (3 females, OPC). Podtatranská kotlina basin, Belá river, Pribylina, 760 m, N49°06'06" E19°48'35", 11.X.1991, leg. P. Chvojka (2 males, 4 females, NMPC). Podtatranská kotlina basin, Studený potok stream, Stará Lesná, 780 m, N49°08'37" E20°17'25", 28.IX.1989, leg. P.

Chvojka (6 males, 6 females, NMPC). High Tatras, Javorinka stream, 1030 m, N49°15'37" E20°08'31", 17.IX.1988, leg. M. Černý (5 males, 6 females, NMPC). Belianske Tatras, Biela river, Ždiar, 880 m, N49°16'09" E20°15'58", 29.IX. + 06.X.1989, leg. P. Chvojka (6 males, 4 females, NMPC). *Ukraine*. Bieszczady Mts (Besszádok), Ung National Park, above Lubnya (Kiesvölgy), N: 49°02' 13,90" E: 22°42' 59,75", 579 m, singled, 20. IX. 2013, leg. J. Oláh, Cs. Balogh, Cs. Deák & I. Meszesán (1 male, OPC).

Remarks. The fine structures of the aedeagus and parameres summarized in the diverged structure matrices are rather stable both inside and among the different populations from the entire distributional area, from England to the Pyrénées and to Albania.



Figures 67–73. *Allogamus auricollis* (Pictet, 1834). 67 = male genitalia in left lateral view, 68 = phallic organ in left lateral view, 69 = left paramere in dorsal view, 70 = aedeagus head in ventral view, 71 = aedeagus head in lateral view; endophallus almost fully erected indicating the ejaculatory duct with gonopore as well as the ventral sclerite in anchor position. 72 = female vaginal sclerite complex profile in lateral view, 73 = vaginal complex profile in dorsal view.



Figures 74–117. *Allogamus auricollis* (Pictet, 1834). Diverged structure matrix of left paramere in dorsal view. 74–79 = England population, 80–87 = France (Pyrénées) population, 88–89 = Czech population, 90–96 = Poland population, 97–101 = Austrian population, 102 = Ukrainian population, 103–106 = Romanian population, 107–111 = Montenegro population, 112–115 = Macedonian population, 116–117 = Albanian population.

Allogamus despaxi Décamps, 1967

(Figures 143–144)

Material examined. The species was described from a single specimen. This holotype was preserved in alcohol and deposited in the author's collection at the Laboratory of Hydrobiology, Paul-Sabatier University, Toulouse. Dr. Décamps retired, a colleague who took care of his collection also retired. The Laboratory of Hydrobiology moved to a new place and the collection was possibly transferred to the Museum of Natural History in Toulouse. By intensive correspondence we have tried to find the holotype at the museum without any success. Finally Dr. Décamps informed us that they are unable to send us any specimen because the collection is probably pending somewhere and nobody is directly in charge of it at present. We have redrawn the phallic organ from the original drawings.

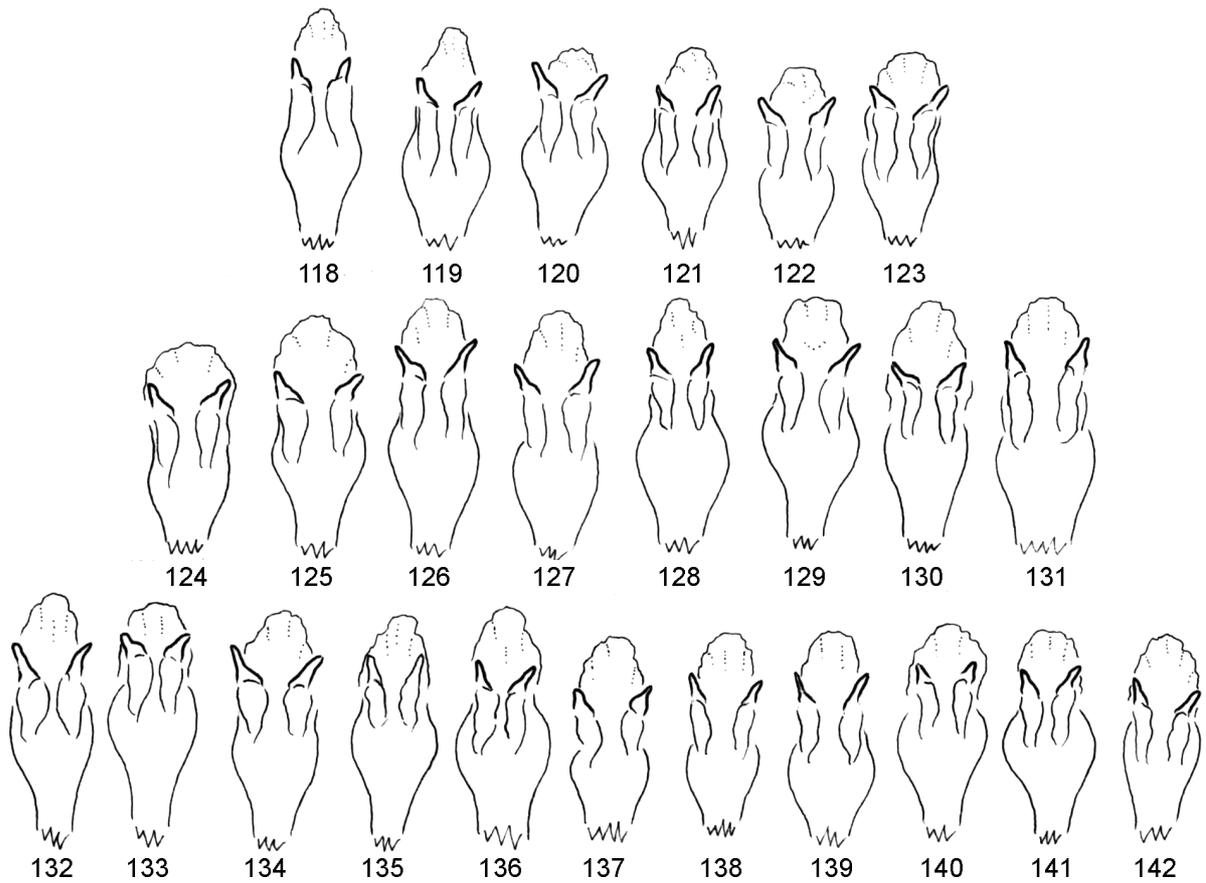
Remarks. This species was collected from Avajan, Neste d'Aure, 900 m, Hautes-Pyrénées.

Its taxonomic status was confirmed by M. D. E. Kimmins (Décamps 1967). Based upon the detailed original description and drawing and the characters of the closely related species from the nearby Valley Ossau *A. zomok* sp. nov. we have placed this species into the *Allogamus auricollis* subgroup.

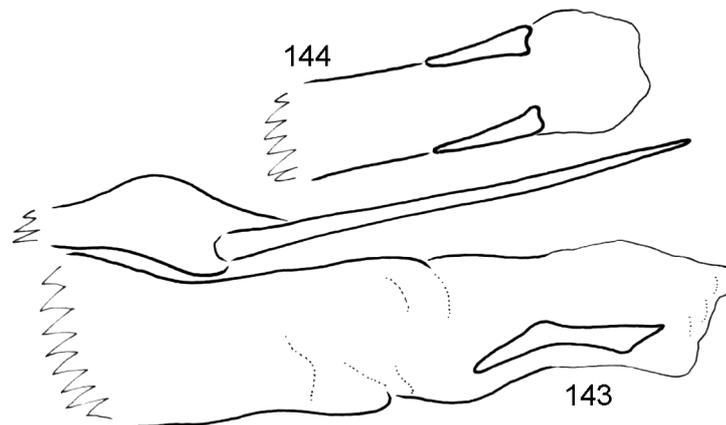
Allogamus zomok Oláh & Coppa sp. nov.

(Figures 145–150)

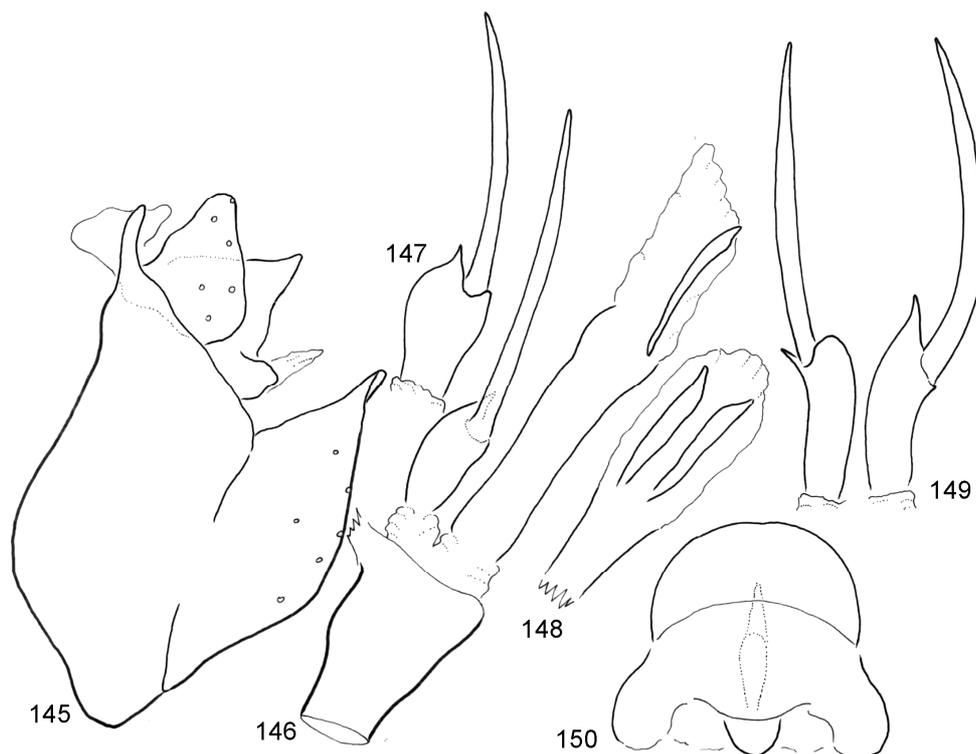
Diagnosis. Similar to *A. despaxi*, but differs by having genital cavity shrunken, almost vestigial, not large and deep; the third segment of the maxillary palp simple, not with unique tridentate distal end; apparent harpago of the gonopods broad rounded, not tapering, accessory process on the paraproctal basal triangle blunt, not slender in lateral view; apicoventral sclerite of the aedeagus differently formed and positioned.



Figures 118–142. *Allogamus auricollis* (Pictet, 1834). Diverged structure matrix of aedeagus head in ventral view. 118–123 = England population, 124–129 = Austrian population, 130 = Czech population, 131 = Ukrainian population, 132–136 = Montenegro population, 137–140 = Macedonian population, 141–142 = Albanian population.



Figures 143–144. *Allogamus despaxi* Décamps, 1967. 143 = male, phallic organ in left lateral view, 144 = aedeagus head in ventral view.



Figures 145–150. *Allogamus zomok* Oláh & Coppa sp. nov. 145 = male genitalia in left lateral view, 146 = phallic organ in left lateral view, 147 = left paramere in dorsal view, 148 = aedeagus head in ventral view, 149 = left and right parameres of paratype in dorsal view. 150 = female vaginal sclerite complex profile in dorsal view.

Material examined. **Holotype.** France, Pyrénées-Atlantiques, Vallée Ossau, 1984, leg. G. Vincon (1 male, OPC). **Allotype.** Same as holotype (1 female, OPC). **Paratypes.** Same as holotype (1 male, 2 females; OPC).

Description. In alcohol both male and female have forewing membrane dark. Forewing length 11 mm. Head, thorax and appendages dark brown.

Male genitalia. Genital cavity abbreviated, shrunken. Cerci subquadrangular. Paraproct triangular in lateral view. Accessory process on the basal triangulum of the paraproct present and blunt. Paramere shaft very short, stocky. Apico-ventral sclerite of the aedeagus narrow elongated.

Female genitalia. External genital structure similar to the species subgroup. Anterior apodemes of the vaginal sclerite complex simple rounded laterad.

Etymology. *zomok* from “zömök” stocky in Hungarian, refers to the reduced, abbreviated, al-

most vestigial genital cavity and the short and dumpy paramere shaft.

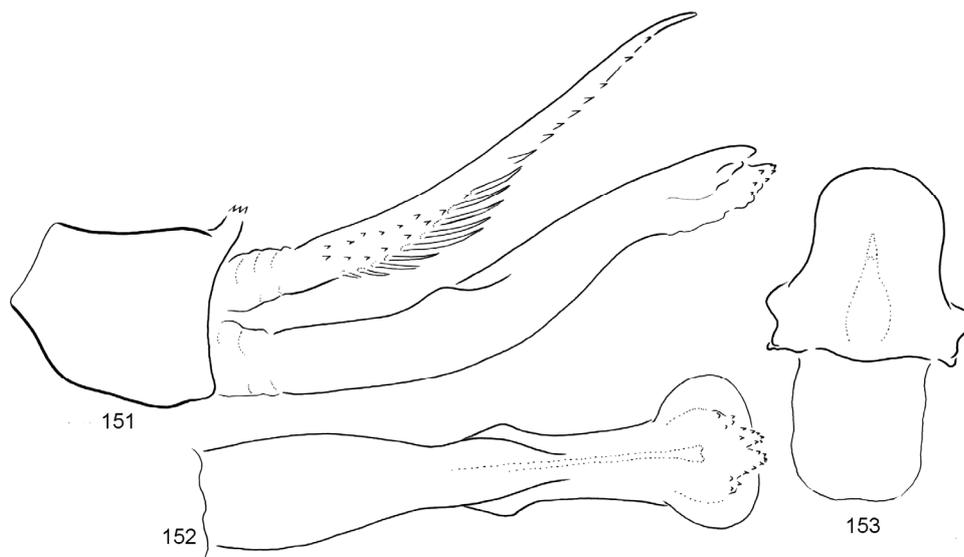
Allogamus hilaris new species subgroup

Light species characterized with a strong paramere shaft without primary seta. Longer secondary setae present midway, shorter setae present basolaterad and ventrad from middle to subapical. Modified accessory duct of female present.

Allogamus hilaris (McLachlan, 1876)

(Figures 151–153)

Material examined. France. Alpes-Maritimes, La Brigue, Torrent de Malaberhe, Lieu dit Vacherie, 24.IX.2008, leg. G. Coppa, (1 female; OPC). Italy. Piemonte-Cuneo, Ormea, rio Armella, N44.1639° E7.8821°, 1000 m, 10.X.2001, light trap, leg. Museo Caffi, Bergamo (2 males, 1 female; OPC). Piemonte-Torino, Ceresole Reale,



Figures 151–153. *Allogamus hilaris* (McLachlan, 1876). 151 = male phallic organ in lateral view, 152 = aedeagus in ventral view. 153 = female vaginal sclerite complex with the anterior tip of the modified accessory duct profile in dorsal view.

Colle di Nivolet, Parco Nazionale del Gran Paradiso, 2700 m, 21.X.1990, leg. Chiappafreddo (1 male; N°1256 CC). Lombardia-Bergamo, Averara, Alpe Cul versante sud, N46.0440° E9.6201°, 1800 m, 23.IX.2004, leg. E. Bertuetti (9 males, 3 females; OPC). Lombardia-Bergamo, Mezzoldo, Alpe Ancogno, 1800 m, light trap, N46,0381° E9,6359°, 3.X.1995, leg. F. Albrici, M. Valle (5 males, 13 females; CNSMB). Liguria-Imperia, Mendatica, torrente Tanarello, 1280 m, light trap, N44,0772° E7,7486°, 10.X.2001, leg. Museo Caffi BG (1 male; CNSMB). Liguria-Imperia, Triora, rio Lazzarin c/o Verdeggia, 1075 m, light trap, N44,0406° E7,7229°, 9.X.2001, leg. Museo Caffi BG (2 males, 1 female; CNSMB). Liguria-Savona, Calizzano, torrente Frassino, N44.2351° E8.1958°, 920 m, 11.X.2001, leg. Museo Caffi, Bergamo (5 males, 8 females; OPC). Liguria-Savona, Sassello, rio del Nido, 1000 m, N 44,4449° E8,5769°, 12.X.2001, leg. Museo Caffi BG (3 males; CNSMB).

Remarks. *Allogamus hilaris* new species subgroup is comprised of the single nominate species. This subgroup is a specialized lineage inside the *Allogamus auricollis* species group. The longer secondary setae and the short tertiary setae together are distributed along the entire ventrum

of the paramere. The pair of the ventral sclerite of the aedeagus is modified into a fused bilobed dentate structure. The semisclerotized dorsal sclerite on the head of the aedeagus has taken over the flexing function forming laterally extended rounded semicircular lobes. Female vaginal sclerite complex has accessory duct modified into an enlarged sac of subquadratic dorsal profile.

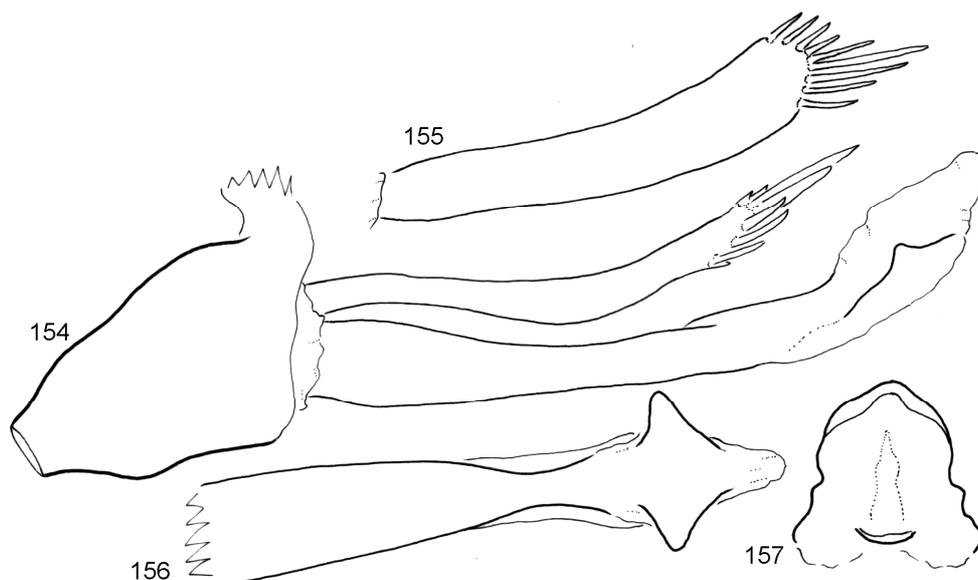
Allogamus ligonifer new species subgroup

Light species characterized with subequal secondary apical setae on the parameres. Modified accessory duct of female lacking.

Allogamus gibraltarius González & Ruiz, 2001

(Figures 154–157)

Material examined. Spain. Cádiz Province, Rio Majaceite, Canuto del Aljibe, N 36° 31' 50" W 5° 35' 07", 320 m, 2. XI. 2007, leg. A. RUIZ, (1 female, OPC). Cádiz Province, Rio Majaceite, Canuto del Aljibe, Guadalete Basin, N36° 32' 21" W 5° 38' 10", 320 m, 27. X. 2013, leg. A. RUIZ (8 males, 5 females DZFCUG; 8 males, 6 females, OPC).



Figures 154–157. *Allogamus gibraltarius* González & Ruiz, 2001. 154 = male, phallic organ in left lateral view, 155 = left paramere in dorsal view, 156 = aedeagus in ventral view, 157 = female vaginal sclerite complex profile in dorsal view.

***Allogamus kefes* Coppa & Oláh sp. nov.**

(Figures 158–160, 161–164)

Diagnosis. Similar to *A. pupos* sp. nov. but differs by having shorter leading seta in the apical seta brush; fused ventral sclerite on the aedeagus differently formed; stem of aedeagus without dorsal hump midway.

Material examined. *Holotype.* France, Drôme Department, Auelon, Le Deves, 19. IX. 2006, leg. G. Coppa (1 male, CPC). *Allotype.* Drôme Department, Montbrun les Bains, Torrent d’Anary Pont D542, 29. X. 2010, leg. G. Coppa (1 female, CPC). *Paratypes.* Same as allotype (1 male, 1 female; OPC).

Description. In alcohol both male and female have forewing membrane light brown with scarcely scattered lighter spots. Forewing length 18 mm. Head, thorax and appendages brown.

Male genitalia. Genital cavity well developed. Cerci rounded subquadrangular. Paraproct triangular in lateral view with small apical hook. Paramere shaft with apical brush of setae, leading seta slightly longer than the others. The pair of apico-ventral sclerites of the aedeagus fused into a

ventral quadrangular plate, lateral tooth moved more anterad.

Female genitalia. External genital structure similar to the species subgroup. Anterior apodemes of the vaginal sclerite complex simple rounded laterad.

Etymology. Epithet *kefes* from “*kefés*” brushy in Hungarian refers to the pattern of the apical setae on the parameres.

***Allogamus laureatus* (Navas, 1918)**

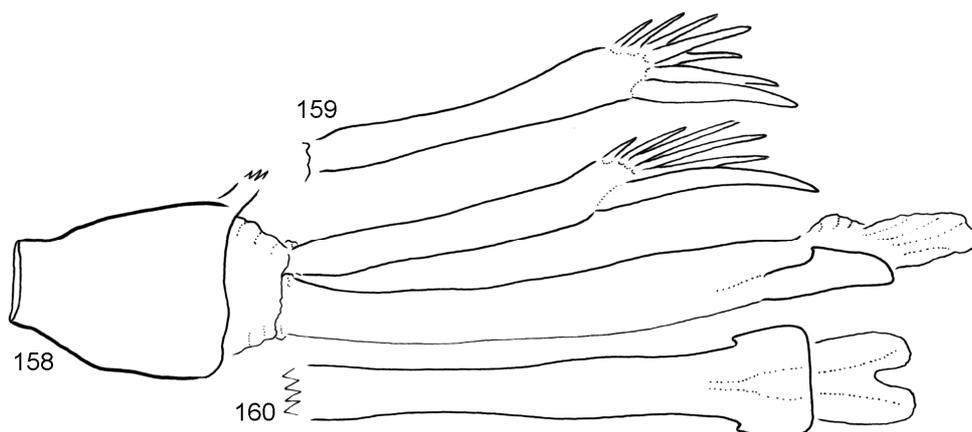
(Figures 165–167)

Material examined. Spain. Orense Province, Serra do Invernadeiro, Seixo Blanco, 998 m, 42°7’1.98” N 7°20’43.60” W, 6.X.2010, leg. M. González & J. Martínez (3 males, 2 females, OPC).

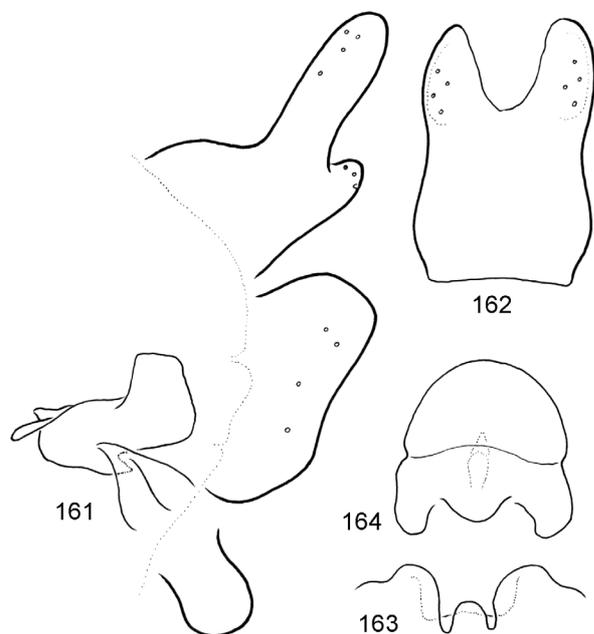
***Allogamus liginifer* (McLachlan, 1876)**

(Figures 168–171)

Material examined. France. Corrèze, Chenaillers Mascheix, Le Chambariol, 28.IX.2010, leg. G. Coppa, (1 male, 1 female, CPC). Pyrénées-Orien-



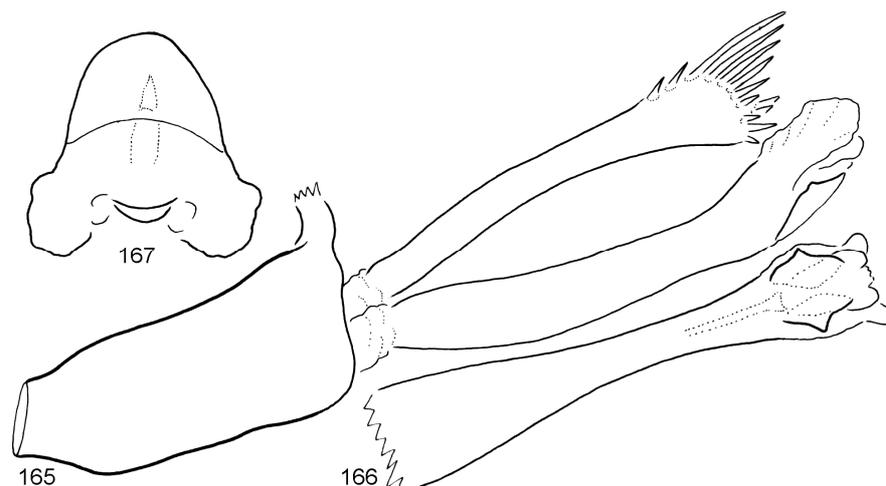
Figures 158–160. *Allogamus kefes* Coppa & Oláh sp. nov. 158 = male, phallic organ in left lateral view, 159 = left paramere in dorsal view, 160 = aedeagus in ventral view.



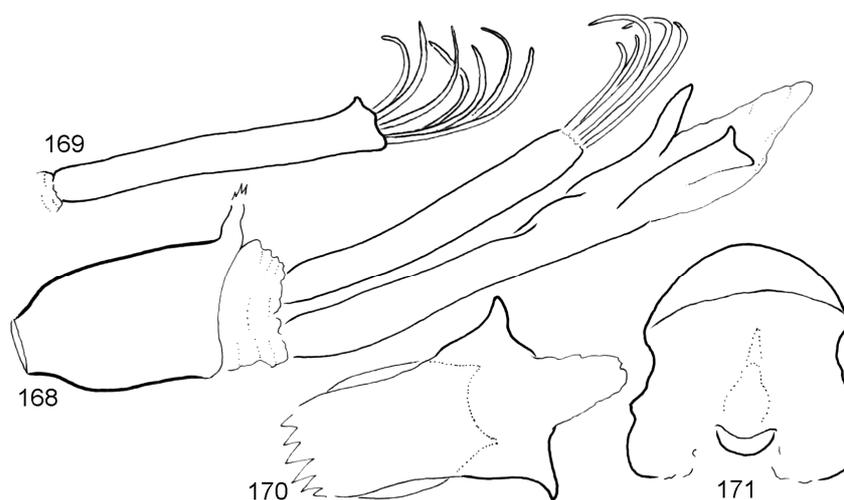
Figures 161–164. *Allogamus kefes* Coppa & Oláh sp. nov. 161 = female genitalia in left lateral view with vaginal sclerite complex, 162 = female anal tube in dorsal view, 163 = female vulvar scale (lower lip) in ventral view, 164 = dorsal profile of vaginal sclerite complex.

tales, Cattlar, La Tet Pont D 616, 28.X.2008, leg. G. Coppa (1 male, 1 female; OPC). Cantal Department, Murat, sur l'Alagnon Pont du Camping, 26.X.2005, leg. G. Coppa (1 male, CPC). Puy-de-Dôme Department, Besse et Saint Anastaise, Lac de Bourdouze, 7.X.2007, leg. G. Coppa (1 male, CPC). Puy-de-Dôme Department, Besse et Saint

Anastaise, Lac de Montcineyre, 7.IX.2007, leg. G. Coppa (1 male, 1 female; OPC). Puy-de-Dôme Department, Saint Germain Lembron, Couse d'Ardes pont D909, 28.X.2005, leg. G. Coppa (1 male, CPC). Corrèze Department, Monceau-sur-Dordogne, D12 le Gand Dordogne, 16.XI.1997, leg. G. Coppa (2 males, 1 female; 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 Vaurs, 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). Lozère Department, Meyrueis, Ru de Bethuzon, 27.X.2010, leg. G. Coppa (1 male, CPC). Lozère Department, Saint Bonnet de Chirac, Les Bories ru Romardies, 25.X.2010, leg. G. Coppa (1 male, CPC). Lozère Department, Saint Bonnet de Chirac, Les Bories Lot, 25.X.2010, leg. G. Coppa (1 female, CPC). Lozère Department, Saint Chely d'Apcher, sur le Chapouillet Confluence avec la Truyère, 18.VIII.



Figures 165–167. *Allogamus laureatus* (Navas, 1918). 165 = male, phallic organ in left lateral view, 166 = aedeagus in ventral view, 167 = dorsal profile of vaginal sclerite complex.



Figures 168–171. *Allogamus ligonifer* (McLachlan, 1876). 168 = male, phallic organ in left lateral view, 169 = left paramere in dorsal view, 170 = aedeagus head in ventral view, 171 = female vaginal sclerite complex profile in dorsal view.

2011, leg. G. Coppa (1 male, CPC). Vosges Department, Valtin, La Meurthe en Amont de l'Etang, 4.X.2010, leg. G. Coppa (1 male, CPC). 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). Haut-Garonne Department, Galie, pas de précision, 13.X.2006, leg. G. Coppa (1 female, CPC). Haute-Garonne Department, Galie, pas de pré-

cision, 30.IX.2006, leg. G. Coppa (1 male, 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 précision, 27.II.2006, leg. G. Coppa (1 male, CPC). Morbihan Department, Inguiniel, sur le Sebrevet le Porz, 22.IV.20106, leg. G. Coppa (1 male, CPC). Languedoc-Roussillon, Dep. Hérault, Saint-Pons-de-Thomières, around camping place, hard leaved forest, at house-

walls and in grassland, 285 m, N43,49037° E 2,78524°, 18.X.2009, leg. A. Schönhofer (3 males; CNSMB).

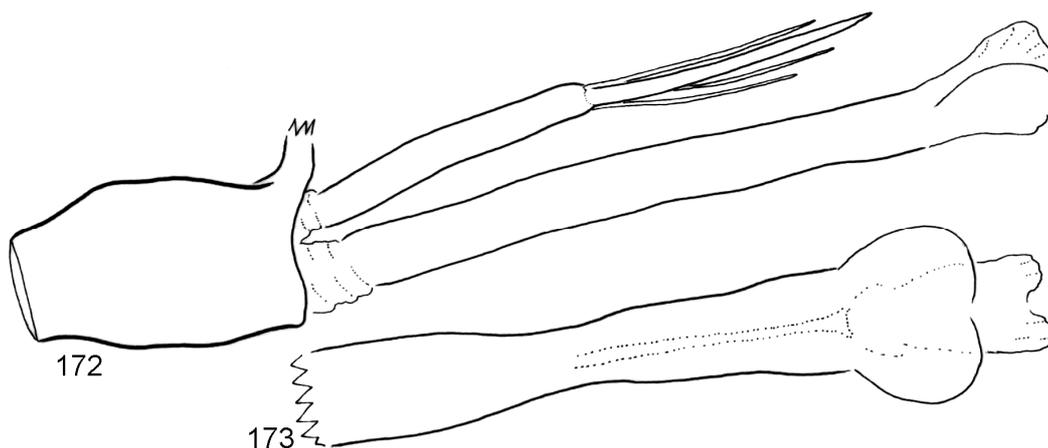
Remarks. There is significant currently segregating standing variation among and inside the examined populations in the shape of dorsal sclerite of the aedeagus, in the apical dorsal pattern of the paramere shaft and in the pointedness of the accessory paraproctal process. Populations from Lozere-Cevennes and Correze-Dordogne have dorsal sclerite with deep mesal excavation and more developed lateral pointed lobes in dorsal view, dorsal pattern of paramere shaft with mesal subapical tooth, accessory paraproctal process is more slender and pointed. Specimens from Vosges, Bretagne and Massif Central have more shallow mesal excavation on the dorsal sclerite, dorsal pattern of paramere shaft with mesal apical tooth, accessory paraproctal process is less pointed.

Besides populations with stable diverged fine structure there is variation detectable also inside populations. This may suggest ongoing diversification in sexual selection processes both on phallic structures and on the paraproctal accessory process. There is possibility also for reinforcement processes under the influence of gene flow by immigrants. A more detailed study of structure matrix 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.

***Allogamus pertuli* Malicky, 1974**

(Figures 172–173)

Material examined. Greece. Karpenision, Mikro Chorio, 700 m, 15.X.1991, leg H. Malicky (1 male, OPC).



Figures 172-173. *Allogamus pertuli* Malicky, 1974. 172 = male, phallic organ in left lateral view, 173 = aedeagus head in ventral view.

***Allogamus pupos* Coppa & Oláh sp. nov.**

(Figures 174–175, 176–179)

Diagnosis. Similar to *A. kefes* sp. nov. but differs by having smaller body, forewing less distinctly spotted; longer leading seta in the apical seta brush; fused ventral sclerite on the aedeagus differently formed; stem of aedeagus with dorsal hump midway.

Material examined. Holotype. France, Alpes-Maritimes Department, Tende, Torneau Aval, 13. XI. 2012, leg. G. Coppa (1 male, CPC). Allotype. Same as holotype (1 female, CPC). Paratypes. Same as holotype (2 males, 1 female, OPC) Vaucluse Department, Fontaine-de-Vaucluse, La Sorgue, 30. X. 2010, leg. G. Coppa (3 males, CPC).

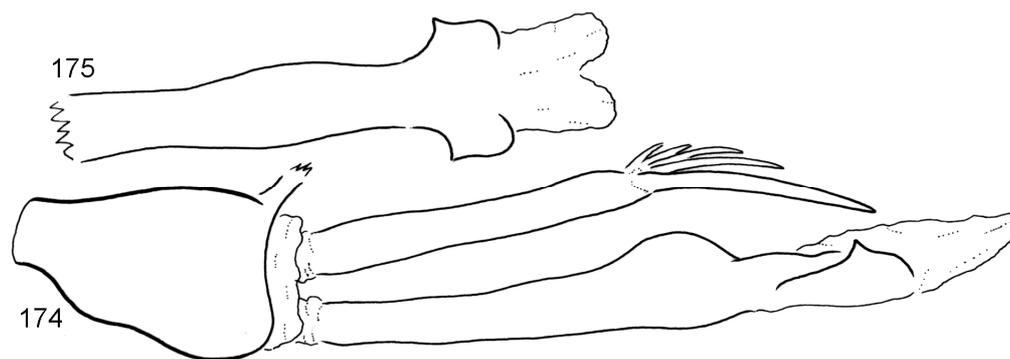
Description. In alcohol both male and female have forewing membrane light brown with un-

distinct lighter spots. Forewing length 14 mm. Head, thorax, and appendages brown.

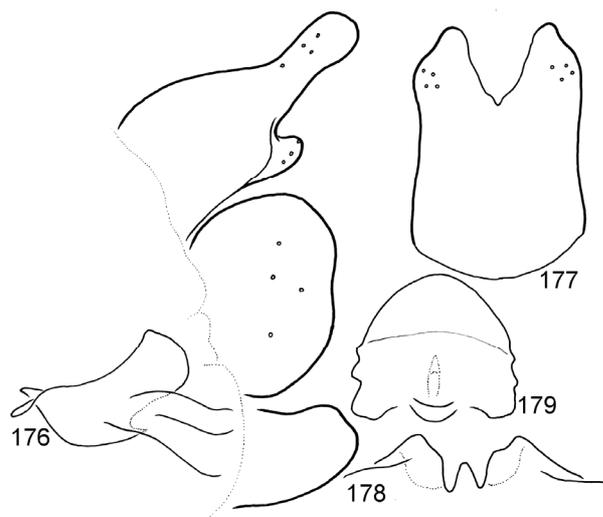
Male genitalia. Genital cavity well developed. Cerci rounded. Paraproct triangular in lateral view with small apical hook. Paramere shaft with apical brush of setae, leading seta much longer than the others. The pair of apicoventral sclerites of the aedeagus fused into a ventral quadrangular plate, lateral tooth moved more posterad.

Female genitalia. External genital structure similar to the species subgroup. Anterior apodemes of the vaginal sclerite complex with small lobes laterad.

Etymology. Epithet *pupos* from “*púpos*” humpy in Hungarian, refers to the dorsal hump on the stem of aedeagus.



Figures 174–175. *Allogamus pupos* Coppa & Oláh, sp. nov. 174 = male, phallic organ in left lateral view, 175 = aedeagus in ventral view.



Figures 176–179. *Allogamus pupos* Coppa & Oláh sp. nov. 176 = female genitalia in left lateral view with vaginal sclerite complex, 177 = female anal tube in dorsal view, 178 = female vulvar scale (lower lip) in ventral view, 179 = orsal profile of vaginal sclerite complex.

Allogamus mortoni new species complex

Light species characterized by the neoformation of pointed accessory paraproctal process.

The modified accessory duct of female is lacking. *Allogamus mortoni* species complex is most related to species *Allogamus lignonifer* based on both male and female genital structures, but differs by having genital cavity more deep and the accessory process strongly developed on the ventral branches of the paraproctal complex, almost as long as the dorsal branch of the paraproct itself. The following description of the male and female genital structures of the new species complex characterizes all of the new species. In the new species description we describe only the separating morphological structures of diversified accessory processes and the female vaginal sclerites.

Male genitalia. Segment IX medium long with more setose apicomarginal depression on the pleural region. Deep genital cavity produced anteriorly as a continuation of the superanal complex with sclerotized mesal septum. Cerci broad foliiform subdivided with a mesal irregular digitiform arm. Dorsal branch of paraproct, (the paraproct sensu stricto) produced as a pair of heavily sclerotized stout spurs with slightly and shortly hooked apex. Ventral branch or the basal triangulum of the paraproct complex (the vestigium of somite X

and XI) produced a pair of pointed accessory process with morphological diversification of species specific shape. Gonopods single segmented; apex of gonopods, the “apparent harpago” turned in coronal plane is the most varying structure of the species complex.

Female genitalia. Anal tube, the fused tergites IX and X bilobed in lateral view and armed ventrobasad with a pair of variously developed or almost reduced setose digitate process. Setose sternite IX large rounded in lateral view flanking the setaless, glabrous supraanal plate, the upper vulval lip. Vulval scale, the lower vulval lip with less produced mesal lobe. The internal genital structure, the well sclerotized vaginal sclerite complex seems species specific, especially the diversified shape of anterior apodemes in dorsal view offers stable trait to separate species. Variability of both external structures and vaginal sclerite complex need more detailed studies on several specimens of more populations. The anterior apodeme of the vaginal sclerite complex may be obscured by residues even after careful clearing and cleaning procedures. The ventrolateral process on female tergite IX seems enlarged (*A. pohos* sp. n., *A. kurtas* sp. n.), thinned (*A. tuskes* sp. n.), abbreviated (*A. kampos* sp.n.), or even vestigial (*A. kettos* sp. n.). However it is probably not stable. Special study is required to examine its stability and its ranges of variability in several populations.

Morphological variability and stability. Both male and female phenotypic variation is rather significant in *Allogamus mortoni* species group. Periphallial organs of cerci and gonopods, the phallic organs of parameres and aedeagus, as well as the external female genital structures are subjects to significant interspecific and intra-specific variabilities.

Detailed molecular genetic survey with neutral markers revealed significant deviations in various *Allogamus mortoni* populations. The measured DNA pattern has not matched the wing or the paramere morphological patterns of the examined populations (Múrria et al. unpublished data). Both

the forewing brown pattern and the paramere apical spine pattern exhibited rather significant random variations among and inside populations. It seems that the parameres are not diverged in *A. mortoni* species complex and its setal pattern not stabilized. Parameres are influenced by neutral non-adaptive processes. The target of the non-neutral adaptive sexual selection processes is not the intromittent phallic organ. We have discovered stable divergences in the shape of the paired accessory processes on the paraproctal complex of the male genitalia. This divergence was accompanied by corresponding morphological diversity on the anterior apodemes of the vaginal sclerite complex of the females.

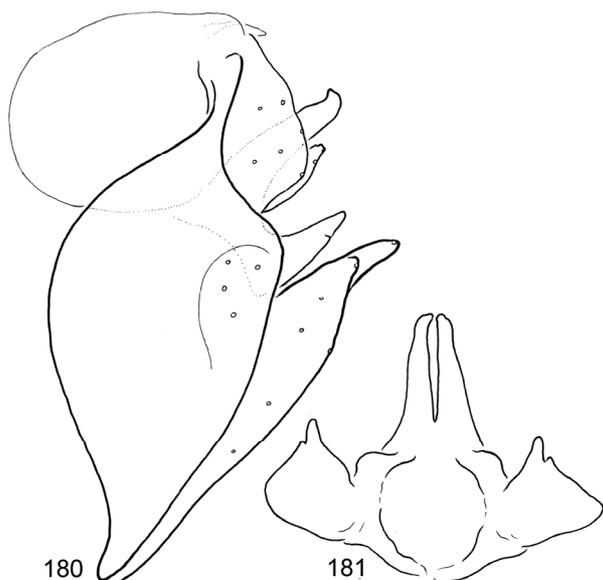
The diverged structure matrices of the pointed accessory process exhibit high stabilities in all the five new species. The fine structure analysis revealed stability, but its high resolution capacity indicates minor deviations for each specimen. There are no two specimens alike. Like every human has different earlobe! Moreover there is possibility to detect reinforcement processes between interacting populations by gene flow of immigrants. All these processes may interfere and can confuse the interpretation of fine structure analysis in routine alpha-taxonomic studies.

***Allogamus kampos* Oláh & Ruiz sp. nov.**

(Figures 180–181, 182–184, 185–188, 189–200)

Diagnosis. Paraproctal basolateral accessory process on the superanal genital complex with subdivided apex. Ventrolateral process on female tergite IX is vestigial. Most close to *A. kettos* sp. nov., but differs by having paraproctal accessory process with less developed lateral division and the anterior apodemes on the vaginal sclerite complex mesad curving and tapering.

Material examined. *Holotype.* Spain, Málaga Province, Rio Hozgarganta, La Saucedá, N36° 31' 50", W5° 35' 08", 510 m, 1.XI.2007, leg. A. Ruiz, (1 male, DZFCUG). *Allotype.* Same as holotype (1 female, DZFCUG). *Paratypes.* Same as holotype (1 male DZFCUG, 1 male, OPC). Cádiz Province, Rio Majaceite, Canuto del Aljibe, N36°



Figures 180–181. *Allogamus kampos* Oláh & Ruiz sp. nov. 180 = male, genitalia in lateral view, 181 = paraproct with the accessory processes in caudal view.

31' 50", W5° 35' 08", 320 m, 2.XI.2007, leg. A. Ruiz, (2 males DZFCUG, 2 males; OPC). Cádiz Province, Rio Majaceite, Benamahoma, N36° 46' 05", W5° 28' 34", 420 m, 2.XI.2007, leg. A. Ruiz, (2 males DZFCUG, 1 male; OPC). Cádiz Province, Rio Majaceite, Canuto del Aljibe, Guadalete Basin, N36° 32' 21", W5° 38' 11", 320

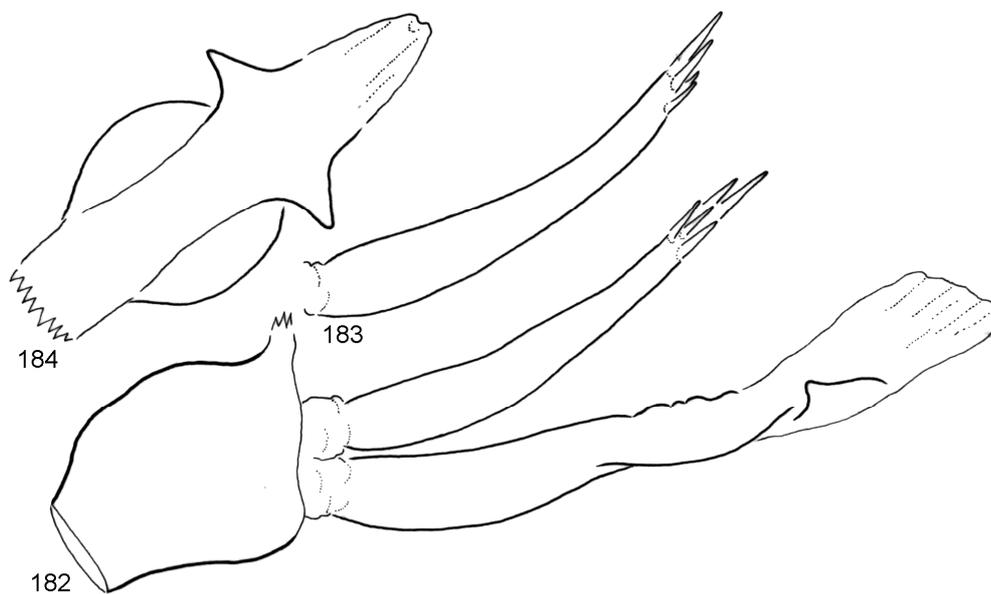
m, 27.X.2013, leg. A. Ruiz, (8 males, 5 females DZFCUG; 8 males, 6 females, OPC). Cádiz Province, Rio del Bosque/Majaceite, Benamahoma, Guadalete, N36° 46' 05", W5° 28' 34", 420 m, 9. XI.2013, leg. A. Ruiz, (8 males, DZFCUG; 8 males, OPC). *Morocco*. Azica, 1600 m, Ketama, 13.XI.2013, leg. W. Graf (2 males, OPC).

Description. Male (in alcohol). Both male and female have forewing membrane marbled and speckled, slightly irrorated. This forewing pattern variously developed at specimens, pharate or newly emerged specimens less or not patterned at all. Forewing length 20 mm. Head, thorax and appendages are stramineous.

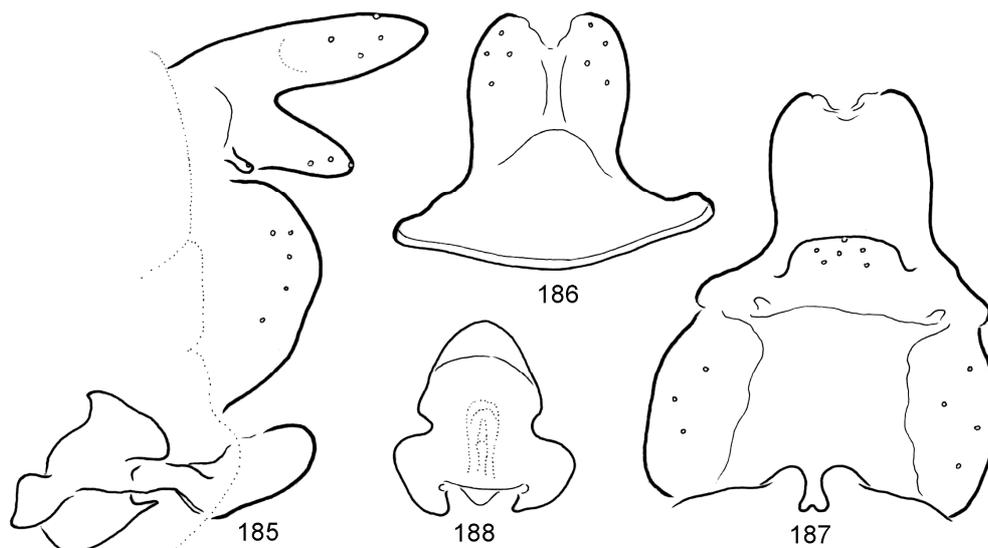
Male genitalia. Periphallic organs as described in the species complex diagnosis. Accessory process on the basal triangulum of the superanal complex with subdivided bifid apex. The lateral division is small, shorter, just discernible.

Female genitalia. Ventrobasal setose process reduced. Anterior apodemes with tapering and mesad turning apex.

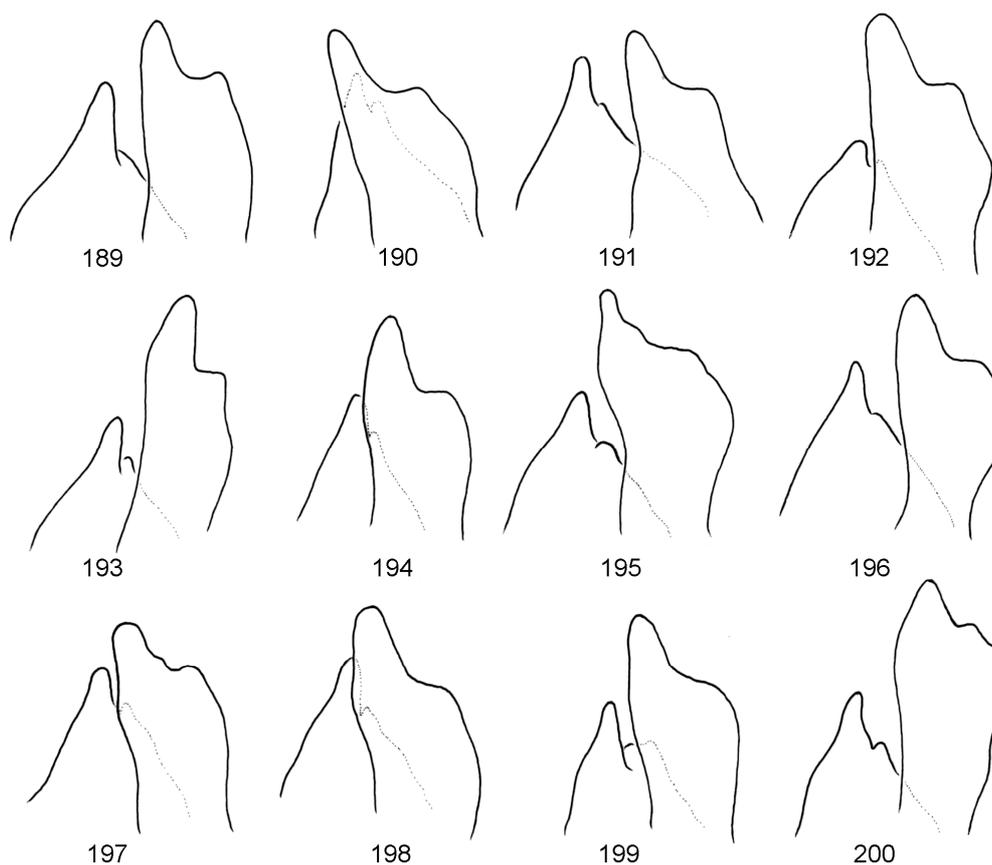
Etymology. Epithet *kamos* is from “*kampós*” hooked in Hungarian, refers to the mesad curving shape of the anterior apodemes of the vaginal sclerite complex.



Figures 182–184. *Allogamus kampos* Oláh & Ruiz sp. nov. 182 = male, phallic organ in left lateral view, 183 = left paramere in dorsal view, 184 = aedeagus head in ventral view,



Figures 185–188. *Allogamus kampos* Oláh & Ruiz sp. nov. 185 = female genitalia in left lateral view with vaginal sclerite complex, 186 = female anal tube in dorsal view, 187 = female genitalia in ventral view, 188 = dorsal profile of vaginal sclerite complex.



Figures 189–200. *Allogamus kampos* Oláh & Ruiz sp. nov. Diverged structure matrix of the right accessory process on the basal triangle of the paraproct together with the apex of the right harpago in caudal view.

***Allogamus kettos* Oláh & Ruiz sp. nov.**

(Figures 201–212, 213–214)

Diagnosis. Paraproctal basolateral accessory process on the superanal genital complex with subdivided apex. Ventrolateral process on female tergite IX reduced, just discernible. Most close to *A. kampos* sp. n., but differs by having paraproctal accessory process with more developed lateral division and the anterior apodemes on the vaginal sclerite complex not curving mesad and not tapering.

Material examined. Holotype. Spain, Sevilla Province, Rivera de Huéznar Basin, Isla Margarita (Cazalla de la Sierra), Rio Rivera de Huéznar, N37° 56' 04", W5° 41' 44", 427m, 2.XI.2013, leg. A. Ruiz, (1 male, DZFCUG). *Allotype.* Same as holotype (1 female, DZFCUG). *Paratypes.* Same as holotype (5 males, 3 females DZFCUG;

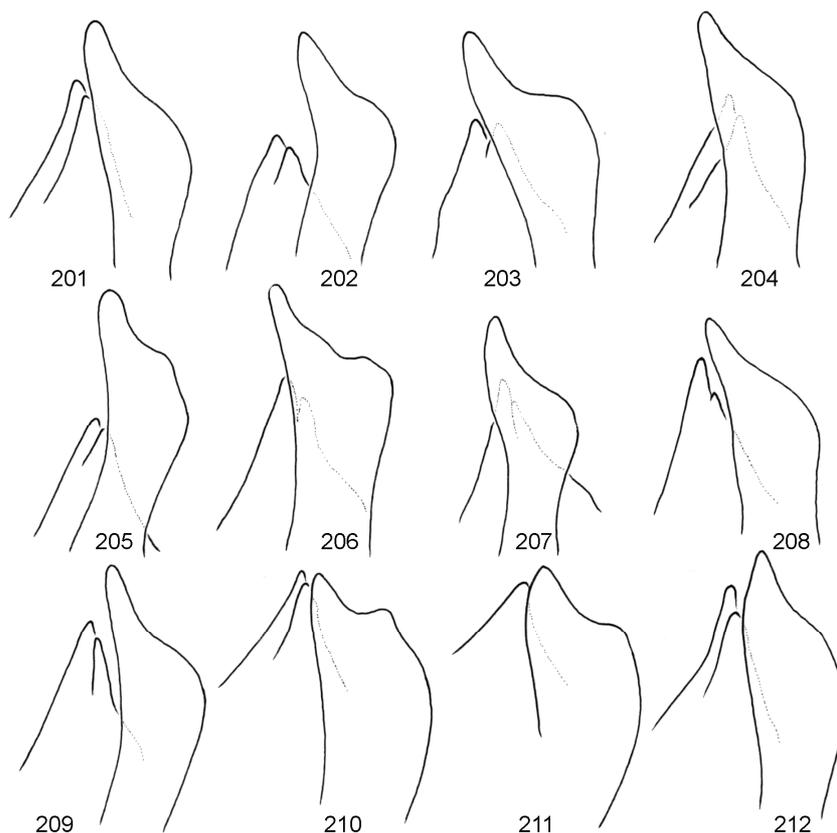
10 males, 5 females, OPC).

Description. Male (in alcohol). Both male and female have forewing membrane marbled and speckled, slightly irrorated. This forewing pattern variously developed at specimens, pharate or newly emerged specimens less or not patterned at all. Forewing length 20 mm. Head, thorax, and appendages are stramineous.

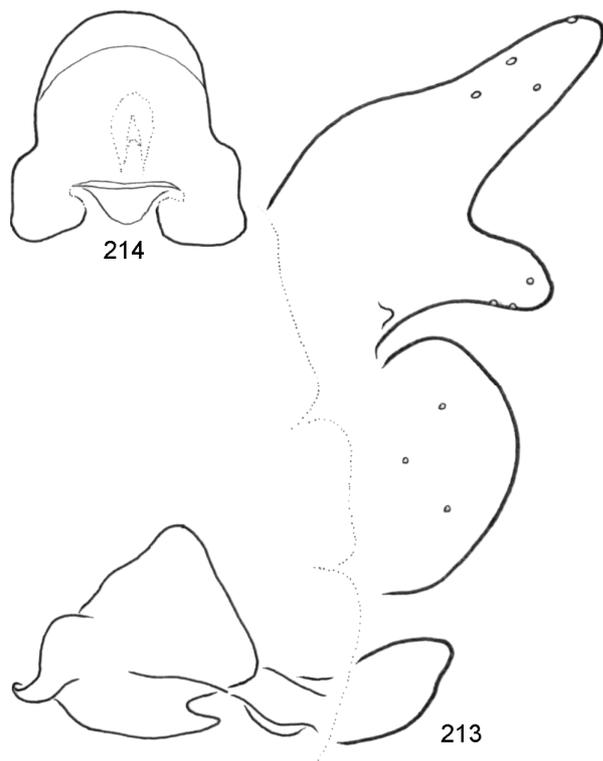
Male genitalia. Periphallic organs as described in the species complex diagnosis. Accessory process on the basal triangulum of the superanal complex with subdivided bifid apex. The lateral division is almost equal long than the mesal division.

Female genitalia. Ventrobasal setose process almost disappeared. Anterior apodemes subquadrangular.

Etymology. Epithet *kettos* is from “*kettős*” doubled in Hungarian, refers to the duplicated tip of the accessory process of the paraproct.



Figures 201–212. *Allogamus kettos* Oláh & Ruiz sp. nov. Diverged structure matrix of the right accessory process on the basal triangle of the paraproct together with the apex of the right harpago in caudal view.



Figures 213–214. *Allogamus kettos* Oláh & Ruiz sp. nov.
213 = female genitalia in left lateral view with vaginal sclerite complex, 214 = dorsal profile of vaginal sclerite complex.

***Allogamus kurtas* Oláh & Zamora-Muñoz sp. nov.**

(Figures 215–226, 227–228)

Diagnosis. Paraproctal basolateral accessory process on the superanal genital complex short triangular. Ventrolateral process on female tergite IX produced and high. Most close to *A. mortoni* Navas, 1907 but differs by the shorter paraproctal accessory process. The anterior apodemes on the vaginal sclerite complex almost regular quadrangular.

Material examined. *Holotype.* Spain, Granada Province, Fardes Basin, Arroyo de Prado Negro stream, Venta del Molinillo, 1201 m, 30.X.2007, leg. C. Zamora-Muñoz (1 male, DZFCUG). *Allotype.* Same as holotype (1 female, DZFCUG). *Paratypes.* Same as holotype (4 males, 1 female;

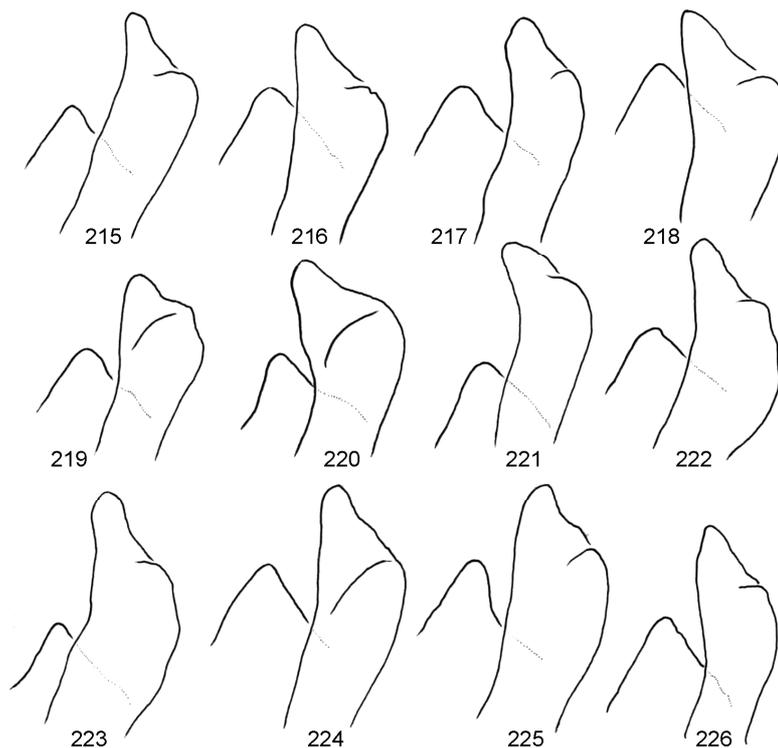
DZFCUG). Granada Province, Fardes Basin, Arroyo de Prado Negro stream, Venta del Molinillo, 1201 m, 9.IX.1995, leg. C. Zamora-Muñoz (3 females, DZFCUG; 3 females OPC). Granada Province, Fardes Basin, Arroyo de Prado Negro stream, Cortijo del Despenadero, N37° 18' 59", W3° 27' 17", 1320 m, 4.X.2000, leg. J. Luzón & P. Jaimez (2 females, OPC). Granada Province, Fardes Basin, Arroyo de Prado Negro stream, Cortijo del Despeñadero, N37° 18' 59", W3° 27' 17", 1320 m, 17.X.1996, leg. J. Luzón & P. Jaimez (1 female, DZFCUG). Granada Province, Fardes Basin, Arroyo de Prado Negro stream, Cortijo del Despeñadero, N37° 18' 59", W3° 27' 17", 1320 m, 19.X.2000, leg. J. Luzón & P. Jaimez (1 female, DZFCUG). Granada Province, Fardes Basin, Barranco de Fuente Grande stream, Fuente de los Potros, N37° 19' 19" W3° 27' 38", 1400 m, 17.X.1996, leg. J. Luzón & P. Jaimez (2 females, DZFCUG). Granada Province, Guadiana Menor Basin, Arroyo Alhorí, Central eléctrica, N37° 8' 59", W3° 11' 57", 1514 m, 14.X.2013, leg. C. Zamora-Muñoz (2 males, DZFCUG). Granada Province, Guadiana Menor Basin, Arroyo Alhorí, Central eléctrica, N37° 8' 59", W3° 11' 57", 1514 m, 18.X.2013, leg. C. Zamora-Munoz (5 males, 2 females; OPC)

Description. Male (in alcohol). Both male and female have forewing membrane marbled and speckled, slightly irrorated. This forewing pattern variously developed at specimens, pharate or newly emerged specimens less or not patterned at all. Forewing length 20 mm. Head, thorax, and appendages stramineous.

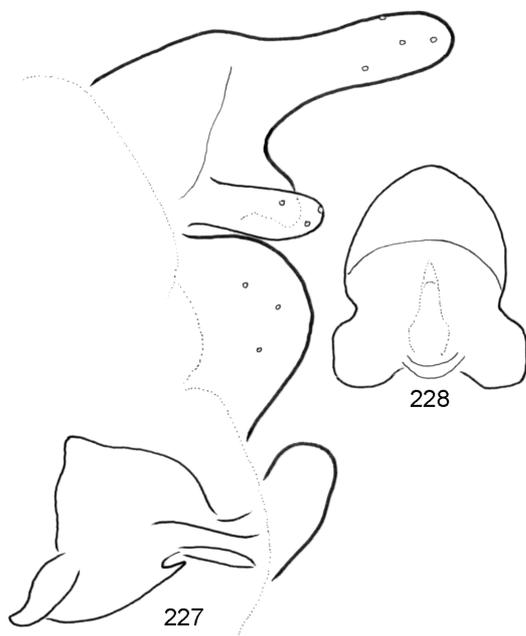
Male genitalia. Periphallic organs as described in the species complex diagnosis. Accessory process on the basal triangulum of the superanal complex short.

Female genitalia. Ventrobasal setose process much developed. Anterior apodemes regular quadrangular.

Etymology. Epithet *kurtas* is from “*kurta*” curt, cutty in Hungarian refers to the low abbreviated accessory basal process of the paraproct.



Figures 215–226. *Allogamus kurtas* Oláh & Zamora-Muñoz sp. nov. Diverged structure matrix of the right accessory process on the basal triangle of the paraproct together with the apex of the right harpago in caudal view.



Figures 227–228. *Allogamus kurtas* Oláh & Zamora-Muñoz sp. nov. 227 = female genitalia in left lateral view with vaginal sclerite complex, 228 = dorsal profile of vaginal sclerite complex.

***Allogamus mortoni* (Navás, 1907)**

Halesus mortoni Navas, 1907: 194–195. „Patria. San Fiel (Portugal), Diciembre de 1907 (!). Cogido por el R.P. Martins, S.J. He dedicado esta especie al distinguido entomólogo señor Morton, de Edimburgo.”

Halesus mortoni Navas, 1907: Schmid 1951a: 46–48. „Le type provient du Portugal: San Fiel XII.1904 (1907 in Navas’s description!). Il est actuellement dans ma collection”

Allogamus mortoni (Navas, 1907): Schmid 1955: 195.

Diagnosis. Nominate species of the group. Similar to *A. kurtas* sp. n. but accessory process on the superanal complex more developed. Female unknown. Type or newly collected material not available.

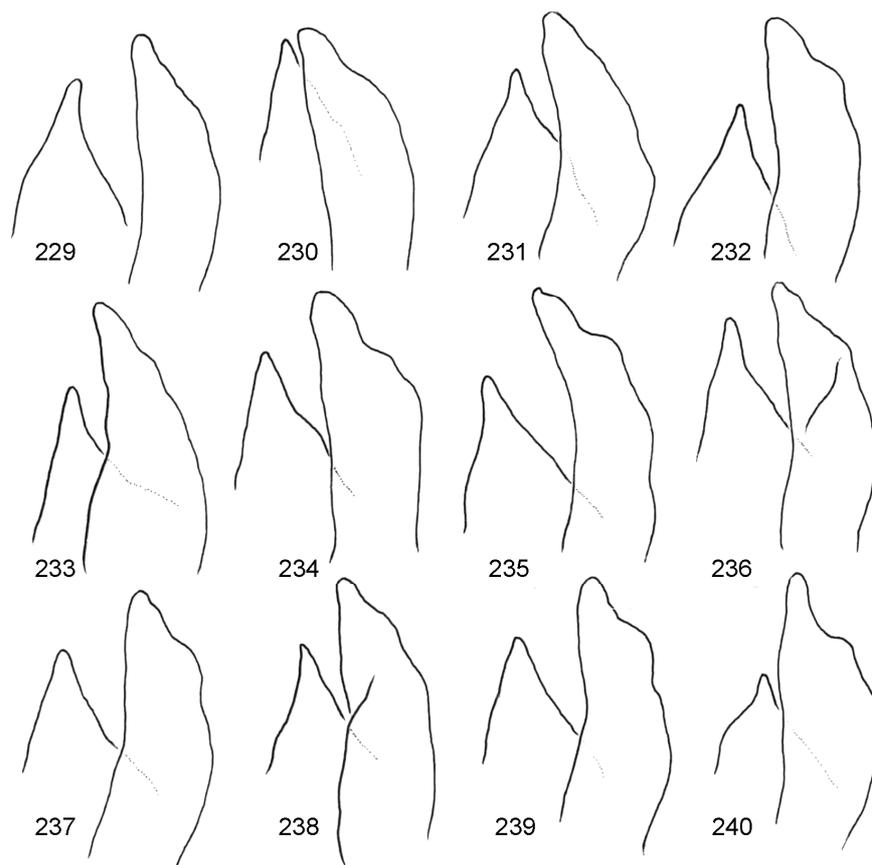
***Allogamus pohos* Oláh & Zamora-Muñoz sp. nov.**

(Figures 229–240, 241–242)

Diagnosis. Paraproctal basolateral accessory process on the superanal genital complex long tri-

angular. Most close to *A. mortoni* Navas but differs by having paraproctal accessory process slender, elongated triangular. Close also to *A. tuskes* sp. n. as well, but apex less pointed, apical third longer slender; apex almost reach the apex of the slender mesal cercal process. However, when the two apices compared it is important to realise that the mesal slender process of the cerci moves together with the dorsal branch of the paraproct and as a result its apex position depends on the

copulation dependent functional state of the superanal complex. Ventrolateral process on female tergite IX produced. The anterior apodemes on the vaginal sclerite complex short and wide without lateral wing; this lateral wing frequently visible on the anterior apodemes of *A. tuskes* representing the anterior end of the wing sclerite and fused to the lateral area of the anterior apodeme, this wing sclerite perform a dorsal stretching function to the membranous vagina.

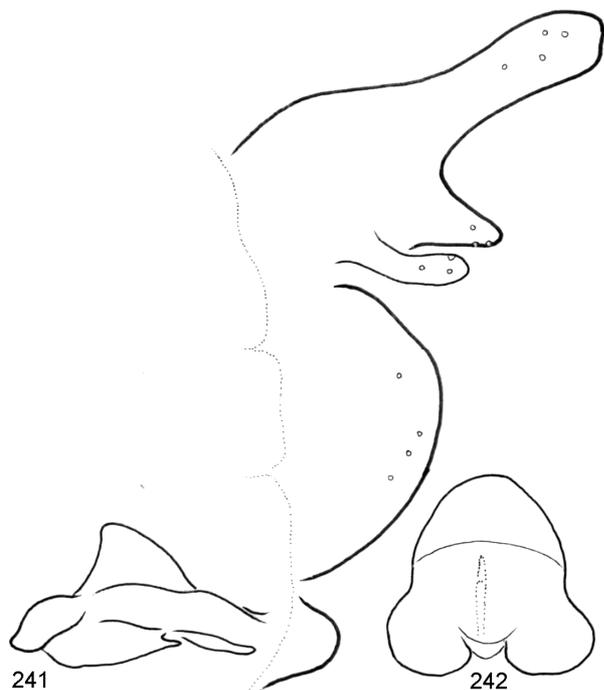


Figures 229–240. *Allogamus pohos* Oláh & Zamora-Muñoz sp. nov. Diverged structure matrix of the right accessory process on the basal triangle of the paraproct together with the apex of the right harpago in caudal view.

Material examined. Holotype. Spain, Jaén Province, Rio Guadalquivir, Nacimiento, N37° 54' 08", W2° 56' 16", 1378 m, 25.IX.2010, leg. C. ZAMORA-MUÑOZ, (1 male, DZFCUG). *Allotype.* Same as holotype, but 5.X.2013 (1 female, DZFCUG). *Paratypes.* Same as holotype (1 male, 1 female, DZFCUG; 1 male OPC). Same as holotype, but 5.X.2013 (7 males, 2 females,

DZFCUG; 7 males, 2 females; OPC). Same as holotype, but 6.X.2013 (6 males, 2 females, DZFCUG).

Description. Male (in alcohol). Both male and female have forewing membrane marbled and speckled, slightly irrorated. This forewing pattern variously developed at specimens, pharate or



Figures 241–242. *Allogamus pohos* Oláh & Zamora-Muñoz sp. nov. 241 = female genitalia in left lateral view with vaginal sclerite complex, 242 = dorsal profile of vaginal sclerite complex.

newly emerged specimens less or not patterned. Forewing length 20 mm. Head, thorax, and appendages are stramineous.

Male genitalia. Periphallic organs as described in the species complex diagnosis. Accessory process on the basal triangulum of the superanal complex elongated triangular.

Female genitalia. Ventrobasal setose process well developed. Anterior apodemes of the vaginal sclerite complex short and wide.

Etymology. Epithet *pohos* is from “*pohos*” bellied in Hungarian, refers to laterad rounded shape of the anterior apodemes of the vaginal sclerite complex.

***Allogamus tuskes* Oláh & Sáinz-Bariáin sp. nov.**

(Figures 243–254, 255–256)

Diagnosis. Paraproctal basolateral accessory process on the superanal genital complex short triangular with needle pointed apex. Most close to

A. kurtas sp. n. but differs by having paraproctal accessory process pointed, not blunt. *A. pohos* sp. n. has accessory process similarly narrowing, but not needle-like pointed and much longer. Ventrolateral process on female tergite IX is slender. The anterior apodemes on the vaginal sclerite complex with lateral wing that is the fused anterior end of the wing sclerite; however, its visibility unstable, depends on view angles.

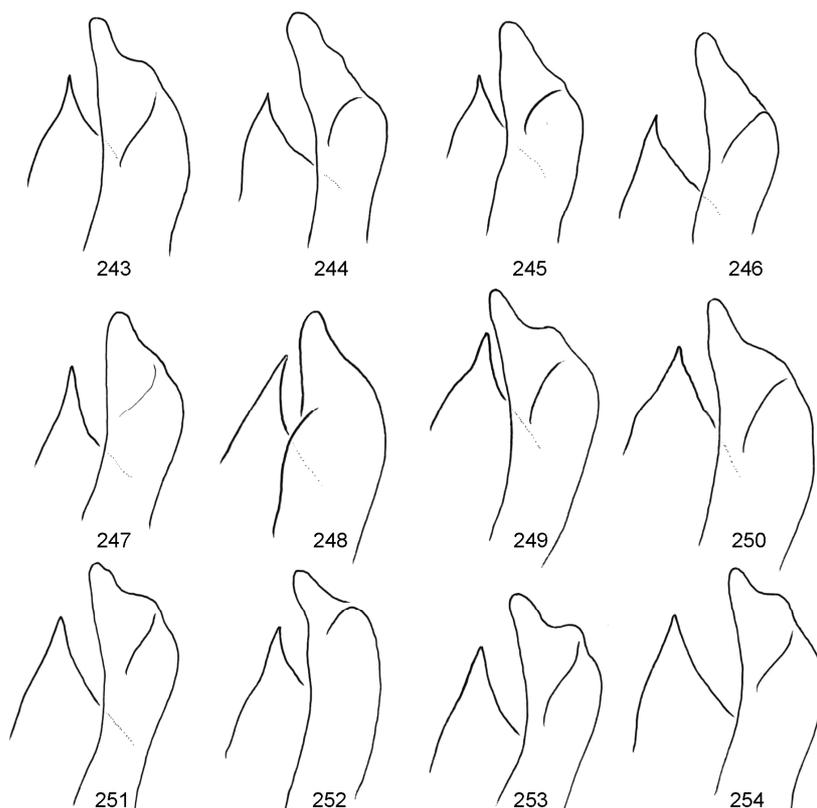
Material examined. *Holotype.* Spain, Granada Province, Cacín Basin, Arroyo Añales stream, Arenas del Rey, N36° 55' 05", W3° 53' 32", 970 m, 28.X.2007, leg. C. Zamora-Muñoz & M. Sáinz-Bariáin (1 male, DZFCUG). *Allotype.* Granada Province, Genil Basin, Rio Aguas Blancas, Quéntar, N37° 13' 17", W3° 25' 10", 1096 m, 21.X.1990, leg. C. Zamora-Muñoz (1 female, DZFCUG). *Paratypes.* Same as holotype (3 males, DZFCUG; 6 males, OPC). Granada Province, Genil Basin, Rio Maitena, Desembocadura, N37° 09' 07", W3° 24' 48", 1060 m, 15.X.2013, leg. M. Sáinz-Bariáin (2 males, DZFCUG; 2 males, OPC). Granada Province, Guadiana Menor, Jérez del Marquesado, Rio de Jérez, 1266 m, collected as larvae, 30.IV.2008 and reared in laboratory, leg. C. Zamora-Muñoz (6 males, 6 females; OPC).

Description. Male (in alcohol). Both male and female have forewing membrane marbled and speckled, slightly irrorated. This forewing pattern variously developed at specimens, pharate or newly emerged specimens less or not patterned at all. Forewing length 20 mm. Head, thorax, and appendages are stramineous.

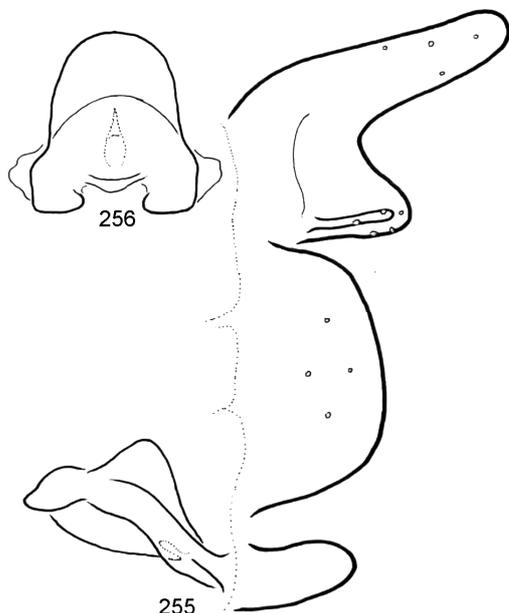
Male genitalia. Periphallic organs as described in the species complex diagnosis. Accessory process on the basal triangulum of the superanal complex triangular with pointed needle-shaped apex.

Female genitalia. Ventrobasal setose process very thin, slender. Anterior apodemes of the vaginal sclerite complex with lateral wings.

Etymology. Epithet *tuskes* is from “*tüskés*” spiny in Hungarian, refers to needle pointed tip of the accessory process of paraproct.



Figures 243–254. *Allogamus tuskes* Oláh & Sáinz-Bariáin sp. nov. Diverged structure matrix of the right accessory process on the basal triangle of the paraproct together with the apex of the right harpago in caudal view.



Figures 255–256. *Allogamus tuskes* Oláh & Sáinz-Bariáin sp. nov. 255 = female genitalia in left lateral view with vaginal sclerite complex, 256 = dorsal profile of vaginal sclerite complex.

***Allogamus corsicus* new species group**

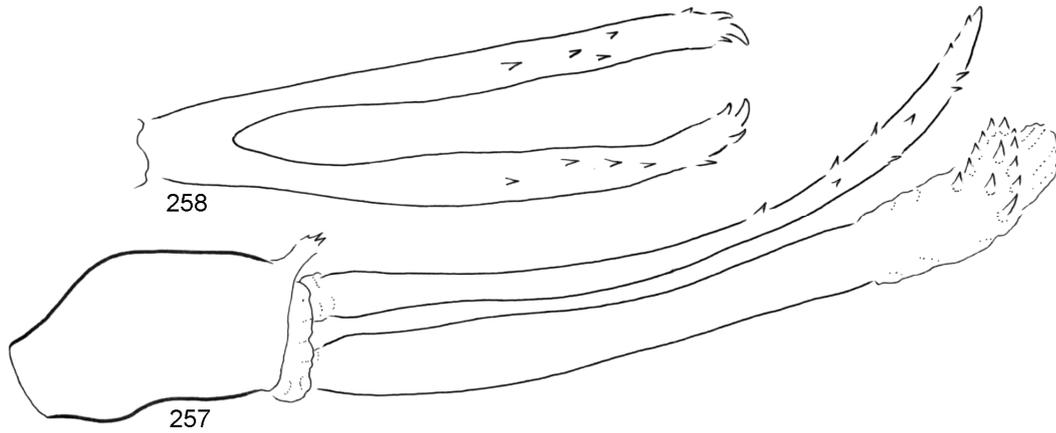
Light species. In this small species group the paired parameres fused basally and diverted apically. Modified female accessory duct lacking.

***Allogamus corsicus* Ris, 1897**

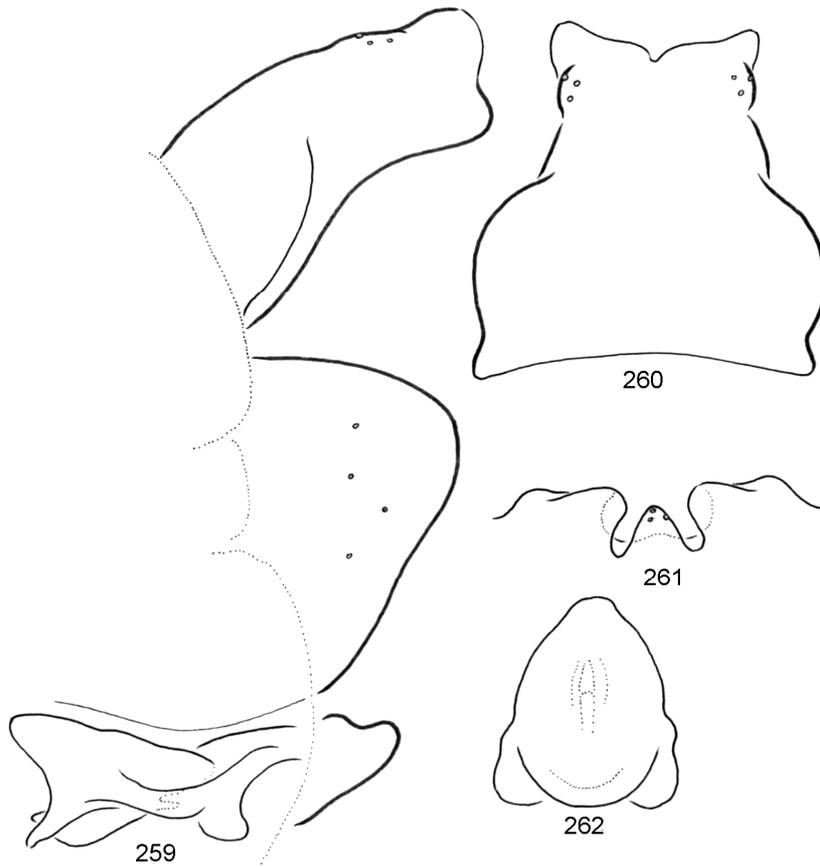
(Figures 257–258, 259–262)

Allogamus corsicus Ris, 1897. Sister-species status between *A. corsicus* and *A. illiesorum* has been reported with new drawings by Botosaneanu (2004: 173–175).

Material examined. France. Corse, Haute-Corse, Mausoleo, fiume Tartagine, 1100 m, N 42.4758° E8.9515°, 28.IX.2000 leg. B. Salmini (74 males, 15 females, CNSMB; 14 males, 7 females; OPC). Corse-Haute Corse, Mausoleo, fiume Tartagine, 1100 m, light trap, N42,4758° E8,9515°, 6.X.1999, leg. S. Benedetta (27 males, 2 females; CNSMB). Corse-Haute Corse, Mausoleo



Figures 257–258. *Allogamus corsicus* Ris, 1897. 257 = male, phallic organ in left lateral view, 258 = the basally fused parameres in dorsal view.



Figures 259–262. *Allogamus corsicus* Ris 1897. 259 = female genitalia in left lateral view with vaginal sclerite complex, 260 = anal tube in dorsal view, 261 = female vulvar scale (lower lip) in ventral view, 162 = dorsal profile of vaginal sclerite complex.

leo, fiume Tartagine, 1100 m, light trap, N 42,4758° E 8,9515°, 28.IX.2000, leg. S. Benedetta (88 males, 22 females; CNSMB). Corse-Haute Corse, Mausoleo, sorgente Tartagine, 1450 m, light trap, N42,4691° E 8,9293°, 6.X.1999, leg. S. Benedetta (11 males, 4 females; CNSMB). Corse-Haute Corse, Mausoleo, sorgente Tartagine, 1450 m, light trap, N42,4691° E 8,9293°, 28.IX.2000, leg. S. Benedetta (33 males, 21 females; CNSMB). Corse-Haute Corse, Mausoleo, P.te sul Melaja, 740 m, light trap, N42,5044° E 8,9777°, 5.X.2000, leg. S. Benedetta (38 males, 18 females; CNSMB). Corse-Haute Corse, Restonica, c/o camping, 650 m, N42,3015° E 9,1522°, 13.XI.2002, leg. L. Dapporto (3 males, 1 female; CNSMB). *Italy*. Sardegna-Sassari, torrente c/o sorg. Monte Limbara, 9.XII.2004, leg. O. Lodovici, P. Pantini (1 male, 2 females CNSMB; 1 male, 2 females; OPC).

Remarks. *A. corsicus* is distinguished from *A. illiesorum* by stable diverged fine structure of parameres and aedeagus head in male and by female tergum IX with rounded lateral shoulders.

***Allogamus illiesorum* Botosaneanu, 1980 stat. rev.**

(Figures 263–264, 265–268)

Allogamus illiesorum Botosaneanu, 1980: 76–77, 80.

Allogamus illiesorum Botosaneanu, 1980. Sister-species status between *A. corsicus* and *A. illiesorum* was confirmed with new drawings by Botosaneanu (2004:173–175).

Allogamus corsicus illiesorum Botosaneanu, 1980. Downgraded to subspecies status by Malicky (2005: 575), without any diagnosis.

Material examined. Italy. Sardegna-Nuoro, Desulo, Rio Melantiagu, N40.0383° E 9.2530°, 970 m, 7.XII.2004, light trap, leg. O. Lodovici & P. Pantini (2 females, CNSMB). Sardegna-Nuoro, Aritzo, 1100 m, 6.X.2002, light trap, leg. F. Fiumi (1 female, CNSMB; 6 males, 1 female; OPC). Sardegna-Nuoro, Fonni, Gennargentu, Rifugio, N40.0424° E 9.3005°, 1550 m, 24.X.2006, trap-pola a vino, leg. F. Fiori (2 males, 1 female, CNSMB). Sardegna-Cagliari, Maracalagonis, Rio

Dominigheddu sopra Geremeas, N39.2516° E 9.4266°, 380 m, 6.XII.2004, leg. O. Lodovici & P. Pantini (8 males, CNSMB; 2 males, 2 females; OPC).

Remarks. *A. illiesorum* is distinguished from *A. corsicus* by stable diverged fine structure of parameres and aedeagus head in male and by female tergum IX with pointed lateral shoulders.

***Allogamus uncatus* species group, rediagnosed**

Schmid (1951a) has separated the „uncatus group” within the *Halesus* genus with all the known species of the present *Allogamus* genus. This species group of the genus *Halesus* was later raised to genus level under the newly erected genus *Allogamus* (Schmid 1955) and the species were listed in the *uncatus* and *auricollis* groups without any group diagnoses. The *Allogamus uncatus* rediagnosed species group has basally fused and apically adhering parameres and a dorsal pair of heavily sclerotized rod-shaped apomorphic processes on the aedeagus. Female anal tube fused, compact.

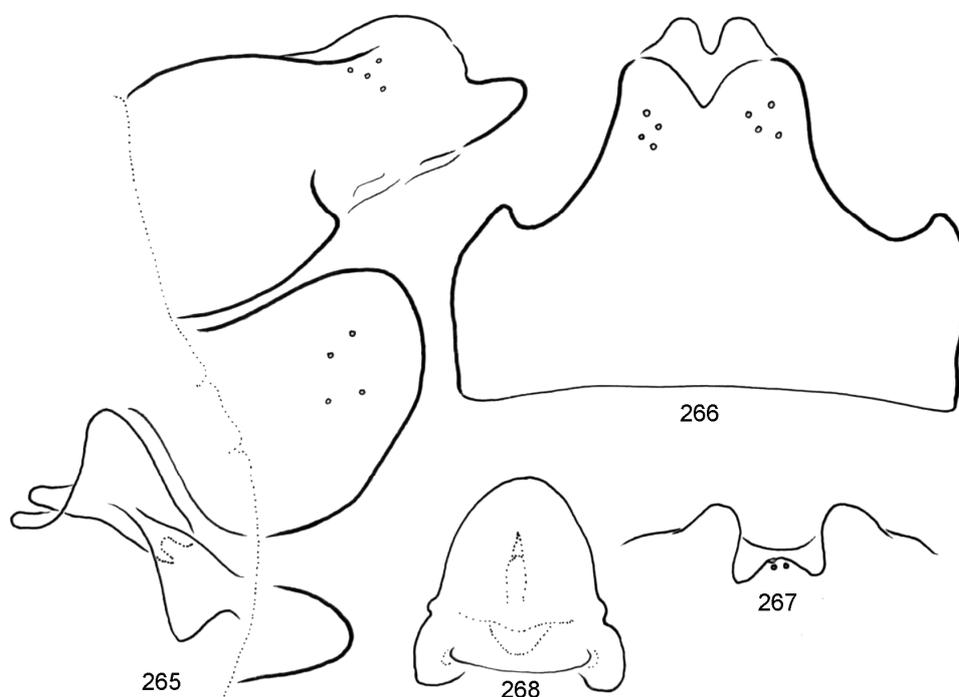
***Allogamus botosaneanui* Moretti, 1991**

(Figures 274, 294)

Material examined. Italy. Toscana-Firenze, Marradi, Monte Bruno, 700 m, N44.0259° E 11.6786°, 6.X.2002 leg. A. Usvelli (10 males, 1 female, CNSMB; 5 males, 4 females; OPC). Toscana-Firenze, Marradi, Monte Bruno, 700 m, N44.0259° E 11.6786°, 26.X.2002 leg. A. Usvelli (1 male; FMNHU). Toscana-Firenze, Marradi, Monte Bruno, 900 m, N 44,0259° E 11.6786°, 28. X.1999 leg. A. Usvelli (1 male; FMNHU). Toscana-Firenze, Marradi, Monte Bruno, rio Canneto, 700 m, N44,0259° E 11,6786°, 13.IX. 2003, leg. A. Usvelli (1 male; CNSMB). Toscana-Firenze, Marradi, Monte Bruno, rio Canneto, 700 m, light trap, N44,0259° E 11,6786°, 30.IX.2003, leg. A. Usvelli (2 males; CNSMB). Toscana-Firenze, Marradi, Monte Bruno, rio Canneto, 700 m, light trap, N44,0259° E 11,6786°, 21.X.2003, leg. A. Usvelli (1 Male; CNSMB). Liguria-Genova, Mezzanego, passo del Bocco, Parco Aveto - Foresta Demaniale Monte Zatta, 1000 m, light



Figures 263–264. *Allogamus illiesorum* Botosaneanu, 1980 stat. rev. 263 = male, phallic organ in left lateral view, 264 = the basally fused parameres in dorsal view.



Figures 265–268. *Allogamus illiesorum* Botosaneanu, 1980 stat. rev. 265 = female genitalia in left lateral view with vaginal sclerite complex, 266 = anal tube in dorsal view, 267 = female vulvar scale (lower lip) in ventral view, 268 = dorsal profile of vaginal sclerite complex.

trap, N44,4055° E9,4513°, 31.X.2009, leg. V. Raineri (2 males; CNSMB). Liguria-Genova, Mezzanego, passo del Bocco, Parco Aveto-Foresta Demaniale Monte Zatta, 1000 m, light trap, N 44,4055° E9,4513°, 2.X.2009, leg. V. Raineri (1 male; CNSMB). Liguria-Genova, Mezzanego,

passo del Bocco, Parco Aveto-Foresta Demaniale Monte Zatta, 1000 m, light trap, N44,4055° E 9,4513°, 30.X.2009, leg. O. Lodovici, V. Raineri, M. Valle (1 male, 1 female; CNSMB). Marche-Fermo, fiume Tenna, 6.XI.1977, leg. Romagnoli, D'Alessandro (1 male; n°1593 CC).

***Allogamus dacicus* (Schmid, 1951)**

(Figures 279, 285, 292)

Material examined. Romania. Argeş county, Făgăraş Mts, Căpătânenii Ungureni, small spring-lake 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 (1 male, 1 female; OPC). Braşov county, Făgăraş Mts, Dejani, right sidebrook of Dejani stream, N45°35.446' E24°56.348', 1755m, 30.VIII.2012 leg. T. Kovács, D. Murányi, J. Oláh (1 male, OPC).

***Allogamus fuesunae* Malicky, 2004**

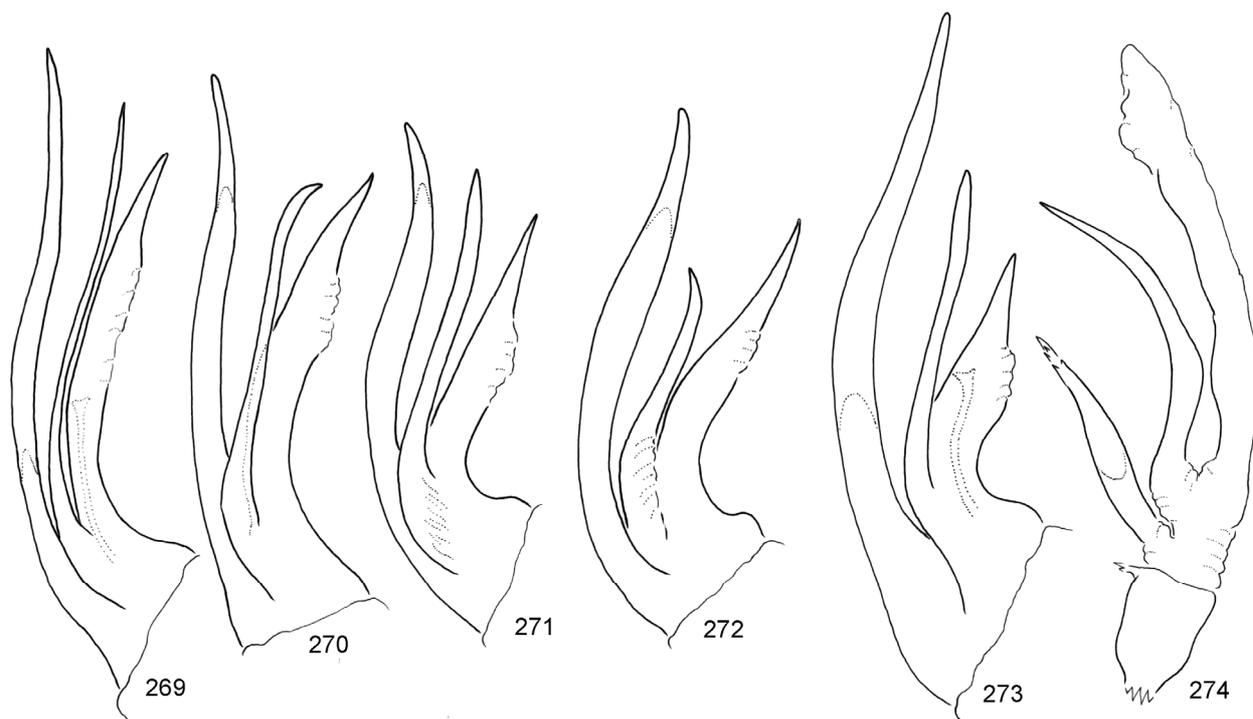
(Figure 275)

Material examined. Andorra. Vall de Ramsol, Riu dels Meners, 1966 m, N42°36.44777' E1°38.2116' 10.IX.1986, leg. M. González (1 male, OPC).

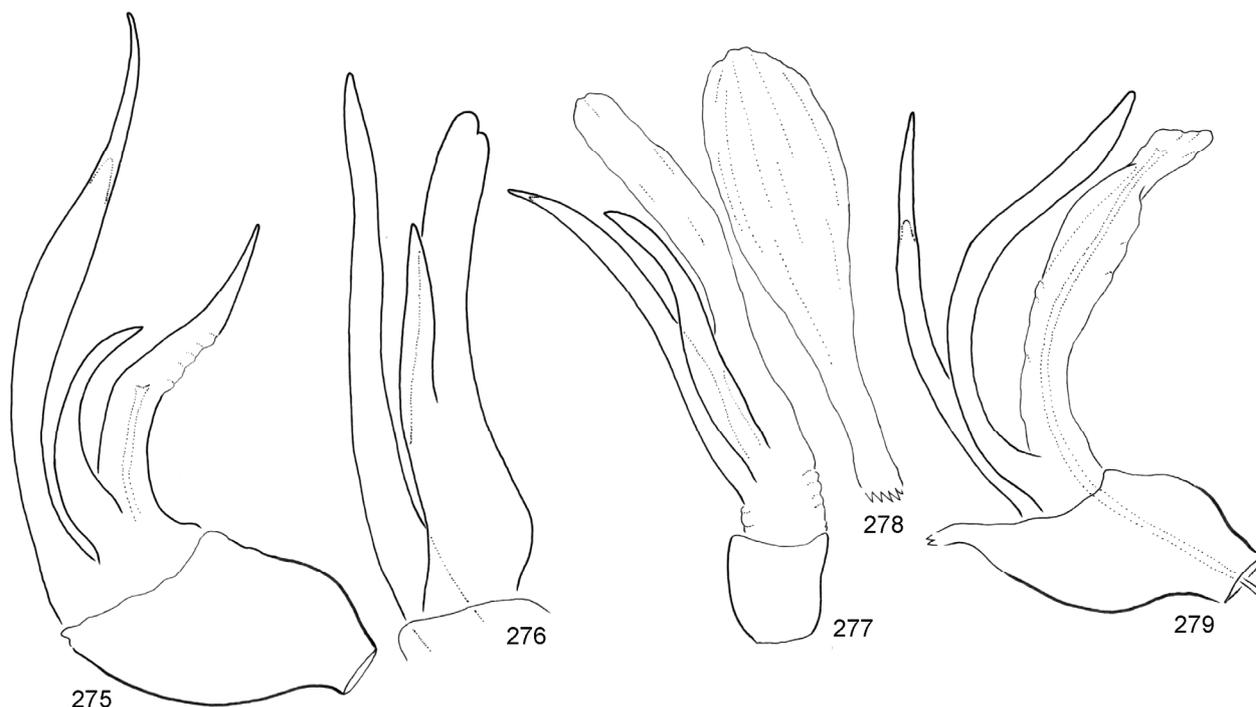
***Allogamus mendax* (McLachlan, 1876)**

(Figures 271, 282, 289)

Material examined. France. Alpes-de-Haute-Provence, Uvernet, Bachelard zone humide, 21. IX.2009, leg. G. Coppa, (2 males, 3 females; OPC). Italy. Piemonte-Cuneo, Crissolo, Pian del Re, fiume Po, N44.7005° E7.0934°, 2020 m, 22. IX.1998, light trap, leg. O. Lodovici (24 males, CNSMB; 12 males, OPC). Piemonte-Cuneo, Crissolo, Pian del Re, fiume Po, N44.7005° E7.0934°, 2020 m, 1.X.1997, light trap, leg. O. Lodovici (8 females, OPC). Piemonte-Torino, Prali, Ribba torrente Germanasca, 1800 m, N44,8575° E7,0372°, 29.IX.2002, leg. G.B. Delmastro, G Vincon (3 males, CNSMB). Valle d'Aosta-Aosta, Cogne, Parco Nazionale Gran Paradiso, 1500 m, 4.X. 1975, leg. M. Valle (1 female, CNSMB). Valle d'Aosta-Aosta, Valsavaranche, Pont, 1980 m, 27.VII.1980, leg. Faraci (4 males, CNHNV).



Figures 269–274. Male, phallic organ of the *Allogamus uncatu* species group in left lateral view. 269 = *Allogamus uncatu* (Brauer, 1857), 270 = *Allogamus stadleri* (Schmid, 1951), 271 = *Allogamus mendax* (McLachlan, 1876), 272 = *Allogamus pantinii* Oláh, Lodovici & Valle sp. nov. 273 = *Allogamus tomor* Oláh, 2012, 274 = *Allogamus botosaneanui* Moretti, 1991.



Figures 275–279. Male, phallic organ of the *Allogamus uncatus* species group in left lateral view. 275 = *Allogamus fuesunae* Malicky, 2004, 276 = *Allogamus periphetes* Malicky, 2004, 277 = *Allogamus starmachi* Szczesny, 1967, 278 = *Allogamus starmachi* Szczesny, 1967, membranous aedeagus in erected state, 279 = *Allogamus dacicus* (Schmid, 1951).

***Allogamus pantinii* Oláh, Lodovici & Valle sp. nov.**

(Figures 272, 283, 290, 295–303)

Diagnosis. This new species with almost unicolour light brown forewing without any distinct pattern is most close to *A. mendax*, but differs by having fused paramere with different arching and longer separated apical portion; paired dorsal branches of the aedeagus shorter and with distinctly laterad arching pattern; aedeagus apex turning slightly upward, not straight; dorsal profile of the vaginal sclerite complex different and the modified accessory duct shorter.

Material examined. *Holotype.* Italy, Piemonte-Cuneo, Briga Alta, affluente Torrente Negrone, N44.1109° E7.7252°, 1600 m, 10.X.2001, light trap, leg. Museo Caffi, Bergamo (1 male, CNS MB). *Allotype.* Same as holotype (1 female, CNS MB). *Paratype.* Same as holotype (1 male,

CNSMB; 1 male, OPC).

Description. Male (in alcohol). Both male and female have forewing membrane light brown without any distinct pattern. Forewing length 19 mm. Head, thorax, and appendages are stramineous.

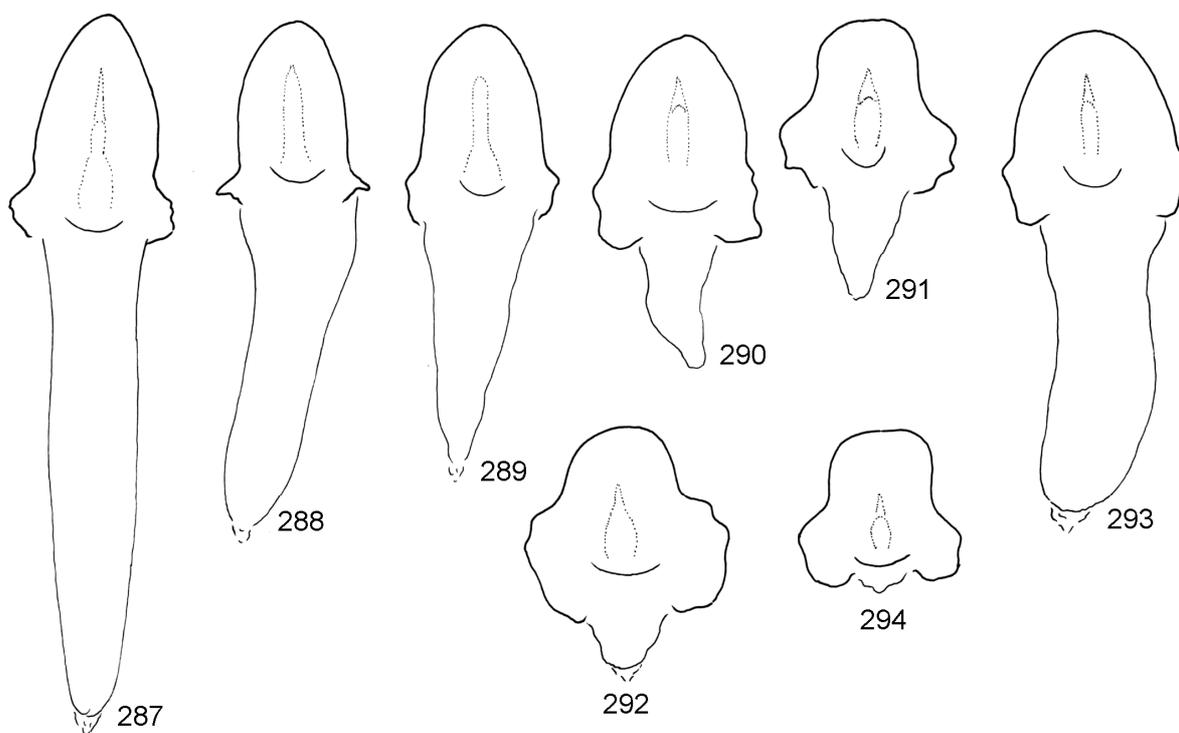
Male genitalia. Periphallic organs as described in the species group rediagnosis. The fused parameres of the phallic organ rather stout, the free bifid apex is short. Dorsal arms of aedeagus with laterad arching apical third. Sclerotized dorsum of aedeagus upward arching.

Female genitalia. Anal tube with rounded basal half in dorsal view. Anterior apodemes of vaginal sclerite complex slightly bilobed laterad, modified accessory duct medium long.

Etymology. The species is dedicated to our colleague and friend Paolo Pantini who, for several years, collaborates with us in collecting caddisflies.



Figures 280–286. Female, anal tube of the *Allogamus uncatus* species group in left lateral view. 280 = *Allogamus uncatus* (Brauer, 1857), 281 = *Allogamus stadleri* (Schmid, 1951), 282 = *Allogamus mendax* (McLachlan, 1876, 283 = *Allogamus pantinii* Oláh, Lodovici & Valle sp. nov. 284 = *Allogamus starmachi* Szczesny, 1967, 285 = *Allogamus dacicus* (Schmid, 1951), 286 = *Allogamus tomor* Oláh, 2012.



Figures 287–294. Female, dorsal profile of the vaginal sclerite complex with the modified accessory duct of the *Allogamus uncatus* species group. 287 = *Allogamus uncatus* (Brauer, 1857), 288 = *Allogamus stadleri* (Schmid, 1951), 289 = *Allogamus mendax* (McLachlan, 1876, 290 = *Allogamus pantinii* Oláh, Lodovici & Valle sp. nov., 291 = *Allogamus starmachi* SZCZESNY 1967, 292 = *Allogamus dacicus* (Schmid, 1951), 293 = *Allogamus tomor* Oláh 2012, 294 = *Allogamus botosaneanui* Moretti 1991.

***Allogamus periphetes* Malicky, 2004**

(Figure 276)

Remarks. Holotype described from Italy, Piemonte and the single paratype from Switzerland. Types were not available for study. In spite of repeated intense collecting effort new material is lacking. Phallic organ is redrawn from the original drawings and description.

***Allogamus stadleri* (Schmid, 1951)**

(Figures 270, 281, 288)

Material examined. France. Puy-de-Dôme, Mont-Dore, Val-de-Courre, 10.X.2007, leg. G. Coppa, (1 male, 2 females, OPC).

***Allogamus starmachi* Szczesny, 1967**

(Figures 277–278, 284, 291)

Allogamus starmachi Szczesny, 1967: 479.

Allogamus lazarei Szczesny, 1967: 480–481. (Botosaneanu & Malicky 1978: 353.)

Allogamus tatricus Szczesny, 1967: 481–482. (Botosaneanu & Malicky 1978: 353.)

Material examined. Poland. High Tatras, Hlindy Valley, 29.IX.1977 leg. Nagy (4 males, 1 female; OPC). High Tatras, above 1000 m, leg. B. Szczesny (11 males, 6 females, OPC).

***Allogamus tomor* Oláh, 2012**

(Figures 273, 286, 293)

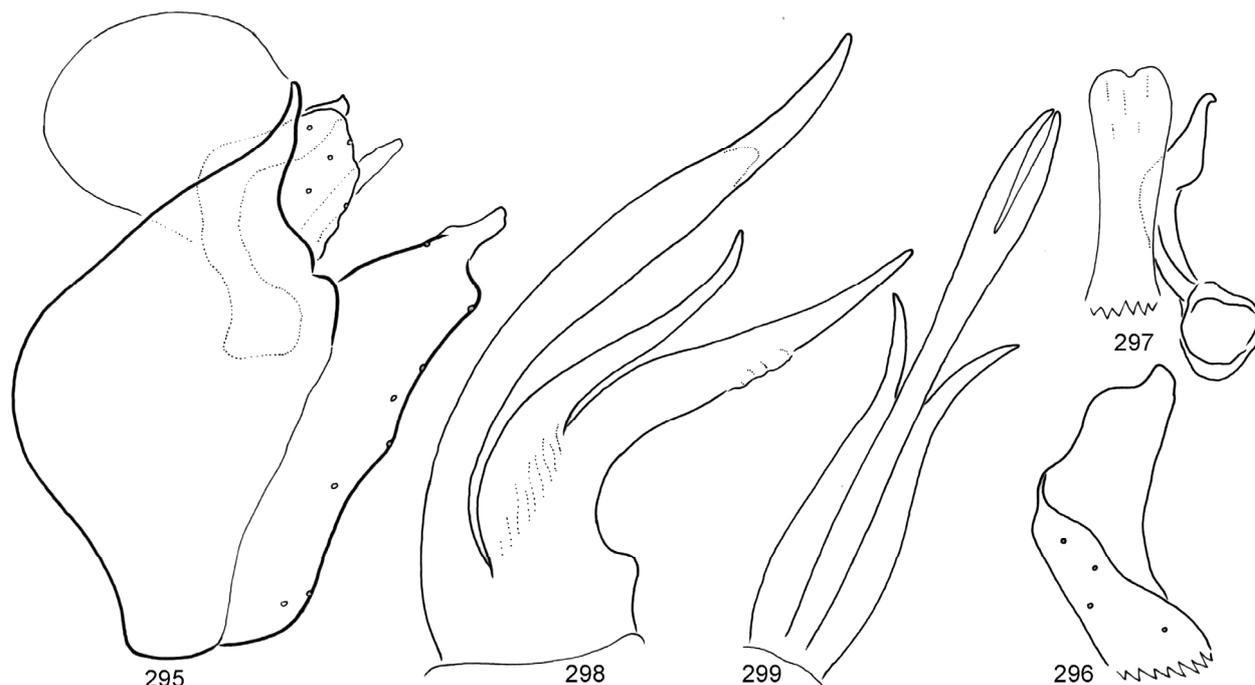
Material examined. Holotyp. Albania, Skrapar district, Ostrovicë Mts, Backë, Krojmbret Spring and its outlet brook NE of the village, N 40° 31.753' E20°25.152', 1965 m, 12.X.2012, leg. P. Juhász, T. Kovács, D. Murányi, G. Puskás (1 male, OPC). *Allotype.* Same as holotype (1 female, OPC).

***Allogamus uncatu* (Brauer, 1857)**

(Figures 269, 287)

Material examined. Albania. Bulqizë district, Çermenikë Mts, open brook beneath Mt. Kaptinë, N41°23.212' E20°17.506', 1610 m, 10.X.2012,

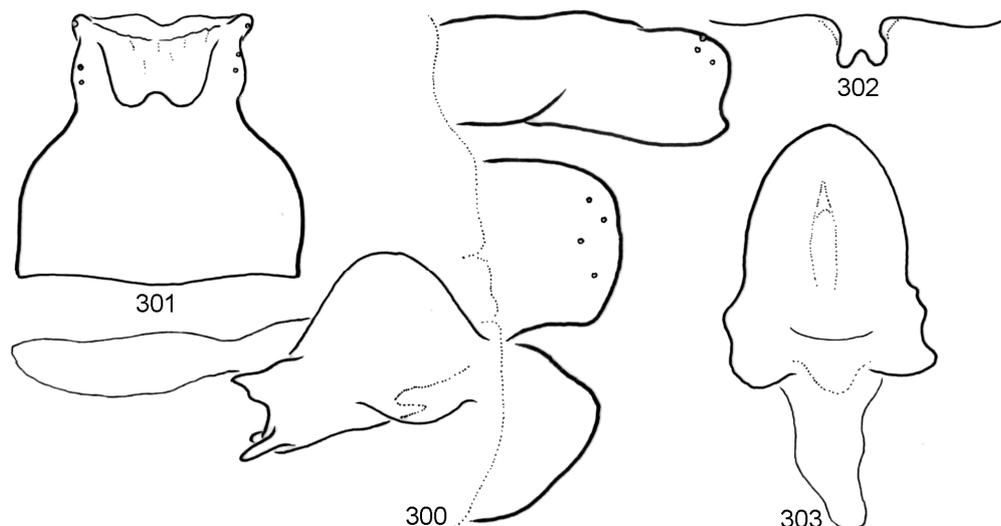
leg. P. Juhász, T. Kovács, D. Murányi, G. Puskás (1 male, OPC). Dibër district, Korab Mts, spring brooks of the bog beneath Mt. Korab, N41° 47.913' E20°33.561', 2165 m, 07.X.2012, leg. P. Juhász, T. Kovács, D. Murányi, G. Puskás (2 females, OPC). Korçë district, Vallamarë Mts, open brook above Lower Lenija Lake, SE of Vallamarë Peak, N40°47.374' E20°28.250', 2100 m, 10.X.2013, P. Juhász, T. Kovács, D. Murányi, G. Puskás, (16 males, 21 females; OPC). *Austria.* Gleinalpe, springs and springbrook 1.4 km above restaurant Krautwaschl, 1172 m, N47°12'15.31", E15°8' 22.14", 22.X.2012, leg. J. Oláh & I. Szivák (1 female; OPC). Koralpe, Handalm, springs near Gösler Hütte (Weinebene), 1784m, N46° 50'35.89", E15°01'18.53", 21.X.2012, leg. J. Oláh & I. Szivák (1 male, OPC). *Bulgaria.* Rila Mts., Borovets, Zavrachitsa hut, Prava Maritsa, 42°10' 04.9", 23°38'28.1", 2200 m, 05.X.2011, light, leg. Á. Ecsedi, T. Kovács, G. Puskás, (2♂, 14♀, OPC). Blagoevgrad province, Pirin Mts, Bansko, stream in pine shrub above the Vihren hut, N41°45.293' E23°24.933', 1995 m, 24.X.2013, leg. J. Kontschán, D. Murányi, T. Szederjesi, (3 females, HNHM). Pazardzhik province, Bataska planina, Batak, forest brook SW of the village, 1520 m, N41°53.412' E24°10.366', 25.X.2013, leg. J. Kontschán, D. Murányi, T. Szederjesi, (1 female; HNHM). *Czech Republic.* Western Bohemia, Krušné hory Mts, brook W of Jelení (NW of Nové Hamry), 900 m, N50°23'47" E12°39'00", 20.X.1993, P. Chvojka leg. (4 males, 4 females, NMPC). Northern Bohemia, Jizerské hory Mts, Ješkrabec brook, Rejdice, 670–750 m, N50°43'58" E15°21'55", 29.IX.2006, P. Chvojka leg. (2 males, 2 females, NMPC). Eastern Bohemia, Orlické hory Mts, brooks, NPR Trčkov reserve SE of Šerlich Mt., 800–850 m, N50°18'50" E16°24'55", 28.X.1994, P. Chvojka leg. (2 males, 3 females, NMPC). Eastern Bohemia, Orlické hory Mts, brook, NPR Bukačka reserve NW of Šerlich Mt., 930–970 m, N50°20'06" E16°22'31", 26.X.1994, P. Chvojka leg. (2 males, 3 females, NMPC). Northern Moravia, Králický Sněžník Mt., Morava river, 750–1100 m, N50°10'00" E16° 49'14", 19.X.2000, P. Chvojka leg. (5 males, 4 females, NMPC). *Italy.* Friuli Venezia Giulia-Udine, Raccolana, Sella Nevea, 1030 m, 23.IX.1995,



Figures 295–299. *Allogamus pantinii* Oláh, Lodovici & Valle sp. nov. Male, 295 = genitalia in left lateral view, 296 = apparent harpago in caudal view, 297 = right paraproct and subanal plate in caudal view, 298 = phallic organ in lateral view, 299 = fused paramere and the dorsal arms of aedeagus in dorsal view.

leg. Á. Uherkovich (1 male, 1 female; OPC). Friuli Venezia Giulia-Udine, Resia, Ucea, rio Bianco, N46.3108 E13.3575, 800 m, 20.IX.1996, leg. P. Pantini & M. Valle (10 males, 7 females, OPC). Friuli Venezia Giulia-Udine, Resia, Alpi Giulie, Sella Carnizza, spring area of River Ucea, N46°20'11.4" E13°19'46.8", 1105 m, 9.XI.2012, leg. T. Kovács & G. Magos (1 female, OPC). Lombardia-Bergamo, Foppolo, epirhitral-sopra il paese, 1700 m, 17.X.2004, leg. P. Pantini, S. Simula (5 females, CNSMB). Lombardia-Bergamo, Premolo, sorgenti torrente Parina, N 45.9240° E9.8246°, 1750 m, 1.X.2003, lighth trap, leg. O. Lodovici, M. Massaro (125 males, 30 females, CNSMB; 20 males, 10 females; OPC). Lombardia-Bergamo, Valbondione, Val Cerviera, 2050 m, light trap, N46,0562° E10,0598°, 2.IX.2003, leg. R. Calandrina (5 males; CNSMB). Lombardia-Bergamo, Parre, c/o Baita di Leten, 1765 m, light trap, N45,9242° E9,8541°, 29.IX.2004, leg. O. Lodovici, M. Massaro, M. Valle (15 males; CNSMB). Lombardia-Brescia, Vione, Val Cané, Rio Cortebona, 1800 m, light trap, N 46,2765° E10,4521°, 20.IX.1982, leg. A. Bona-

cina, M. Valle (1 male; CNSMB). Lombardia-Sondrio, Val Masino, La Rasica, 1150 m, N46.2638° E9.6774°, 21.X.2007, leg. M. Valle (13 males, 1 female; CNSMB). Lombardia-Sondrio, Valfurva, Passo Gavia, bordo lago, 2650 m, N46,3446° E10,4916°, 10.IX.2011, leg. W. Zucchelli (3 males; CNSMB). Veneto-Belluno, Feltre, sorgenti torrente Colmeda, N46.0764° E11.8709°, 750 m, 14.X.2002, lighth trap, leg. O. Lodovici, P. Pantini (2 males, OPC). Macedonia. Pelagonia region, Pelister Mts, Nižepole, open brook at the ski station, N40°58.787' E21°15.218', 1375m, 2.X.2013, leg. T. Kovács, D. Murányi, (19 males, 16 females; OPC). Montenegro. Prokletije Mts. Vusanje S 2 km, Oko spring and grlja stream, 1034 m, N42° 30.704' E19° 50.088', 12.X.2008, leg. L. Dányi Z. Fehér, J. Kontschán & D. Murányi (1 male, HNHM). Velika E, Murino 18 km toward Čakor-pass, N42° 40.001' E19° 59.800', 1554 m, 5.X.2005, leg. T. Deli, Z. Eröss, Z. Fehér & D. Murányi (1 male, HNHM). Vojnik Mts. Mokro, ca. 5 km S of Savnik, spring and its outlet brook in beech forest, 1062m, N42° 56.858' E19° 05.463', 9.X.2008, leg. L. Dányi, Z. Fehér,



Figures 300–303. *Allogamus pantinii* Oláh, Lodovici & Valle sp. nov. Female, 300 = genitalia in left lateral view with the vaginal sclerite complex, 301 = anal tube in dorsal view, 302 = vulvar scale (lower lip), 303 = dorsal profile of vaginal sclerite complex with the modified accessory duct.

J. Kontschán & D. Murányi (1 male, HNHM). Bjelasica Mts, Stevanovac, Lepešnica, 42°59' 28.2", 19°32'48.8", 1050 m, 04.11.2011, leg. KOVÁCS, T. MAGOS, G. (2 males, 2 females; OPC). *Poland*. Koscielsko, Chocholowska Valley, 15.IX.1989, leg S. Nógrádi & Á. Uherkovich (1 female; OPC). *Romania*. Transylvania, leg. L. Peregovits & L. Ronkay (1 male, OPC). *Slovakia*. Stratena valley, toward Hrabusice, 26.IX.1984, leg. Á. Uherkovich (2 females, OPC). Svermovo (=Telgárt), Hron Spring, 19.IX.1985, leg. Á. Uherkovich (8 males, OPC). Podbanske, 14.X. 1989, leg. S. Nógrádi & Á. Uherkovich (1 male, 1 female; OPC). Stratena, Dobsinska Ladova Jaskyna, 11.X.1987, leg. Á. Uherkovich (1 male, 1 female; OPC). Tatranska Polianka, 10.X.1987, leg. Á. Uherkovich (3 males, OPC). High Tatra, Hliny Valley, 29.IX.1977, leg. Nagy (8 males, females, OPC). Oravské Beskydy Mts, left tributary of Bystrá stream below Babia hora Mt., 1000–1300 m, N49°33'39" E19°30'47", 15.X. 1991, leg. P. Chvojka (13 males, 5 females, NMPC). High Tatras, brook W of Biely Váh river, 1320 m, N49°08'00" E20°01'00", 07.X. 1990, leg. P. Chvojka (3 males, 1 female, NMPC). High Tatras, Biely Váh river, 1280 m, N49°08' E20°01', 07.X.1990, leg. P. Chvojka (4 males, 2 females, NMPC). High Tatras, Biely Váh river,

1350 m + 1440 m, N49°08'10" E20°01'04", 07.X. 1990, leg. P. Chvojka (5 males, 4 females, NMPC). Belianske Tatras, Čierna voda stream S of Tatranská Kotlina, 860 m, N49°12'32" E20° 18'36", 13.X.1990, P. Chvojka leg. (4 males, 7 females, NMPC). Tributary River Lupcianska, Liptovska Luzna, Narodny Park Nizke Tatry, 830 m, 11.X.2008, leg. Richabun team (1 male, OPC). Rejdova (Sajóréde), Mlynná stream, below spring, at bridge, N48°46'16" E20°13'31" 1250 m, 3. X. 2013, singled leg. J. Oláh & J. Kecskés (2 females; OPC). Rejdova (Sajóréde), right tributary of Mlynná stream, at bridge, N48°46' 16" E20°13'31" 1250 m, 3. X. 2013, singled leg. J. Oláh & J. Kecskés (5 males, 4 females; OPC). Rejdova (Sajóréde), Slana (Sajó) stream, below spring, N48°47'6" E20°12'18", 1120 m, 3.X. 2013, singled leg. J. Oláh & J. Kecskés (2males, OPC). Rejdova (Sajóréde), right tributary of Slana (Sajó) stream, lower reach, N48°48'53" E20°15' 51" 680 m, 3. X. 2013, singled leg. J. Oláh & J. Kecskés (1 male, 4 females, OPC). Rejdova (Sajóréde), Slana (Sajó) stream, lower reach, N48°48'15" E20°13'33" 910 m, 3. X. 2013, singled leg. J. Oláh & J. Kecskés (1 male, OPC). Banskobystrický region, Poľana Mts, Hriňová, Bystré, spring brook of Bystrý Stream, N48° 37.569' E19°29.261', 1025 m 8.X.2013, singled

leg. J. OLÁH & L. SZÉL (2 males, OPC). *Slovenia*. Pohorje Mt., below Pesek, spring area of river Oplotnica, 1345 m, 46°28'24,8" 15°20'55,9", 8. XI.2012, leg. T. Kovács & G. Magos (1 female, OPC). *Ukraine*. Ukrainian Carpathians, Pod Dan-cerz, 11.IX. 1908 (2 males, K375, K376; NMPC). Ukrainian Carpathians, Forestanka, 12 IX. 1908 (1 male, K377; NMPC)

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