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Questions of Molecular Evolution of Pheromone Communication in Caddisflies and Lower Moths (Insecta: Trichoptera, Lepidoptera)

V. D. Ivanov and S. I. Melnitsky

Department of Entomology, St. Petersburg State University, St. Petersburg, Russia
e-mail: v--ivanov@yandex.ru

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Abstract—Recent GS-MS and GC-EAD studies of pheromone production and perception in caddisflies and lower moths have shown that these insects use a rather limited selection of volatiles as attractants. Most of them are alcohols and ketones, although the diversity of chemicals produced by sternal glands of abdominal segment V is much wider, especially in the lower Trichoptera. Sternal pheromone glands produce only short-chain polymers in all Amphiesmenoptera. These glands are part of the ground-plan for the related orders, Trichoptera and Lepidoptera, occurring in both sexes and producing similar but not identical sets of components in males and females. The presence of pheromone volatiles is shown to be restricted to the gland segments (Fig. 1), although some other short-chain polymers do occur in the head of females of *Molanna angustata* (Molannidae). The pheromone blends of lower Trichoptera (Glossosomatidae, Rhyacophilidae, and Philopotamidae) are multi-component and resemble plant volatiles in composition. A hypothesis of the origin of pheromone communication is proposed postulating basic resemblance of early pheromones and plant volatiles in variety and chemical composition. These pheromones were detected by non-specialized receptors of the amphiesmenopteran ancestor and served as guides for insect aggregation on plants as well as on shores of reservoirs, marking the places suitable for a wide variety of species. The primary aggregation function of pheromones was changed in more advanced communication systems to the species-specific signaling with sex-related asymmetry of signals, although the aggregation significance persisted in some species. Pheromone communication has disappeared in some most advanced lineages (e.g., Leptoceridae) with parallel reduction of glands, secretion, and antennal receptors. The pheromone composition does not show gradual divergent evolution in related species; instead, abrupt transformation of pheromone blends with persistence of major components in remote families seems to be the typical case.

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A pheromone is typically a mixture of compounds which includes the principal components prevailing by mass, and minor components. Each component of the pheromone blend may perform several functions (Jacobson, 1976). Pheromones of insects are detected by various specialized receptors which are often concentrated on the cephalic sensory appendages and other body parts (Ivanov, 1969, 2000; Elizarov, 1978).

Moths and butterflies (Lepidoptera) and caddisflies (Trichoptera) are two closely related orders which diverged from a common ancestor in the Mesozoic (Ivanov and Sukacheva, 2002; Kozlov et al., 2002) and are presently united in the superorder Amphiesmenoptera (Kristensen, 1997; Kristensen and Skalski, 1999). The phylogenies of the orders and relationships of the families have been quite reliably determined for caddisflies (Kjer et al, 2002; Ivanov and Sukacheva, 2002) and lower moths (Kristensen, 1984), whereas the family-level phylogenetic system of the higher lepidopterans is still far from being complete (Kozlov et al., 2002, etc.).

The studies of pheromones of Lepidoptera, and to a much lesser degree, Trichoptera have an extensive history. No less than 38% of all the studies of animal pheromones (Symonds and Elgar, 2008) are carried out on Lepidoptera but almost exclusively on the higher Ditrysia, whereas communication of more primitive families is more poorly studied (Kozlov et al., 1996). Pheromone compounds vary greatly in their chemical structure though the set of their functional types is limited; the best studied in Amphiesmenoptera are attractant pheromones, most of which belong to the classes of alcohols, aldehydes, ketones, and fatty acid esters and are highly specific. The di-

versity of chemical communication signals increases due to isomerism; precise recognition of species is sometimes based on proportions of specific isomers and the ratio of the major and minor components of the pheromone blends (Wilson and Bossert, 1963; Skirkevicius, 1986, 1988; Löfstedt et al., 1994, Billen and Morgan, 1998; Ayasse et al., 2001; El-Sayed, 2013).

The chemical structure of the sternal pheromone gland products has been determined for a number of caddisfly species (Duffield et al., 1977; Ansteeg and Dettner, 1991; Löfstedt et al., 1994; Bjostad et al., 1996; Bergmann et al., 2001, 2002, 2004; Bergmann, 2002) and several species of primitive moths of the families Eriocraniidae and Nepticulidae (Toth et al., 1995; Zhu et al., 1995; Kozlov et al., 1996). Such information is available for more than 1500 species of Lepidoptera, mostly the higher groups (Byer, 2006), and new data are added every month. It has been shown that the pheromones of caddisflies and lower moths are similar in the chemical composition and are produced by the sternal glands in the middle part of the abdomen; by contrast, the pheromones of the higher Ditrysia are chemically different and are secreted by the tergal glands on the tip of the abdomen (Löfstedt, 1991; Kozlov et al., 1996). Therefore, we will consider the factual data and evolutionary trends in caddisflies and non-ditrysian moths, using the data on Ditrysia only for comparison. The main goal of this paper is to review the diversity of pheromones in these groups and to outline the possible ways of their evolution.

In our analysis we used, first, the data from scientific publications and open access databases on insect pheromones (El-Sayed, 2013) and, second, our original data obtained by a variety of methods, including gas chromatography with mass spectrometry and electroantennographic detection (GC-MS, GC-EAD), field experiments with pheromones, and an extensive set of microscopic techniques. The methods used were described in detail in the previous publications (Ivanov and Melnitsky, 2002, 2011; Ivanov et al., 2008; Löfstedt et al., 2008). The morphology of the sternal pheromone glands was studied in more than 400 species of caddisflies and primitive moths (Ivanov and Melnitsky, 1999, 2002, and unpublished data).

The structure and topography of sensilla on the cephalic sensory appendages were studied in more than 80 species of caddisflies (Melnitsky and Ivanov, 2010; Ivanov and Melnitsky, 2011). Comparative analysis of the gland products and the structure of antennal and palpal receptors has shown that structural changes in the signal and receptor components of the chemical communication system of caddisflies are weakly interdependent. If certain volatiles are not synthesized in one sex (e.g., in males of *Molanna angustata* Curtis and other Molannidae), individuals of the other sex lack the corresponding specialized sensilla on their antennae. Complete reduction of the sternal glands in Leptoceridae (Ivanov and Melnitsky, 2011) is correlated with disappearance of the antennal chemoreceptors. However, in most cases, changes in the pheromone composition in different species are not accompanied by considerable changes in the antennal sensory apparatus.

The Diversity of Sternal Gland Products in Amphiesmenoptera

The chemical composition of the pheromone gland products in Trichoptera is unevenly studied: such data are available for 4 species from 3 genera of Psychomyiidae, 4 species from 3 genera of Polycentropodidae, 3 species from 2 genera of Hydropsychidae, 3 species from 2 genera of Philopotamidae, 3 species from 1 genus of Rhyacophilidae, 2 species from 1 genus of Glossosomatidae, 3 species from 2 genera of Phryganeidae, 10 species from 7 genera of Limnephilidae, and for one species from each of the families Hydroptilidae, Goeridae, Molannidae, and Odontoceridae (Duffield et al., 1977; Ansteeg and Dettner, 1991; Löfstedt et al., 1994; Bjostad et al., 1996; Bergmann et al., 2001, 2002, 2004; our unpublished data). Among the lower moths, data on the pheromone composition are available for the families Eriocraniidae (Zhu et al., 1995; Kozlov et al., 1996) and Nepticulidae (Toth et al., 1995). It should be noted that researchers usually provide data only on the acting components available for analysis or on the most abundantly released compounds, but do not describe all the secretions of the pheromone glands.

The pheromones of most caddisfly species studied in this respect are short-chain (with less than 10 carbon atoms) alcohols or ketones (Löfstedt et al., 1994, 2008; Bjostad et al., 1996; Bergmann et al., 2001, 2002; Ivanov et al., 2008; Djernaes and Sperling, 2012). The pheromone gland secretion can also include organic acids, aldehydes, and some other classes of organic compounds but their exact functions are still to be determined. The primitive Lepidoptera also

use alcohols or ketones as pheromones; in particular, the pheromones of the three studied species of the family Nepticulidae are alcohols (Toth et al., 1995), whereas the pheromone blends of the representatives of Eriocraniidae contain both alcohols and ketones (Zhu et al., 1995; Kozlov et al., 1996). Long-chain organic compounds are used as a source for pheromone synthesis by higher lepidopterans (Roelofs and Bjostad, 1984; Symonds, 2008); they also seem to be the precursors of alcohols, ketones, and other compounds secreted by caddisflies and lower moths, but reliable data on the biosynthesis of short-chain pheromones are lacking.

In a detailed recent study of pheromone communication in the caddisfly *Molanna angustata* Curtis (Löfstedt et al., 2008), its sex attractants were identified as nonan-2-ol (the main component) and heptan-2-ol, although the corresponding ketones were also present in the glands. Additional, previously unpublished data on the pheromone gland products of this species are given in Fig. 1. These data show that short-chain alcohols and ketones are synthesized only in the sternal pheromone glands of the females, whereas the males have neither such compounds nor glands. The females do not possess any other source of attractant pheromones besides the sternal glands, but their cephalic tissues can produce some other volatiles (heptanal, nonanal, and 3-hydroxy-2-butanol); functions of them have not been studied in this species. The alcohols and ketones synthesized by the pheromone glands of *M. angustata* females equally affect the antennal receptors of the males (Fig. 2), but in the experiments the mixture of alcohols and ketones was found to be less attractive than the blend including only alcohols. In dense populations, caddisflies may accidentally get into the control traps as the result of their seeking behavior; the presence of ketones was found to decrease the frequency of such captures (i.e., ketones acted as repellents), but statistical demonstration of this phenomenon requires additional experiments.

Analysis of the chemical structure of pheromones in representatives of the family Limnephilidae has shown that this group of caddisflies is distinguished by the presence of alcohols and ketones with the methyl radical at the 3rd, 4th or 6th carbon atom. The data of behavioral and electro-physiological experiments indicate that the role of sex attractants in Limnephilidae belongs to the methylated components of the pheromone blends. In particular, the female secretions of the well-studied species *Anabolia laevis* Zett. (Ivanov et al., 2000, 2008; Bergmann, 2002) contain (3S,4S)-4-methylhexan-3-ol, 3-hydroxybutan-2-one, (3R,4S)-4-methylheptan-3-ol, 6-nonen-2-one, and 6-nonen-2-ol. Two methylated components, (3S,4S)-4-methylhexan-3-ol and (3R,4S)-4-methylheptan-3-ol, act as distant attractants while other compounds induce no behavioral response. Moreover, the complete blend including all the five sternal gland products considerably decreased the attractiveness of pheromone traps for males (Ivanov et al., 2008). Thus, not all pheromone gland secretions showing olfactory activity are attractants; instead, these compounds may have different biological effects. The secretions of *Chaetopteryx villosa* (F.) (Limnephilidae) were found to contain both saturated and unsaturated methylated derivatives of butan-2-one, which had been previously recorded in other members of the family but not in this particular species (Bergmann, 2002), and also derivatives of hexan-3-one and heptan-3-one which act as sex attractants in other representatives of Limnephilidae. The chemical information in caddisflies, even in the evolutionarily advanced families, seems to be encoded by a small set of components.

The products of the sternal pheromone glands of caddisflies may include dozens of components. This situation is observed, for example, in the females of *Agapetus fuscipes* Curtis (Glossosomatidae); the antennae of the males respond to 12 of these components (Fig. 3). Unfortunately, not all of the compounds produced by the females can be reliably identified. According to our data, such diversity of the products is also characteristic of some other species, including relatively primitive ones, such as *Rhyacophila nubila* Zett., *Rh. fasciata* Hag. (Rhyacophilidae), *Hydroptila forcipata* (Eaton) (Hydroptilidae), *Philopotamus montanus* Don., and *Wormaldia* spp. (Philopotamidae), and advanced ones, such as representatives of the family Limnephilidae. In general, diversity of the products of synthesis is very typical for caddisflies, especially in more primitive families.

It has been known for a long time that as a rule, caddisflies of both sexes possess sternal glands but their secretions are different (Ansteeg and Dettner, 1991; Löfstedt et al., 1994). However, the secretions of both sexes may also be similar to some extent, for example, in caddisflies of the family Hydropsychidae (Löfstedt et al., 1994). According to our data, the blend produced by the male of *Psychomyia pusilla* (F.) (Psychomyiidae) included 12 components, and that produced by the female, 9 components. Some of the

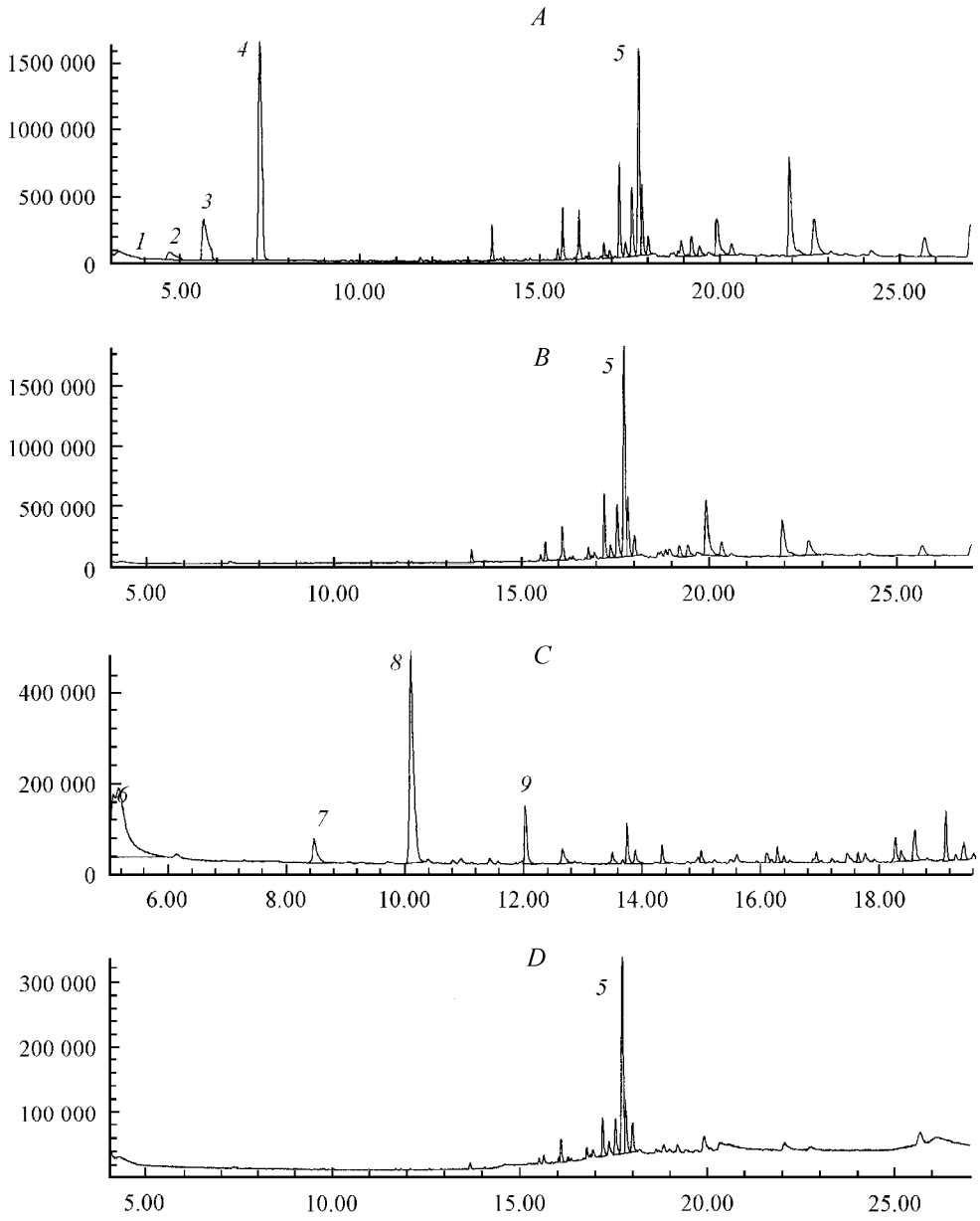

Fig. 1. Results of analysis of extracts of different body parts of *Molanna angustata* Curt. by the GC-MS method (gas chromatography with mass spectrometry). Abscissa: retention time (min.); ordinate: total ion yield (arbitrary units). The peaks correspond to individual components of the volatile mixture. Body parts: (*A*) abdominal sternites IV and V of females; (*B*) abdominal segments VII, VIII, and IX of females; (*C*) heads of females; (*D*) abdominal sternites IV and V of males. Components: (*1*) heptan-2-one; (*2*) (S)heptan-2-ol; (*3*) nonan-2-one; (*4*) (S)nonan-2-ol; (*5*) fatty acid mixture; (*6*) chlorinated organic compounds (contamination); (*7*) heptanal; (*8*) 3-hydroxy-2-butanone; (*9*) nonanal.

alcohols and ketones were identical in the pheromone blends of the two sexes: the gland extract of the male was found to contain 3-penten-2-ol, methyl-2-hexanol, and heptan-2-one, and that of the female, methyl-2-hexanol and heptan-2-one. Similar components were found in females of different species of the genus *Tinodes*: the gland secretions of *T. pallidulus* McL. and *T. rostocki* McL. contained heptan-2-one, nonan-2-one, nonanal (*T. pallidulus*), and menthone (*T. rostocki*), but it was heptan-2-one that acted as an attractant in both species (Bergmann, 2002). The antennae of the males of *Tinodes waeneri* (L.), studied by us, responded to three components produced by the female glands: heptan-2-one, (E)-3-nonen-2-one, and nonan-2-one. The main component present with the highest concentration in the females of this species, heptan-2-one, was also found in the males though in a lower concentration. Thus, production of heptan-2-one is not

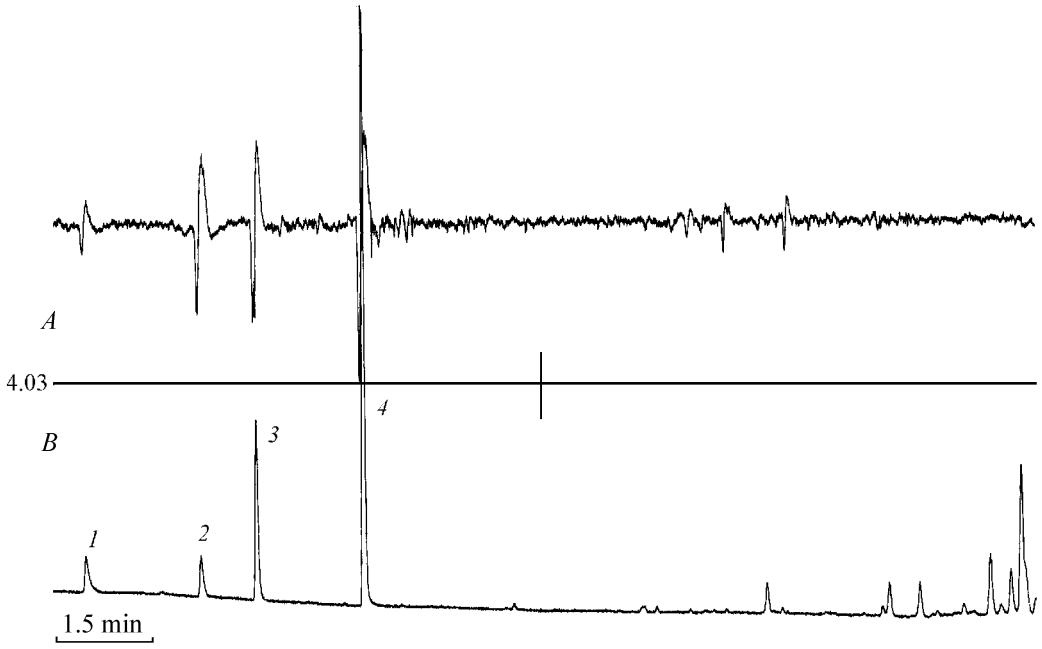

Fig. 2. Results of the experiment with the antenna of the male of *Molanna angustata* Curt. by the GC-EAD method (gas chromatography with electroantennographic detection). (*A*) electric activity of the antenna (the receptor potential) in response to the volatile components of the extract of the female sternal glands; (*B*) chromatogram of this extract. Components (*1–4*) are the same as in Fig. 1 (modified after Löfstedt et al., 2008).

only typical for the females of all the studied species of this genus but also possible in the males. The only olfactory active component in the females of *Hydropsyche angustipennis* (Curt.) (Hydropsychidae) is nonan-2-one; the males also produce this component, in greater quantities than do females, and four more types of ketones (Löfstedt et al., 1994). Similarly, according to our data, nonan-2-one is the main pheromone component of both sexes of *Hydropsyche siltalai* Döhler, its concentration being much higher in the male than in the female. The antennae of males of *Agapetus fuscipes* respond to a variety of compounds produced by the females (Fig. 3), of which nonan-2-one and nonan-2-ol were also identified by us in the gland extract of the males. Similar products were also found in the pheromone glands of both sexes of *Limnephilus politus* McL. In these cases, realization of species-specific behavior may depend on the ratio of compounds in the pheromone blend and on the presence of additional components which are not necessarily detected by antennal receptors. Contrary to what was observed in species of the families Psychomyiidae and Hydropsychidae, we did not find any similar components in the sternal gland secretion of conspecific males and females of such representatives of Annulipalpia as *Polycentropus flavomaculatus* (Pict.) (Polycentropodidae) and *Wormaldia subnigra* McL. (Philopotamidae).

In the above cases, the attractants were saturated compounds; however, in a number of families of Annulipalpia (Philopotamidae, Hydropsychidae, Polycentropodidae, and Psychomyiidae) and Integripalpia (Limnephilidae) the gland secretion includes unsaturated compounds as well. Such compounds are present as minor admixtures in most species but they prevail in some representatives of Philopotamidae, in particular *Philopotamus montanus*. Unsaturated compounds form the main components of the pheromone blends of lower moths of the family Eriocraniidae; comparison with caddisflies shows this family to be the most similar to Philopotamidae, both in the pheromone composition and in the gland structure.

The Glands Producing Pheromones

Sex pheromones in caddisflies and primitive moths are produced by specialized sternal glands with ducts open in the anterolateral parts of abdominal sternite V while their reservoirs may extend into segment IV. The morphology of sternal pheromone glands and associated cuticular structures has been studied in sufficient detail for representatives of 55 families, including some fossil caddisfly taxa (Ivanov and Melnitsky, 1999, 2002, 2013a; Melnitsky, 2004; Djernes and Sperling, 2012). The cytological structure of pheromone glands of caddisflies and primitive moths has been studied in more than 20 species (Melnitsky,

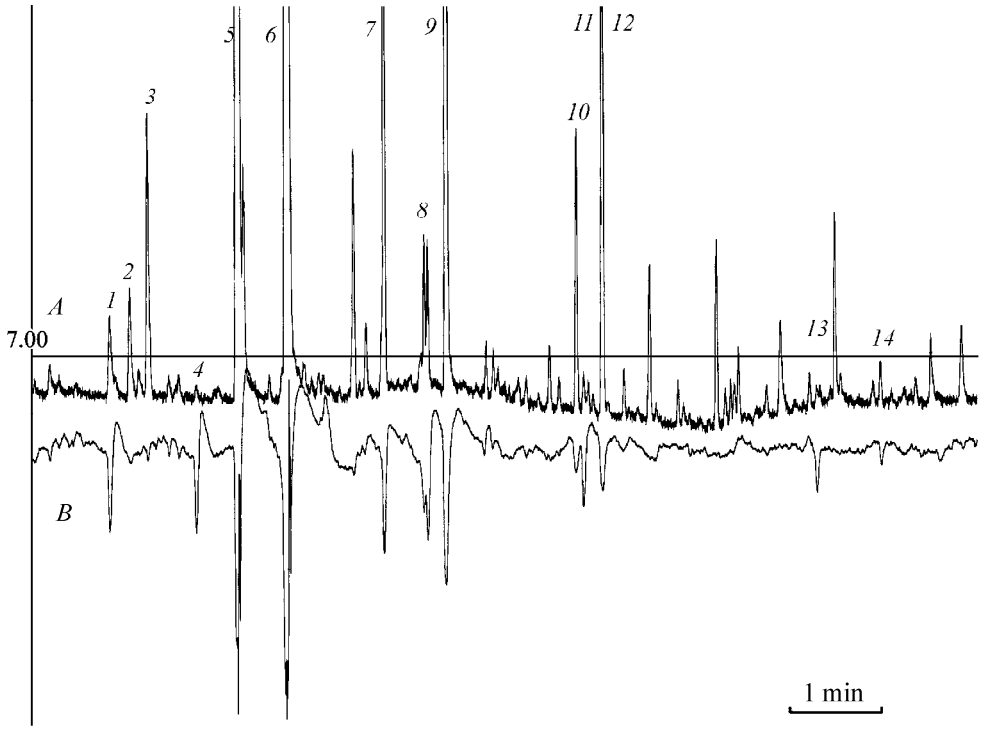

Fig. 3. Results of the experiment with the antenna of the male of *Agapetus fuscipes* Curt. by the GC-EAD method (gas chromatography with electroantennographic detection) and the extract of the female sternal glands. (*A*) chromatogram; (*B*) activity of the antenna. Components: (*1*, *8–14*) unidentified components [(*8*) possibly an unsaturated derivative of nonanol; (*9*) an ester; (*10*) a mixture of cyclic molecules]; (*2*) 3-methyl-2-butanol; (*3*) heptan-2-ol; (*4*) hexanol; (*5*) nonan-2-one; (*6*) hexenyl ester of butane acid; (*7*) nonal-2-ol.

2001; Hashimoto and Kobayashi, 2009; Melnitsky and Deev, 2009; Melnitsky and Ivanov, 2011; Djernes and Sperling, 2011). By their origin, the sternal glands are sac-like invaginations of the cuticle; their secretory parts consist of hypodermal (integumental) cells which form exocrine glands. Comparative studies have shown that the exocrine glands in insects have a uniform structure (Nasonov, 1901; Noirot and Quennedey, 1974; Quennedey, 1984, 1991, 1998, 2000; Noirot, 1995). They are based on integumental hypoderm, both parts of which, the epithelium and its cuticular derivatives, have been transformed into a specialized organ. In the simplest glands (type C1), the secretory cells are slightly modified epithelial cells; in more complex glands (type C2), the cells lie within the hypoderm layer but lack direct contact with the exterior, their products being released via the hemolymph or other cells. The most complex glands (type C3) consist of three types of cells forming a multilayered structure; the products are directed into the gland reservoir by canals formed by specialized cells. The largest cells (the terminal secretory cells) in type C3 glands have cavities with numerous microvilli where the components of the pheromone blend seem to accumulate. It is possible that pheromone synthesis is partly accomplished in the cell cavity. Cells of the second type, the canal ones, play an accessory role, forming a thin canal for releasing the secretion from the cavity and an additional sheath of this canal. The cuticular reservoir is formed by the third type of cells, namely unspecialized hypodermal cells. The sternal glands of Amphiesmenoptera belong to type C3 (Melnitsky and Deev, 2009). In addition, the glands may have muscles of their own, which are usually associated with the efferent ducts (Djernes and Sperling, 2011), whereas in species of the families Phryganeidae (Ivanov and Melnitsky, 2002; Melnitsky et al., 2011) and Stenopsychidae (Hashimoto and Kobayashi, 2009) the muscle fibers lie below the terminal secretory cells.

Four types of sternal pheromone glands are present in Amphiesmenoptera: tubular (the first type), saccular (the second type), reniform (the third type), and fenestrated (the fourth type) (Ivanov and Melnitsky, 1999). Glands of the second type have been found only in Trichoptera, in particular, in many evolutionary lineages of the suborder Integripalpia. The reniform glands also occur only in caddisflies, namely, some Limnephiloidea (Ivanov and Melnitsky, 2002). The

higher lepidopterans possess terminal glands on the dorsal surface of the last abdominal segments (Löfstedt, 1991).

The Functions of the Gland Products

The results of chemical analysis of the pheromone gland secretions give no idea of the biological role of the products, and should be therefore supplemented by studies of their effects on the living insects. In the literature there are data on pheromone communication in 13 species from 6 families of caddisflies, based on experiments with pheromone traps (Löfstedt et al., 1994, 1998; Bjostad et al., 1996; Bergmann et al., 2001, 2002; Ivanov et al., 2008). Among the lower moths, there are reliable data for some species of Eriocraniidae (Zhu et al., 1995; Kozlov et al., 1996). In all these cases, the goal of the experiments was to demonstrate distant attraction of males by the sternal gland secretions of females. At the same time, despite the use of standard techniques and the confirmed presence of pheromone glands, pheromone communication could not be experimentally demonstrated in a number of species of caddisflies and primitive moths (Resh et al., 1987; Solem and Petersson, 1987; Löfstedt et al., 1994; Kozlov and Zvereva, 1999; our unpublished data). It can therefore be assumed that caddisflies and primitive moths may possess some still unknown factors modifying the attractiveness of mates (Ivanov and Melnitsky, 2002), or that they may have some special pheromone glands not homologous to those on abdominal sternite V.

One of the little discussed functions of the sternal glands is signaling aimed not at attracting the sexual partner (the typical role of a distant sex attractant) but at aggregation of conspecific individuals in certain parts of the landscape. The gland secretion in this case acts as an aggregation pheromone. According to our observations, aggregation of adults occurs already in representatives of relatively primitive caddisfly families: Philopotamidae, Rhyacophilidae, Glossosomatidae, and Psychomyiidae. Aggregation was also described in the evolutionarily advanced families Hydropsychidae (Ivanov, 1985; Löfstedt et al., 1994; Ivanov et al., 1996) and Leptoceridae (Solem, 1978); chemical stimuli playing the main role in the former family, and visual ones, in the latter. Aggregations of caddisflies may be quite loose, with adults concentrating in a certain area, usually in the crowns of one or several neighboring trees, and being absent within many hundreds of meters outside this limited territory. We observed such groups, for example, in *Agapetus ochripes* Curt. (Glossosomatidae), *Anabolia laevis* Zett. (Limnephilidae), and species of the genus *Gunungiella* Ulmer (Philopotamidae). Among the lower moths, aggregation is typical for species of the genus *Micropterix* Hübn. (Micropterigidae).

The use of the sternal gland products as repellents against predators has been discussed in the literature for a long time (Ansteeg and Dettner, 1991, and references therein). The sternal gland secretions were shown to be toxic to invertebrates when applied on the cuticle. According to our observations, abundant sternal secretion of large species, such as *Phryganea bipunctata* Retz. (Phryganeidae) provided effective protection from attacks by birds, in particularly gulls, which caught the adult caddisflies in flight but dropped them immediately. In a different case, an attack of the same species by the ants *Formica rufa* L. ended in the death of the attackers. However, an abundant release of sternal gland products accompanied by a sharp smell can be observed only in species of a few advanced families: Polycentropodidae (*Polycentropus* Curt.), Phryganeidae, and Limnephilidae, but this method of defense is not typical for most other families. The very position of the glands in the ventral part of the body under the wings is not conducive to their use for defense.

Due to their repellent action, the sternal gland products might be also used to mark an already fertilized female or to prevent the attacks of males on the copulating pair. Observations of a number of species (*Phryganea bipunctata* Retz., *Ph. grandis* L., *Rhyacophila nubila* Zett., and different species of *Hydropsyche* Pict., in particular *H. contubernalis* McL. and *H. nevae* Kol.) showed that soon after the beginning of copulation, the numerous males present near the receptive female or even attacking the copulating pair stopped their attacks and moved away. The role of pheromone secretion of the sternal glands in this process of behavior modification remains to be studied.

The Possible Ways of Origin and the Early Evolution of Pheromone Secretion

The presence of sternal pheromone glands is a well-established synapomorphy of Trichoptera and Lepidoptera (Kristensen, 1984); these glands were already developed by the moment of divergence of these orders in the Mesozoic, whereas no sternal glands have been found in their Paleozoic ancestors, Protomeropina (Ivanov and Sukacheva, 2002). The pheromone

glands must have appeared as novel structures in the common ancestor of Trichoptera and Lepidoptera in the Permian and Triassic. The structures associated with abdominal sternal glands were discovered in the fossil caddisflies of the families Philopotamidae, Polycentropodidae, Ecnomidae, Hydropsychidae, and Glossosomatidae (Ulmer, 1912; Ivanov and Melnitsky, 2005, 2006, 2013a). Caddisflies were probably able to produce pheromones already in the Mesozoic.

The ways of origin and the early steps of evolution of the sternal glands are still hypothetical. The complex apparatus of the glands is similar in species of different orders and must have been the result of long evolution. The products of these glands may also be similar (El-Sayed, 2013): for example, (S)-heptan-2-ol is produced by the glands of 2 species of caddisflies from unrelated families, 2 species of beetles, 3 species of hymenopterans, and 1 species of primitive moths; (S)-nonan-2-ol was found in 2 species of caddisflies and 4 species of hymenopterans; 3-hydroxy-2-butanon is produced by caddisflies, lepidopterans, dipterans, beetles, hymenopterans, and cockroaches. The methylated compounds present in the secretions of *Anabolia laevis* were also found in beetles and hymenopterans. Nonan-2-one occurs in the representatives of 6 families of caddisflies, 6 families of beetles, 4 families of hymenopterans, and 1 family of dipterans, whereas outside the class of insects it is present in acarines, whip scorpions, rodents, and bats. It may be assumed that the genetic information on the synthesis of volatiles is preserved in the genome for a long time and is used when the need arises.

The development of specialized glands and pheromones synthesized by them should be supported both by the receptors (scent perception by specialized sensilla) and by the CNS (interpretation of the olfactory signal). Thus, the appearance of specialized glands and their products cannot by itself give impetus to the development of a communication system without the previous development of its sensory component. In fact, the logic of the process suggests that formation of the sensory part of the communication system should precede the pheromone glands and their products.

One may consider two sources of chemical stimuli which predated the appearance of specialized sex attractant pheromones in Amphiesmenoptera: the odor of the insect itself and the odor of its habitat. Data on volatile production in caddisflies lacking sternal glands, for example, in the abdomen of males of *Mollanna angustata* and in the terminal abdominal segments of females of this species, reveal the presence of only long-chain fatty acids which do not excite olfactory receptors. It is much more probable that the antennae of the ancestral forms responded to the ambient odors, particularly to the volatiles of plants on which the insects usually found shelter. This hypothesis is supported by similarity between insect pheromones and plant volatiles. In particular, according to the Pherobase (El-Sayed, 2013), the volatile components produced by the sternal glands of *M. angustata* are also present in a wide range of plants. Other volatiles found in the insect pheromone blends are also produced by various plants. On the other hand, many components produced by the glands of lower caddisflies and detected by their antennae have their analogs among the various volatiles of plant origin. For example, the snakeshead *Arum maculatum* L. produces dozens of volatiles (Kite, 1995), including the same ketones that occur in the pheromones of *M. angustata* and other caddisflies.

The aggregation concept can be proposed as a working hypothesis of the origin of pheromone communication in Amphiesmenoptera and possibly other groups of insects. This concept assumes that the initial stages in the development of communication were determined by the specific odor of the places where the mates met. The ancestral forms could find such places using a wide range of stimuli including olfactory ones. Later in the course of evolution, the odor of the patches of vegetation inhabited by caddisflies could be intensified due to additional production of plant volatiles or similar compounds by the insects themselves. At this stage, the pheromones promoted aggregation and served as markers of a favorable biotope, their "meaning" being the same for both sexes and even for different species. Thus, the signal produced by one species could be used by other species as an additional identifier of the meeting place. Another case of different species using similar signals, though for a completely different purpose, is known as Müllerian mimicry. The aggregation hypothesis explains the abundance of common components in the pheromone blends of different insects: these compounds were used in the past as markers of favorable habitats, facilitating concentration of individuals and the meeting of mates. Moreover, the pheromones released by different caddisfly species aggregated on the banks of reservoirs might attract individuals of other species, preventing them from moving far away from the reser-

voir in search of mates. This was promoted by abundant sternal gland secretion in both sexes. Asymmetrical perception of components produced by different sexes and different species facilitated the meeting of mates despite a high level of chemical "noise" created by the vegetation and individuals of other species. This concept is supported by the fact that in primitive caddisflies, not all the components of the gland secretion affect the antennae of the opposite sex (Fig. 3, components 2 and 3).

Insects seem to synthesize and release a greater number of compounds than are detected by their olfactory receptors. This diversity creates the basis for further evolution of chemical communication. In some cases, however, it is not clear whether the presence of specific components is a side effect of pheromone synthesis in the ancestral forms, or these compounds are detected by still unknown receptors positioned on some other body parts.

The role in communication has been demonstrated for some but not all components of the gland secretion. The observed redundancy in production and perception of pheromones could have been initially determined by the need to recognize complex odors of the plants, by some components playing the same role (e.g., due to different volatility at different temperatures) or by low reliability of signal recognition by weakly specialized receptors against the background of plant odors. The compounds constantly present in caddisflies, of which the most common ones are nonan-2-one, nonan-2-ol, heptan-2-one, heptan-2-ol, and some other alcohols and ketones, may have formed a universal attractive signal and served as the starting point for further evolution of pheromone signals.

The Main Directions of Specialization in the Evolution of Pheromone Communication

The details of evolution of the pheromone system are difficult to discuss due to a great degree of similarity in the pheromone composition of remotely related species, which may be regarded as parallelism. Comparative analysis does not demonstrate any divergent events in the pheromone evolution of caddisflies, but it does reveal the tendency of species from related families to use a certain set of components. For example, representatives of Annulipalpia more extensively use unsaturated alcohols and ketones, which creates an superficial resemblance to lower moths of the family Eriocraniidae and supports the concept according to which the primitive evolutionary state was characterized by glands of the 4th type producing unsaturated alcohols and ketones (Djernaes and Sperling, 2011). The limnephiloid families are distinguished by methylated components of the pheromone blend playing the main role in communication (Ivanov and Melnitsky, 2011).

The classical cladistic approach to pheromone evolution is complicated by numerous parallelisms in the gland product composition and the common occurrence of unsaturated and methylated short-chain alcohols and ketones among the volatiles of insects. In view of this, we cannot support the hypothesis of Djernaes and Sperling (2011) and assume instead that the pheromone secretions of the primitive Amphiesmenoptera consisted of a wide range of components, including both saturated and unsaturated compounds. The subsequent evolution of the pheromone communication system probably involved specialization of the products and reduction of their quantities, a decrease in the diversity of components, and an increase in the sensitivity of the antennae.

Enhanced gland secretion with a defensive function occurs in the families Phryganeidae and Polycentropodidae. In the first case, quickly evaporating droplets of secretion with a sharp odor can be observed. In the second case, namely, in polycentropodid caddisflies of the genera *Polycentropus* Curt. and *Neureclipsis* McL. (but not *Cyrnus* Steph. and *Plectrocnemia* Steph.) and some species from different genera of Limnephilidae, the odor is present but droplets of secretion do not appear. This effect can also be observed, though to a much lesser degree, in some species of other families, such as Psychomyiidae, Hydropsychidae, and Rhyacophilidae. The defensive function of the sternal glands requires a special quantitative study.

Sex-related asymmetry in the degree of gland development, the chemical composition of their secretion, and the production of pheromones is a common phenomenon among the lower Amphiesmenoptera. There are distinct differences in the chemical composition: even in cases when identical components occur in males and females (for example, in Hydropsychidae: Löfstedt et al., 1994; our unpublished data), chemical asymmetry is manifested in the number and relative abundance of the components. Asymmetry is much less noticeable in the gland structure: the glands of both sexes always belong to the same morphologi-

cal and, evidently, histological type, differing only in size and proportions.

Reduction of the sternal glands proceeds in parallel in Trichoptera and Lepidoptera. It may be accompanied by the appearance of secondary glands: terminal glands in higher lepidopterans, eversible structures at the tip of the abdomen in species of the genus *Phylloicus* Muell. (Calamoceratidae) (Prather, 2003), fenestrated structures on the basal abdominal sternites in caddisflies of the genus *Athripsodes* Billberg and some lower moths, including *Catapteryx* Zagulajev et Sinev and species of the family Nepticulidae (Löfstedt and Kozlov, 1997). The chemical composition of pheromones changes drastically in the evolution of Lepidoptera: the highly volatile alcohols and ketones are replaced by fatty acid esters (the main pheromone class in the lower Ditrysia) and, finally, by various epoxides and even long-chain aliphatic hydrocarbons (Löfstedt and Kozlov, 1997). These compounds are characterized by high molecular weights and are synthesized in very small quantities. The new terminal pheromone glands have a simple structure, possibly due to low toxicity and extremely small amounts of the pheromones produced. The transition to new low-volatile pheromones in Ditrysia is based on the use of acetates and other derivatives of fatty acids: these acids are present in great quantities in the hemolymph of the adults where they function as reserve nutrients. Fatty acids have low volatility but their esters are more volatile.

Fatty acids can be easily transformed by acetylation or deacetylation, during which their chains are enlarged or reduced by two carbon atoms at once (Symonds and Elgar, 2008; Liénard and Löfstedt, 2010). Pairs of ketones and alcohols differing by two carbon atoms are very common in the pheromone blends of caddisflies, indicating that this mechanism of synthesis may also occur in caddisflies and thus may be typical of Amphiesmenoptera as a whole. The hemolymph of caddisflies contains great quantities of fatty acids (see Fig. 1) which may serve as a basis for pheromone synthesis.

The processes of oxidation, changes in the length of the carbon chain, and formation of double bonds in the pheromone molecules are accomplished by enzymes. The diversity of components synthesized in the primitive families of caddisflies indicates that the sternal glands of the ancestors of Trichoptera and Lepidoptera already contained a wide range of these enzymes. Further evolution, as shown by comparison of species from different taxa, led to specialization, possibly limiting the diversity of biosynthetic processes. The details of this evolution will become clear only after further studies of pheromones in caddisflies and lower moths.

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