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## Ethological defence mechanisms in insects. III. Chemical defence

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Etologiczne mechanizmy obronne owadów. III. Obrona chemiczna

### SUMMARY

Based on literature data, the chemical defence against predators employed by some insect species is presented in this paper. Active and passive forms of chemical defence based on allomones synthesized *de novo* by insects and allomones acquired from plant and animal food and symbiotic bacteria have been discussed.

**Keywords:** insects, chemical defence, allomones

### STRESZCZENIE

W oparciu o dane z piśmiennictwa przedstawiono stosowaną przez wybrane gatunki owadów chemiczną obronę przed drapieżnikami. Uwzględniono czynne i bierne formy obrony chemicznej w oparciu o allomony syntetyzowane przez owady *de novo* i allomony, których źródłem jest pokarm roślinny i zwierzęcy, a także symbiotyczne bakterie.

**Słowa kluczowe:** owady, obrona chemiczna, allomony

Insects exhibit diverse strategies of defence against insectivorous animals (4, 17, 18). One of the ways to avoid and prevent predators' attacks is the chemical strategy. Insects employ a rich arsenal of chemical weapons such as gases, poisons, and burning and foul-smelling liquids. Chemical defence can be both passive and active. The first form does not require behavioural engagement;

it is typical of insects whose tissues are saturated with toxic substances. The other type of defence associated with activation of specific behavioural mechanisms is displayed by insects, which produce and store abhorrent foul-smelling toxic substances in hemolymph, diverticula, or special glands, and release them only when threatened. Chemical defence is associated with high costs. Continuous synthesis of defensive substances in the organism is energy-consuming. Activation of toxin release is connected with high expenditure; additionally, questing is then disturbed, which may lead to a reduced rate of growth and development (34).

Defensive substances released by disturbed insects often act as stimuli attracting predators' attention to the bright contrasting colouration of the prey (scarlet, yellow, black, purple). The chemical defence in insects is frequently associated with their defensive warning or aposematic colouration that is easy to remember and discourages the predators to give up the preys even upon the first attempt to attack. Therefore, chemical defence follows the principle "I am not tasty", "I am dangerous" (4). For instance, the bright colouration of ladybirds has become a "we-are-not-tasty" signal for birds and an effective tactic. Another advantage of chemical defence is the fact that substances that are repulsive in taste and smell offer the victim a chance to be released by the predator.

Several hundred defensive chemical compounds, collectively known as allomones (the term relates to all chemical substances employed in the contact between animals belonging to various species), have been identified so far (4). Allomones may be *de novo* synthesized by insects or may be exogenous, i.e. acquired from the plant and animal food source.

#### ENDOGENOUS ALLOMONES

To protect its eggs and larvae, the earwig *Forficula auricularia* (Forficulidae) uses its long pincers, but when attacked it twists the abdomen towards the attacker and releases a foul-smelling liquid (35, 4). The brightly coloured lubber grasshopper *Romalea microptera* (Arcididae), a representative of Orthoptera and one of the two biggest North American grasshoppers, wards its enemies off by releasing toxic froth from its mouthparts. The froth contains air bubbles and a mixture of phenols, terpenes, and benzoquinon; when they burst, they release a cloud of gas around the insect. When the attacker insists, the insect employs another type of chemical weapon, i.e. it vomits a drop of repellent liquid (23).

The bombardier beetle (*Brachinus exploadens*), a representative of carabids (Carabidae), repels the attacker by a toxic liquid produced by abdominal glands located near the anus. The gland consists of two parts: the atrium and the vestibule separated by a mobile muscular valve. Some atrial cells produce hydrogen peroxide (25%), while others hydroquinone (75%); when the insect is in danger, these substances are forced to the "combustion chamber" or "explosion chamber"

lined up by a thick chitin heat-resistant layer. The inner walls of the chamber contain glands that secrete catalases and peroxidases. Catalases decompose hydrogen peroxidise, while peroxidases oxidize hydroquinone to the proper defensive substance, i.e. benzoquinone. The temperature of the mixture in this exothermic reaction may reach 100°C. A considerable amount of oxygen is produced in the process, which combined with its high temperature and pressure results in discharging the reaction products, benzoquinone and oxygen, through two orifices located at both sides of the anus. The reaction is accompanied by an explosive sound that can be heard from 0.5 m, a distance at which the insect aims at its predator. The mobile nozzle-like abdomen tip, a “revolving turret”, provides the bombardier beetle precision of the shot. Therefore, the beetle can direct its “missiles” both backwards and sideways. The number of consecutive shots may reach up to 50. The attacker is confused by simultaneous noise, high temperature, and a cloud of white-blue irritant vapours that blind it temporarily (12, 14, 4, 21, 28).

The American stick insect *Anisomorpha buprestoides* (Pseudophasmatidae) releases a defensive substance, terpene dialdehyde, from abdominal apertures. The stick insect can shoot its venom towards its pursuer, i.e. another insect, bird, or mammal, before it is captured. While the predator begins cleaning, the stick insect has enough time to escape (11).

To defend against enemies, the rose aphid (*Macrosiphum rosae*) (Aphididae) uses its cornicles located on the sixth tergite of the abdomen to exude a substance that coagulates and forms a waxy plaque (5).

Caterpillars of the South American moth *Lonomia achelous* (Saturniidae) are equipped with venom glands at the base of warts (bristles) releasing a potent anticoagulant substance that can cause serious haemorrhages in their enemies, including humans (25).

When threatened by ants, the dirty white larvae of the poplar leaf beetle (*Melasoma populi*) from the chrysomelid family (Chrysomelidae) release large drops of pungent almond oil-smelling liquid from black dorsal warts and withdraw them into the warts when the danger passes (5, 35).

The domestic bug (*Cimex lectularius*) (Cimicidae) produces its chemical weapons in the thoracic glands. The characteristically odourous fluid is contact venom for ants, spiders, scorpions, and even bats (5, 35).

Termite soldiers are potent defence forces. These sterile males and females fed with a special liquid substance by workers constitute a caste whose aim is to self-sacrifice for the benefit of the others. Their only role is to ensure safety of colony members when these are invaded by their traditional predators, i.e. ants. The heads of termite *Nasutitermes corniger* (Termitidae) soldiers have the shape of a bottle neck resembling a glue tube filled with a toxic corrosive terpenoid substance which is shot at the predator with great precision. Ants that have entered

the termite mound are glued to the walls by the substance. Although the liquid is effective against any enemy, it does not affect termite workers, which in groups of 6 hold down the invader with their legs and emit a scent signal to call the soldier. The substance does not block either the gland or the nozzle through which it is released by the soldier (15). Therefore, the substance does not pose danger to the *N. corniger* soldiers. The greatest sacrifice to the colony is the suicide they commit in order to destroy the invader. This form of chemical defence is typical of the termite *Globitermes sulphureus*. By abdominal wall muscle contraction, the soldiers of this species expel yellow exudate while attacking the enemies. The defensive liquid solidifies in the air, thus becoming a death trap also for the soldiers themselves. The force of muscle contraction is sometimes so powerful and violent that both the gland and the defender's body explode (39). A similar defence tactics is employed by termites from the genus *Anoplotermes* inhabiting Africa and South America; they have no soldier caste, therefore the duty of defence is taken over by infertile male and female workers, which become kamikazes when threatened. The moment they are touched by invaders, e.g. ants, they contract their abdominal muscles and this leads to body rupture and spraying the enemy with a sticky liquid, a mixture of digestive tract content and body fluids (15).

Suicidal soldiers are typical of other insects as well, e.g. ants from the genus *Camponotus* inhabiting the humid rainforest zones in Malaysia. The kamikazes are recruited amongst a special caste of females equipped with two defensive mandibular glands filled with a sticky substance and located along the soldier's body. The substance is released by rupture of the body integument between the abdominal segments due to sudden contraction of muscles induced by contact with the intruder, which has no escape as the liquid hardens within a few minutes (19, 15).

An interesting and complex system of nest and territory defence is employed by the African weaver ant *Oecophylla longinoda* (Formicidae), which defends its terrain against intruders, including members of other colonies of the same species. The defence system involves four pheromones that have different roles and ranges of diffusion in the air. When disturbed by an enemy, the ant releases the pheromone mixture from glands located at the base of the mandibles. The quickest and most volatile substance is hexanal, an aldehyde evoking symptoms of anxiety reflected by movements of the antennae in workers waiting for the scent of other pheromones. At an appropriate concentration, the second component of the defence system with a smaller area of activity, i.e. hexanol, mobilizes ants to march towards the source of the alarm, where they enter the range of 3-undecanone, the third pheromone. This component of the defence system encourages sister-ants to attack any foreign object with their mandibles. The fourth pheromone, 2-butyl-2-octenal, enhances aggression in ants attacking the invader (19, 42).

When threatened, the beetle *Staphylinus olens* (Staphylinidae) raises the abdomen perpendicularly and, without interrupting the escape run, releases a pungent liquid containing iridodial (terpenes) and ketones from pygidial glands. The toxins are highly irritating to animal mucous membrane and skin. The beetle's chemical defence is assisted by mandibles directed against the predator and the sound it produces (5, 35, 21).

The chemical defence strategy exhibited by adults, larvae, and eggs of ladybirds (Coccinellidae) relies on alkylpyrazine alkaloid compounds produced in the insect fat body. A disturbed individual releases a defensive substance together with drops of orange-coloured hemolymph from femoral-tibial joints. The amount of released hemolymph can reach even 20% of the beetle body weight. Particular genera and even species of ladybirds produce various alkaloids, which give hemolymph specific smell and bitter taste. In its hemolymph, the seven-spotted ladybird (*Coccinella septempunctata*) releases coccinelline, an alkylpyrazine alkaloid from the azophylene group, a warning substance against ants and birds. The two-spotted ladybird (*Adalia bipunctata*) employs another defensive alkaloid, adaline (a derivative of azabicyclonane), which is less toxic than coccinelline but is released in larger amounts (20, 8, 27).

Two species of the long-horn beetle, *Stenocentrus ostricilla* and *Syllitus grammicus* (Cerambycidae), have mandibular glands, i.e. very long containers of oily liquid with pores located at the anterior surface of the head. The discharge secreted by these glands contains o-cresol and toluene. Volatilization of the toxin is enhanced by cuticular appendices at the gland orifice; hence, the smell of these goat-insects is distinct and effective in repelling invaders. Another representative of the long-horn beetle, i.e. the musk beetle (*Aromia moschata*) takes its name after the musk odour of the body. The beetle attacks its predators by discharging large amounts of salicylaldehyde and iridodial produced in glands whose orifices are located in the posterior part of the metasternum (32).

Adult Colorado potato beetles (*Leptinotarsa decemlineata*) (Chrysomelidae) defend themselves by releasing highly toxic 7-glutamyl dipeptide from cuticular glands (33).

When disturbed, *Agrypnus murinus*, a representative of elaterids (Elateridae) releases dimethyl sulphide and indole, substances characterized by extremely fetid odour, from its eversible glands (9).

Representatives of the family of fireflies (Lampyridae) from the genus *Photinus* produce toxic steroid substances – lucibufagins. In a stressful situation, they are released with hemolymph at the edges of pronotum integument and antennae. The cuticle in these structures is very thin and becomes ruptured during the release of the substances. The toxins evoke vomiting, or even death, in vertebrates (24).

Representatives of blister beetles (Meloidae), e.g. *Epicauta funebris*, produce cantharidin, a substance from the monoterpene group. The highest concentration of the substance has been found in the beetle integument, but other body parts are infiltrated by with it as well. Eggs and hence larval bodies also contain the compound. The toxin is only synthesized and stored in reproductive system glands by adult males. During copulation, males transfer the toxin with spermatophores to females, which in turn deposit it in eggs. Thus, the male invests in the female and offspring. Additionally, males release cantharidin for defence. It emerges on the cuticle surface with hemolymph from the area around the knee joints. One *Epicauta funebris* male can store up to 30 mg of this monoterpene. In larvae, the toxin is deposited in the digestive tract; when threatened, they release cantharides through the mouth orifice. Cantharidin is a powerful poison for many invertebrate and vertebrate animals, but not for humans (7, 4, 21).

The weapon against attacking ants and birds used by the beetle *Necrodes surinamensis* (Silphidae) is a mixture of caproic and caprylic organic acids and terpenoids. The insect can eject the contents of the rectal gland at a considerable distance and direct its weapon backward and forward by raising the abdomen over the elytra (16).

An interesting mechanism of chemical defence is employed by the death's-head hawk moth *Acherontia atropos* (Sphingidae). Although it is attacked by worker bees, it enters the hive thanks to the thick cuticle and resistance to bee venom. Inside the hive, the moth is practically ignored by bees. The moth is undisturbed in the hive thanks to the ability to generate sounds resembling those produced by the bee queen and, first of all, to produce a mixture of scents. Investigations have revealed that the four components of the mixture are identical to substances contained in the bee body. Hence, the death's-head hawk moth is regarded as a hive-mate and is allowed to feed on nectar and honey freely (29).

#### EXOGENOUS CHEMICAL COMPOUNDS (EXOGENOUS ALLOMONES)

In chemical defence, many insect species employ secondary metabolites of foreign origin, and thus lower the costs of defence (21). Defensive substances are usually acquired from plant or, less frequently, animal food sources. Numerous insects choose plants with high levels of alkaloids. Toxins absorbed by caterpillars are often accumulated in their bodies, reaching concentrations exceeding those in the diet, or they are used for formation of new compounds. The saying "you are what you eat" is adequate in the case of e.g. caterpillars of the pine sawfly (*Diprion pini*) from the family Tenthredinidae. The caterpillars form clusters of thousands of individuals on pine tree branches in the forests of Europe and Africa. Their potential enemies are ants *Formica aquilonia* (Formicidae). When a scout ant finds sawfly larvae, it runs to the nest leaving odour traces along the way, which

will enable worker ants to find the rich source of nutrition. Unlike other insects, sawfly larvae are not equipped with either large mandibles or a sting containing toxic substances; however, they are not completely helpless in the face of danger. The defence strategy consists in intoxication of scout ants by covering their heads and antennae with a small amount of a rubber substance in order to prevent them from informing the colony about the location of the larvae. The rubber substance is produced from chewed resin collected from pine needles and mixed with a special substance produced in the digestive tract. Both these components are stored in the utricle – a special part of the digestive tract. The mixture produced by sawfly caterpillars has similar properties as the substance used by ants as a warning signal. Ant scouts covered by the substance are confused to such an extent that they are unable to find the way back to the nest. Even if they manage to get back to the nest, the warning scent stimulates other ants to attack and kill them as they are regarded as enemy scout ants (outside the nest, the smell denotes a signal to escape). Therefore, no member of the colony follows the traces left by the scout ant along the way back from the sawfly larvae to the nest. The large horde of sawfly larvae may continue feeding safely (1, 3, 35).

Although fireflies from the genus *Photurius* do not produce lucibufagin, they can contain this substance as they are predators, and the diet of females includes males of the genus *Photinus*. By emitting sequences of flashes that are characteristic of *Photinus*, *Photurius* females attract males, feed on them, and ingest their toxin. This method of acquiring toxic substances is referred to as aggressive mimicry (24).

The hemolymph of *Paederus melanurus* from the rove beetle family (Staphylinidae) contains a toxin called pederin (pederon and pseudopederin) from the group of cyclic amides. A key role in its synthesis is played by endosymbiotic bacterial flora from the *Pseudomonas* group detected in *P. melanurus* hemolymph. Not all individuals are infected with the bacterial microflora; hence, not all of them have the toxin. Treatment of “positive” beetles with an appropriate antibiotic renders them “negative”. The *Paederus melanurus* beetles have a delicate cuticle, which becomes disrupted when the insect is removed from the body surface, hair, or clothes. Then, pederine is released together with hemolymph and it comes into contact with the skin. It is highly irritating and causes extensive vesicular dermatitis. Due to its toxicity, pederine belongs to the most potent animal-derived toxins. It is an inhibitor of protein synthesis; hence it exhibits cytotoxic activity and causes inhibition of epithelial cell proliferation already at the concentration of 1–1.5 ng/ml (21, 41).

In butterflies from the genus *Heliconium* (Nymphalidae) related to our peacock butterfly, both adults and larvae feed on the sap of the *Passiflora* plant growing in Central and South America. The plant produces a strong toxin which protects it against all insects, except for the aforementioned species. The

beautifully coloured butterflies accumulate the toxin in their organisms and thus become inedible to birds (14, 26, 37).

The monarch butterfly (*Danaus plexippus*) (Nymphalidae) inhabiting the area between Canada and Argentina as well as Hawaii, Indonesia, Australia, and South Europe is unpalatable to insectivores. Females lay eggs on the leaves of the common milkweed *Asclepias syriaca*, a plant containing a toxic alkaloid cardiac glycoside, i.e. cardenolide glycoside. The monarch butterfly is the only insect that is insensitive to the alkaloid. The caterpillar accumulates the acquired toxin in the body integument and thus becomes toxic to insectivorous reptiles, birds, bats, predatory beetles, and ants. Active glycoside molecules are transferred to the adult males and females. Thus, both genders participate in protection of eggs and caterpillars. In the adult form, glycosides are deposited in special glands located on the wings and abdomen. A threatened monarch butterfly instantly releases a stinging fetid liquid. A bird that attacks any stage of the butterfly spits it out immediately; a novice predator which swallows the insect will instantly vomit. *Danaus plexippus* butterflies with damaged or pierced wings, evidence of a bird attack, have been seen. A subsequent attempt to capture the butterfly will fail as the bird avoids not only monarch butterflies but also other similarly coloured species (2, 29, 38). The predator's education takes place at capturing the first prey, which additionally bears characteristic colouration (4, 22).

In turn, the *Danaus chrysippus* and *Danaus gilippus* species related with the monarch butterfly (Nymphalidae) exhibit a remarkable efficiency of detoxification of toxic compounds from the group of pyrrolizidine alkaloids (PA) responsible for a large number of deaths among domestic animals in various regions of the world. Only males of the species accumulate toxic substances and become unpalatable to insectivorous animals. The butterflies have warning colouration similar to that of the monarch butterfly. Males utilize the acquired alkaloids to produce pheromones to attract females. During copulation, males transmit over half of the toxin with sperm to females, which then deposit it in eggs, thus protecting them against predators. Therefore, the gift provided by males is a major contribution to the survival of the next generation. The more alkaloid males collect, the more pheromone they produce, thus attracting females effectively and ensuring greater safety to eggs (29). Pyrrolizidine alkaloids (PA) save the lives of moths from the genus *Cretonotos*, whose caterpillars absorb the toxin with food. Males use alkaloids for production of a sexual attractant released by an organ consisting of four plumose appendages located at the posterior part of the abdomen. The size of this structure depends on the amount of accumulated toxins – the bigger the content of glycoside in the plant ingested by the caterpillar, the greater effectiveness in attracting the female (29). PA also saves the life of the *Macrosiphum albifrons* aphid (Aphidae), a lupine pest. The more toxin is contained in the plant, the more readily aphids feed on it, as they are offered protection against the hostile beetles from

the *Carabus problematicus* species (29, 40). Toxin compounds from this group are also utilized by adult flea beetles *Longitarsus parvulus* (Chrysomelidae). Non-toxic plant substances are converted into highly toxic alkaloids in the digestive tract of these beetles. In some species of the flea beetle, the alkaloid concentration is much higher than that in the host plant (10).

Females of the cabbage butterfly (*Pieris brassicae*) (Pieridae) lay 600 eggs in batches of 40–100 on brassicaceae plants, particularly on the leaves of the common cabbage, as they are attracted by sinigrin, an attractant with a mustard oil smell (4). The glycosides of mustard oils present in cabbage are accumulated in the insect bodies; therefore, neither caterpillars nor butterflies are an attractive prey for lizards and birds. Yet, the cabbage butterfly has many enemies among insects (4, 5, 36).

Chemical defence is characteristic of various members of the family Dytiscidae. Their glands form a pocket lined with secretive cells. These glands open behind the head on the dorsal part of the pronotum. When disturbed, they produce light-milky secretion that is toxic for fish and amphibians. It contains steroids produced from their precursors, e.g. cholesterol, contained in food (4, 21).

Larvae of the family chrysomelid beetles (Chrysomelidae), for instance *Chrysomela tremulae*, feed on willow leaves from which they absorb the input product – salicin – and produce salicylates; the latter compounds are transferred to nine defensive glands, where under the impact of  $\beta$ -glucosidase and oxidase enzymes, salicylic aldehyde, a weapon against ants and birds, is produced (21).

Black-yellow caterpillars of the *Malacosoma americanum* moth (Lasiocampidae) spin a thread and build a thick tent to share for effective protection against ants and insectivorous birds. Sometimes the whole tree or even neighbouring trees are wrapped in the thread. Under the cocoon cover, larvae initially eat egg envelopes, buds, and leaves covered with the thread. When the food runs out, they leave the safe place and set off to look for food elsewhere. Although they are well visible, the larvae are still safe. In their glands, many caterpillars have managed to accumulate toxic cyanides contained in leaves. When threatened, they regurgitate the toxic liquid and spray the attacker. The liquid is poisonous and has a repulsive taste. Predators learn quickly that they should leave the caterpillars undisturbed. Equipped with such a chemical weapon, the larvae feed safely and practically leave the whole tree leafless (3).

In the world of insects, there are other ways of getting defensive substances. Larvae of the green lacewing *Chrysopa slossonae* (Chrysopidae) take advantage of the defensive substances of aphids that they feed on. While attacking aphids, the green lacewing might become a prey for ants that protect aphids and their sweet secretion – a valuable source of food. Yet, green lacewing larvae cover their whole bodies with wax produced by aphids, thus masking their own smell and

avoiding the danger. Ants treat them as aphids and protect them accordingly (31). Similar strategies of masking with aphid wax to avoid attacks from predatory ants and other insects are employed by chrysopa larvae. Within 20 minutes, chrysopa larvae manage to collect sufficient amount of wax to ensure not only safety but also access to food (29).

Insects from the family Reduviidae employ sophisticated tactics to reach food and defence. They cover their bodies with debris of termitaries and enter them safely, where they feed on worker termites without being attacked themselves (30).

Any survival strategy to avoid attacks is associated with costs that are difficult to estimate. They depend on the level of risk, the physiological condition of the victim and predator, and environmental conditions (6). Natural old-age related animal death is a rare phenomenon in nature. Each species feeds on some others and serves as food for some others. It is sometimes difficult to distinguish between the predator and the victim, as the same individual can be both of them; therefore, nature has equipped each animal species that could potentially be too powerful with some limitation or disability. Defectiveness or modest mediocrity is to some extent favoured; hence, victims coexist with threatening predators in natural conditions (13). The armament process continues.

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