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Ethological defence mechanisms in insects. I. Passive defence

Etologiczne mechanizmy obronne owadów. I. Obrona bierna

SUMMARY

The review article describes the ethological defence mechanisms in insects. This group of animals live in all climatic zones and have conquered all the habitats therein. In order not to become prey, insects employ various defence mechanisms – passive and active – or both these forms simultaneously or in a definite order. Because of their great variety, we have focused on passive defence only: the external structure of the body of animals, concealed life (anachoresis), cryptic colouring and body's form (mimetism), imitation of species with abilities for defence (mimicry).

STRESZCZENIE

W artykule przeglądowym przedstawiono etologiczne mechanizmy obronne owadów. Ta grupa zwierząt występuje we wszystkich strefach klimatycznych i opanowała wszystkie środowiska każdej z nich. By nie stać się ofiarami drapieżców, owady stosują bogactwo różnorodnych form obrony biernej, czynnej, a także obydwie te formy jednocześnie lub w określonej kolejności. Z uwagi na to w artykule ograniczono się do omówienia mechanizmów biernych obejmujących: strukturę zewnętrzną powłok ciała, ukryty sposób życia (anachoreza), kryptyczne ubarwienie i kształt ciała (mimetyzm), naśladownictwo gatunków zwierząt zdolnych do obrony (mimikra).

Key words: insects, passive defence, external structure of the body, anachoresis, mimetism, mimicry

Defence against natural enemies is one of the basic needs in animal life. The mutual dependence between carnivorous animals and their prey is reflected in the mutual adaptation of their morphology, physiological traits, lifestyle and behaviour. In many cases it is difficult to distinguish the predator from the prey, as the same individual may potentially be both of them: it preys on other animals and is preyed on.

Insects constitute a big percentage of the animal world. They are the most diverse group among the invertebrates. These animals live in all climatic zones and have conquered all the habitats therein. Their remarkable expansion and the great numbers of individuals and species are provided by, on the one hand, high reproduction and diversity and, on the other hand, by incredible defence mechanisms.

Insects have enemies among numerous animal species. They are food for amphibians and reptiles; half of all bird species and most bats would not survive without them. Even people in some regions of the world eat insects. Insects are also preyed on by spiders and other insect species. In order not to become prey, insects employ various defence mechanisms – passive and active – and also both these forms simultaneously or in a definite order.

Passive defence includes 1) the external structure of animals, 2) concealed life (anachoresis), 3) cryptic colouring which conveys the meaning "I am not here" (mimetism), 4) imitation of other species – "I am something else, I am distasteful or dangerous" (mimicry).

1. Protective role of the external structure

The insect body is covered with a hard covering built of chitin and proteins. It has a function of an exoskeleton to protect animals against loss of water and against predators ' attack.

A strong exoskeleton is the best protection from even the most pertinacious predators. A praying mantis has such hard body covering that a hornet is unable to pierce it and loses the fight. The larva of the Australian butterfly *Liphyra brassolis* (*Lycaenidae*) is a pest of *Oecophylla smaragdina* ants, and the strong, although flexible, body covering protects it against their attack. The covering is composed of a thick cuticle and crust. The ants' fierce bites and the acrid liquid that they discharge are not able to damage the leathery larval crust. In myrmecophilous butterfly species, a newly transformed imago is capable of defence against ants. The still crumpled wings and legs of the butterfly are covered with greasy scales and the abdomen – with twisted hairs which fall out at the slightest touch. After the attack, ants remove butterfly's scales and hairs from their mouths, while the butterfly spreads its wings, gets stronger and starts the first flight (Attenborough, 1993; Pabis, 2008).

Certain traits of the body parts ensure insects' safety. For instance, the final segments of some cockroaches are covered by slimy secretion from special glands which makes it difficult for predators to catch the potential prey and allows the insect to escape. The mandibles of termite "soldiers" are not only used to grasp food but also for defence (Fig. 1). The long hind legs (10 cm – twice as long as the body) of the cricket-like *Deinacrida heteracantha* insect from New Zealand have a locomotion function and ensure its safety. They are covered with spikes, similar to those in roses, which prevent the predator from catching the prey or even hurt it. Defence-efficient spikes and hairs of various kinds, are also found on the body of larvae of some butterflies (Wojtusiak, 1991).

The pressure of the enemy exerts and the period of its intensification affects the degree of prey's defensive power. For example, in *Crictocopus sylvestris* fly larvae from the family *Chironomidae*, often are preyed on by a dangerous predator – the hydra, the length of abdominal hairs which block access to the larval body undergoes changes. From autumn to spring, in the periods of high abundance of the hydra, the insect larvae have thick setae, whereas in summer, when the number of hydras is significantly smaller, the larval setae are sparse and short. It is interesting that the longest setae are seen in young larvae of the fly, which are highly exposed to predators' attack due to the small size of their bodies (Hershey and Dodson, 1987). Larvae of the white-faced darter

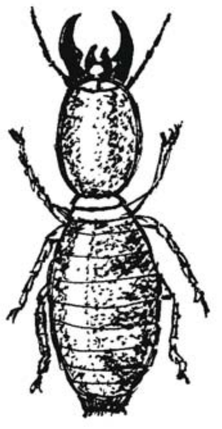

Fig. 1. Termite soldier equipped with strong mandibles

Leucorrhinia dubia dragonfly are a good example of the dependence between the degree of prey's defensive power and predator's pressure. The larvae which live in fish-lakes, compared to the larvae from fishless habitats, have longer and stronger spikes on the dorsal and lateral line of the abdominal segments. The longest spikes are formed in larvae under the influence of a chemical signal sent out by the predator fish – a perch; it should be noticed that their length is not dependent on the larval body size (Arnqvist and Johansson, 1998).

2. Concealed life (anachoresis)

Another form of passive defence is concealed life. Many insect species inhabit zones that are inaccessible or hardly accessible to predators. The safe zone of a habitat may serve as a permanent living site only to these species whose needs it fulfils.

Larvae of numerous root sap sucking insect species, e.g. cicada, spend their lives in the ground, (Attenborough, 1979). The larvae of the European June beetle (*Amphimallon solstitialis*) hatch from eggs laid in the soil, where they dwell relatively safely for two years before they transform into an adult insect. Mayfly larvae stay hidden under stones in water for 2–3 years (Sandner, 1990).

Insects do not only take advantage of natural shelters but also form such safe sites. Various plant galls, pathological bubbles or withered leaves are examples of such forms. For instance, when females from the *Cynipidae* group – cynip *Diplolepis quercusfolii* lay eggs with the ovipositor into the tissues of the ventral side of the leaves, they simultaneously inject a substance which induces an outgrowth – a gall (Fig. 2). Tissue outgrowth is also caused by embryonic and larval excretions which affect plant enzymes and hormones. The form of these outgrowths is specific and permanent for individual species of this insect group. Galls provide protection from predators and environmental factors for eggs, larvae and pupae and are a rich source of food for larvae (Sandner, 1990).

The female of hazel leaf-roller *Byctiscus betulae* also builds a shelter for its larvae (Fig. 3). It carefully selects the leaf to hide the eggs, sits on its petiole and makes two incisions across the leaf, one on each side. The leaf bends and withers at the damage site and the female usually curls the outer surface of the leaf inside. A sticky substance which sticks the roll is secreted at the leaf rim. Simultaneously, the female lays 2–4 eggs; these are immediately inseminated by the male which accompanies the female. The shelter leaf sometimes falls onto the ground. The hatched larvae are

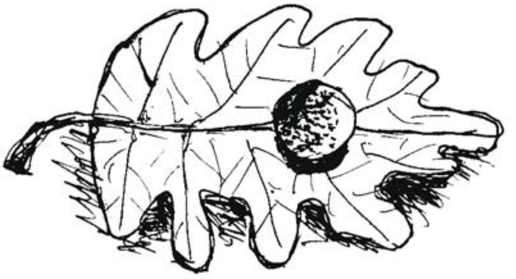

Fig. 2. The gall on an oak leaf offers shelter to an egg, a larva and a pupa

Fig. 3. The hazel leaf-roller undergoes larval development in a shelter built by the mother

safe and they nourish on the decaying roll. Pupation takes place in the soil (Bauer, 1956; Sandner, 1990).

Inside leaves of trees and other plants live larvae of a small *Nepticulidae* butterfly with wings reaching the size of 1 cm. They bore winding corridors – tunnels, which become increasingly wider as the larvae grow (Fig. 4). These tunnels are called mines; they end at a site where the larva leaves the leaf and climbs down to the ground on a silky thread. The various species of this butterfly form specific patterns of the corridors.

The larvae and pupae of *Lipara* genus flies undergo metamorphosis in a hiding place. First instar larvae of *L. lucens* hatch from eggs laid on the surface of common reed leaves; they enter the leaf sheath and move between the young leaves. Inside the stalk, the larvae moult and enter the second and the third instar. The first and second instar larvae feed on young leaves that grow at the apex (phytophages), while the third instar larvae eat both live and dead fragments of the plant (phytosaprophages). Hidden in the reed stalk, the third instar larvae overwinter and in spring pupae appear. Larval feeding activity leads to higher density of internodes at the tip of the stalk, which is

Fig. 4. A mine bored by a growing caterpillar

visible as a conspicuous cigar-shaped deformity (gall) (Fig. 5). Both the second and the third larval instar contribute to formation of the gall. The imago leaves the deformed stalk and starts laying eggs instantly (Grochowska, 2006).

Larvae of *Ipidae* woodworm (Fig. 6), e.g. bark beetle (*Ips typographus*) undergo the developmental stages in a hidden place. Before ovipositioning, the female bores a maternal chamber in the bark of the damaged tree and makes small incisions – grooves bored at similar distances on its sides.

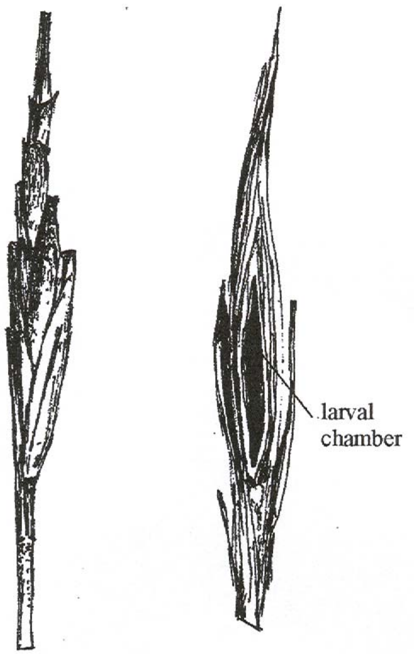

Fig. 5. The *Lipara lucens* L. gall A – external view B – longitudinal section

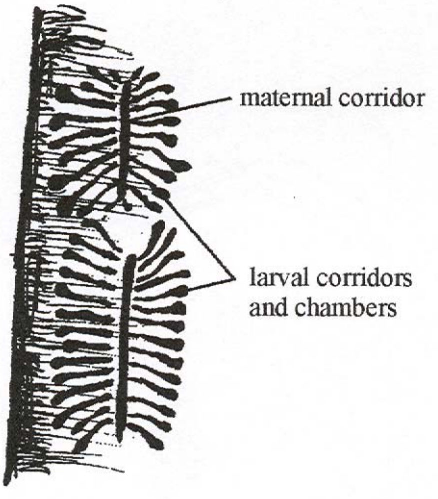

Fig. 6. Bark beetles bore corridors under the tree bark

Here, the female lays one egg in each groove, a total of 20–40, and leaves the tree. The hatched larvae bore tunnels in the tree directed off the maternal chamber. They are narrow initially, but they enlarge along with larval growth and end with a chamber in which pupation commences.

An interesting way to hide from enemies such as ants is displayed by the larva of the spittlebug (*Philaenus spumarius*) from the *Homoptera* order; in fact it makes the larva better recognised that adult forms of the insect. The larva is almost all hidden in saliva-like whitish spittle (Fig. 7). It is produced in an early period of its life from the secretion of the abdominal wax glands that is saponified with liquid excrements. This product is saturated with air in the respiration process and soon gets hardened in the air. The produced cocoon protects the larva not only against enemies, but also against drying-up (Brehm, 1968; Sandner, 1990).

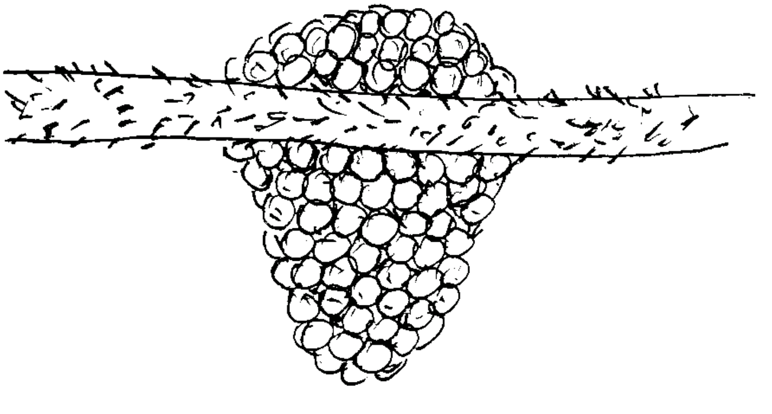

Fig. 7. A spittlebug larva hidden in whitish saliva-like spittle

3. I am not here (mimetism)

In order to protect themselves against enemies, insects in all developmental stages and in all habitats exhibit mimetism, which is reflected in unusual shapes, colours and patterns that they adopt to imitate the background. While observing insects in nature, one is often amazed by their great assimilation of the appearance and behaviour with the natural surroundings. Good camouflage is the result of quiet struggle between the prey and the predator. Caterpillars of the pine beauty moth (*Panolis flammea*) disperse after hatching, and their dark-green colour makes them look so similar to pine needles among which they live that single individuals are difficult to spot (Sandner, 1990).

Larvae of the tortoise beetle (*Cassida nebulosa*), which belongs to *Chrysomelidae*, have upward- and forward-bent fork-like spikes at the posterior part of the body. Successive moults inserted into one another are left on these spikes and covered with excrements thus forming a perfect cover for the larva by imitating a lump of dirt in which the larva is not distinguishable. *Cassida murrarea* larvae are similarly camouflaged (Brehm, 1968).

The horned treehopper (*Centrotus cornutus*), a representative of *Membracidae* is difficult to spot. It has three projections on the prothorax: two laterally bent and the third, bigger one running backwards. When standing motionlessly, the insect resembles a thorn on the plant stem. Caterpillars of the *Geometridae* butterflies, e.g. *Ennomos illustraria*, resemble twigs not only in their colour, but also the texture of the body coverings and body position. They often hold a twig with the abdominal prolegs and bend at an angle that is exactly the same as that of small twigs and leaves, it is therefore difficult to notice them (Fig. 8) (Fabre, 1925). Day butterflies are able to hide because the upper, colourful surface of the wings is visible only during flight; when the butterflies rest and the wings are folded, only the lower camouflage-coloured surface that facilitates blending with the environment can be seen. For instance, a red underwing butterfly (*Catocala nupta*) sitting on a tree trunk is invisible as its upper forewings have the colour of the bark.

Fig. 8. A *Geometridae* butterfly caterpillar mimics a twig

Highly advanced mimetism is found in numerous exotic insects, among others in the representative of *Nymphalidae – Kallima inachus formosana* butterfly. While sitting on a tree branch with the wings folded, it resembles a dry leaf in its colour and shape. There is nearly absolute similarity, because the wing venation resembles the medial and lateral leaf venation in a most delusive way. The short appendage of the hind wings imitates a petiole and a few dark spots emphasize similarity of this butterfly to dry leaves (Sandner, 1990).

Most beetles from the family *Buprestidae* are as glossy as jewels, although not all of them. The African *Julodis klugi* is hairy and thanks to this it collects considerable amounts of pollen on the dorsum, which are abundant enough to cover the insect while visiting flowers. The Shield Mantis *Choeradodis rhombicollis* from Costa Rica is a master of camouflage – its flattened body, stalk-like legs and the green colour make her resemble a leaf. A representative of the family *Rhopalidae* bugs – rhopalid *Chorosoma schillingi* lives in sandy habitats overgrown with dry grass. Its slender body resembles a piece of dry grass stalk.

The Brazilian bush cricket *Ommatoptera pictifolia* displays an interesting way of hiding against predators. When it remains motionlessly on a twig, it resembles an old dried-up leaf, which does not attract other animals. When in danger, it jumps high and raises the hind wings demonstrating the brown and red spots which are meant to intimidate the attacker. Another grasshopper, the brown *Sathrophylia rugosa* from India is invisible when it sits close to a twig. Its body perfectly mimics the background, and the various patterns and spots on its wings imitate the tree bark. In its light-brown colour, the South American *Flatoides delbatus* resembles lichens on the tree bark and is therefore very difficult to notice. It is not simple to tell the difference between lichens and the longhorn beetle *Lithinus nigrocristatus*. The spotted patches of lichens offer these insects a disguise.

Mimetism ensures safety to the larvae of the butterfly *Trichoplusiani* (*Noctuidae*). The female of this species does not lay eggs carefully, but she scatters them. The hatched larvae may have different colours as they mimic the colour of the host plant. Such highly advanced critical colouring is determined by feeding on the first host plant only (Sittenfield et al., 2002).

An example of interesting camouflage is provided by the caterpillar of the *Nemoria arizonaria* moth from the family *Geometridae* living in the south-western states of the USA and in Mexico. Females of this moth lay eggs on oaks twice a year – in spring and summer. Caterpillars hatched in spring live and feed on the nodular, yellow oak inflorescences, which they mimic. The larval body coverings are almost indistinguishable from the inflorescences. Their surface is yellow and covered with red-brown nodules which imitate flower stamina. Caterpillars which hatch in summer may only feed on leaves; although initially they resemble the spring generation, later they adopt the appearance of young, green shoots and mimic them even by orienting their bodies in the same angle as that between young twigs and bigger branches (Greene, 2000). Experimental investigations on alteration of food in two generations demonstrated that caterpillars' appearance depends solely on the substances contained in the food (Greene, 1996; Koszteyn, 2005).

Despite the considerable size of the body (reaching approximately 20 cm) and lack of active defence means, representatives of phasmids (*Phasmida*) prove to be real masters of camouflage. Both the shape and the colour of the body play a protective role. Phasmids' bodies display two types of structure: either elongated and slender or flattened and cylindrical; therefore, some of these insects mimic twigs (Fig. 9) and others resemble leaves. When disturbed, the stick-insect *Bacillus rossi* or *Caransia morosus* hold their legs and antennae along the body and pretends to be another twig. In its shape and colour, *Phyllium biocilatum* resembles a leaf as its body and legs are flattened (Fig. 10). It leads a nocturnal life-style, but at dawn, it becomes immobile and cataleptic. In this condition it is possible to orient its legs in any position. When the twig the phasmid is sitting on is touched, the insect sways along. That is why Indians believe that these insects emerge from leaves. The species is characterised by wind mimetism (Brehm, 1968; Boczek, 1990; Sandner, 1990).

Mimetism based on a transparent body is quite exceptional. This simplest way of matching the body colour to the background is represented by the larvae of the angle shades *Phlogophora meticulosa*. Its transparent body shows a large digestive tract filled with green contents, which ensures invisibility among leaves. Another example of mimetism based on a transparent body is provided by the *Cithaerias esmeralda (*Nymphalidae*)* butterfly from the Monteverde Mountains in Costa Rica. Due to a small numbers of scales, its wings are nearly transparent and make the insect less visible.

Fig. 9. A stick-insect with its folded legs looks like a shrub twig

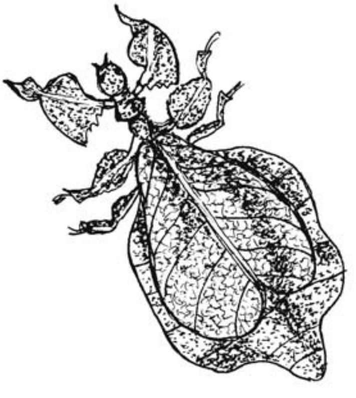

Fig. 10. The leaf insect mimics a leaf by its shape and colour (acc. to Boczek, 1990)

Some animal species achieve safety by the so-called refractive colouring, which facilitates blurring of the body contour (Wojtusiak, 1991). For example, in *Melanolophia canadaria* and *Catocala ultronia* butterflies, the arrangement of dark stripes and marks on the wings corresponds with the vertical grooves in the tree bark. At a longer distance, it is difficult to spot the triangular shape of the moth's body on the tree trunk. Similarly, the moth *Catocala relicta*, which has white striped wings, blends with the birch bark. When the fragment of trunk was devoid of the white bark, the moth was observed to change the resting place so as to find on a lighter patch.

Young caterpillars of the European butterfly *Hyloicus pinastri* have white and green stripes along the body; the body remains in a parallel position to tree needles among which they live. The last instar larvae, which have no parallel stripes on the body, do not stay among needles but on branches, where they are less visible.

Despite the body colour camouflage of the insect with the background, stereoscopic vision would enable predators to spot the prey, if there were no phenomenon of the counter-shade. This means of defence is typical of caterpillars in some insect species. When lighted, the darker dorsal part of the body seems to be less convex than the lighter ventral part which remains in shade. The larva in this position loses its three-dimensional appearance and as a two-dimensional form is not an attractive prey any more even for such perfect predators as birds. Caterpillars of some moth species from family *Notodontidae*, e.g. the puss moth *Dicranura vinula,* have a darker ventral part of the body which they turn towards light after feeding; thus they take advantage of counter-shade as a form of defence. Caterpillars of the brimstone *Gonepteryx rhamni* from the family *Pieridae* have a dark dorsal part and are therefore safe in the "normal" position. Apart from this contrast, caterpillars' similarity to leaves is additionally enhanced by stripes on the lateral side and by its colour. The colour of caterpillars' body is provided by dyes contained in food which are absorbed selectively by their organisms and deposited in the body coverings (McGowan, 2000). Such visual effects are called chiaroscuro by painters (Sandner, 1990; Wojtusiak, 1991).

Hairy caterpillars are also provided with a considerable safety thanks to reduction of the body shade. The big number of short setae on the lateral side contributes to blurring of the frontier between the body and the milieu when the animal moves along a suitable background.

Many insects inhabiting different habitats in various regions of a given country are characterized by different body colouring. This is referred to as polymorphism.

The yellow shell moth *Camptogramma bilineata* from the *Geometridae* family, which is usually light yellow, has its dark variety living on the dark rocks of the island of Jersey and on the dark peat bogs of Connemara in Ireland and a light-coloured form which lives in the light-grey calcareous rocks of the neighbouring regions. Light-coloured individuals are more visible against the dark background and are therefore eliminated by insectivorous birds. Individuals of the grayling (*Hipparchia semele*) living on the area of cretaceous rock have a lighter ventral side and the colour of this part of the body in those inhabiting heath is more brown. A locust remaining in an area of burnt-out savannah changes its colour from dirty-white through yellow and brown to reach black within a few days. It loses this ability in the migratory phase. The colouring of the white-faced darter (*Leucorrhinia dubia*) larvae may fluctuate between yellow-brown to vivid green and always corresponds to the colour of the background (Rutkowski, 1999). The ability to change colour was also observed in the larvae of the North American *Ischnura vericalis* dragonfly.

The so-called industrial melanism, i.e. appearance of dark butterflies in highly polluted areas, is worth mentioning. This phenomenon was observed in the middle of the 19th century in the industrial regions of Great Britain. As a result of soot- and smoke-borne industrial pollution, lichens on tree trunks disappeared and butterflies' resting sites became darkened. The peppered moth (*Biston betularia*) is an example proving that colouring helps butterflies to survive. The light forms of this insect are perfectly invisible on a tree bark overgrown with lichens and on grain stalks. Factory smoke in the industrial areas of England changed the selection conditions of the peppered moth, which gave way to the dark-brown forms. The chances of survival and reproduction of the dark pepper moth is three-fold greater than of the light-coloured varieties. Industrial melanism has also been reported in *Boarmia punctinalis.*

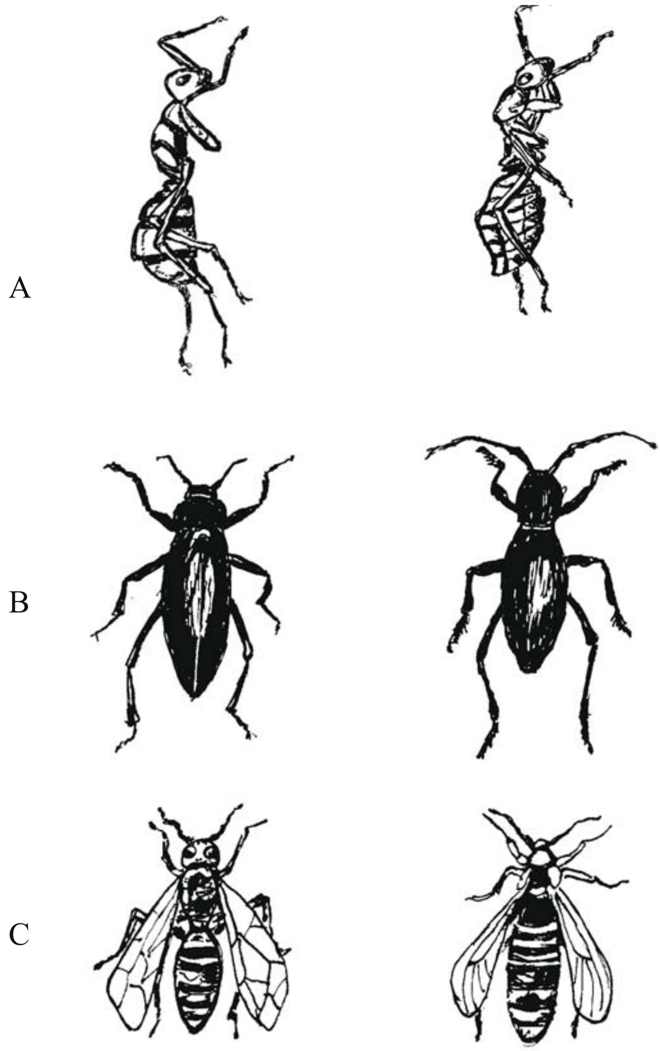

Fig. 11. Examples of Batesian mimicry in insects on the right (acc. to Boczek, 1990)
A – the hemipteran insect from the family *Miridae* mimics an ant;
B – a defenceless longhorn of the stinky beetle;
C – a hornet moth mimics a hornet

4. I am something else (mimicry)

A common insect defence mechanism is mimicry, which attracted Bates' attention in the middle of the 19th century. Harmless insects look and behave as poisonous or stinging animals (Batesian mimicry). Insects convey the information that they are inedible with the use of sounds, a specific colour and body structure (Fig. 11) (Kaleta, 2003; Koszteyn, 2005). For instance, a hemipteran insects from the family *Miridae* resembles an ant in terms of body form and structure (Fig. 11 A).

Longhorn beetles are a group of beetles exposed to predators' attack because they spend a considerable part of life on tree trunks. However, they are safe because they imitate poisonous or stinging insects (Fig. 11 B). At first sight, it is difficult to distinguish the Borneo longhorn beetle *Nothopeus fasciatipennis* from the wasp *Hemipepsis speculifer*. Representatives of the family *Sesiidae*: the lunar hornet moth *Trochilium craboniformis* or the hornet moth *Aegeria apiformis* (Fig. 11 C) resemble a hornet, wasp or bee rather than a butterfly. The black and yellow pattern of the abdomen and narrow transparent wings contribute to their similarity to hymenopteran insects. The latter trait is a result of "windows", i.e. areas devoid of scales. Thanks to this advanced mimicry, defenceless butterflies avoid being eaten by insectivorous animals. Bearing in mind the unpleasant experience, a predator which has once hunted for a wasp will never prey on any of them again (Boczek, 1990).

Other non-stinging insects, e.g. the drone fly *Eristalis tenax* from the family *Syrphidae* have evolved colours that delusively resemble a bee – black and yellow, contrastive and distinct stripes. The fly resembles a bee not only by the colours but also by the size and posture while sitting on flowers. Higher mimicry was reported from the South American saltatoria. It is not only coloured similarly to a wasp, but also pretends to have a powerful weapon – it walks on five legs and holds the sixth one stiff behind the body, which gives the impression of a sting. When in danger, the caterpillar from the *Sphingidae* family from Central America "transforms" into a venomous snake. At first it becomes motionless as if it pretended a twig. If the predator does not give up, the caterpillar bends its head inward simultaneously showing the ventral part of its body. Thus it shows the predator a colourful picture of "a head with two eyespots" and wriggles the posterior part of the body as if it were the bifid tongue of a snake. The feeling of fear of venomous snakes, which is so common in the animal world, ensures the insect safety (Attenborough, 1979). Caterpillars of the *Sphingidae* butterflies from Galapagos have a picture of snake's scales and eyes painted on the body. As shown in investigations, such appearance reduces the frequency of predator attack by 76% (Birkhead et al., 1994). The African grasshopper *Myrmecophana fallax* mimics a venomous ant. The insect has a wider "waist" than an ant, but the camouflage provided by white colouring of the lateral sides effectively produces the look of an ant. The hemipteran insects from family *Miridae* also mimic ants.

The butterfly *Caligo eurilochus* from the family *Nymphalidae* living in Honduras and Columbia has a picture of a big, yellow-rimmed "eye" on both hind wings. When it folds them, it resembles an owl and thus intimidates predators effectively (Sandner, 1990). When in danger, one of the Brazilian beetles immediately folds up its legs, lies on one side, displays the white ventral part of its body and holds one of its forelegs flattened on the background. Thus, the beetle imitates fresh birds' dung on the ground.

Sometimes insects cooperate with each other in order to deceive the enemy. The Madagascan Auchenorrhyncha suborder *Homoptera* have brightly coloured wings. To deceive the insectivorous birds, they cluster together and resemble inflorescences. In *Ityraea gregorii*, each individual takes the role of a petal. Some of them have yellow wings and others – green, and when they sit tightly next to one another, they create a partially developed bud with yellow petals emerging from green sepals. They retain the ability of collective camouflage also during flight (Cuisin and Albert, 1993).

The defence mechanisms described above are only a small part of the insect defence arsenal. These animals employ not only passive, but also highly diversified active forms of defence.

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