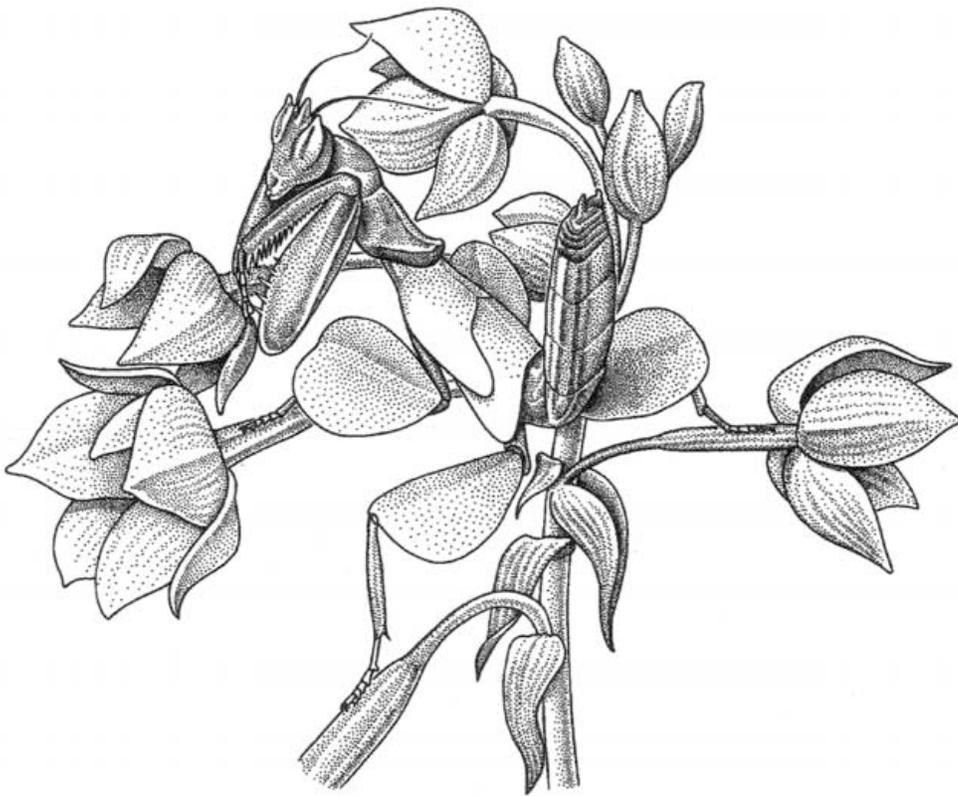


INSECT DEFENCE

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*Cryptic mantid among orchid flowers*

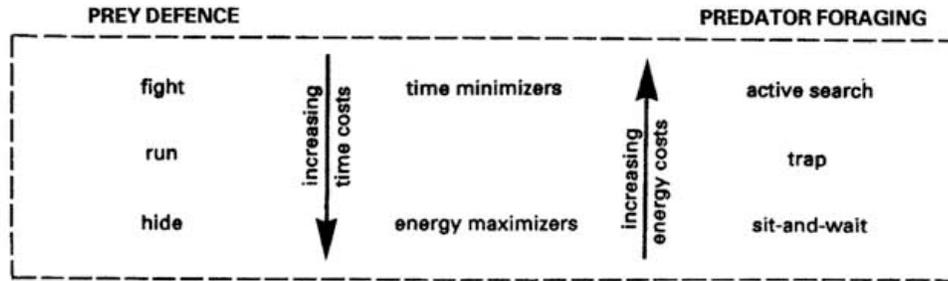


Fig. 13.1 The basic spectrum of prey defence strategies and predator foraging, varying according to costs and benefits in both time and energy. (After Malcolm, 1990.)

Although some humans eat insects (Chapter 1), many 'western' cultures are reluctant to use them as food. This aversion extends no further than humans. For very many organisms, insects provide a substantial food source: they are nutritious, abundant and diverse, and they are found everywhere. Some animals, termed **insectivores**, rely almost exclusively on a diet of insects; omnivores may eat them opportunistically and many herbivores unavoidably consume insects. Insectivores may be vertebrates or invertebrates, including arthropods – insects certainly eat other insects. Even plants lure, trap and digest insects; for example, pitcher plants (both New World Sarraceniaceae and Old World Nepenthaceae) digest arthropods, predominantly ants, in their fluid-filled pitchers (section 10.4.2), and the flypaper and Venus flytraps (Droseraceae) capture many flies. Insects, however, actively or passively resist being eaten, by means of a variety of protective devices – the insect defences that are the subject of this chapter.

Before continuing, some commonly used terms discussed in Chapter 12 should be reviewed. A predator is an animal that kills and consumes a number of prey animals during its life. Animals that live at the expense of another animal but do not kill it are parasites, which may live internally (endoparasites) or externally (ectoparasites). Parasitoids are those which live at the expense of

one animal that dies prematurely as a result. The animal attacked by parasites or parasitoids is a host. All insects are potential prey or hosts to many kinds of predators (either vertebrate or invertebrate), parasitoids or, less often, parasites.

Many defensive strategies exist, including specialized morphology, behaviour, noxious chemicals and responses of the immune system. This chapter deals with aspects of defence that include death feigning, autotomy, crypsis (camouflage), chemical defences, aposematism (warning signals), mimicry and collective defensive strategies. These are directed against a wide range of vertebrates and invertebrates but, since much study has involved insects defending themselves against insectivorous birds, the role of these particular predators will be emphasized. Immunological defence against microorganisms is discussed in Chapter 3 and those used against parasitoids are considered in Chapter 12.

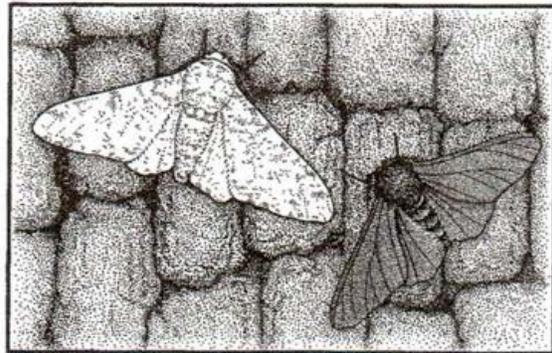
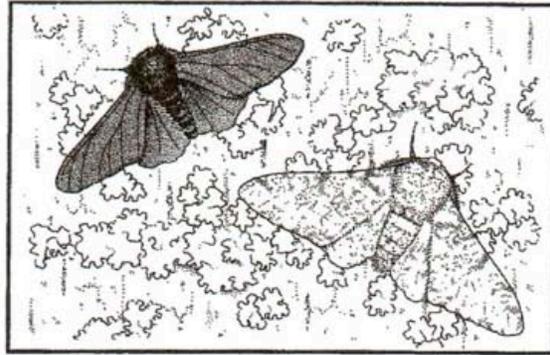
A useful framework for discussion of defence and predation can be based upon the time and energy inputs to the respective behaviours. Thus hiding, escape by running or flight, and defence by staying and fighting involve increasing energy expenditure but diminishing costs in time expended (Fig. 13.1). Many insects will change to another strategy if the previous defence fails: the scheme is not clear-cut and it has elements of a continuum.

## BOX 13.1

## INDUSTRIAL MELANISM – A BLACK-AND-WHITE CASE?

Britain's long history of enthusiastic amateur lepidopteran studies has allowed the detection of a fascinating case of apparent evolution of a novel pattern in a moth as a response to selective predation. The peppered moth (Geometridae: *Biston betularia*) was known to be a light-coloured moth with a habit of resting cryptically against the pale lichens of tree trunks. In 1848, in the heyday and heartland of the Industrial Revolution in Manchester, England, a **melanic** (dark) morph was reported for the first time. Although the melanic form increased in industrial areas (**industrial melanism**), this change was not followed in detail. Retrospectively, it seemed that these dark *carbonaria* forms of *B. betularia* were differentially successful in eluding bird predation as they rested on lichenless tree trunks blackened by soot. Their pale relatives, which were cryptically protected in clean areas, stood out and were picked off dark trunks by predators. In post-industrial Britain, following reduction in smoke emissions and restriction of air pollution, the frequency of melanics has declined. Experimental manipulations showed that moths settled on the appropriately coloured dark or light background, and when moths of each morph were placed on pale and dark tree trunks, as illustrated here, birds were shown to select inappropriately coloured morphs.

Re-examination, stimulated by discovery of pre-industrial melanism in museum-preserved specimens and recent observation of unpredicted proportions of light and dark morphs, has



cast doubts on the simplicity of this often cited example of evolution through natural selection. Firstly, the moths settle primarily under the shoulder (where a tree branch joins the trunk) rather than exposed on the trunk. At this joint, melanic moths are more cryptic than pale ones, even on pale trees in unpolluted areas. Furthermore, if consideration is given to the reflectance of the wings, the pale morph is most cryptic on a grey background of 30% reflectance (100% is pure white and 0% black) rather than white. In appropriately designed choice experiments, moths respond predictably with the pale

BOX 13.1—*continued*

morphs favouring somewhat darker backgrounds than pure white ones. If these factors are included in calculations of selective advantage, the previous curious excess of dark morphs in unpolluted rural areas becomes explicable.

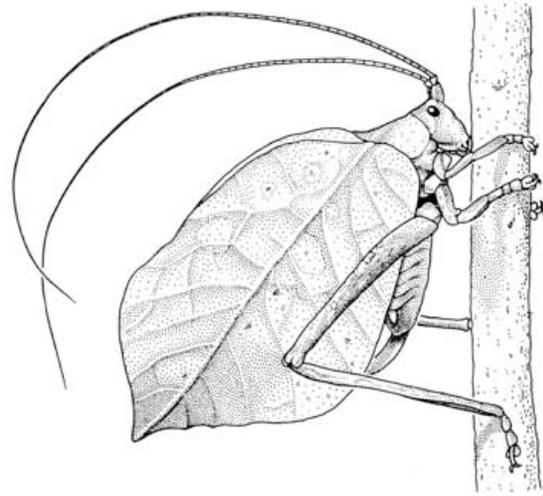
## 13.1 DEFENCE BY HIDING

In common language a **cryptic** insect, that is, a well-concealed insect that looks very much like its general background environment, is said to 'mimic' its surroundings. However, crypsis is usually excluded from definitions of true mimicry, which is restricted to animal resemblance to another animal that is recognizable by natural enemies (section 13.5).

Insect crypsis can take many forms. The insect may adopt **camouflage**, making it difficult to distinguish from the general background in which it lives, by:

- resembling a uniform coloured background, such as a green geometrid moth on a leaf;
- resembling a patterned background, such as a mottled moth on tree bark (Box 13.1);
- being countershaded – light below and dark above – as in some caterpillars and aquatic insects;
- having a pattern to disrupt the outline, as is seen in many moths that settle on leaf litter; or
- having a bizarre shape to disrupt the silhouette, as demonstrated by some membracid leafhoppers.

In another form of crypsis, termed **masquerade** or **mimesis** to contrast with the camouflage described above, the organism deludes a predator by resembling an inedible object that is a specific feature of its environment – something that is of no inherent interest to a predator. This feature may be an inanimate object, such as the bird dropping resembled by young larvae of some butterflies



**Fig. 13.2** A leaf-mimicking katydid, *Mimetica mortuifolia* (Orthoptera: Tettigoniidae) in which the fore wing resembles a leaf even to the extent of leaf-like venation and spots resembling fungal mottling. (After Belwood, 1990.)

like *Papilio aegaeus* (Papilionidae), or an animate object. 'Looper' caterpillars (the larvae of geometrid moths) resemble twigs, membracid homopterans imitate thorns arising from a stem and many stick-insects look very much like sticks and may even move like a twig in the wind. Many insects, notably amongst the lepidopterans and orthopteroids, look like leaves, even to the similarity in venation (Fig. 13.2). These may appear to be dead or alive, mottled with fungus, or even partially eaten as if by a herbivore.

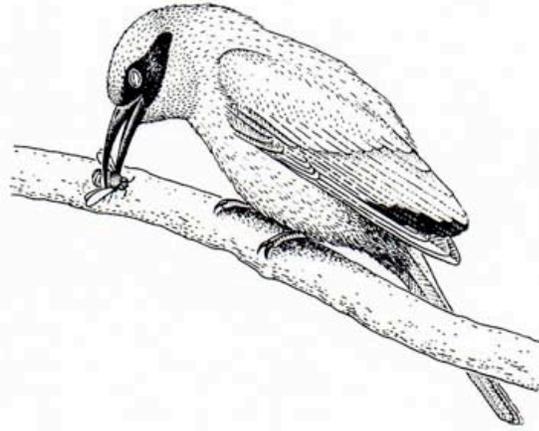
Crypsis is a very common form of insect concealment, particularly in the tropics and

BOX 13.2  
 AVIAN PREDATORS AS SELECTIVE AGENTS FOR INSECTS

Henry Bates, the first person to suggest a theory for mimicry, argued that it arose through agents selecting among different butterflies, based upon their association of mimetic patterns and unpalatability. Birds, it is contended, are crucial agents in the evolution of insect defences, and examination of the role of avian predators has always been central to these studies.

Two early views appeared to counter the selective importance of birds. The first, that birds do not prey on aposematic monarch butterflies or on either morph of *Biston betularia* (Box 13.1), can be dismissed as due to poor observation. The second, that the total observed insect food items of birds reflected the proportional availability of insect prey, regardless of whether protected or not, was taken to imply that birds could not be selective feeders. Actually, this result is unsurprising if birds exhibit the full range of foraging behaviours shown in Fig. 13.1. The problem is that combining dietary intakes – the results of the many different feeding strategies of insectivorous birds – reveals nothing of the specificity and effectiveness of predator–prey interactions, which relate to prey defence and total prey availability.

Thus winter-roosting monarch butterflies are fed upon by black-backed orioles (Icteridae) that browse selectively on poorly-defended individuals, while black-headed grosbeaks (Fringillidae) appear to be completely insensitive to the toxins. Old World bee-eaters (Meropidae) and neotropical jacamars (Galbulidae) are specialized predators,



able to deal with the stings of hymenopterans (the red-throated bee-eater, *Merops bullocki*, is shown here destinging a bee on a branch, after Fry *et al.*, 1992) and toxins of butterflies respectively; a similar suite of birds is able to feed selectively on noxious ants. The ability of these specialist predators to distinguish between varying patterns and edibilities makes them important selective agents in the evolution and maintenance of defensive mimicry.

Birds are observable insectivores for field and laboratory studies: their readily recognizable behavioural responses to unpalatable foods include head-shaking, disgorging of food, tongue-extending, bill-wiping, gagging, squawking, and ultimately vomiting. For many birds, a single learning trial with noxious (Class I) chemicals appears to lead to long-term aversion to the particular insect, even with a substantial delay between feeding and illness. However, manipulative studies of bird

BOX 13.2—*continued*

diets are complicated by their fear of novelty (neophobia) leading to rejection of startling and frightening displays (section 13.2).

It is unlikely that any insect has completely escaped the attentions of predators and certain birds can overcome even the most severe insect defences. For example, the lubber grasshopper (Acrididae: *Romalea guttata*) is large, gregarious and aposematic and it squirts volatile, pungent chemicals accompanied by a hissing noise when attacked. The lubber is extremely toxic and is avoided by all lizards and birds except one, the loggerhead shrike (Laniidae: *Lanius ludovicianus*), which snatches its prey, including lubbers, and impales them 'decoratively' upon spikes with minimal handling time. These impaled items serve both as food stores and in sexual or territorial displays. *Romalea*, which are emetic to shrikes when fresh, become edible after two days of lardering, presumably by denaturation of the toxins. Impaling behaviour thus proves to be preadaptive, permitting feeding upon an extremely well-defended insect. No matter how good the protection, there is no such thing as total defence in the coevolutionary arms race between prey and predator.

amongst nocturnally active insects. It has low energetic costs but relies on the insect being able to select the appropriate background. Experiments with two differently coloured morphs of *Mantis religiosa* (Mantidae), the European praying mantid, have shown that brown and green morphs placed against appropriate and inappropriate coloured backgrounds were fed upon in a highly selectively manner by birds: they removed all 'mismatched' morphs and found no camouflaged ones. Even if the right background is chosen, it may be necessary to orientate correctly: moths with disruptive outlines or with striped patterns resembling the bark of a tree may be concealed only if orientated in a particular direction on the trunk.

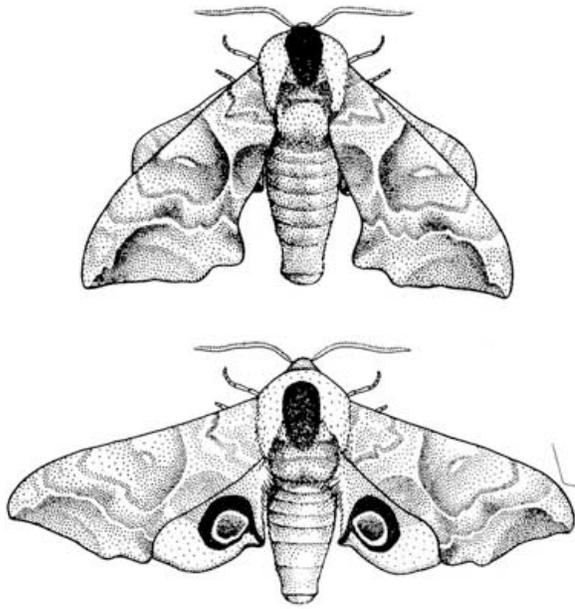
In the vignette at the head of this chapter, a nymph of the Indomalayan orchid mantid *Hymenopus coronatus* (Hymenopodidae) is shown blending beautifully with the pink flower spike of an orchid. The crypsis is enhanced by the close resemblance of the femora of the mantid's legs to the flower's petals. Crypsis enables the mantid to avoid detection by its potential prey (flower visitors)

(section 12.1.1) as well as to be concealed from predators.

## 13.2 SECONDARY LINES OF DEFENCE

Little is known of the learning processes of inexperienced vertebrate predators, such as insectivorous birds. However, studies of the gut contents of birds show that cryptic insects are not immune from predation (Box 13.2). Once found for the first time (perhaps accidentally), birds subsequently seem able to detect cryptic prey via a 'search image' for some element(s) of the pattern. Thus, having discovered that some twigs were caterpillars, American blue jays were observed to continue to peck at sticks in a search for food. Primates can identify stick-insects by one pair of unfolded legs alone, and will attack actual sticks to which phasmatid legs have been affixed experimentally. Clearly, subtle cues allow specialized predators to detect and eat cryptic insects.

Once the deception is discovered, the insect prey may have further defences available in reserve. In the energetically least demanding



**Fig. 13.3** The eyed hawk moth, *Smerinthus ocellatus* (Lepidoptera: Sphingidae): top, the brownish fore wings cover the hind wings of a resting moth; bottom, when the moth is disturbed, the black and blue eyespots on the hind wings are revealed. (After Stanek, 1977.)

response, the initial crypsis may be exaggerated, as when a threatened masquerader falls to the ground and lies motionless. This behaviour is not restricted to cryptic insects: even visually obvious prey insects may feign death (**thanatosis**). This behaviour, used by many beetles (particularly weevils), can be successful, as predators lose interest in apparently dead prey or may be unable to locate a motionless insect on the ground. Another secondary line of defence is to take flight and suddenly reveal a flash of conspicuous colour from the hind wings. Immediately on landing the wings are folded, the colour vanishes and the insect is cryptic once more. This behaviour is common amongst certain orthopterans and underwing moths; the colour of the flash may be yellow, red, purple or, rarely, blue.

A third type of behaviour of cryptic insects upon discovery by a predator is the production of a **startle display**. One of the commonest is to open the fore wings and reveal

brightly coloured 'eyes' that are usually concealed on the hind wings (Fig. 13.3). Experiments using birds as predators have shown that the more perfect the eye (with increased contrasting rings to resemble true eyes) the better the deterrence. Not all eyes serve to startle: perhaps a rather poor imitation of an eye on a wing may direct pecks from a predatory bird to a non-vital part of the insect's anatomy.

A quite extraordinary type of insect defence is the convergent appearance of part of the body to a feature of a vertebrate, albeit on a much smaller scale. Thus the head of a species of fulgorid bug, commonly called the alligator bug, bears an uncanny resemblance to that of a caiman. The pupa of a particular lycaenid butterfly looks like a monkey head. Some tropical sphingid larvae assume a threat posture which, together with false eyespots that actually lie on the abdomen, give a snake-like impression. These resemblances may deter predators (such as birds that search by 'peering about') by their startle effect, with the incorrect scale of the mimic being overlooked by the predator.

### 13.3 MECHANICAL DEFENCES

Morphological structures of predatory function, such as the modified mouthparts and spiny legs described in the previous chapter, may also be defensive, especially if a fight ensues. Cuticular horns and spines may deter a predator or have use in fighting, for example, in defence of territory or in combating a rival. For ectoparasitic insects, which are vulnerable to the actions of the host, one line of defence is given by the body shape and sclerotization. Fleas are laterally compressed and biting lice dorsoventrally flattened – shapes that make these insects difficult to dislodge from hairs or feathers. Furthermore, many ectoparasites have resistant bodies, and the heavily sclerotized cuticle of certain beetles must act as a mechanical anti-predator device.

Many insects construct retreats which can deter a predator that fails to recognize the structure as containing anything edible or that is unwilling to eat inorganic material. The cases of caddisfly larvae (Trichoptera), constructed of sand grains, stones or organic fragments (Fig. 9.6) may have originated in response to the physical environment of flowing water but certainly have a defensive role. Similarly, a portable case of vegetable material bound with silk is constructed by the terrestrial larvae of bagworms (Lepidoptera: Psychidae). In both caddisflies and psychids, the case serves to protect during pupation.

Artificial shields are constructed by some insects; for example, the larvae of certain lacewings cover themselves with the sucked-out carcasses of their insect prey or with lichens, and some larvae of chrysomelid beetles use their faeces for the same purpose. These may not act as barriers to a determined predator but will give a first mouthful of inedible material. The waxes and powders secreted by many homopterans (such as scale insects, woolly aphids, whiteflies and fulgorids) may function similarly, and also may entangle the mouthparts of a potential arthropod predator.

Body structures themselves, such as the scales of moths, caddisflies and thrips, can protect since they detach readily to allow the escape of a slightly denuded insect from the jaws of a predator, or the sticky threads of spider webs or the glandular leaves of insectivorous plants such as the sundews. A mechanical defence which seems at first to be maladaptive is **autotomy**, the shedding of limbs, as demonstrated by stick-insects (Phasmatodea) and perhaps crane flies (Diptera: Tipulidae). The upper part of the phasmatid leg has the trochanter and femur fused, with no muscles running across the joint. A special muscle breaks the leg at a weakened zone in response to a predator grasping the leg. Immature stick-insects and mantids can regenerate lost limbs at moulting, and certain

autotomized adults can induce an adult moult at which the limb can regenerate.

Secretions of insects can have a mechanical defensive role, acting as a glue or slime that ensnares predators or parasitoids. Certain cockroaches have a permanent slimy coat on the abdomen that confers protection. Lipid secretions from the **cornicles** (also called **siphunculi**) of aphids may gum up predator mouthparts or small parasitic wasps. Termite soldiers have a variety of secretions available to them in the form of cephalic glandular products, including terpenes that dry on exposure to air to form a resin. In *Nasutitermes* (Termitidae) the secretion is ejected via the nozzle-like **nasus** (a pointed snout or rostrum) as a quick-drying fine thread that impairs the movements of a predator such as an ant. This defence counters arthropod predators but is unlikely to deter vertebrates. Mechanical-acting chemicals are only a small selection of the total insect armoury that can be mobilized for chemical warfare.

#### 13.4 CHEMICAL DEFENCES

Chemicals play vital roles in many aspects of insect behaviour. Chapter 4 dealt with the use of pheromones in many forms of communication, including alarm pheromones elicited by the presence of a predator. Similar chemicals, called allomones, play important roles in the defences of many insects, notably amongst many Heteroptera and Coleoptera. The relationship between defensive chemicals and those used in communication may be very close, sometimes with the same chemical fulfilling both roles. Thus a noxious chemical that repels a predator can alert conspecific insects to the predator's presence and may act as a stimulus to action. In the energy/time dimensions shown in Fig. 13.1, chemical defence lies towards the energetically expensive but time efficient end of the spectrum. Chemically-defended insects tend to have high **apparency** to predators, that is, they are usually non-cryptic, active, often relatively

large, long-lived and frequently aggregated or social in behaviour. They often signal their distastefulness by **aposematism** – warning signalling usually involving bold colouring but sometimes including odour and perhaps sound production.

#### 13.4.1 Classification by function of defensive chemicals

Amongst the diverse range of defensive chemicals produced by insects, two classes of compounds can be distinguished by their effects on a predator. Class I defensive chemicals are noxious because they irritate, hurt, poison or drug individual predators. Class II chemicals are innocuous, being essentially antifeedant chemicals that merely stimulate the olfactory and gustatory receptors, or aposematic indicator odours. Many insects use mixtures of the two classes of chemicals and, furthermore, Class I chemicals in low concentrations may give Class II effects. Contact by a predator with Class I compounds results in repulsion through, for example, emetic (sickening) properties or induction of pain, and if this unpleasant experience is accompanied by odorous Class II compounds, predators learn to associate the odour with the encounter. This conditioning results in the predator learning to avoid the defended insect at a distance, without the dangers (to both predator and prey) of having to feel or taste it.

Class I chemicals include both **immediate**-acting substances which the predator experiences through handling the prey insect (which may survive the attack), and chemicals with **delayed**, often systemic, effects including vomiting or blistering. In contrast to immediate-effect chemicals sited in particular organs and applied topically (externally), delayed-effect chemicals are distributed more generally within the insect's tissues and haemolymph and are tolerated systemically. Whereas a predator rapidly learns to associate immediate distastefulness with particular prey (especially if it is aposematic), it is

unclear how a predator identifies the cause of nausea some time after the predator has killed and eaten the toxic culprit, and what benefits this action brings to the victim. Experimental evidence from birds shows that these predators are indeed able to associate a particular food item with a delayed effect, perhaps through taste when regurgitating the item. Too little is known of feeding in insects to understand if this applies similarly to predatory insects. Perhaps a delayed poison that fails to protect an individual from being eaten evolved through the education of a predator by a sacrifice, thereby allowing differential survival of relatives (section 13.6).

#### 13.4.2 The chemical nature of defensive compounds

Class I compounds are much more specific and effective against vertebrate than arthropod predators. For example, birds are more sensitive than arthropods to toxins such as cyanides, cardenolides and alkaloids. Cyanogenic glycosides are produced by zygaenid moths (*Zygaenidae*), *Leptocoris* bugs (*Rhopalidae*) and *Acraea* and *Heliconius* butterflies (*Nymphalidae*). Cardenolides are very widespread, occurring notably in monarch butterflies (*Nymphalidae*), certain cerambycid and chrysomelid beetles, lygaeid bugs, pyrgomorphid grasshoppers and even an aphid. Similarly, a variety of alkaloids are acquired convergently in many coleopterans.

Possession of Class I emetic or toxic chemicals is very often accompanied by aposematism, particularly coloration if directed against visual-hunting diurnal predators. However, visible aposematism is of no use at night, and the sounds emitted by nocturnal moths such as certain *Arctiidae* when challenged by bats may be aposematic, warning the predator of a distasteful meal.

Class II chemicals tend to be volatile and reactive organic compounds with low molecular weight, such as aromatic ketones, aldehydes, acids and terpenes. Examples include

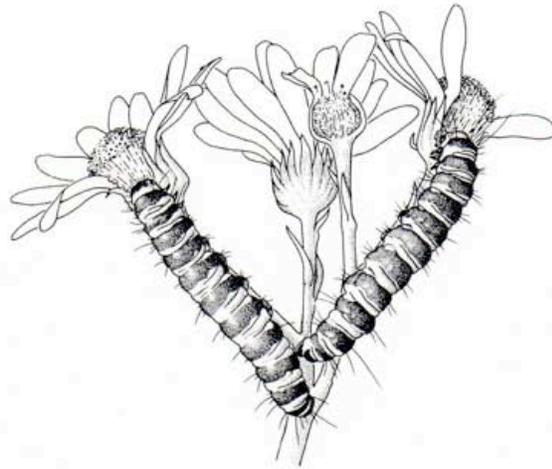
the stink gland products of Heteroptera and the many substances of low molecular weight such as formic acid, emitted by ants. Bitter-tasting but non-toxic compounds like quinones are commonly occurring Class II compounds. Many defensive secretions are complex mixtures that can involve synergistic effects. Thus the carabid beetle *Heluomorphodes* emits a Class II compound, formic acid, which is mixed with *n*-nonyl acetate that enhances skin penetration of the acid to give a Class I painful effect.

The role of these chemicals in aposematism, warning of the presence of Class I compounds, was considered above. In another role, these Class II chemicals may be used to deter predators such as ants that rely on chemical communication. For example, prey such as certain termites, when threatened by predatory ants, release mimetic ant alarm pheromones, thereby inducing inappropriate ant behaviours of panic and nest defence. In another case, ant-nestinquilines, which might provide prey to their host ants, are unrecognized as potential food because they produce chemicals that appease ants.

Class II compounds alone appear unable to deter many insectivorous birds. For example, blackbirds (Turdidae) will eat notodontid (Lepidoptera) caterpillars that secrete a 30% formic acid solution; many birds actually encourage ants to secrete formic acid into their plumage in an apparent attempt to remove ectoparasites (so-called 'anting').

#### 13.4.3 Sources of defensive chemicals

Many defensive chemicals, notably those of phytophagous insects, are derived from the host plant upon which the larvae (Fig. 13.4) and, less commonly, the adults feed. Frequently a close association is observed between restricted host-plant use (monophagy or oligophagy) and the possession of a chemical defence. An explanation may lie in a coevolutionary 'arms race' in which a plant develops toxins to deter phytophagous



**Fig. 13.4** The distasteful and warningly coloured caterpillars of the cinnabar moth, *Tyria jacobaeae* (Lepidoptera: Arctiidae), on ragwort, *Senecio jacobaeae*. (After Blaney, 1976.)

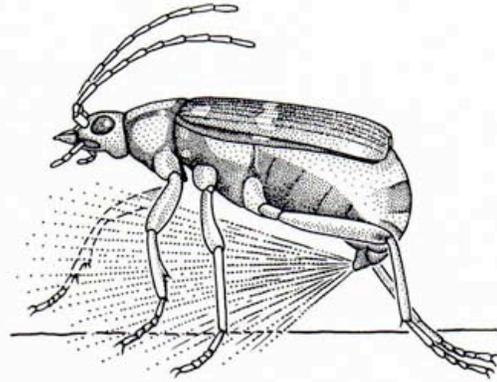
insects. A few phytophages overcome the defences and thereby become specialists able to detoxify or sequester the plant toxins. These specialist herbivores can recognize their preferred host plants, develop on them and use the plant toxins (or metabolize them to closely related compounds) for their own defence.

Although some aposematic insects are closely associated with toxic food plants, certain insects can produce their own toxins. For example, amongst the Coleoptera, meloid beetles synthesize cantharidin, buprestids make buprestin, and some chrysomelids can produce cardiac glycosides. The very toxic staphylinid *Paederus* synthesizes its own blistering agent, pederin. Experimentally it has been shown that certain insects which sequester cyanogenic compounds from plants can still synthesize similar compounds if transferred to toxin-free host plants. If this ability preceded the evolutionary transfer to the toxic host plant, the possession of appropriate biochemical pathways may have preadapted the insect to using them subsequently in defence.

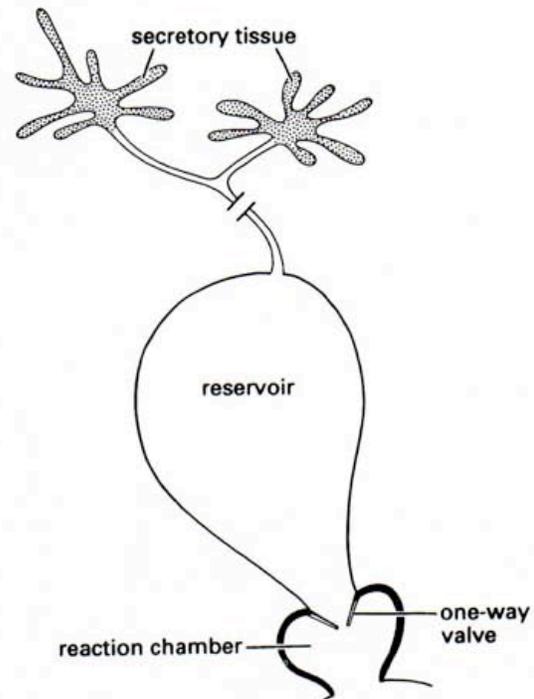
BOX 13.3  
INSECT BINARY CHEMICAL WEAPONS

The common name of bombardier beetles (Carabidae: including genus *Brachinus*) derives from the observations by early naturalists that the beetles released volatile defensive chemicals which appeared like a puff of smoke, accompanied by a 'popping' noise resembling gunfire. The spray, released from the anus and able to be directed by the mobile tip of the abdomen, contains *p*-benzoquinone, a deterrent of vertebrate and invertebrate predators. This chemical is not stored; when required, it is produced explosively from components held in paired glands. Each gland is double, comprising a muscular-walled, compressible inner chamber containing a reservoir of hydroquinones and hydrogen peroxide, and a thick-walled outer chamber containing oxidative enzymes. When threatened, the beetle contracts the reservoir, and releases the contents through the newly opened inlet valve into the reaction chamber. Here an exothermic reaction takes place, resulting in the liberation of *p*-benzoquinone at a temperature of 100 °C.

Studies on a Kenyan bombardier beetle, *Stenaptinus insignis*, (illustrated here, after Dean *et al.*, 1990) showed that the discharge is pulsed: the explosive chemical oxidation produces a build-up of pressure in the reaction chamber which closes the one-way valve from the reservoir, thereby forcing discharge of the contents through the anus (as shown by the beetle directing its spray at an antagonist in front of it). This relieves the pressure, allowing the valve to open, permitting refilling of the



bombardier beetle



reaction chamber from the reservoir (which remains under muscle pressure). Thus the explosive cycle continues. By this mechanism a high-intensity pulsed

BOX 13.3—*continued*

jet is produced by the chemical reaction, rather than requiring extreme muscle pressure. Humans discovered the principles independently and applied them to engineering (as pulse jet propulsion) some millions of years after the bombardier beetles developed the technique.

Amongst the many unusual means of obtaining a defensive chemical, that used by *Photurus* fireflies (Lampyridae) is one of the most bizarre. Many fireflies synthesize deterrent bufadienolides, but *Photurus* females cannot do so. Instead they acquire their supplies by eating male *Photinus* fireflies, which are lured to their deaths by the *Photurus* females that mimic the flashing sexual signal of the *Photinus* female.

#### 13.4.4 Organs of chemical defence

Endogenous defensive chemicals (those synthesized within the insect) are generally produced in specific glands and stored in a reservoir (Box 13.3). Release is through muscular pressure or by evaginating the organ, rather like turning the fingers of a glove inside out. The Coleoptera have developed a wide range of glands, many eversible, that produce and deliver defensive chemicals. Many Lepidoptera use urticating (itching) hairs and spines to inject venomous chemicals into a predator. Venom injection by social insects is dealt with in section 13.6.

In contrast to these endogenous chemicals, exogenous toxins, derived from external sources such as foods, are usually incorporated in the tissues. This makes the complete prey unpalatable but requires the predator to test at close range in order to learn, in contrast to the distant effects of many endogenous compounds. However, the larvae of some swallowtail butterflies (Papilionidae) that feed upon distasteful food plants concentrate the toxins and secrete them into a thoracic pouch

called an **osmeterium**, which is everted if the larvae are touched. The colour of the osmeterium is often aposematic, reinforcing the deterrent effect on a predator (Fig. 13.5). Larval sawflies (Hymenoptera: Pergidae), colloquially called 'spitfires', store eucalypt oils, derived from the leaves that they eat, within a diverticulum of their foregut and ooze this strong smelling, distasteful fluid from their mouths when disturbed (Fig. 13.6).

#### 13.5 DEFENCE BY MIMICRY

The theory of **mimicry** is an interpretation of the close resemblances of unrelated species and was an early application of the theory of evolution. Bates, a naturalist studying in the Amazon in the mid nineteenth century, observed that many similar butterflies, all slow-flying and brightly coloured, seemed to be immune from predators. Although many species were common and related to each other, some were rare and belonged to quite distantly related families. Bates believed that the common species were chemically protected from attack, and this was advertised by their aposematism – high apparency (behavioural conspicuousness) through bright colour and slow flight. The rarer species, he thought, probably were not distasteful but gained protection by their superficial resemblance to the protected ones. On reading the views that Darwin had newly proposed in 1859, Bates realized that his own theory of mimicry involved evolution through natural selection. Poorly protected species gain increased immunity from predation by

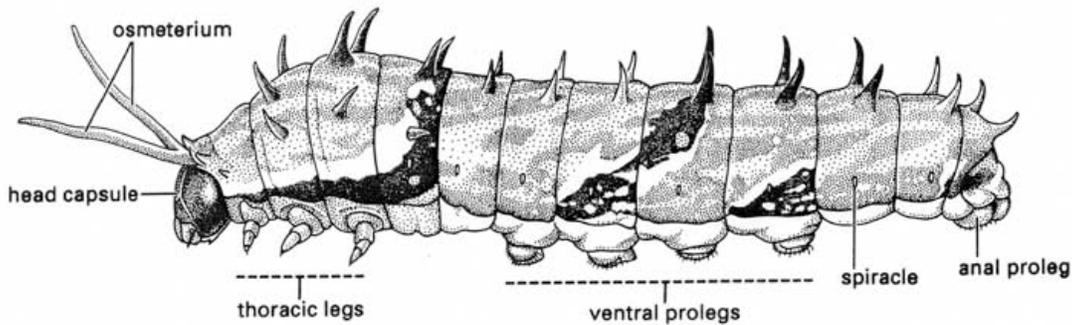


Fig. 13.5 A caterpillar of the orchard butterfly, *Papilio aegaeus* (Lepidoptera: Papilionidae), with the osmeterium everted behind its head. Eversion of this glistening, bifid organ occurs when the larva is disturbed; it is accompanied by a pungent smell.

differential survival of subtle variants that more resembled protected species in either appearance, smell, taste, feel or sound. The selective agent is the predator that preferentially eats the inexact mimic. Since that time, mimicry has been interpreted in the light of evolutionary theory, and insects, particularly butterflies, have remained central to mimicry studies.

Understanding mimicry systems requires recognition of three basic components: the **model**, the **mimic** and the **observer**. These components are related to each other through signalling and receiving systems, of which the basic association is the warning signal given by the model (e.g. aposematic colour which warns of a sting or bad taste) perceived by the observer (e.g. a hungry predator). The naive observer must learn of the association between aposematism and subsequent pain or distaste. When learnt, the observer will thereafter avoid the model. The model clearly benefits from this coevolved system, in which the observer can be seen to gain by not wasting time and energy chasing an inedible prey.

Once such a mutually beneficial system has evolved, it is open to manipulation by others. The third component is the mimic: an organism that parasitizes the signalling system through deluding the observer, for example, by false warning colouration. If this provokes



Fig. 13.6 An aggregation of sawfly larvae (Hymenoptera: Pergidae: *Perga*) on a eucalypt leaf. When disturbed, the larvae bend their abdomens in the air and exude droplets of sequestered eucalypt oil from their mouths.

a reaction from the observer similar to true aposematic colouration, the mimic is dismissed as unacceptable food. It is important to realize that the mimic need not be perfect, as long as it can elicit the appropriate avoidance response from the observer. Only a limited subset of the signals given by the model may be required. For example, the black and yellow banding of venomous wasps is an aposematic colour pattern that is displayed by countless species from amongst many orders of insects. The exactness of the match, at least

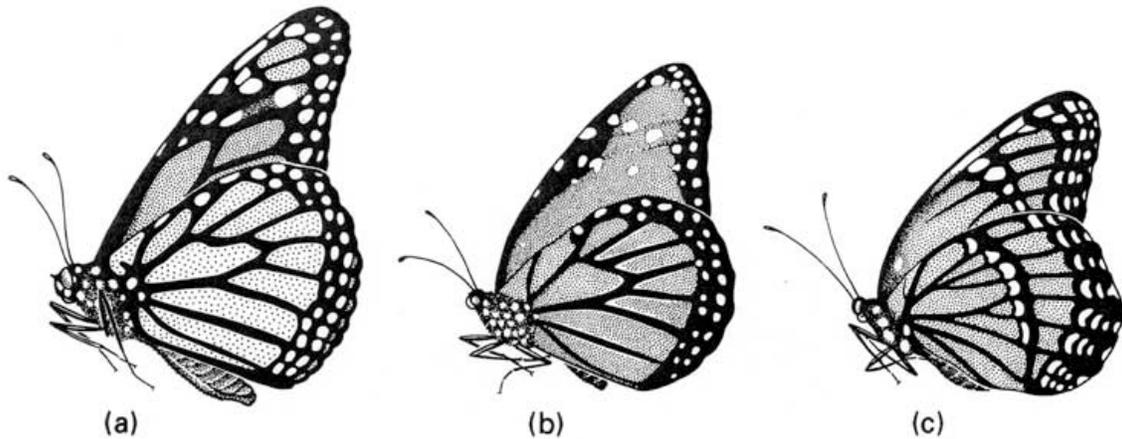


Fig. 13.7 Three nymphalid butterflies that are Müllerian co-mimics in Florida: (a) the monarch (*Danaus plexippus*); (b) the queen (*D. gilippus*); (c) the viceroy (*Limenitis archippus*). (After Brower, 1958.)

protection varies greatly. In the species involved, the warning signal of the co-models differs markedly from that of their close, non-mimetic relatives.

Interpretation of mimicry may be difficult, particularly distinguishing protected from unprotected mimetic components. For example, a century after discovery of one of the seemingly strongest examples of Batesian mimicry, recent studies have cast doubt on the classical interpretation. The system involves two North American danaine butterflies, *Danaus plexippus*, the monarch, and *D. gilippus*, the queen, which are chemically defended models that are mimicked by nymphaline viceroy butterflies (*Limenitis archippus*) (Fig. 13.7). Historically, based on observation of the viceroy's larval food plants and taxonomic affiliation, the butterflies were considered to be palatable, and therefore Batesian mimics. Ideas on palatability were overturned after an experiment in which isolated butterfly abdomens were fed to natural predators (wild-caught red-winged blackbirds). It was impossible that previous exposure to aposematism deterred feeding birds because the aposematically patterned butterfly wings had been removed. Viceroys were found to be as unpalatable as monarchs, and queens were least unpalatable. In Florida populations and

with this particular predator, the system now seems to be Müllerian. The viceroy and monarch are co-models and the queen is a less well chemically protected member that benefits through the asymmetry of its palatability relative to the others. Appropriate experiments to assess palatability, using natural predators and avoiding problems of previous learning by the predator, are uncommon. Other strictly designed tests may show more 'Batesian' systems to be Müllerian.

It has been reasoned that, if all members of a Müllerian mimicry complex are aposematic and distasteful, then an observer (predator) is not deceived by any member and this cannot be mimicry but rather shared aposematism. However, equality of distastefulness across all members of a complex is unlikely. Furthermore, some observers (e.g. specialist predators) may find the least well defended part of the complex to be edible. Thus definitions of mimicry that take into account the range of all possible observers will include Müllerian mimicry.

### 13.5.3 Mimicry as a continuum

The practicality and even the significance of differentiating two forms of defensive mimicry can be questioned but each gives a

different interpretation of the ecology and evolution of the components, and makes quite dissimilar predictions concerning life histories of the participants. For example, the theory of Müllerian mimicry makes predictions that there ought to be certain characteristics:

- Limited numbers of co-modelled aposematic patterns, reducing the number that a predator has to learn.
- Behavioural modifications to 'expose' the pattern to potential predators, such as conspicuous display rather than crypsis, and diurnal rather than nocturnal activity.
- Long post-reproductive life, with prominent exposure to encourage the naive predator to learn of the distastefulness on a post-reproductive individual.

In Batesian mimicry, the model may exhibit characteristics 2 and 3 above. In addition, Batesian mimicry ought to involve mimetic polymorphism, sex-limited (female-only) mimicry and divergence of the model's pattern away from that of the mimic (evolutionary escape). Although all these predictions are met in some mimetic species, there are some exceptions to all of them. Evidently, the rigid demarcation of mimicry into two types is an oversimplification.

Amongst the lycid beetles there are many aposematically odoriferous and warningly coloured species that demonstrate a range of mimetic relationships. The Australian lycid *Metriorrhynchus rhipidius* is protected chemically by odorous methoxy-alkylpyrazine, and by bitter principles and acetylenic antifeedants. Species of *Metriorrhynchus* provide models for mimetic beetles from at least six distantly related families (Buprestidae, Pythidae, Meloidae, Oedemeridae, Cerambycidae and Belidae) and at least one moth. All these mimics are convergent in colour; some have nearly identical alkylpyrazines and distasteful chemicals; others share the alkylpyrazines but have different distasteful chemicals; and some have the odorous chemical but appear to lack

any distasteful chemicals. These aposematically coloured insects form a mimetic series. The oedemerids are clearly Müllerian mimics, modelled precisely on the local *Metriorrhynchus* species and differing only in using cantharidin as an antifeedant. The cerambycid mimics use different repellent odours, whereas the buprestids lack warning odour but are chemically protected by buprestins. Finally pythids and belids are Batesian mimics, apparently lacking any chemical defences. After careful chemical examination, what appears to be a model with many Batesian mimics, or perhaps a Müllerian ring, is revealed to demonstrate a complete range between the extremes of Müllerian and Batesian mimicry.

Although the extremes of these two prominent mimicry systems are well studied, and in some texts appear to be the only systems described, they are but two of the possible permutations involving the interactions of model, mimic and observer. Further complications ensue if model and mimic are of the same species, as in automimicry, or if there is sexual dimorphism and polymorphism. All mimicry systems are complex, interactive and never static, because population sizes change and relative abundance of mimetic species fluctuate so that density-dependent factors play an important role. The defence offered by shared aposematic colouring, and even shared distastefulness, can be circumvented by a specialized predator able to cue on the warning, overcome the defences and eat selected species in the mimicry complex (Box 13.2).

### 13.6 COLLECTIVE DEFENCES IN GREGARIOUS AND SOCIAL INSECTS

Chemically defended, aposematic insects are often clustered rather than uniformly distributed through suitable habitat. Thus unpalatable butterflies may live in conspicuous aggregations as larvae and as adults; the winter congregation of migratory adult

monarch butterflies in California and Mexico is an example. Many chemically defended homopterans aggregate on individual host plants and some vespid wasps congregate conspicuously on the outside of their nests (seen in the vignette of Chapter 11). Orderly clusters occur in the phytophagous larvae of sawflies (Hymenoptera: Pergidae; Fig. 13.6) and some chrysomelid beetles that form defended circles (**cycloaalex**). Some larvae lie within the circle and others form an outer ring with either their heads or abdomens directed outwards, depending upon which end secretes the noxious compounds. These groups often make synchronized displays of head and/or abdomen bobbing, which increase the apparency of the group.

Formation of such clusters is sometimes encouraged by the production of aggregation pheromones by early arriving individuals (section 4.3.2(b)), or may result from the young failing to disperse after hatching from limited egg batches. Benefits to the individual from the clustering of chemically defended insects may relate to the dynamics of predator training. However, these may also involve kin selection in subsocial insects, in which aggregations comprise relatives that benefit at the expense of an individual 'sacrificed' to educate a predator.

The latter scenario for the origin and maintenance of group defence certainly seems to apply to the eusocial Hymenoptera (ants, bees and wasps) as seen in Chapter 11. In these insects, and in the termites (Isoptera), defensive tasks are usually undertaken by morphologically modified individuals called soldiers. In all social insects, excepting the army ants, the focus for defensive action is the nest, and the major role of the soldier caste is to protect the nest and its inhabitants. Nest architecture and location are often a first line of defence, with many nests buried underground, or hidden within trees, with a few easily defensible entrances. Exposed nests, such as those of savanna-zone termites, often have hard, impregnable walls.

Termite soldiers can be male or female; they may have weak sight or be blind, and have enlarged heads (sometimes exceeding the rest of the body length). Soldiers may have well-developed jaws, or be **nasute**, with small jaws but an elongate 'nasus' or rostrum. They may protect the colony by biting, by chemical means or, as in *Cryptotermes*, by **phragmosis** – the blocking of access to the nest with their modified heads. Amongst the most serious adversaries of termites are ants, and complex warfare takes place between the two. Termite soldiers have developed an enormous battery of chemicals, many produced in highly elaborated frontal and salivary glands. For example, in *Pseudacanthotermes spiniger* the salivary glands fill nine-tenths of the abdomen, and *Globitermes sulphureus* soldiers are filled to bursting with sticky yellow fluid used to entangle the predator – and the termite, usually fatally. This suicidal phenomenon is seen also in some *Camponotus* ants which use

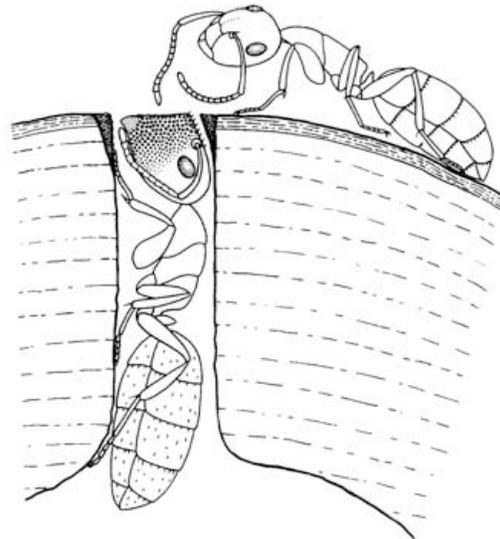
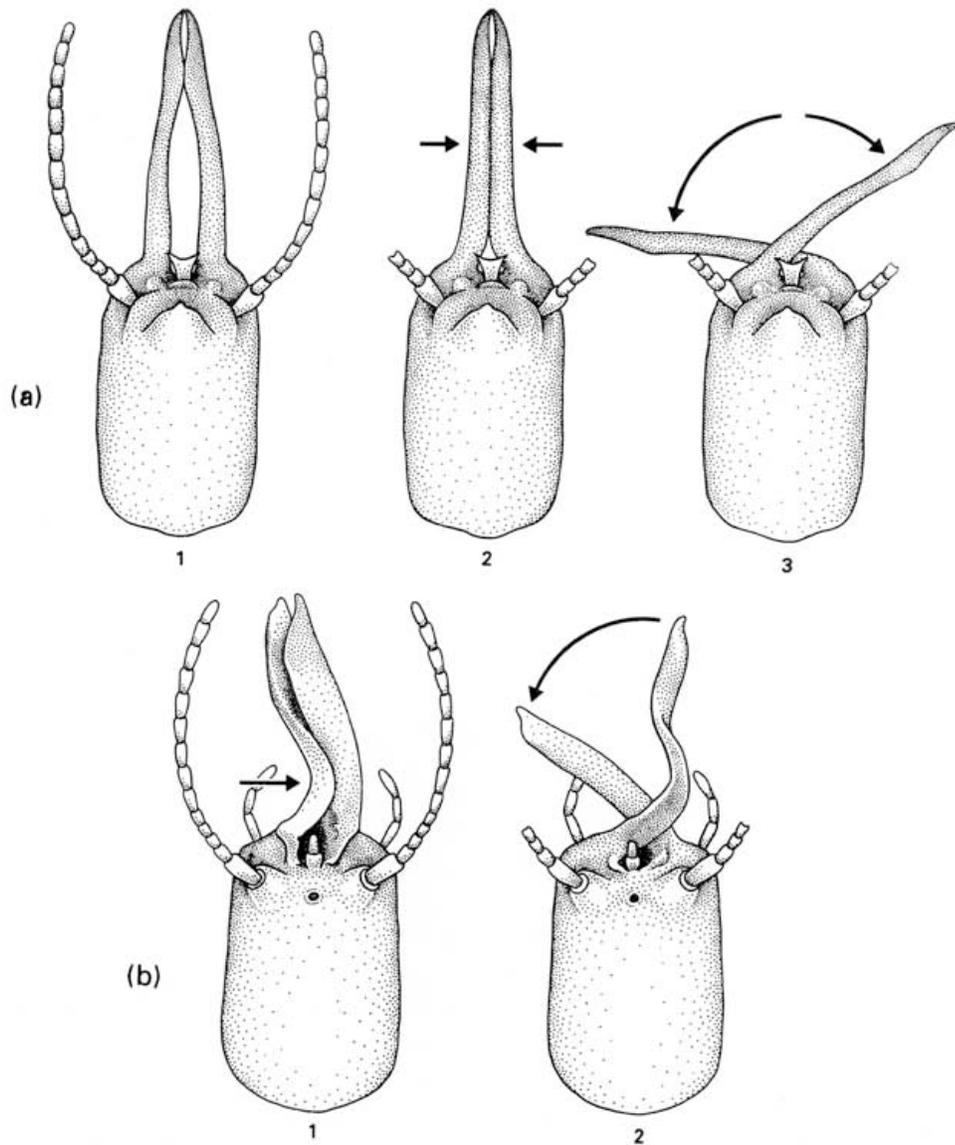


Fig. 13.8 Nest guarding by the European ant *Colobopsis truncata*: a minor worker approaching a soldier that is blocking a nest entrance with her plug-shaped head. (After Hölldobler and Wilson, 1990, from Szabó-Patay, 1928.)



**Fig. 13.9** Defence by mandible snapping in termite soldiers: (a) a symmetric snapping soldier of *Termes* in which (1) the long thin mandibles are pressed hard together, and thus (2) bent inwards, before (3) they slide violently across one another; (b) an asymmetric snapping soldier of *Homalotermes* in which force is generated in the flexible left mandible by (1) being pushed against the right one, until (2) the right mandible slips under the left one to strike a violent blow. (After Deligne *et al.*, 1981.)

hydrostatic pressure in the gaster to burst the abdomen and release sticky fluid from the huge salivary glands.

Some of the specialized defensive activities used by termites have developed convergently amongst ants. Thus the soldiers of

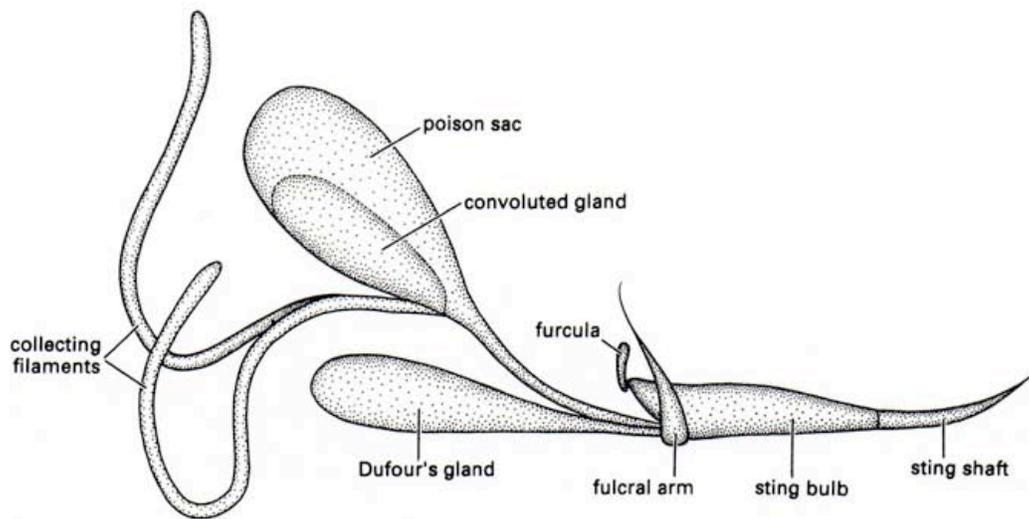


Fig. 13.10 Diagram of the major components of the venom apparatus of a social aculeate wasp. (After Hermann and Blum, 1981.)

Other glands in social hymenopterans produce additional defensive compounds, often with communication roles, and including many volatile compounds that serve as alarm pheromones. These stimulate one or more defensive actions: they may summon more individuals to a threat, marking a predator so that the attack is targeted, or, as a last resort, they may encourage the colony to flee from the danger. Mandibular glands produce alarm pheromones in many insects and also substances that cause pain when they enter wounds caused by the mandibles. The metapleural glands in some species of ants produce compounds that defend against microorganisms in the nest through antibiotic action. Both sets of glands may produce sticky defensive substances and a wide range of pharmacological compounds is currently under study to determine possible human benefit.

Even the best defended insects can be parasitized by mimics (section 13.5), and the best of chemical defences can be breached by a predator (Box 13.2). Although the social insects have some of the most elaborate defences seen in the Insecta, they remain

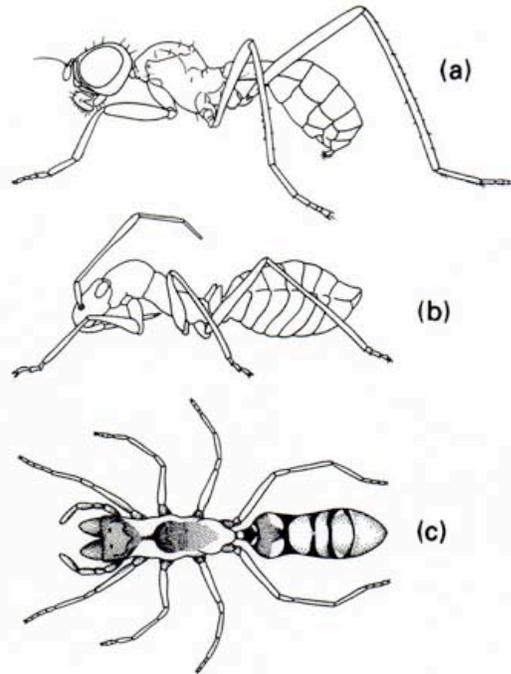


Fig. 13.11 Three ant mimics: (a) a fly (Diptera: Micropezidae: *Badisis*); (b) a bug (Hemiptera: Miridae: Phylinae); (c) a spider (Araneae: Clubionidae: *Sphecotypus*). (After (a) McAlpine, 1990; (b) Atkins, 1980; (c) Oliveira, 1988.)

vulnerable. For example, many insects model themselves on social insects, with representatives of many orders converging morphologically on ants (Fig. 13.11), particularly with regard to the waist constriction and wing loss, and even kinked antennae. The aposematic yellow-and-black patterns of vespid wasps and apid bees provide models for hundreds of mimics throughout the world. Not only are these communication systems of social insects parasitized, but so also are their nests, which provide many parasites andinquilines with a hospitable place for their development (section 11.3).

Defence must be seen as a continuing coevolutionary process, analogous to an 'arms race', in which new defences originate or are modified and then are selectively breached, stimulating improved defences.

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