

# Aposematic (Warning) Coloration in Plants

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**Abstract** Aposematic (warning) coloration is a common defense in plants, although it was largely ignored before 2001. The fact that many aposematic animals use both plant-based pigments and sequestered poisonous molecules to become aposematic emphasizes the absurdity of neglecting the aposematic nature of so many plants. Similar to the situation in animals, aposematic coloration in plants is commonly yellow, orange, red, brown, black, white, or combinations of these colors. Aposematic coloration is expressed by thorny, spiny, prickly and poisonous plants, and by plants that are unpalatable for various other reasons. Plants that mimic aposematic plants or aposematic animals are also known. Many types of aposematic coloration also serve other functions at the same time, such as physiological, communicative and even other defensive functions. It is therefore difficult in many cases to evaluate the relative functional share of visual aposematism in various color patterns of plants and the specific selective agents involved in their evolution. Aposematic coloration is part of a broader phenomenon of defensive coloration in plants; this topic has also received only limited attention, as is evident from the lack of a regular and systematic description of these color patterns in published floras.

## 1 Introduction

Most land plants have organs or tissues with colors other than green that should have both a cost and an advantage. The cost to the plant of producing colored organs has three aspects. First, it requires the allocation of resources to synthesize the pigments.

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Second, any color of an organ of a nonwoody aerial plant other than green may in many cases (but certainly not all, see Chalker-Scott 1999; Matile 2000; Hoch et al. 2001, 2003; Lee and Gould 2002; Gould et al. 2002a, b; Close and Beadle 2003; Gould 2004; Ougham et al. 2005; Hatier and Gould 2008) be linked to lower photosynthesis. Third, conspicuousness may attract herbivores. In general, the benefits of coloration should be higher than the costs in order for such character to evolve.

Plant pigments and coloration caused by air spaces or other physical effects serve many physiological and communicative functions, such as photosynthesis, defense from UV light, scavenging of oxygen radicals, pollination, seed dispersal, thermoregulation and defense (e.g., Gould et al. 2002a; Close and Beadle 2003; Lee 2007). Gould et al. (2002b), Lev-Yadun et al. (2002, 2004), Lev-Yadun (2006a), Schaefer and Wilkinson (2004) and Lev-Yadun and Gould (2007, 2008) have already argued that nonphotosynthetic plant pigments have the potential to serve more than one function concurrently. I stress that I fully agree with Endler (1981), who proposed in relation to animal coloration that “we must be careful not to assume that because we have found one apparent function to a color pattern, it necessarily means that we have a complete explanation.” Thus, various hypotheses concerning the coloration of leaves and other plant parts need not contrast with or exclude any other functional explanation of specific types of plant coloration, and traits such as coloration that may have more than one type of benefit may be selected for by several agents. Consistent with Grubb’s (1992) view that defense systems are not simple, I consider that the evolution of plant coloration reflects an adaptation to both physiological pressures and to relations with other organisms.

Here I will describe and discuss the facts and questions related to aposematic coloration in plants in an attempt to outline this phenomenon and compare it with the broad knowledge of visual aposematism in animals. I will refer to aposematic coloration in the broadest sense, considering any visual warning phenomenon associated with unpalatability that may deter herbivores. The goal of this chapter is to stimulate further research into this generally overlooked phenomenon in plant biology.

## ***1.1 Partial Descriptions of Color Patterns in Floras***

One major obstacle to studies of defensive plant coloration in general and aposematic coloration in particular is provided by the fragmentary and inconsistent descriptions of plant coloration, especially of vegetative organs. Taxonomists have usually referred only to flower colors, and even this character has not always been fully described. Thorn, spine and prickle color, unripe and ripe fruit color, leaf colors, bark color and color changes in all of these organs have usually not been systematically described. In his seminal book on plant demography, Harper (1977) commented as follows on the possibility that defensive plant coloration operates: “botanists were reluctant to accept things that are commonplace for zoologists.” The surprisingly small number of papers in botany related to defensive coloration

as compared to zoology is clearly reflected in the annotated bibliography by Komárek (1998), which has thousands of related publications on animals and only a few about plants. The significant progress made in understanding the defensive role of pigmentation in zoology and the basics of the genetic mechanisms involved took over a century to achieve (e.g., Majerus 1998; Ruxton et al. 2004; Hoekstra 2006), and the effort needed to reach the same level of progress in botany is probably not any smaller. Lev-Yadun and Gould (2008) emphasized that in spite of all of the current difficulties involved in accepting, understanding and proving defensive plant coloration, there is no reason to continue with the long tradition of botanists (or, to give them their current popular name, “plant scientists”) of neglecting the study of defensive plant coloration including aposematism. Moreover, even zoologists studying animal aposematism who studied plant–animal interactions related to herbivory overlooked this issue. An intermediate stage of imperfect explanations, which in any case are common in many areas of biology and other sciences, will still allow progress to be made in the issue of aposematic coloration and may stimulate thinking by other scientists who may develop even better theoretical or experimental ideas than the ones that exist today.

## 2 Aposematism

Aposematic (warning) coloration is a biological phenomenon in which poisonous, dangerous or otherwise unpalatable organisms visually advertise these qualities to other animals (Cott 1940; Edmunds 1974; Gittleman and Harvey 1980; Ruxton et al. 2004). The evolution of aposematic coloration is based on the ability of target enemies to associate the visual signal with risk, damage, or nonprofitable handling, and thus to avoid such organisms as prey (Edmunds 1974; Gittleman and Harvey 1980; Ruxton et al. 2004). Typical colors of aposematic animals are yellow, orange, red, purple, black, white and brown, or combinations of these (Cott 1940; Edmunds 1974; Wickler 1968; Savage and Slowinski 1992; Ruxton et al. 2004). The common defense achieved by aposematic coloration has resulted in the evolution of many mimicking animals. The mimics belong to two general categories, although there are intermediate situations. One is Müllerian mimics: here, defended animals mimic each other, sharing the cost of predator learning among more participants. The other is Batesian mimics, which are undefended animals that benefit from the existence of common defended aposematic models (Cott 1940; Edmunds 1974; Wickler 1968; Savage and Slowinski 1992; Ruxton et al. 2004).

### 2.1 *Olfactory Aposematism*

While this chapter is dedicated to visual aposematism in plants, olfactory aposematism, whereby poisonous plants deter mammalian or insect herbivores, has also

been proposed (Eisner 1964; Rothschild 1972, 1973, 1986; Levin 1973; Atsatt and O'Dowd 1976; Wiens 1978; Eisner and Grant 1981; Harborne 1982; Rothschild et al. 1984; Guilford et al. 1987; Rothschild and Moore 1987; Kaye et al. 1989; Moore et al. 1990; Woolfson and Rothschild 1990; Launchbaugh and Provenza 1993; Provenza et al. 2000; Massei et al. 2007). It is probable that—similar to pollination (Faegri and van der Pijl 1979; Dafni 1984; Jersáková et al. 2006) and seed dispersal (Pijl 1982), where certain plants use both visual and olfactory signals simultaneously for animal attraction—double signaling also holds for plant aposematism. In the case of the very spiny zebra-like rosette annual *Silybum marianum* (Asteraceae), which was proposed to use visual aposematic markings—white stripes (Lev-Yadun 2003a), Rothschild and Moore (1987) proposed that it uses olfactory aposematism via pyrazine. It is likely that both types of aposematism operate simultaneously in the case of *Silybum*, possibly towards different herbivores. The possibility that thorny, spiny and prickly plants use visual and olfactory aposematism simultaneously should be studied systematically. I should stress that olfactory aposematism is especially important as a defense against nocturnal herbivores, as has been shown for many fungi (Sherratt et al. 2005).

## 2.2 *The Anecdotal History of Discussions of Aposematic Coloration in Plants*

A database search of “aposematism in plants” does not yield anything earlier than the year 2001. After it became clear to me in January 1996, following compelling evidence in the field, that aposematic coloration probably exists in many thorny, spiny and prickly plants, 12 years of thorough library study resulted in a very short pre-2000 list of authors who discussed it (usually very briefly) in poisonous plants (Cook et al. 1971; Hinton 1973; Harper 1977; Wiens 1978; Rothschild 1980, 1986; Harborne 1982; Williamson 1982; Knight and Siegfried 1983; Smith 1986; Lee et al. 1987; Givnish 1990; Tuomi and Augner 1993). Moreover, several of these references (Knight and Siegfried 1983; Smith 1986; Lee et al. 1987) dismissed the existence of aposematic coloration in the plants they studied. These few early mentions of visual aposematism in plants referred to poisonous ones, while papers published since 2001 have given more attention to thorny, spiny and prickly ones (Lev-Yadun 2001, 2003a, b, 2006b; Midgley et al. 2001; Gould 2004; Midgley 2004; Lev-Yadun and Ne'eman 2004, 2006; Rubino and McCarthy 2004; Ruxton et al. 2004; Speed and Ruxton 2005; Halpern et al. 2007a, b; Lev-Yadun and Gould 2008; Lev-Yadun and Halpern 2008) and less attention to poisonous ones (Lev-Yadun and Ne'eman 2004; Hill 2006; Lev-Yadun 2006b; Lev-Yadun and Gould 2007, 2008).

Cook et al. (1971) is the earliest reference I managed to find that briefly proposed that aposematic coloration occurs in poisonous seeds of the plant *Eremocarpus setigerus* (Euphorbiaceae). Seeds of this plant are either camouflaged by mottling when less poisonous, or are much more poisonous and have a plain gray color that does

not camouflage them much. The mountain dove (*Zenaidura macroura*) rejects the gray seeds and eagerly eats the mottled ones, leading Cook et al. (1971) to propose that they are aposematic. Hinton (1973), who was a zoologist, gave the first detailed hypothesis for a possible defense from herbivory of yellow, red and other types of vivid flower coloration. Hinton proposed that colorful poisonous flowers should be considered to be aposematic and that they probably have mimics. His review of deception in nature was published in a book about illusion which was not a biology book, but rather dealt with art. This hypothesis, which was also briefly referred to by the very influential Miriam Rothschild (1980) when she discussed the roles of carotenoids, did not cause botanists or zoology-oriented ecologists to pursue this issue. It seems that the relevant community was willing to consider plant coloration only for physiological issues, or when plant–animal relations were considered, mostly to attract pollinators and seed dispersers. Later, Rothschild (1986) proposed that red may serve as an aposematic color in poisonous plants, without giving examples. Harper, who wrote his comment about botanists that were reluctant to accept things that are commonplace for zoologists around the same time (1977), did not explain why zoologists who dealt with animal aposematism and were also involved in research on plant–animal interactions had not recognized how common these phenomena are in many plant habitats. The fact that many aposematic animals use both plant-based pigments and sequestered poisonous molecules to become aposematic highlights the absurdity of neglecting the aposematic nature of so many plants. Wiens (1978), in his review on mimicry in plants, mentioned that many examples of striking, contrasting, and often variegated or mottled patterns of coloration characterize plants, particularly leaves, and asked if they serve aposematic functions. He proposed that if herbivores primarily orient their feeding selection visually, these patterns should function aposematically. Wiens (1978) gave several examples of poisonous plants with patterned leaf coloration, such as *Caladium* and *Dieffenbachia*, and colorful poisonous seeds of various plants including *Ricinus*. Wiens (1978) also mentioned personal communication with C. Dodson that suggested that young red leaves in tropical plants may also be aposematic. Eisner (1981), without using the term aposematic, actually described visual aposematism in the thorny plant *Schrankia microphylla*, which folds its leaves when touched, further exposing its thorns. Harborne (1982), in his book on chemical ecology, proposed that the brightly colored, purple-black berries of the deadly *Atropa belladonna* warn grazing mammals of the dangers of consuming them. Williamson (1982) also briefly proposed that brightly colored (red or red and black) seeds lacking an arillate or fleshy reward (e.g., *Erythrina*, *Ormosia*, and *Abrus*) might be aposematically colored to warn seed eaters of their toxicity. Knight and Siegfried (1983) raised the question of whether green fruits signal unpalatability, and concluded that green does not provide enough contrast to be aposematic in the forest canopy. Smith (1986) hypothesized that leaf variegation may be aposematic in theory, but concluded that for the vine species (*Byttneria aculeata*) he studied, the variegation was actually related to defense from herbivory, mimicking leaf mining damage but not actually aposematic. Although Smith rejected the operation of aposematism in the plant species he studied, he gave a clear and detailed formulation of the aposematic hypothesis for poisonous plants:

“The benefits to the plant of chemical defense against herbivores would be greater if herbivores avoided such plants altogether, rather than testing leaves for palatability, and so causing some damage. A distinct leaf color pattern linked with chemical defense might function in this way. Polymorphism for leaf color should then coincide with polymorphisms for chemical defense. Müllerian and Batesian mimicry could result in evolution of similar patterns of variegation, with or without associated toxicity, among other species which have herbivore species in common with the model species” (Smith 1986). Lee et al. (1987) concluded that anthocyanins in developing leaves of mango and cacao are not aposematic. Givnish (1990) noted that Smith’s (1986) rejected hypothesis regarding the aposematic value of leaf variegation should be considered, but did not elaborate on this issue when he proposed that the understory herbs he studied use leaf variegation as camouflage. Tuomi and Augner (1993) mentioned a possible association between bright colors in plants and toxicity. Augner (1994) modeled and discussed the conditions needed for the operation of aposematism in plants, focusing on chemical-based aposematism with no direct reference to a visual one, although it can be understood from the text that visual aposematism was not opposed. Augner and Bernays (1998) modeled the possibilities of plant defense signals and their mimics, and although they did not refer directly to visual aposematism, it is again clear from the text that they concluded that Batesian mimics of plant defense signals may be common (see proposed Müllerian and Batesian mimics in Lev-Yadun 2003a, 2006b; Lev-Yadun and Gould 2007, 2008). Archetti (2000), in his discussion of red and yellow autumn leaves that were proposed to signal aphids about the defensive qualities of trees, rejected the possibility that these leaves are aposematic.

Another issue of importance concerning poison-related aposematism is the relativity of aposematism. Deciding that a certain branch, root, leaf, flower, fruit or seed is poisonous or unpalatable is a relative issue. Certain frugivores can consume fruits that are poisonous to other animals (Janzen 1979), and the same is true of any plant organ or tissue. Therefore, a chemically defended plant that is aposematic for certain animal taxa may be edible and nonaposematic for other taxa.

### ***2.3 Aposematic Coloration in Thorny, Spiny, and Prickly Plants***

There are three terms for sharp defensive plant appendages: thorns, when they are made of branches; spines, when they are made of leaves; and prickles, when they are made of cortical tissues (e.g., in roses). Thorns, spines and prickles provide mechanical protection against herbivory (Janzen and Martin 1982; Janzen 1986; Tomlinson 1990; Myers and Bazely 1991; Grubb 1992; Rebollo et al. 2002) because they can wound mouths, digestive systems (Janzen and Martin 1982; Cooper and Owen-Smith 1986; Janzen 1986), and other body parts of herbivores. Thus, theoretically, once herbivores learn to identify thorns, spines and prickles (and their bright colors or associated markings should help in their recognition), they can avoid the harmful plants advertising them. The fact that thousands of

thorny, spiny and prickly species have colorful and sharp defensive structures or that they are otherwise conspicuous due to their white or colorful markings somehow escaped the notice of botanists and zoologists, although cacti and other spiny taxa are found in the majority of botanical gardens.

Since what is toxic to one animal might be harmless to another (Laycock 1978; Janzen 1979; Gleadow and Woodrow 2002), chemical-based aposematism may not operate for all herbivores. For sharp defensive organs, the situation is somewhat different. There are differences in the sensitivity of herbivores to sharp objects, but even specialized mammalian herbivores like woodrats and collared peccaries, which are well adapted to deal with and exploit very spiny *Opuntia* plants, tend to choose the less spiny ones (Brown et al. 1972; Theimer and Bateman 1992). The need to touch and ingest sharp objects makes all large vertebrate herbivores sensitive to such plants. Thorns, spines and prickles may therefore be more universal than poisons in relation to aposematism.

The recent proposals that thorny, spiny and prickly plants may be visually aposematic (Lev-Yadun 2001, 2003a, b, 2006b; Midgley et al. 2001; Gould 2004; Midgley 2004; Lev-Yadun and Ne'eman 2004, 2006; Rubino and McCarthy 2004; Ruxton et al. 2004; Speed and Ruxton 2005; Halpern et al. 2007a, b; Lev-Yadun and Gould 2008; Lev-Yadun and Halpern 2008) were based on the fact that thorns, spines and prickles are usually colorful or are conspicuous because they are marked by various types of associated coloration in the tissues that form them, including white markings. Similarly, it has also recently been proposed that many spiny animals have colorful spines and so they are aposematic (Ruxton et al. 2004; Inbar and Lev-Yadun 2005; Speed and Ruxton 2005), a fact that was discussed only briefly in the classic monograph by Cott (1940).

After realizing that the thorns, spines and prickles of many wild plants in Israel are usually colorful or are associated with conspicuous white or colorful markings, I decided to examine whether this principle is true in four very spiny taxa (cacti, *Agave*, *Aloe*, *Euphorbia*). When the examination of many species of these taxa clearly indicated that the sharp defensive appendages are usually conspicuous, I proposed that these plants are visually aposematic (Lev-Yadun 2001).

Lev-Yadun (2001) showed that two types of thorn conspicuousness are typical of many plant species: (1) colorful thorns and spines, and (2) white and colorful spots and stripes associated with thorns and spines in leaves, stems, and fruits. Both types of aposematic coloration dominate the spine systems of taxa rich in spiny species: cacti and the genera *Agave*, *Aloe*, and *Euphorbia*. It has been recorded in over a thousand species originating in America and Africa. The colorful spine systems are commonly multicolored (spines are brown, yellow, red, white, gray, pink, black, and tan). For instance, in cacti (the spiniest taxon), in more than 50% of the species for which there are detailed data (e.g., Benson 1982), the spines are pigmented with 3–7 colors, and 88.6% of the 973 cacti species described in Preston-Mafham and Preston-Mafham (1994) have white markings associated with their spines (Lev-Yadun 2001). It has been proposed that conspicuous spines are beneficial for plants, since herbivorous vertebrates remember the signal and thus tend to avoid sampling these conspicuous spiny plants subsequently. Furthermore,



herbivores may pass over the aposematic individuals and eat their nonaposematic neighbors, thus reducing competition between aposematic and their neighboring plants (Lev-Yadun 2001). Rubino and McCarthy (2004) tested Lev-Yadun's (2001) aposematic hypothesis by examining the presence of aposematic coloration in thorny, spiny, and prickly vascular plants of southeastern Ohio, and because of their similar field results, reached the same conclusions.

This phenomenon of aposematism in thorny, spiny and prickly plants, which seems to be very common, has been described and discussed at three levels: (1) the floristic approach, where it is studied across large taxa (Lev-Yadun 2001) or floras or ecologies (Lev-Yadun and Ne'eman 2004; Rubino and McCarthy 2004); (2) the individual species level (Lev-Yadun 2003a; Lev-Yadun and Ne'eman 2006; Halpern et al. 2007a, b), and; (3) mimicry of the phenomenon (Lev-Yadun 2003a, b, 2006b; Lev-Yadun and Gould 2008). Although Midgley et al. (2001) and Midgley (2004) did not use the word aposematic, they described the typical conspicuous white thorns of many African *Acacia* trees as visually deterring large herbivores, supporting the aposematic hypothesis. Ruxton et al. (2004) and Speed and Ruxton (2005) elaborated on the principle that, unlike poisons, aposematic thorns advertise their own dangerous quality (self-advertisement).

Lev-Yadun (2003a) showed that the rosette and cauline leaves of the highly thorny winter annual plant species of the Asteraceae in Israel (*S. marianum*) resemble green zebras. The widths of typical variegation bands were measured and found to be highly correlated with leaf length, length of the longest spine at leaf margins, and the number of spines along the leaf circumference. Thus, there was a significant correlation between the spininess and strength of variegation. Lev-Yadun (2003a) proposed that this was a special case of aposematic (warning) coloration. However, additional defensive and physiological roles of the variegation, such as mimicry of the tunnels of flies belonging to the Agromyzidae, reducing the number of insects landing on the leaves in general, just as zebra stripes defend against tsetse flies (Lev-Yadun 2003a and citations therein), were also proposed.

## **2.4 Pathogenic Bacteria and Fungi and Thorns**

Three recent publications showed that spines harbor an array of pathogenic bacteria and fungi (Halpern et al. 2007a, b; Lev-Yadun and Halpern 2008). Spines from date palm (*Phoenix dactylifera*) trees, thorns from common hawthorn (*Crataegus aronia*) trees and two thorny shrub species, thorny burnet (*Sarcopoterium spinosum*) and manna tree (*Alhagi graecorum*), were sampled in Israel. Every typical mature individual of these trees and shrubs carries hundreds or even thousands of conspicuous and therefore potentially aposematic spines or thorns. The severity and frequency of infections among orchard workers in Israel following date-palm spine wounding has necessitated the costly practice of removing all of the millions of spines from many of the orchards using mechanical saws. Even the small number of spines and thorns studied resulted in a list of aerobic and anaerobic bacteria species including *Clostridium perfringens*, *Bacillus anthracis* and *Pantoea agglomerans* (Halpern et al. 2007a, b).



*C. perfringens* is known to be a flesh-eater in that it can produce a necrotizing infection of the skeletal muscle called gas gangrene (Shimizu et al. 2002). *Clostridium tetani*, the etiological agent of tetanus, a serious disease in humans and animals, can be fatal when left untreated. Thorn injuries have been known to cause tetanus in the USA, Ethiopia, and Turkey (Hodes and Teferedegne 1990; Ergonul et al. 2003; Pascual et al. 2003). *B. anthracis* is the etiological agent of anthrax, a notoriously acute fatal disease in both domesticated and wild animals, particularly herbivorous ones, and humans (Jensen et al. 2003). The cutaneous form of the disease is usually acquired through injured skin or mucous membranes, a typical thorn injury. None of the published medical data discussed ecological or evolutionary issues or aposematism, but were instead only published in the interests of medical practice. However, these data showed that plant thorns, spines and prickles may regularly harbor various toxic or pathogenic bacteria (Halpern et al. 2007a, b).

In their review of the medical literature, Halpern et al. (2007b) found that septic inflammation caused by plant thorn injury can result from not only bacteria but also pathogenic fungi. Dermatophytes that cause subcutaneous mycoses are unable to penetrate the skin and must be introduced into the subcutaneous tissue by a puncture wound (Willey et al. 2008).

## ***2.5 Do Spiny Plants Harbor Microbial Pathogens on their Spines, Unlike Nonspiny Plants?***

Given that microorganisms are generally ubiquitous, there is no reason to assume that only specific plants or specific plant organs will be rich in microorganisms. Despite this ubiquitous occurrence, however, certain plants or plant organs may have specific chemical components or structures on their surfaces that either reduce or increase the possibility that microorganism taxa will survive. Microorganisms can grow on plant surfaces in biofilms, which are assemblages of bacterial cells that are attached to a surface and enclosed in adhesive polysaccharides excreted by the cells. Within the biofilm matrix, several different microenvironments can exist, including anoxic conditions that facilitate the existence of anaerobic bacteria. Considering the findings of Halpern et al. (2007a, b) in regard to spines and thorns, it is clear that anaerobic bacteria can survive on these defensive structures. Although it is assumed that an array of biofilm types is formed on plant surfaces, this issue should be studied systematically in relation to defense from herbivory in order to gain a better understanding of the antiherbivory role of microorganisms.

## ***2.6 Silica Needles and Raphids Made of Calcium Oxalate***

An obvious question concerning the potential defensive role of pathogenic microorganisms on plant surfaces concerns those not found on thorns, spines and prickles.

The positive answer in many cases is simple. Thousands of plant species have a sharp microscopic alternative to insert the pathogens into the tissues of the herbivores.

Lev-Yadun and Halpern (2008) proposed that many plant species without thorns, spines, or prickles possess an alternative: one of two types of usually internal (but sometimes external), sharp, microscopic defensive structures: silica needles and raphids (which are needles made of calcium oxalate). Silica bodies in plants are formed by the ordered biological deposition of silicon that enters the plant via the roots (Richmond and Sussman 2003). Silica bodies have several known functions: structural, serving as cofactors in the detoxification of heavy metals, and defense from herbivory (e.g., Richmond and Sussman 2003; Wang et al. 2004). Lev-Yadun and Halpern (2008) discussed their specific potential defensive function: enabling the penetration of microorganisms into the bodies of herbivores. Thousands of plant species belonging to many families produce raphids (Franceschi and Horner 1980). Usually, raphids are formed in specific parenchymal cells that differ from their neighboring cells and are called idioblasts (Fahn 1990). The raphids are formed in idioblasts in large numbers and are packed compactly (aligned parallel to each other), but spread when the tissue is wounded. Raphids are always elongated, needle-shaped, and have two sharp, pointed ends. This, however, is not the whole structural story. Studies conducted with a scanning and transmission electron microscope have revealed that, in many cases, the raphids may be barbed or may have deep grooves along them. The grooves serve as channels through which plant toxins are introduced into the tissues of the herbivores (Sakai et al. 1972; Franceschi and Horner 1980). Like silica bodies in plants, calcium oxalate bodies have several functions, including tissue calcium regulation, defense from herbivory, metal detoxification, and structural functions (Franceschi and Horner 1980; Ruiz et al. 2002; Nakata 2003; Franceschi and Nakata 2005).

In addition to the ability of both types of internal microscopic spines (raphids and silica needles) to introduce plant toxins into the wounded tissues of the herbivore by causing mechanical irritation, Lev-Yadun and Halpern (2008) proposed that they are also able to introduce pathogenic microorganisms. Because of their small size, raphids and silica needles can internally wound the mouth and digestive systems of not only large vertebrates but also insects and other small herbivores that manage to avoid thorns, spines and prickles by passing between them. Through the wounds inflicted by the silica needles and raphids, microorganisms found on the plant surfaces themselves as well as in the mouth and digestive tract of the herbivore may cause infection. Like thorns, spines and prickles, the raphids and silica needles actually inject the pathogenic microorganisms into the sensitive mouth and digestive tract of the herbivore.

The use of pathogenic microorganisms to harm animals by wounding is already known from zoology. For instance, the huge predaceous lizard known as the Komodo dragon (*Varanus komodoensis*) seems to use the pathogenic bacteria found in its saliva as an additional advantage in hunting, like snake's venom. Animals wounded by a bite from the Komodo dragon commonly suffer from bacteremia and thus can be caught later after being incapacitated if not killed by the primary attack (Montgomery et al. 2002).

## ***2.7 Plant Biological Warfare: Thorns Inject Pathogenic Bacteria into Herbivores, Enhancing the Evolution of Aposematism***

The physical defense provided by thorns, spines, prickles, silica needles, and raphids against herbivores might be only the tip of the iceberg in a much more complicated story. All of these sharp plant structures may inject bacteria into herbivores by wounding, enabling the microorganisms to pass the animal's first line of defense (the skin), and in so doing may cause severe infections that are much more dangerous and painful than the mechanical wounding itself (Halpern et al. 2007a, b; Lev-Yadun and Halpern 2008).

Another theoretical aspect is the delay between the thorn's contact and wounding and the microorganism's action. While the pain induced by contact with thorns is immediate, the microorganism's action is delayed. However, the same is true for the delayed action of poisons in aposematic poisonous organisms, and yet there is general agreement that colorful poisonous organisms are aposematic (e.g., Cott 1940; Edmunds 1974; Gittleman and Harvey 1980; Harvey and Paxton 1981; Ruxton et al. 2004). Therefore, there is no reason to view a microorganism's contamination and its delayed action any differently.

Lev-Yadun and Halpern (2008) proposed that thorns, spines, prickles, silica needles and raphid-injected microorganisms play a considerable potential role in antiherbivory, actually serving as a biological warfare agent, and they may have uniquely contributed to the common evolution of aposematism (warning coloration) in thorny plants or on the surfaces of plants that have internal microscopic spines (Halpern et al. 2007a, b; Lev-Yadun and Halpern 2008). While it now seems clear that thorny plants are aposematic, the issue of potential aposematism in plants with microscopic internal spines in the form of raphids and silica needles has not yet been systematically addressed.

## ***2.8 Color Changes in Old Aposematic Thorns, Spines, and Prickles***

Among the various colorful plant/animal communication systems, adaptive color changes are known to take part in the two extensively studied gene dispersal systems: pollination and frugivory. Young and unrewarding animal-pollinated flowers and young and unripe fleshy fruits are usually green and cryptic. Flowers usually become colorful and conspicuous only towards anthesis, when they open and offer nectar and pollen as rewards to pollinators. Many flowers retain their conspicuous advertising colors until they wilt. However, many others change color after pollination (Weiss 1991, 1995; Weiss and Lamont 1997). A change in flower color that occurs during an inflorescence may reduce the flower's advertising intensity, and thus its detectability by pollinators. On the other hand, retaining the coloration after pollination, or after such flowers turn unreceptive, may reduce pollinator visits to

unpollinated flowers, thus diminishing the plant's reproductive success. By simultaneously reducing the reward after pollination and their attractiveness by changing their color, plants direct pollinators to unpollinated flowers within the same inflorescence or plant. Floral color change is a well-documented phenomenon in various taxa and life forms on all continents except Antarctica (Weiss 1991, 1995; Weiss and Lamont 1997; Bradshaw and Schemske 2003). Fleshy fruits usually become colorful (yellow, pink, orange, red, brown, blue, purple and black) only toward ripening, when they become edible by lowering the content of protective, poisonous, and otherwise harmful secondary metabolites, and by increasing their sugar, protein and fat contents as well as their flavor and softness (Ridley 1930; van der Pijl 1982; Snow and Snow 1988; Willson and Whelan 1990; Schaefer and Schaefer 2007), a phenomenon that is also considered to be at least partly adaptive (Willson and Whelan 1990).

While the adaptive significance and the broad occurrence of color change in flowers (Weiss 1991, 1995), fruits (van der Pijl 1982; Willson and Whelan 1990) and leaves (Matile 2000; Archetti 2000; Hamilton and Brown 2001; Hoch et al. 2001; Lee et al. 2003; Schaefer and Wilkinson 2004; Lev-Yadun and Gould 2007) has been widely discussed, the phenomenon of color change in thorns, spines and prickles has only recently been described as being a widespread phenomenon and discussed as such (Lev-Yadun and Ne'eman 2006).

Patterns of color changes of senescent colorful aposematic thorns, spines and prickles were described in Lev-Yadun and Ne'eman (2006). Color changes make them less conspicuous, and they lose most or even all their aposematic character. The scale of this phenomenon on a taxon, flora, continent or global scale is still unknown. Lev-Yadun and Ne'eman (2006) emphasized that color changes in thorns, spines and prickles are not mandatory. Color changes and the aposematic character losses occur when the defended organs become less edible to large herbivores because of their increased size, mechanical rigidity or chemical defense, or when there is no need for defense. Reducing the cost of defense seems to be the reason for the ephemeral nature of the conspicuousness of plant thorns, spines and prickles (Lev-Yadun and Ne'eman 2006). The adaptive value may lie in reducing the investment in coloration, since a thin ephemeral coloration layer demands fewer resources. Keeping a thorn, spine, or prickle colorful for a long time is more costly, and the benefit of being aposematic is smaller in older, larger, or otherwise better protected organs. The tendency of plants to lower the cost of defense by thorns, spines and prickles is a well-known phenomenon. For instance, African acacias and other woody plants have longer thorns on the lower branches than on the higher ones (Cooper and Owen-Smith 1986; White 1988; Milewski et al. 1991; Brooks and Owen-Smith 1994; Young and Okello 1998; Gowda and Palo 2003). Certain trees (e.g., various citrus and palms) have large thorns or spines only when juvenile and none or fewer when mature (e.g., Kozłowski 1971; Cooper and Owen-Smith 1986; Cornett 1986; Clement and Manshardt 2000). Moreover, like several other types of induced defenses, thorns and spines are known to increase in size and number following herbivory (e.g., Milewski et al. 1991; Perevolotsky and Haimov 1991; Young et al. 2003). There is no theoretical difficulty in proposing that color

changes in thorns, spines and prickles also reflect conservation of resources (Lev-Yadun and Ne'eman 2006). However, a simple alternative explanation exists: the thorns, spines, and prickles are colorful simply because the hard polymers composing them are colorful by nature. Lev-Yadun and Ne'eman (2006) dismissed this possibility because the thorns, spines and prickles that lose or change color remain hard and functional. The layer of coloration does not seem to have a significant, or even any, role in producing their sharpness. The broad taxonomic distribution of color changes in thorns, spines and prickles indicates that this character has evolved repeatedly and independently (convergent character) in both gymnosperms and angiosperms, probably in response to selection by visually oriented herbivores.

## ***2.9 Biochemical Evidence of Convergent Evolution of Aposematic Coloration in Thorny, Spiny and Prickly Plants***

There is very strong indirect evidence for the operation of aposematic coloration in thorny and spiny plants and its convergent evolution in the fact that conspicuous thorn and spine coloration is found in angiosperm taxa that have mutually exclusive biochemical pathways of pigmentation. For instance, taxa belonging to the Caryophyllales (e.g., Cactaceae, Caryophyllaceae, Chenopodiaceae) produce yellow and red pigments via the betalain pathway (Stafford 1994). Most other angiosperm families use anthocyanins for similar patterns of coloration. The fact that spines of cacti are usually conspicuous because of their coloration (Lev-Yadun 2001), commonly including yellow, orange and red coloration resulting from betalain derivatives, indicates that this group of pigments may, among their various functions, be involved in aposematic coloration. By contrast, in Rosaceae, Asteraceae and Fabaceae as well as in many other angiosperm families that use anthocyanins for yellow, orange, pink, red, blue and black coloration of thorns, spines and prickles, the chemical origin of the aposematic coloration is different (Lev-Yadun 2001, 2006b; Lev-Yadun and Gould 2008). It seems therefore that the aposematic coloration of thorny, spiny and prickly plants is a good case of convergent evolution.

## ***2.10 Mimicry of Aposematic Thorns, Spines, and Prickles***

Mimicry of aposematic animals is very common (Cott 1940; Edmunds 1974; Wickler 1968; Ruxton et al. 2004), and several authors have already proposed that mimicry also operates in plants as an antiherbivore mechanism. Wiens (1978) estimated that about 5% of land plants are mimetic, listing several types of defensive plant mimicry. For instance, mimicry of host leaf morphology is common in mistletoes and was proposed to give rise to crypsis and thus to reduce herbivory (Ehleringer et al. 1986). Since there are so many colorful (aposematic) thorns,

spines and prickles, mimics of them are expected. Indeed, various plant taxa from several continents mimic thorns, spines and prickles. Lev-Yadun (2003b) described two types of thorn mimicry: (1) a unique type of weapon (spine) automimicry (within the same spiny or prickly individual), a phenomenon previously known only in animals (e.g., Guthrie and Petocz 1970), and (2) mimicry of aposematic colorful thorns, spines and prickles by colorful elongated and pointed plant organs (buds, leaves and fruit), which, despite their appearance, are not sharp. The discussion of mimicry of thorny, spiny, and prickly plants may be addressed at different taxonomic levels: (1) Müllerian mimicry among thorny, spiny and prickly plant taxa, (2) weapon (spine and prickle) automimicry (within the same individual), and (3) Batesian mimicry, when nonspiny plants mimic thorny, spiny and prickly ones. Interestingly, some insects mimic colorful aposematic plant thorns to escape predation (Purser 2003).

When the proportion of aposematic spiny plants in a given habitat increases for a period that is long enough for an evolutionary change, Müllerian mimicry may lead to the establishment of defense guilds (see Waldbauer 1988). Müllerian mimicry does indeed seem to occur within the group of spiny plants; for instance, there are three very spiny zebra-like annual rosette plant species in the eastern Mediterranean region (*S. marianum*; *Notobasis syriaca*; *Scolymus maculatus*, all of the Asteraceae), and it has been proposed that a defense guild has evolved in these plants (Lev-Yadun 2003a). Similarly, the white spines of many African acacias (Midgley et al. 2001; Midgley 2004) and the yellow, orange, red, brown and black spines of cacti (Lev-Yadun 2001) can all be considered Müllerian mimicry rings of aposematically and physically defended plants.

Weapon (spine) automimicry (within the same individual) occurs when impressions (with or without color printing) of the real spines form on leaves during their development. The developmental mechanism that allows the weapon automimicry to appear is simple. In most if not all *Agave* species, the developing leaves press hard against each other, the spines found along the margins press into the surface of the same or adjacent leaf, and their pattern is copied as a sunken negative and retained along the nonspiny parts of the leaves. For instance, in *Agave americana*, a common ornamental in Israel, the spine copies are seen in many leaves. The species showing the most remarkable spine mimicry is *A. impressa*, in which it is very conspicuous because of a white material that is printed on the false spines. The same type of colorful spines along the margins of the petiole and their mimicry by impression is obvious in the American palm *Washingtonia filifera* (Palmaceae), a common ornamental as well as a feral tree in Israel, and in *Aloe* sp. (Liliaceae) (Lev-Yadun 2003b). This spine automimicry is a vegetal parallel to the “weapon automimicry” of horns or canine teeth known in several mammalian species (Guthrie and Petocz 1970). Weapon (spine) automimicry was found in dozens of species of *Agave*, one species of *Aloe*, and a palm species, which all have spine-like imprints or colorations on their leaves, giving the impression of more extensive spininess (Lev-Yadun 2003b). The mimicry of aposematic colorful thorns, spines and prickles by nonspiny plants is a simple and typical case of Batesian mimicry, but the spine automimicry is a special intraorganismic Batesian mimicry. Lev-Yadun

(2003b, 2006b) proposed that both types of mimicry serve as antiherbivore mechanisms.

When nonthorny plants mimic thorny ones with colorful elongated and pointed plant organs, which despite their appearance and conspicuous coloration are not sharp at all, Batesian mimicry occurs (Lev-Yadun 2003b). Simple mimicry by colorful thorn-like structures was found in several wild species growing in Israel. For example, in several *Erodium* sp. (Geraniaceae), the elongated fruits, which are several centimeters long, beak-like, pointed, and self-dispersing (by drilling into the soil), are red. In *Sinapis alba*, an annual of the Brassicaceae, the elongated and pointed distal part of the fruit, when fully developed but not yet ripe, looks like a spine and is colorful (yellow, red, purple, or various combinations of these). In *Limonium angustifolium*, a wild and domesticated perennial of the Plumbaginaceae, the distal part of its large leaves is red and looks like a spine, although it is soft (Lev-Yadun 2003b).

Lev-Yadun (2006b) and Lev-Yadun and Gould (2008) proposed that there are two possible evolutionary routes towards the mimicry of colorful thorns, spines, or prickles. In the first, an aposematic thorny plant may have lost its thorny character but retained the shape and aposematic signal. In the second, a nonaposematic and nonthorny plant can acquire the signal, becoming a primary mimic. Alternatively, the thorn or spine-like structure and its coloration may have a different, unknown function. There are no field, developmental, or genetic data that may help in distinguishing between these options for any plant species. Concerning aposematism, Ruxton and Sherratt (2006) proposed that defense preceded signaling, which supports both proposed evolutionary routes. In general, the evolution of aposematism in plants is a neglected subject that needs considerable research effort for even a basic level of understanding.

### 3 Aposematic Coloration in Poisonous Flowers, Fruits, and Seeds

Flower and fruit colors and their chemical defenses were commonly discussed as mechanisms for filtering pollinators and seed dispersers rather than concerning aposematism (Ridley 1930; Faegri and van der Pijl 1979; Herrera 1982; Willson and Whelan 1990; Weiss 1995; Clegg and Durbin 2003; Schaefer et al. 2004, 2007). However, in many cases, the combination of visual signaling and chemical defense and the unpalatability of flowers and fruits should have led to the view that they are aposematic. I will describe the meager information concerning aposematic reproductive structures in plants.

As described above, poisonous seeds were probably the first plant parts that were proposed to be visually aposematic because they are both poisonous and colorful (Cook et al. 1971; Wiens 1978; Williamson 1982). However, aposematism was mentioned only briefly in each of these three papers and further research was not done. The second plant part proposed to be poisonous and colorful and therefore aposematic was the flower (Hinton 1973; Rothschild 1980), but again, this hypothesis was not pursued further. Concerning fruits, Harborne (1982) proposed that the



brightly colored, purple-black berries of the deadly *A. belladonna* warn grazing mammals of the dangers of consuming them. Aposematism in fruits mimicking thorns (Lev-Yadun 2003b) or aposematic caterpillars (Lev-Yadun and Inbar 2002) are discussed in other sections of this chapter. Schaefer and Schmidt (2004), without using the term aposematic, actually described visual aposematism in chemically defended fruits, like Eisner concerning the thorny plant *S. microphylla* (1981), and like Midgley et al. (2001) and Midgley (2004) concerning the conspicuous white thorns of many African *Acacia* trees, who described aposematism without mentioning it. Only Hill (2006) experimentally examined the aposematic function of poisonous and colorful fruits and gave good indications for the warning function of the coloration.

There is a large body of evidence for the operation of olfactory and visual aposematism in both flowers and fruits, although the authors of these studies referred to filtering of pollinating and dispersing animals rather than to aposematism. For instance, Pellmyr and Thien (1986), in a broad theoretical study on the origin of angiosperms, proposed that floral fragrances originated from chemicals serving as deterrents against herbivore feeding. In a much more focused study of flower defense in the genus *Dalechampia*, Armbruster (1997) and Armbruster et al. (1997) proposed that defensive resins have evolved into a pollinator-reward system, and that several defense systems have evolved from such advertisement systems. However, the possibility of dual signaling systems that serve to simultaneously attract some animals and repel others has not received much research attention. Pollen odors in certain wind-pollinated plants that do not attract pollinators are rich in defensive molecules such as  $\alpha$ -methyl alcohols and ketones (Dobson and Bergström 2000). The dearomatized isoprenylated phloroglucinols may visually attract pollinators of *Hypericum calycinum* by their UV pigmentation properties, but at the same time the plant may use this pigmentation as a toxic substance against caterpillars, defending the flowers from herbivory (Gronquist et al. 2001). The dual action of attracting pollinators while deterring other animals was also found in other taxa, e.g., *Catalpa speciosa* and *Aloe vryheidensis* (Stephenson 1981; Johnson et al. 2006; Hansen et al. 2007). Thus, floral scents may have a defensive role (Knudsen et al. 2006; Junker et al. 2007) in addition to their known attracting function. A similar double strategy of using signals to attract certain animals and repel others occurs in fruits (Cipollini and Levey 1997; Tewksbury and Nabhan 2001; Izhaki 2002). Altogether, in spite of the huge body of research conducted to characterize visual and chemical signaling by plants to animals in flower and fruit biology, the aposematic hypothesis for these very important plant organs, which are commonly visually and chemically conspicuous, has received very little attention.

#### **4 Undermining Insect Camouflage: A Case of Habitat Aposematism**

It has recently been suggested that many patterns of plant coloration may undermine the camouflage of small invertebrate herbivores (Lev-Yadun et al. 2004). This hypothesis attempted to provide a unifying general explanation for many of the

vegetal coloration types found in nature. The essence of the hypothesis is based on a simple principle that many types of plant coloration undermine the camouflage of small invertebrate herbivores, especially insects, thus exposing them to predation, and in addition causing them to avoid plant organs with unsuitable coloration, to the benefit of the plants. Undermining camouflage is a special case of “the enemy of my enemy is my friend,” and a visual parallel of the chemical signals that plants emit to call wasps when attacked by caterpillars (Kessler and Baldwin 2001; Kappers et al. 2005). Moreover, this is a common natural parallel to the well-known phenomenon of industrial melanism (e.g., Kettlewell 1973; Majerus 1998), which illustrates the great importance of plant-based camouflage for herbivorous insect survival and can serve as an independent test for the insect camouflage undermining hypothesis. It was proposed that the enormous variations in coloration of leaves, petioles and stems, as well as of flowers and fruits, undermine the camouflage of invertebrate herbivores, especially insects (Lev-Yadun et al. 2004). For instance, if a given leaf has two different colors—green on its upper (adaxial) side and blue, brown, pink, red, white, yellow or just a different shade of green on its lower (abaxial) side—a green insect (or one of any color) that is camouflaged on one of the sides will not be camouflaged on the other. The same is true for vein, petiole, branch, stem, flower, or fruit coloration. These differences in color are common across diverse plant forms, from short annuals to tall trees, and in various habitats, from deserts to rain forests and from the tropics to the temperate region. Furthermore, leaf color frequently changes with age, season, or physiological condition. Young leaves of many tropical trees and shrubs (Richards 1996; Dominy et al. 2002; Lee 2007)—as well as of many nontropical plants—are red, and later become green, whereas leaves of many woody species in the temperate zones change to yellow and red in autumn (Matile 2000; Hoch et al. 2001).

In heterogeneous habitats, optimal camouflage should maximize the degree of crypsis in the microhabitats used by the prey, and so herbivores may enjoy better crypsis in heterogeneous habitats (Endler 1984; Edmunds and Grayson 1991; Merilaita et al. 1999). Therefore, a plant with many colors may under certain conditions provide better crypsis than a monocolored one. However, the ratio between the size of the herbivore and the size of the color patches on the plants determines whether a certain coloration pattern will promote or undermine crypsis of the herbivore (Lev-Yadun 2006b). Since insects are in general smaller than many of the color patches of leaves, flowers, fruits or branches, they will often be exposed to predators and parasites and will not become more cryptic and better defended. Indeed, certain types of variegation that form small-scale mosaics are not considered to operate to undermine insect camouflage, as has been partly addressed by Schaefer and Rolshausen (2006). The relative colored areas of plant organs (especially leaves) and the sizes of relevant herbivorous invertebrates should be documented and analyzed under natural and experimental conditions to allow a better understanding of the camouflage issue.

Plants provide habitat and food for many animals, so it is logical to assume that visual perception of animals (both herbivores and predators) coevolved with plants. Intuitively, the common optimal camouflage for herbivorous insects should be

green, and many insects, e.g., aphids, caterpillars and grasshoppers, have indeed evolved green coloration (Cott 1940; Purser 2003). The effectiveness of green camouflage or gray colors that match bark is impaired by diverse nongreen backgrounds, or even by a variety of green shades of plant background, as was evident with industrial melanism (Kettlewell 1973; Majerus 1998). It has therefore been suggested (Lev-Yadun et al. 2004) that all herbivores that move, feed or rest during the day on plant parts that have different colorations from their own immediately become more conspicuous to their predators. The same is true for insect egg color, which should match the background color for defense. Many plants are simply too colorful to enable a universal camouflage of herbivorous insects and other invertebrates to operate successfully, and so they force small herbivores to cross “killing zones” with colors that do not match their camouflage. Since the variable coloration is usually either ephemeral (red young leaves or red or yellow autumn leaves) or occupies only a small part of the canopy (young leaves, petioles, flowers, and fruits), the gains for insects that have evolved to match such ephemeral or less common coloration are low (Lev-Yadun et al. 2004), and with low gains it is difficult to overcome this type of plant defense by evolution. The excellent color vision possessed by many predators of insects, in particular insectivorous birds (the most common and significant predators of herbivorous invertebrates) (Van Bael et al. 2003), probably makes undermining herbivores’ camouflage highly rewarding for plants (Lev-Yadun et al. 2004).

I conclude that since insects, like many other animals, tend to avoid surfaces that don’t match their coloration (e.g., Cott 1940; Kettlewell 1973; Endler 1984; Stamp and Wilkens 1993; Carrascal et al. 2001; Ruxton et al. 2004), plant coloration that undermines camouflage can be viewed as habitat aposematism.

## 5 Delayed Greening as Unpalatability-Based Aposematism

Delayed greening of young leaves of various conspicuous colors (white, pink, very light green) is a common phenomenon in the tropics (Richards 1996). The hypothesis that delayed greening is associated with low nutritive value in young leaves of tropical plants, and that this property defends them from herbivory (Kursar and Coley 1991, 1992, 2003; Coley and Barone 1996), is a special case of a more general hypothesis that low nutritive value acts as a defense (Feeny 1976; Moran and Hamilton 1980; Augner 1995). A similar principle is known to operate well as a defense in many leaves, stems, and young fruit that produce high levels of tannins and other protease inhibitors that decrease protein availability during digestion (Robbins et al. 1987; Bernays et al. 1989; Ryan 1990). Numata et al. (2004) showed that seedlings of various species of the genus *Shorea* (Dipterocarpaceae) that express delayed greening suffer less damage from insect herbivory than species with regular greening. A similar phenomenon occurs in the intraspecific polymorphic *Conocarpus erectus* (buttonwood) leaf color. Some individual plants are silvery and some are green, but some change from green when young to silvery later.

Silvery leaves in buttonwood suffer less insect herbivory (Schoener 1987, 1988; Agrawal and Spiller 2004). Yet, despite the high likelihood that delayed greening is effective and probably also operates outside the tropics, this hypothesis has not received the attention it merits. I propose that the association of being unpalatable with conspicuous colors (delayed greening) may act as a signal to herbivores regarding the lower nutritive value, a typical aposematism. At the same time, such coloration may undermine herbivorous insect camouflage (Lev-Yadun et al. 2004; Lev-Yadun 2006b).

## 6 Colorful Autumn Leaves

The liveliest recent discussion on defensive plant coloration has centered on the phenomenon of red and yellow autumn leaves. For many decades most people believed that these colors simply appear after the degradation of chlorophyll, which masked these pigments, and that they have no function. However, physiological benefits of autumn leaf coloration, such as protection from photoinhibition and photooxidation, are well indicated (e.g., Chalker-Scott 1999; Matile 2000; Hoch et al. 2001, 2003; Lee and Gould 2002; Gould et al. 2002ab; Close and Beadle 2003; Gould 2004; Ougham et al. 2005; Hatier and Gould 2008). So far, six defensive roles of this coloration against insect herbivory have been proposed. (1) The first, and most discussed, is that the bright colors of autumn leaves signal that the trees are well defended and that this is a case of Zahavi's handicap principle (Zahavi 1975, 1977, 1991; Grafen 1990; Zahavi and Zahavi 1997) operating in plants (Archetti 2000; Hamilton and Brown 2001; Archetti and Brown 2004). (2) Schaefer and Rolshausen (2006) formulated the "defense indication hypothesis." (3) Lev-Yadun and Gould (2007) proposed that the function of the bright autumn leaf coloration may in some cases represent aposematism or its mimicry. (4) Lev-Yadun and Gould (2007) also proposed that the colorful autumn leaves signal that they are going to be shed soon. (5) Yamazaki (2008) proposed that autumn leaf coloration employs plant-ant mutualism via aphids. (6) The last hypothesis concerning the defensive role of bright autumn coloration addresses the undermining of herbivorous insect camouflage (Lev-Yadun et al. 2004), which was discussed above. There are several additional subhypotheses of the defensive role of red and yellow autumn leaves that will not be discussed here because they are less relevant to the discussion on aposematic coloration.

Concerning Zahavi's handicap principle operating in colorful autumn leaves (Archetti 2000, 2007a, b; Hamilton and Brown 2001; Hagen et al. 2003, 2004; Archetti and Brown 2004, 2006; Archetti and Leather 2005; Brown 2005), the idea was partly (Lev-Yadun and Gould 2007, 2008; Ougham et al. 2008; Ramirez et al. 2008) or wholly (Holopainen and Peltonen 2002; Wilkinson et al. 2002; Schaefer and Wilkinson 2004; Ougham et al. 2005; Schaefer and Rolshausen 2006, 2007; Sinkkonen 2006a, b; Chittka and Döring 2007; Rolshausen and Schaefer 2007; Schaefer and Gould 2007; Hatier and Gould 2008; Yamazaki 2008) discounted.

Lev-Yadun and Gould (2007, 2008) emphasized that the operation of aposematism does not exclude the possible simultaneous operation of any other types of visual or nonvisual defense in autumn leaves (see also Hatier and Gould 2008).

The opposition to the handicap hypothesis is based on the complicated biological facts involved (which are also not yet well understood), and on the simultaneous operation of various and sometimes contrasting physiological and defensive functions of autumn leaf coloration. The various functions probably differ in their importance over time, even in a single leaf, let alone in a flora or a broad geographical region (see Lev-Yadun and Gould 2007; Ougham et al. 2008). Holopainen and Peltonen (2002) suggested that leaves that have just turned yellow are a good indication to aphids of the nitrogen available in them in the form of amino acids, an attracting rather than a repelling signal. Wilkinson et al. (2002) held that rather than signaling defensive qualities to aphids, especially since these are drawn to yellow leaves, this coloration serves as a sunscreen (a physiological role), and red colors help to warm leaves, and also function as antioxidants. Ougham et al. (2005) stressed the importance and good documentation of the physiological role of autumn leaf coloration. They argued that the signal is not costly, which, according to the most common view (but not all views, see Lachmann et al. 2001), is a basic feature of signals involved in the operation of Zahavi's handicap principle (Zahavi 1991; Zahavi and Zahavi 1997).

Elaborating on a previous idea by Fineblum and Rausher (1997) about the shared biochemical pathways for flower color and defensive molecules, Schaefer and Rolshausen (2006) formulated the "defense indication hypothesis," a hypothesis of defensive plant coloration, focusing on anthocyanins. It posits that fewer herbivorous insects will feed on plants with strong anthocyanin coloration because it correlates with defensive strength. The biochemical basis for this correlation is that anthocyanins and a number of defense chemicals such as tannins stem from the same biosynthetic pathways. Schaefer and Rolshausen (2006) clearly state that since, according to their understanding, autumn leaf coloration has evolved primarily because of physiological roles, and not as a defense against herbivores, this coloration is not a signal (it is not aposematic), and may be used only as a cue by the insects.

Contrasting views on the phenomenon of bright autumn leaf coloration were presented concerning the hypothesis that these bright leaves may be aposematic. Archetti (2000) specifically rejected the possibility that autumn leaf coloration is aposematic, and aposematism was not discussed in other studies that favored the signaling hypothesis (Hamilton and Brown 2001; Hagen et al. 2003, 2004; Archetti and Brown 2004, 2006; Archetti and Leather 2005; Brown 2005; Archetti 2007a, b). Lee and Gould (2002), Lee (2002), Gould (2004), Sherratt et al. (2005) and Schaefer and Rolshausen (2007) interpreted the hypothesis of handicap-related autumn coloration presented in the papers by Archetti (2000) and Hamilton and Brown (2001) as a case of aposematism, notwithstanding the different views of the authors. Lev-Yadun and Gould (2007), however, proposed that the function of the bright autumn leaf coloration may in many cases represent aposematism or its mimicry. Lev-Yadun and Gould (2007, 2008) proposed that if

the defense indication hypothesis is accepted, it directly follows that plant parts rich in anthocyanins may serve in many cases as aposematic (warning) coloration for chemical-based unpalatability. If the red-colored autumn leaves are well defended by various chemicals, as proposed by Schaefer and Rolshausen (2006), or even if red and old yellow autumn leaves are just of low nutritive value (two cases of unpalatability), many bright autumn leaves should be considered aposematic (Lev-Yadun and Gould 2007).

The reason why yellow or red autumn leaves in species that are chemically well defended or unpalatable should be considered aposematic is obvious. Moreover, as in other cases of aposematism (Cott 1940; Wickler 1968; Lev-Yadun 2003b), it is tempting to postulate that mimics of true aposematic autumn leaves also exist. Lev-Yadun and Gould (2007) proposed that the widespread phenomenon of red autumn leaves in some areas may be partly the result of Müllerian and Batesian mimicry. When toxic or unpalatable red leaves of different species mimic each other, they should be considered Müllerian mimics, and when nontoxic and palatable leaves mimic toxic ones, they should be considered Batesian mimics. The question of the potential role of mimicry in the evolution of red (or yellow) autumn coloration is still an enigma. If old yellow leaves are unpalatable, while leaves that have just turned yellow are rich with free amino acids (e.g., Holopainen and Peltonen 2002), then Batesian mimicry by the newly formed yellow leaves seems to operate with the yellow leaves formed earlier on the same tree, or among various trees of the same species that differ in yellowing time, or even among different species. The potential involvement of olfactory cues in autumn leaf aposematism should be studied. Again, Lev-Yadun and Gould (2007) emphasized that the lack of strong attacks on red or yellow autumn leaves does not necessarily prove that there is no risk of herbivory. The possibility of olfactory aposematism of yellow and red autumn leaves operating simultaneously with visual aposematism in unpalatable leaves was not discussed in depth. The fact that there are good physiological indications of significant volatile release from such leaves (Keskitalo et al. 2005) supports such a possibility.

## **7 Animal and Herbivore Damage Mimicry May Also Serve as Aposematic Coloration or Aposematic Visual Signals**

It is probable that various types of defensive mimicry by plants may trick animals into behaving according to the plant's interests, just as they are tricked by bee mimicry of orchid flowers during pollination (e.g., Dafni 1984; Jersáková et al. 2006). Defensive animal mimicry by plants exists in several forms: (1) egg-laying mimicry, (2) ant mimicry, (3) aphid mimicry, (4) caterpillar mimicry, and (5) animal chewing or tunneling damage mimicry.

Butterfly egg mimicry in plants was proposed as a way to reduce egg laying by *Heliconius* butterflies (Benson et al. 1975; Gilbert 1980; Shapiro 1981a, b; Williams and Gilbert 1981).

Three types of visual defensive insect mimicry have been described. In the first type, plants have dark spots and flecks in the epidermis of stems, branches, and petioles that resemble ant swarms in size, shape, and pattern (Lev-Yadun and Inbar 2002). In the second type, dark anthers are the size, shape, and color of aphids, and they sway in the wind like swiveling aphids (Lev-Yadun and Inbar 2002). Finally, stipules along the branches of *Passiflora caerulea* look like caterpillars, slugs or snails climbing along the stems (Rothschild 1974, 1984), and immature pods of several annual legumes have conspicuous reddish spots, arranged along the pods, causing them to look like aposematic lepidopteran caterpillars (Lev-Yadun and Inbar 2002).

It is well known that ants defend plants from insect or mammalian herbivory, and in certain cases their relations with their hosts have been recognized as being mutualistic (e.g., Madden and Young 1992; Jolivet 1998). The potential benefit of ant-attendance mimicry is obvious. Ants bite and sting and are aggressive, and so many animals, including herbivores, will avoid them. Thus, ants have become models for a variety of arthropods that have evolved to mimic them (Wickler 1968; Edmunds 1974). The importance of ants in defending plants was demonstrated in a field experiment in which ant and aphid removal resulted in a 76% increase in the abundance of other herbivores on narrow-leaf cottonwoods (Wimp and Whitham 2001). Many plant species invest resources in attracting ants, providing them with shelter, food bodies and extrafloral nectaries (Huxley and Cutler 1991). Certain plants tolerate aphid infestation to gain antiherbivore protection from aphid-attending ants (Bristow 1991; Dixon 1998). Thus, it is not surprising that ant mimicry is found in plants. Ant mimicry has been found so far on the stems and petioles of *Xanthium trumarium* (Asteraceae) and *Arisarum vulgare* (Araceae) growing in Israel. The ant mimicry was in the form of conspicuous, dark-colored spots and flecks, usually 2–10 mm in size on the epidermis, resembling ants in size, shape and in the direction of their spatial patterns, which resemble a column of ants. Dots predominate in some individual plants; flecks in others (Lev-Yadun and Inbar 2002). Ant swarms are typically composed of many moving dark flecks, each varying in size from several millimeters to over a centimeter. The swaying of leaves, stems or branches in the wind in combination with the dark spots and flecks, many of which are arranged in lines, may give the illusion that the “ants” move. Again, the possibility of the involvement of olfactory mimicry of ants has not been studied yet. In any case, the aggressive and efficient antiherbivore activities of ants seem to make it beneficial for plants to mimic ant attendance in order to deter herbivores (both insects and vertebrates) without paying the cost of feeding or housing them (Lev-Yadun and Inbar 2002).

A mimicry phenomenon similar to ant mimicry is aphid mimicry. Lev-Yadun and Inbar (2002) described aphid mimicry in *Paspalum paspaloides* (= *P. distichum*), where the dark anthers are the size, shape and color of aphids and the anthers sway in the wind like swiveling aphids. Similarly, the stems of *Alcea setosa* are also covered with dark flecks that look like aphids. It has been proposed by Lev-Yadun and Inbar (2002) that plants that look infested may be left untouched by both mammalian grazers and aphids or various other insects. Several studies have



shown that early infestation by aphids and other homopterans has a negative impact on host plant preferences and larval performance of other insect herbivores. Finch and Jones (1989) reported that large colonies of the cabbage aphid *Brevicoryne brassicae* and the peach aphid *Myzus persicae* deter ovipositioning by the root fly *Delia radicum*. Inbar et al. (1999) demonstrated that homopterans (whiteflies) not only alter adult cabbage looper (*Trichoplusia ni*) host selection, but also actually reduce the feeding efficiency of their offspring. Aphids respond to crowding by enhanced dispersal (Dixon 1998), and so it is also probable that they may avoid already infested or infestation-mimicking hosts. This clear zoological data set supports the hypotheses about the potential defensive value of aphid mimicry, but experimental data is needed to fully accept this hypothesis. Again, the possible involvement of olfactory cues should not be ruled out.

The third case of conspicuous coloration that mimics insects for defense is that of caterpillar mimicry. It was proposed to operate in two types of mimicry: (1) stipules along the branches of *P. caerulea* look like caterpillars, slugs or snails climbing along the stems, and were proposed to deter butterflies searching for laying sites (Rothschild 1974, 1984); (2) immature legume pods of several wild annual legumes (*Lathyrus ochrus*; *Pisum elatius*; *P. humile*; *Vicia peregrina*) look like aposematic poisonous lepidopteran caterpillars ornamented with spiracles or other spots on their sides due to the presence of conspicuous spots in various shades of red and purple arranged along the pods (Lev-Yadun and Inbar 2002), which may serve as herbivore-repellent cues and form part of the defense system of the plants. Caterpillars employ a large array of defenses that reduce predation. Unpalatable caterpillars with stinging and irritating hairs, functional osmeteria or body-fluid toxins often advertise their presence by aposematic coloration and aggregation (Cott 1940; Bowers 1993; Eisner et al. 2005). The usual warning colors of caterpillars are yellow, orange, red, black and white with stripes along the body and/or arranged in spots, especially around the abdominal spiracles. To conclude the cases of defensive insect mimicry by plants, Lev-Yadun and Inbar (2002) suggested that the cases of ant, aphid and caterpillar mimicry may signal unpalatability (aposematism) to more than one group of animals in two ways: first, insect mimicry may reduce attacks by insect herbivores that refrain from colonizing or feeding on infested plants (because of competition, cannibalism and/or induced plant defenses); and second, where the insect mimicked is aposematic, this could deter larger herbivores from eating the plants. None of these hypotheses about the various types of defensive insect mimicry was tested directly. It has however been shown that ungulates may actively select leaves in the field by shape and color and avoid spotted ones (e.g., Cahn and Harper 1976), but there seems to be no published data on the response of mammalian herbivores to aposematic (or cryptic) caterpillars. Again, the possible involvement of olfactory deterrence was not studied.

Mimicry of feeding damage by caterpillars as the reason for the formation of leaf lobes in some Moraceae (Niemelä and Tuomi 1987) or mimicry of chewed leaf ends in certain palms (Dirzo 2002) has also been posited. The mimicry of tunneling (Smith 1986; Lev-Yadun 2003a; Lee 2007; Campitelli et al. 2008; Soltau et al. 2009) was described above.

A related phenomenon, the use of aposematic insects to defend plants from large herbivores, has been proposed by Rothschild (1972, 1986). Various poisonous aposematic insects aggregate on poisonous plants, adding to the plant's aposematic odor and possibly to its coloration. This type of mutualism via aposematism deserves much more descriptive, theoretical and experimental studies.

## 8 Plant Aposematism Involving Fungi

The possibility that plants have mutualistic relationships with various fungi including pathogenic ones is not new. Most suggestions for such relations were based on the chemical defenses provided by endophytic or parasitic fungi (Clay 1990; Bush et al. 1997; Omacinn et al. 2001; Clay and Schardl 2002). Recently, there were two suggestions that fungal pigmentation, with or without known toxins, is used as a type of aposematic coloration. In the first case, Lev-Yadun and Halpern (2007) proposed that the very poisonous purple–black sclerotia of the infamous fungus *Claviceps purpurea* (ergot) and many other *Claviceps* species are aposematic. Very toxic fungal sclerotia are associated with conspicuous colors (black, yellow, purple, reddish, brown, violet, white and their combinations), and they severely harm herbivores that consume the infected plants, thus meeting the criteria for aposematism. These fungi, which only moderately reduce the reproductive capacity of their hosts, can protect the host plants from herbivory and weaken the evolutionary tendency of their hosts to evolve better resistance to infection. Moreover, by doing so, the fungi defend the host plant that is their habitat. In the second case, Lev-Yadun (2006a) proposed that whitish-colored plants may appear to be infested by fungal disease. Because there are very good indications that plant parts that may be infested by fungi are rejected by animals—frugivores avoid eating damaged fruits (Janzen, 1977; Herrera, 1982; Manzur and Courtney, 1984; Borowicz, 1988; Buchholz and Levey, 1990)—Lev-Yadun (2006a) proposed that white plant surfaces that mimic fungus-infested plants may reduce the tendency of herbivores to consume such plants. This is a type of visual aposematism.

## 9 Distance of Action of Aposematic Coloration (Crypsis Versus Aposematism)

The difference between a smart person and a wise one is that the wise one will not get into the difficult situation from which the smart one can find his way out. Ruxton et al. (2004) named their book about defensive mechanisms *Avoiding Attack*. Camouflage of various types is a good way to escape attack, but when it fails, aposematism may operate at close range in various animals (e.g., Mappes et al. 2005; Tullberg et al. 2005). The different visual and cognitive abilities of various animal taxa add to the significance of the variability of aposematic signaling (Endler and Mappes 2004); this is probably also true when plants have several colors in their spine system (Lev-Yadun 2001). While this double strategy (camouflage

versus aposematism) has not yet been studied in plants, there are indications that it may operate. For instance, certain cacti use their spines for camouflage from a distance (Benson 1982), while they may be colorful and aposematic at close range (e.g., Lev-Yadun 2001). This issue deserves descriptive, theoretical and experimental studies so that it can be better understood.

## 10 Aposematic Trichomes: Probably an Overlooked Phenomenon

Trichomes, the unicellular and multicellular appendages of the epidermis (Fahn 1990), are well known for their multiple functions in plants. Trichomes may serve in protecting plants from excess sun irradiation of various wavelengths, including UV (Fahn and Cutler 1992; Manetas 2003); secrete toxic ions, especially in saline habitats (Fahn 1988); function in water absorption (Fahn and Cutler 1992); reduce transpiration (Fahn and Cutler 1992; Werker 2000); defend from insect or other herbivorous invertebrates by reducing accessibility or by actually trapping their legs or by chemical means (Levin 1973; Fahn 1979, 1988; Werker 2000); and defend from large herbivores when they sting, as in *Urtica* (Thurston and Lersten 1969; Levin 1973; Fahn 1990; Fu et al. 2006). In addition, in certain carnivorous plants like *Drosera* and *Dionea*, they may take part in the attraction, capture and digestion of insects (Juniper et al. 1989; Fahn 1990). Many plant trichomes are colorful (red, yellow, orange, blue, white) and very conspicuous. In certain cases, such as in cotton plants, pigmented trichomes produce toxins that defend from caterpillars (Agrawal and Karban 2000). In addition, the trichomes have conspicuous red markings at their base in various plants, e.g., *Echium angustifolium* (Boraginaceae) and *Echinopsadenocaulos* (Asteraceae). Thorns, spines and prickles are large and usually spaced, and their ability to defend from insects is limited (e.g., Potter and Kimmerer 1988), whereas trichomes—because of their size, density and chemical composition—may commonly defend plants from insects (e.g., Levin 1973; Fahn 1979, 1988; Werker 2000). I propose that colorful and poisonous or sticky trichomes may deter insects and serve as aposematic coloration. Because many insects see UV (Briscoe and Chittka 2001), the possibility that trichomes may deter insects in the UV channel should be considered and studied. The possibility that trichomes produce olfactory aposematic signals in addition to visual ones should also be considered, in light of the secretive nature of many trichomes (Fahn 1979, 1988).

## 11 Experimental Evidence

The experimental evidence for the operation of aposematic coloration in plants is meager. Cook et al. (1971) showed that poisonous gray seeds of *Eremocarpus setigerus* are rejected by the mountain dove. Cahn and Harper (1976) showed that sheep

avoid *Trifolium repens* plants with leaf marks, but did not discuss aposematism. Lev-Yadun and Ne'eman (2004) showed that sheep, goats, camels, donkeys and cattle reject conspicuous green plants in the yellow desert in the summer. Numata et al. (2004) found that leaves with delayed greening suffer lower levels of insect damage when they are still young. Hill (2006) showed that the Florida scrub jay (*Aphelocoma coerulescens*) rejects poisonous red fruit. Karageorgou and Manetas (2006) showed that young red leaves of the evergreen oak *Quercus coccifera* are attacked less than green ones by insects, but rejected the aposematic coloration hypothesis. Similar results were found for other species in Greece (Karageorgou et al. 2008). Recently, additional data about the defensive operation of white variegation that mimics insect damage in leaves was published (Campitelli et al. 2008; Soltau et al. 2009). The possibility of olfactory aposematism was not tested in any of these cases.

## 12 Conclusions

Aposematic (warning) coloration seems to be a common defense in plants, even though it was practically ignored by botanists and zoologists until recently. The first papers fully dedicated to visual aposematism in plants were published after the year 2000. Similar to the situation in animals, aposematic (warning) coloration (yellow, orange, red, brown, black and white, and combinations of these colors) seems to be a common defense in plants, although (except for anecdotal mentions) it has been practically ignored by botanists and zoologists until recently. The fact that many aposematic animals use both plant-based pigments and sequestered poisonous molecules to become aposematic highlights the absurdity of neglecting the aposematic nature of so many plants. Aposematic coloration was referred to here in the broadest sense, considering any visual warning phenomenon that may deter herbivores. Aposematic coloration is expressed by thorny, spiny and prickly plants, by poisonous ones, and by plants that are unpalatable for various reasons. Plants that mimic aposematic plants or aposematic animals are probably common, despite the small number described so far. Colorful mimicry of insect infestation or herbivore damage to tissues in order to repel herbivores is also found in plants. Many types of aposematic coloration simultaneously serve other functions, such as physiological, communicative and even other defensive functions. It is therefore difficult in many cases to evaluate the relative functional share of aposematism in various color patterns of plants and the specific selective agents involved in their evolution. Aposematic coloration is part of a broader phenomenon of defensive coloration in plants, which has also received insufficient attention. The fact that botanists have not usually considered the operation of aposematic coloration or other types of defensive coloration is evident from the lack of a regular and systematic description of these color patterns in the majority if not all of the thousands of published floras. The related phenomenon of olfactory aposematism of poisonous plants has also received very little attention. Simultaneous operation of visual and olfactory

aposematism in the same plant is also proposed. Many theoretical aspects of aposematism that were and are currently being studied experimentally in animals have almost never been studied in plants. Aposematic coloration in animals has been broadly studied since the nineteenth century and is still not fully understood. The effort needed to understand aposematic coloration in plants is probably not any smaller. This situation provides the opportunity for ambitious scientists to express their capabilities. Thus, there appears to be a colorful future for the study of aposematic coloration in plants.

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