

and supporting essential gestational processes and optimal secretion of gestational hormones. The placenta is the organ of transport of fetal nutrients and wastes. As an interface between mother and fetus, it shelters the fetus from physical adversity and immunological rejection; it may also serve more complex defense mechanisms. Microorganisms in the placenta may conceivably impair these multiple functions to the detriment of the fetus.

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*et al.* (4), predators can learn an avoidance response based on odor alone, then one can easily envision the evolution of imitation of warning odors by palatable species (Batesian mimicry) and convergence of odor in unrelated distasteful species (Müllerian mimicry). Such olfactory mimicry has indeed been invoked to account for apparent similarities in odor in certain chemically protected insects (7). The increasingly sensitive analytical techniques now available to the natural product chemist may make it possible to determine whether such presumed chemical mimicry has a basis in fact. It is particularly tempting to predict that olfactory mimicry, both Batesian and Müllerian, should be commonplace in plants.

The preceding is not meant to imply that odors are invariably aposematic or that olfactory aposematism can be achieved only through de novo evolution of warning chemicals. Odor is a consequence of the chemical emission that characterizes all forms of life, and most biological odorants are undoubtedly without signal function. Aposematic odors, one might imagine, could in many instances be no more than odors of incidental origin that have only secondarily, under appropriate predation pressure, and with or without chemical elaboration, taken on a communicative role. Pheromones, it has been hypothesized, could in some cases have had a comparable origin (8).

We also do not mean to imply that olfactory aposematism can occur only in association with slow-acting toxins. Noxiousness manifests itself in many ways in organisms, as through distastefulness, contact irritancy, pugnaciousness, and possession of defensive glands or mechanical weaponry. Body odors could take on a warning function in all such cases.

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## Toxicity, Odor Aversion, and "Olfactory Aposematism"

Many plants and animals are chemically protected against predation by slow-acting systemic poisons present in their tissues and body fluids. These compounds are commonly bitter tasting but nonvolatile, and hence odorless. Some examples are well known: nicotine in tobacco plants (*Nicotiana* spp.), morphine in the opium poppy (*Papaver somniferum*), quinine in the cinchona tree (*Cinchona officinalis*), and strychnine in *Strychnos* spp. Less familiar examples include emetine in the roots of *Uragoga ipecacuanha* (1), emetic steroids in fireflies (*Photinus* spp.) (2), and cantharidin in meloid beetles (3).

Often the organisms involved are identifiable by odors unrelated to the toxins. There is no evidence to indicate that the odors themselves, at their natural concentrations, are intrinsically repellent to predators or play any direct role in chemical defense. In fact, no satisfactory biological explanation appears to have been advanced to account for such odors.

Palmerino *et al.* (4) have reported that if laboratory rats first exposed to a neutral odor while drinking sugar water are subsequently made ill, the odor becomes conditioned as a drinking deterrent. This result suggests that the characteristic odors of poisonous plants and animals may have evolved as the olfactory concomitants of bitter, odorless toxins and that they may function as conditioned

stimuli for the deleterious effects of the ingested poisons, should the bitter taste itself be insufficient to deter the predator. Experienced predators would thereby be warned to search for food elsewhere. Warning by odor may appropriately be called olfactory aposematism, in analogy to the well-known alternative forms of aposematism shown by animals that warn their predators by visual or acoustic means (5, 6).

Odor, visual appearance, sound, taste, and tactile properties can all be thought of as elements of an "aposematic gestalt" that a predator makes use of to "key out" and appraise a potential prey item. The prey's odor, visual appearance, and sound would normally be the first of these elements encountered by the predator. Because it is obviously to the advantage of the prey to discourage the predator at the earliest possible stage of their interaction, one would expect all three modalities—odor, coloration, and sound—to enter into the elaboration of aposematic signals in nature. In plants, in which acoustic aposematism is nonexistent and visual aposematism relatively rare (at least of the vegetative parts), olfactory aposematism may well be the primary form of warning.

Visual mimicry is a well-studied consequence of the ability of predators to learn to avoid distasteful prey on the basis of appearance and coloration (5). If, as might be inferred from Palmerino

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