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SHORT COMMUNICATION

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Conspicuous and aposematic spines in the animal kingdom

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Abstract Spines serve as a common physical defence mechanism in both the plant and animal kingdoms. Here we argue that as in plants, defensive animal spines are often conspicuous (shape and colour) and should be considered aposematic. Conspicuous spines may evolve as signals or serve as a cue for potential predators. Spine conspicuousness in animals has evolved independently across and within phyla occupying aquatic and terrestrial ecosystems, indicating that this convergent phenomenon is highly adaptive. Still, many spines are cryptic, suggesting that conspicuity is not simply constrained by developmental factors such as differences in the chemical composition of the integument. Aposematism does not preclude the signalling role of conspicuous spines in the sexual arena.

Introduction

Aposematic colouration is a well-known and widespread defensive phenomenon found across the animal kingdom, including invertebrates and vertebrates in marine as well as in terrestrial ecosystems (Lindquist and Hay 1996; Mallet and Joron 1999). Aposematism refers to animals that possess or mimic (Batesian mimicry) traits which are unpalatable or dangerous to potential predators and that advertise them with a variety of signals, mainly bright and contrasting colours, i.e. red, orange, yellow, black and white, but also sound and odour (Cott 1940; Guilford 1990). Unpalatability punishes the predator and thus facilitates an efficient associative learning that reduces further attacks. Unpalatability is a variable trait that is sometimes hard to define (Lindquist and Hay 1996; Mallet and Joron 1999), and has been considered as a general defence mechanism (Edmunds 1974), including behavioural, physical and chemical traits. The vast majority of studies on aposematism of animals associated warning colouration with chemical defence, in particular in insects, amphibians, reptiles and larvae of marine invertebrates (Rothschild 1972; Edmunds 1974; Guilford 1990; Bowers 1993; Lindquist and Hay 1996). Recently, Lev-Yadun (2001) suggested that many spiny higher plants are aposematic since spines are usually conspicuous because of their own bright colours or because of their association with conspicuous markings. It has been proposed that this may deter large mammalian herbivores and accelerate their learning to avoid spiny plants (Lev-Yadun 2001). Surprisingly, a review of some 5,000 relevant references that were published in the last two centuries (Komárek 1998) revealed that the role of colourful animal spines as both physical weaponry and warning colouration have been widely ignored. It should be mentioned that Cott (1940, p 259) gave a few examples of defensive and conspicuous integuments. Here we propose that, as in plants, the phenomenon of colourful, conspicuous spines is also common in the animal kingdom.

Results

The colours and shape of spines in animals tend to be conspicuous and different from the colour of the adjacent body parts. The different colours (e.g. yellow, orange, red, blue, black, white and their combinations) that make spines more conspicuous are illustrated below for several taxa (Fig. 1).

In the phylum Arthropoda, conspicuous spines (i.e. spines that visually contrast with adjacent body parts) can be seen on the exoskeleton of many Crustaceans, such as crabs and lobsters (e.g. the Caribbean spiny lobster, *Panulirus argus*) and on the legs of several insects such as mantids and many orthopterans (katydids, crickets, stick insects, etc.) (see plates in Rentz 1996). Interestingly, in

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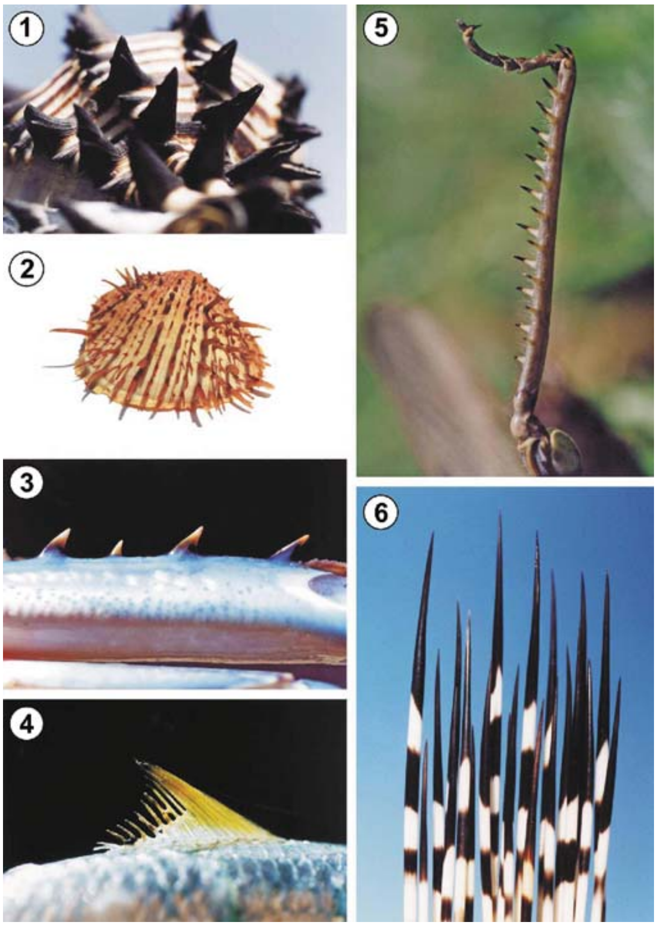

Fig. 1 Conspicuous spines across the animal kingdom; illustrations from aquatic and terrestrial habitats. *1 Muricanthus nigritus* (Mollusca: Gastropoda), *2 Spondylus* sp. (Bivalvia: Gastropoda), *3* legs of the swimming crab *Callinectes sapidus* (Arthropoda: Crustacea), *4* dorsal spines of a mullet *Mullus* sp. (Teleostei: Mullidae), *5* hind tibia of the grasshopper *Anacridium aegypticum* (Insecta), *6* black and white spines of the Indian crested porcupine *Hystrix indica* (Mammalia) (photographs: S L-Y.)

land arthropods, spines (regardless of conspicuity), are primarily limited to these insect groups (and lepidopteran larvae) and few spiders. Similarly, in the phylum Mollusca, defensive conspicuous spines of various bright colours are found on the shells of, for example, the true cowries, class Gastropoda, and in the spiny oysters (e.g. *Spondylus* spp., Spondylidae), class Bivalvia (George and George 1979; Lamprell and Healy 1998; Stix et al. 1968). The phenomenon of conspicuous spines is also highly pronounced and widely distributed in the spiny-skinned animals, phylum Echinodermata. Classic examples are the starfishes *Acanthaster planci* and *Metrodira subulata*, which have red spines, and the yellow-spined *Gomophia aegypticana* (George and George 1979). Spines are also abundant in the phylum Chordata. Perhaps the most diverse group of spiny vertebrates is the bony fishes, many of which are armed with tough, usually dorsal spines. The conspicuousness of the spines (and often rays) can be clearly demonstrated in members of the families Scorpaenidae, Serranidae, Siganidae, Sparidae, Tetraodontidae, Trachinidae (see photographs in Smith and Heemstra 1986). Classic examples are the porcupine fish, *Sebastes crameri* and the yellow spotted burrfish *Chilomycterus spilostylus* (Golani and Darom 1999). Several reptile lineages are protected by hard and relatively short spines. Crocodilians are armed with dorsal spines distributed along the back and tail, and in several species they are visually pronounced by orange colouration, as in the Cuvier's dwarf caiman *Paleosuchus palpebrosus* (Zug et al. 2001). Similarly, the spines of certain turtles, such as the yellow spines of cogwheel turtle, *Heosemys spinosa* (Cogger et al. 1998) are highly conspicuous. The sole representative of the ancient taxon tuataras, the *Sphenodon punctatus* from New Zealand, has brightly coloured erect spines on the nape and back. The bodies of several lizards (Squamata) are covered with conspicuous spines. The horned lizards (e.g. *Phrynosoma asio*), iguanas and species of the genus *Uromastyx*, especially Dabb's mastigure, *U. acanthinurus*, have orange and yellow spines on their tails (Zug et al. 2001). In the class Mammalia, spines are rare, but they have developed in hedgehogs (Insectivora) and porcupines (Rodentia). Similar spine colouration is found in the living fossil, the primitive member of the Monotremata, the spiny anteater *Tachyglossus aculeatus*. Because most spiny mammal species are nocturnal, their spines are advertised by contrasting bands of black and white colouration.

Discussion

Spines are an important anti-predator physical defence in animals (Edmunds 1974). We suggest that this defensive trait is in many cases aposematic because of the conspicuous shape and colouration of spines. Although not all spines are conspicuous the phenomenon is general and convergently evolved in numerous cases and habitats. In both plants and animals visually oriented animal predators or herbivores have selected for this conspicuous and colourful trait. In chemically defended aposematism, the entire body is advertised and the animals are highly conspicuous. On the other hand, in spine-defended animals (and plants) sometimes only the weapon is advertised. In grasshoppers and mantids for example, cryptic colouration can be maintained whereas warning coloured spines (on the legs) are displayed only after they are discovered or attacked by predators.

Because of their defensive role, spines are often harder and tougher than adjacent integument. This function requires physical and chemical modification in the spine. For example, the hardness of spines in rodents is achieved by their shape, development of thick septae, and expansion of cortical layers (Chernova and Kuznetsov 2001). In insects, the hardness of spines (and integument) is derived from modifications of the protein matrix in which the chitin–chain microfibrils are embedded (Borror et al. 1989). This may suggest that the conspicuity of spines is constrained by their modified chemical and physical structure. However, because many spines are cryptic it appears that the relationship between colour and the hardness and sharpness of spines is not fixed.

In unpalatable animals, the chemical defence may evolve independently from the colour signal leading to the classic non-honest Batesian mimicry (Maynard Smith and Harper 2003). Conspicuous spines, on the other hand, may serve as a direct cue for defence ability. Nevertheless, it is highly possible that as in chemically defended aposematic organisms, Batesian mimicry based on faked spines may have evolved as aposematic signals (see also Lev-Yadun 2003 for such phenomenon in plants).

Still, many spines and spiny species are not conspicuous, a fact that is not surprising as no adaptation is universal. Future examination of life history traits of closely related species bearing cryptic vs. conspicuous spines (e.g. crustaceans, orthopterans and fish) should help us understand the driving forces behind this variation. Nevertheless, because, as in plants, spine conspicuousness in animals has evolved independently in numerous lineages, across phyla and contrasting ecologies, in both terrestrial and aquatic ecosystems, this indicates that the phenomenon is highly adaptive. In addition to their defensive significance, it is clear that conspicuous (colours and shape) organs may have an important role in other signalling contexts, such as sexual communication.

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