

scribes the same region as having a central core (of fine structure which we cannot readily relate to our observations) joined by radially directed fibrils to dense little rods distributed around part of the periphery of the cell. Viewed through the electron microscope, Brunotte's lamellar body is seen to be a cavity in the cell cytoplasm filled by a stack of about 400 disc-shaped, membranous sacs with their somewhat undulating faces perpendicular to the optical axis of the cell. The cytoplasmic wall of the cavity is invested at one side with about 400 centripetally pointing ciliary basal bodies; each sac of the cavity is the expanded and flattened outer membrane of one of these cilia (Fig. 2).

Inside the cytoplasm the basal bodies, which seem to lack striated rootlets, have nine triplets of fibrils in a cartwheel arrangement; one filament of each triplet is lost as the cilium emerges into the cavity. There are no central filaments.

The discs are closely stacked so that their membranes (about 60 to 70 Å thick) are separated by a constant (about 20 to 30 Å) distance. Their internal space, which is continuous with that of the cilium, is of more variable dimension (12 to 1000 Å) and includes the extensions of the axial filaments of the cilia. These become progressively disorganized and terminate one by one, having penetrated a third of the disc diameter.

A detailed report on these photoreceptors is in preparation.

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Defensive Spray of a Phasmid Insect

Abstract. *The walkingstick, Anisomorpha buprestoides, has two defensive glands in its thorax from which it ejects an aimed spray when disturbed. Contact stimulation is the usual trigger for the discharge, but birds may elicit the spray by merely approaching the insect. The secretion proved effectively deterrent to ants, predaceous beetles, mice, and blue jays, but not to an opossum.*

The large Southern walkingstick, *Anisomorpha buprestoides*, is known to eject a defensive spray when disturbed (1). The secretion is lachrymogenous, and its vapors are painfully irritating when inhaled. The active principle, anisomorphal, is a terpene dialdehyde (2), chemically allied to nepetalactone (catnip) and certain other cyclopentanoid monoterpenes produced by insects and plants (3). This report deals with the remarkable adaptive refinements of this chemical defense mechanism.

The secretion is produced and stored in two elongate, sac-like glands situated behind the head (Fig. 1B). Discharge is effected by appropriate compressor muscles that surround the glands (Fig. 1C). All instars of both sexes possess functional glands.

Anisomorpha discharges instantly in response to mild traumatic stimulation as, for example, when individual legs are pinched with forceps, or when the body is tapped or persistently prodded. Against a dark background, the spray is clearly visible. Ejection is from one gland or from both, depending on whether the stimulus is applied unilaterally or bilaterally (Fig. 2). Marksmanship is precise: the spray invariably drenches the particular instrument used for stimulation.

As many as five consecutive bilateral discharges may be elicited from an adult female before the glands are depleted. Within 7 to 15 days, her secretory supply is restored. The male

is considerably smaller, and usually sprays only once or twice. Interestingly, the male is nearly always found astride the female (Fig. 1A), even while not mating; the sexes are often found already associated in this fashion while still in their immature nymphal stages. Whether the "pooling" of defensive resources is an important adaptive justification of the partnership remains to be seen.

To determine the defensive effectiveness of the spray, individual adult females of *Anisomorpha* were offered to a variety of caged predators, including ants (*Formica exsectoides*, *Pogonomyrmex badius*), carabid beetles (*Calosoma prominens*), mice (*Peromyscus leucopus*), a mouse-opossum (*Marmosa demararae*), and blue jays (*Cyanocitta cristata*) (4).

The ants and beetles were instantly repelled by the aimed discharges induced by them whenever they bit one of the walkingstick's appendages. The mice approached the walkingsticks and sniffed them on contact but were promptly sprayed, and they fled before inflicting injury. The spray caused pronounced cleansing activities in these three types of predators (5), but no detectable permanent ill-effects. Individuals of *Anisomorpha* with depleted glands were overcome and eaten.

The opossum proved to be an unusually persistent predator. It initiated its attack by grasping the walkingstick in its jaws, and in return was invariably sprayed on the head (Fig. 1E). It then scurried about in obvious discomfort, attempting to cleanse itself of secretion by rubbing its muzzle in the litter on the floor of the cage, but, instead of abandoning the insect, it held it tenaciously with a front paw (Fig. 1F). Squeezed in this fashion, the walkingstick continued spraying, but its discharges were now aimed at the relatively insensitive paw of the opossum and appeared to miss the sensitive eyes and snout. Eventually, after its secretion was ineffectually expended in this fashion, the walkingstick was eaten (Fig. 1G). Additional walkingsticks were offered daily over a period of a week, but the results remained essentially identical; the opossum became no less aggressive with time.

The results with the jays were especially dramatic because the birds often (15 of 21 instances) received the full impact of an aimed discharge before they actually contacted the walkingsticks. Sometimes the birds

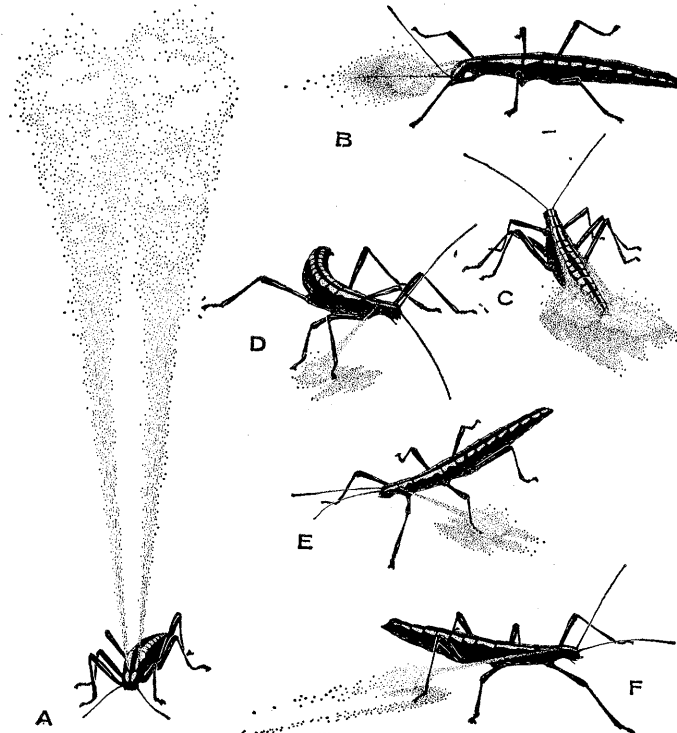
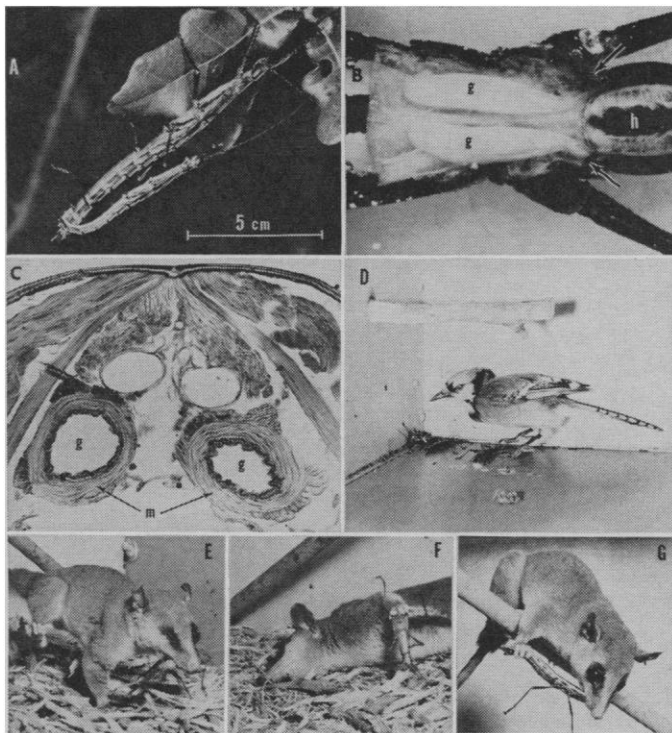
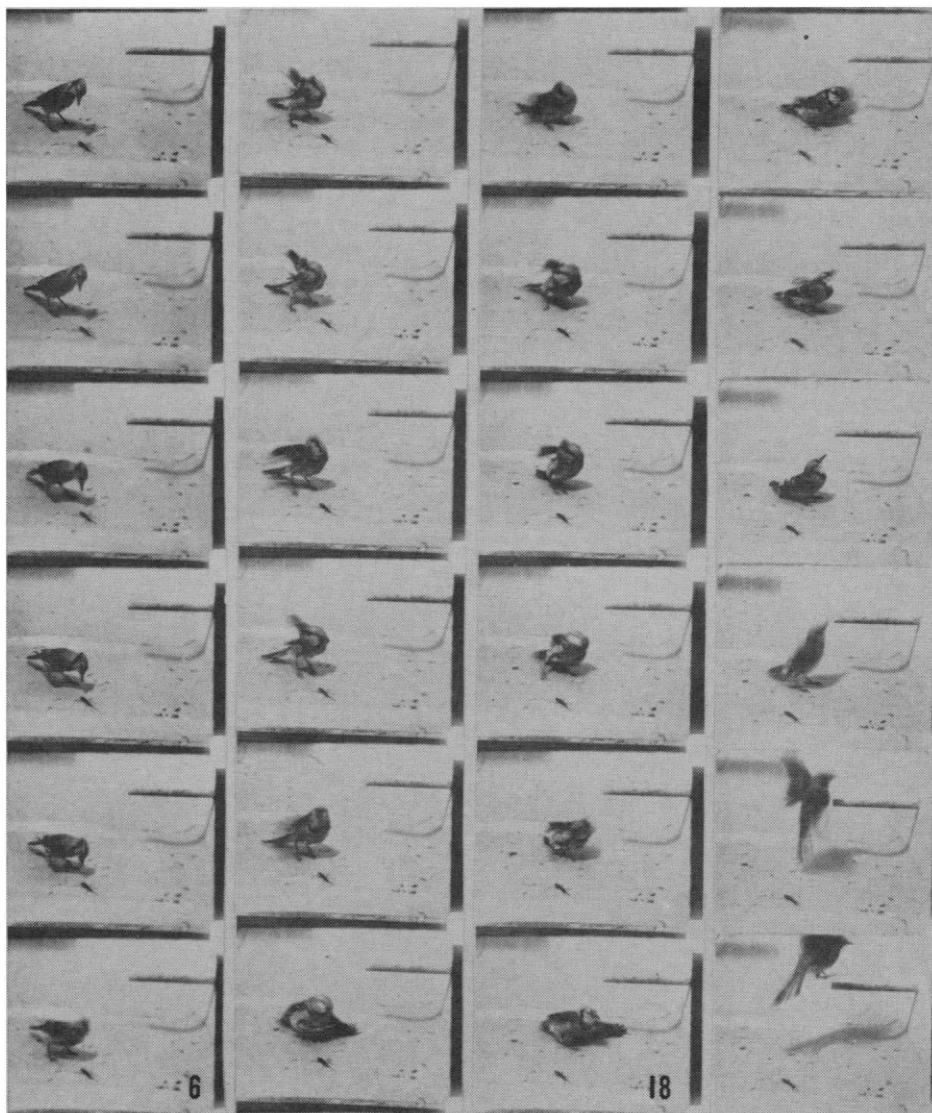


Fig. 1 (top left). A, Pair of *Anisomorpha* on food plant at night. B, The two defensive glands (g) exposed by removal of the dorsal thoracic cuticle; arrows point to gland openings; (h), head. C, Histological cross-section through thorax, showing glands (g) with surrounding musculature (m). D, A blue jay hopping backward at the instant of being sprayed by *Anisomorpha*; the "veiled" appearance of the eye is attributable to the nictitans which, already in action, is shown drawn across the eyeball. E-G, Three stages in the attack of *Marmosa* upon *Anisomorpha*; in E, the opossum has been sprayed in the eye after the initial seizure of the insect; in F, it is running about wiping itself, without releasing its prey; in G, it is eating the insect.

Fig. 2 (top right). *Anisomorpha* spraying in response to stimuli applied in various ways. A-C, Bilateral discharges, elicited by tapping the dorsal thorax (A), touching both antennae with a heated probe (B), or pinching rear of abdomen (C). D-F, Unilateral discharges, induced by pinching respectively the right foreleg (D), the left middle leg (E), and the right hind leg (F).

Fig. 3 (right). Motion picture sequence (18 frames per second) showing a blue jay being sprayed by *Anisomorpha* (the four strips of film are read downward from the left). Note that the bird has been sprayed (frame 6) before touching the insect. After violent head-shaking, during which it almost loses its footing and props itself with one wing (frame 18), the bird flees to its perch.



were sprayed the very instant they descended from their perch and landed on the floor of the cage beside the insects. Other times they hopped around and inspected the walkingsticks at close range, only to be sprayed just before initiating the actual pecking (Fig. 3). At the instant of discharge, the bird was always closer than an estimated 20 cm from the insect and therefore well within the usual range (30 to 40 cm) of the spray. Whatever sensory input *Anisomorpha* relies upon in "recognizing" and "getting its bearings" on the approaching bird, it is clear that no crude combination of vibrational and visual cues is involved. In the laboratory, attempts to elicit discharges by waving objects in the vicinity of walkingsticks, or by tapping the substrate around them, or by doing both these things simultaneously, almost always met with failure. In the field, I have on rare occasions been sprayed on the hand while reaching to seize a walkingstick, and in crowded laboratory cages individuals sometimes spray when the cages are merely jolted or opened, but as a rule the animals never discharge until they are touched. A jay is evidently "betrayed" from a distance by peculiar characteristics of its own.

When hit by the spray, a jay typically jumps back, shakes its head vigorously, and attempts to cleanse it by wiping it against the plumage on its back; it then flees to its perch. Some secretion inevitably hits the eyes, and for seconds or even minutes thereafter the nictitating membranes are seen to be drawn back and forth over the eyeballs in a rapid wiping action (Fig. 1D). All three jays tested were quick to learn to discriminate against *Anisomorpha*. Even when consecutive trials with the same jay were spaced at intervals of 2 to 3 weeks, the bird sometimes remained on its perch and refused to attack.

Anisomorpha is a nocturnal herbivore, yet birds might be among its chief natural enemies. In the environs of Lake Placid, Florida, where I have observed the insects during summer, they are occasionally very abundant and may form dense aggregations feeding on various shrubs at night. They continue feeding until well after dawn, and are then clearly silhouetted against their food plants at a time when bird predation is at a peak. Later in the day they seek shelter from the scorching sun by moving to the base of the plants, only to emerge again after dark.

Anisomorpha is already endowed with secretion and able to spray when it hatches from the egg. In the laboratory, newly hatched nymphs effectively repelled single attacking ants (*Pogonomyrmex badius*). Since the eggs normally hatch at ground level, where foraging ants usually abound, this "inborn" defensive capability must be a major adaptive asset.

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Serologic Codes: Interpretation of Immunogenetic Systems

Abstract. *Transformations of serologic reaction patterns into verbal codes are analyzed. Two equally consistent and complementary models are compared. A model based on the assumption that antibodies are complex (cross-reacting) permits simpler, more uniform, and less prejudicing interpretations of immunogenetic systems than when antibodies are regarded as simple (specific).*

The interpretation of serologic reactions is founded on many assumptions, the arbitrariness of which is not always recognized. It is frequently assumed that there is a one-to-one relation between standard typing reagents and their corresponding antigens. When this assumption proves invalid, complexities of the antigens are usually

assumed. However, the same reaction pattern may instead indicate complexities of the antibodies or complexities of both antibodies and antigens (1).

The existence of complex antigens (antigens with more than one kind of "antigenic determinants," "factors," or "combining sites") as well as complex antibodies (antibodies able to "cross-react" with antigens which with other antibodies appear to be serologically unrelated) is well documented (2, 3).

The ability of one kind of antibody molecules to react with two serologically different antigens can consequently be symbolically expressed in at least two different ways which I call simple-complex and complex-simple. According to the simple-complex code, the simple (specific) antibody (anti-Q) reacts with the complex (related) antigens QT and QU because these antigens have a property in common. According to the complex-simple code it is instead stated that the complex (cross-reacting) antibody (anti-ab) reacts with the simple (unrelated) antigens a and b because the antibody is cross-reacting (Table 1).

Evidently these two interpretations are equally consistent with the observed reaction patterns (+ + - and + - +) in Table 1. The apparent discrepancy between the interpretations is due only to two different methods of codifying the reaction patterns into verbal symbols.

For the simple-complex code a one-letter symbol is assigned to the *antibodies* (anti-Q, anti-T, anti-U), and the antigens are labeled QT (+ + -) and QU (+ - +) corresponding to their ability to react with the antibodies. In contrast, for the complex-simple code a one-letter symbol is assigned to the *antigens* (a and b), and the antibodies are labeled anti-ab (+ +), anti-a (+ -), and anti-b (- +) corresponding to their ability to react with the two antigens.

Both models give oversimplified and conceptually different pictures of reality. The conventional simple-complex model is idealized (and thus falsified) in one direction in that simple (specific) antibodies are assumed. The new complex-simple model is idealized (and thus falsified) in the opposite direction, in that simple antigens (antigens with only one kind of antigenic determinants) are assumed. Both of these models are consequently restricted and complementary.

In order to classify and discuss quali-