sults on multiaction cells in the buccal ganglia to those obtained on cell L10, a multiactioned cholinergic neuron in the abdominal ganglion of *Aplysia* (*2, 3*). In both ganglia a single presynaptic neuron can act on inhibitory and excitatory receptors in different follower cells to produce opposite synaptic actions. In addition, some follower cells in each ganglion have both types of receptors to ACh so that the presynaptic cell can mediate opposite synaptic actions to a single follower cell. In the dual follower cell of the abdominal ganglion the two types of receptors have different kinetic properties so that an action potential in the presynaptic cell produces depolarizing PSP's at low rates of firing and hyperpolarizing PSP's at high rates of firing (*3*). The excitatory receptors have a low threshold for activation but are desensitized at high rates of stimulation; the inhibitory receptors have a higher threshold for activation and their action becomes most apparent at high rates of stimulation. By contrast, in the dual follower cells of the buccal ganglia the two receptor types have similar thresholds to ACh so that a single presynaptic action potential activates both sets of postsynaptic receptors concomitantly, producing a diphasic PSP. As a result of these differences, the sign of the abdominal ganglion dual synapse is frequency dependent, excitatory at low frequencies and inhibitory at high frequencies, whereas the sign of the buccal ganglion dual synapse is dependent on membrane potential as well as frequency. The buccal ganglion dual synapse tends to be primarily excitatory near the resting membrane potential and to become progressively more inhibitory as the membrane is depolarized, by other inputs or by injected current, and the threshold is raised by accommodation. The buccal ganglion synapse is also sensitive to the frequency of firing of the presynaptic neuron. At high rates of firing both components decrease but the second component is more affected because the inhibitory receptors appear to desensitize more rapidly than the excitatory receptors. It therefore appears possible for a nervous system to employ otherwise similar receptor components in very different ways by varying the sequence of their activation and their kinetics for desensitization.

One of the striking features to emerge from studies of these several cholinergic neurons in *Aplysia* (*2, 3, 5, 10*) is that a large variety of synaptic actions can be triggered by a single chemical transmitter compound. In principle it therefore appears possible to construct a ganglionic mass or even a whole nervous system by using only one transmitter substance and by simply varying the types of receptor, the combination of receptors, and their sequence of activation in the postsynaptic cells. That this is not generally the case suggests that different transmitters may be necessary for other purposes, such as cellular recognition or trophic maintenance of synaptic contacts, than for providing different types of synaptic actions.

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4. To obtain a more reliable measure of the reversal potential the two components were examined separately by using hexamethonium (10^{-4} g/ml) to block the excitatory component and *d*-tubocurarine (5×10^{-5} g/ml) to block the inhibitory component.
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7. In addition to having been described in the abdominal ganglion of *Aplysia* (*3*) diphasic ACh responses have been noted in neurons of *Navanax* (H. Levitan and L. Tauc, personal communications) and in dissociated mouse neuroblastoma cells [P. G. Nelson, J. H. Peacock, T. Amano, *J. Cell Physiol.* **77**, 353 (1971)]. Diphasic responses to *l*-glutamate are seen in neurons of *Anisodoris* [A. L. F. Gorman and M. F. Marmor, *Fed. Proc.* **30**, 323 (1971)]. Finally, biphasic PSP's have been found in the left pleural ganglion of Aplysia [G. M. Hughes and L. Tauc, *J. Physiol. London* **197**, 511 (1968)]. These PSP's are mediated by electrotonic coupling between cells, and not by the action of a chemical transmitter [M. Biedebach, J. M. Meunier, L. Tauc, *J. Physiol. Paris* **60**, 220 (1968)].
8. In five paired experiments the reversal potentials for both PSP and ACh response were directly compared. With hexamethonium in the seawater the reversal potential for the inhibitory component was -62.8 ± 6.3 mv for the PSP and -61.0 ± 6.3 mv for the ACh response. With *d*-tubocurarine in the seawater the extrapolated reversal potential for the excitatory component was -12.4 ± 5.9 mv for the PSP and -18 ± 6.1 mv for the ACh response. The values for the PSP and ACh responses were not significantly different ($P > .1$). In some experiments, desensitization rather than *d*-tubocurarine was employed to isolate the ACh excitatory component.
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Cholesteric Liquid Crystal-Like Structure of the Cuticle of Plusiotis gloriosa

Abstract. *The toroidal but parallel array of planes of unidirectionally oriented molecules believed to characterize cholesteric liquid crystals also gives rise to certain geometrical patterns. The reality of this structure is demonstrated by micrographic evidence.*

Michelson (*1*) was first to note that the shell of the beetle *Plusiotis resplendens* reflects circularly polarized yellow light when white light is incident on the shells. Later, Friedel and others (*2*) noted this phenomenon in cholesteric crystals. Shortly afterwards, Gaubert (*3*) studied the phenomenon as represented by a variety of beetles.

Robinson (*4*) has treated and related the combined phenomena, as shown by polypeptide solutions, beetles, and cholesteric liquid crystals, and concluded that "further research into the nature and origin of these irridescent [beetles'] elytra would be repaying." More extensive optical data of Neville and Caveney (*5, 6*) seem to confirm the conclusion.

Thus the concept that cholesteric liquid crystals effect the selective reflection of light of limited color is now even more convincing as being due to their layered structure whose periodicity approximates the wavelength of the band reflection maximum (for a medium of the average refractive index of the liquid crystal). However, the selective reflection of this light of limited color as circularly polarized light of a spe-

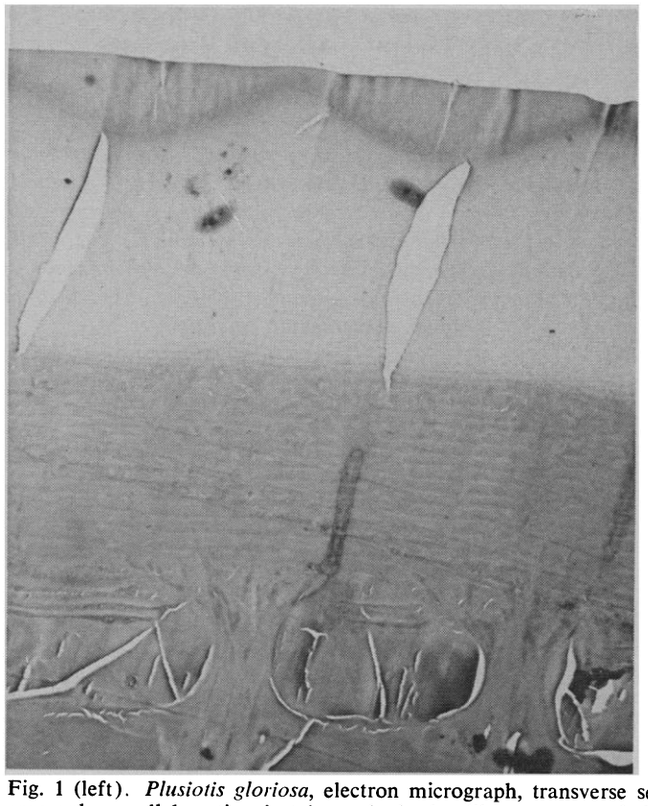

Fig. 1 (left). *Plusiotis gloriosa*, electron micrograph, transverse section of elytra.

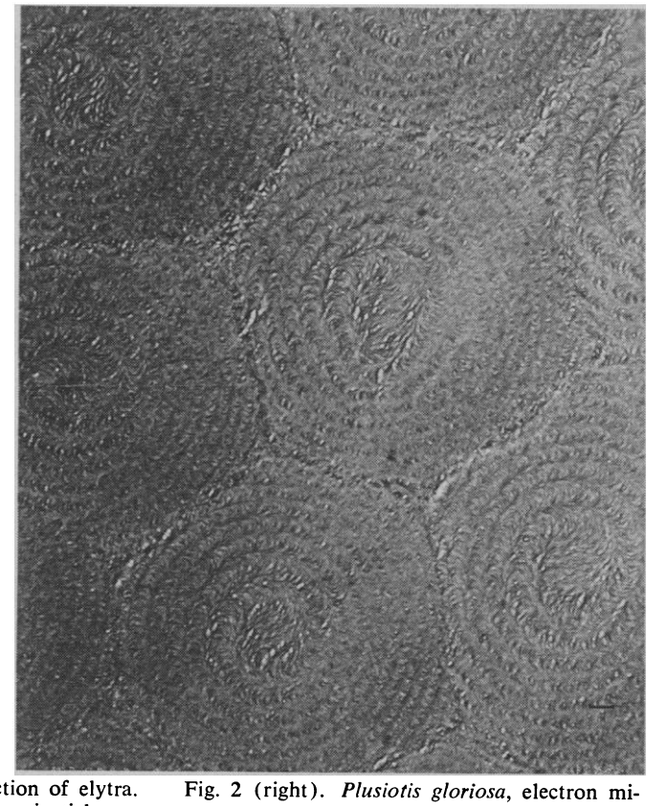

Fig. 2 (right). *Plusiotis gloriosa*, electron micrograph, parallel section just beneath the lenslike structure of the epicuticle.

cific handedness is somewhat more obscure (*7*).

The nature of periodicity peculiar to the liquid crystal systems resides in the fact that their molecules are parallel and in a plane. Successive planes (layers) of these are believed to differ from each other by a constant angle of rotation of the direction of the molecules and of a single-handedness (*7*). (The rotation is either right-handed or left-handed and varies with wavelength, usually being nonrotary for some wavelength.) Neville, Caveney, and others observe that the Scarabaeidae show left-handed reflection with few exceptions. Caveney's (*6*) study includes several different species; and, most significantly, he attributes most of the reflected polarized light of all of these examples to the presence of uric acid (50 to 70 percent of the structure by volume). At the same time, his electron micrograph of a diagonal section of the cuticle of *Plusiotis resplendens* shows exceptionally well the helicoidal layered structure characteristic of cholesteric liquid crystals, suggested by models and examples of Bouligand (*8*), and which had been considered to account for all of the polarizing character until Caveney's paper appeared.

My photographs (Figs. 1 to 3) are studies of *Plusiotis gloriosa*, a satiny green and silver striped species also studied by Caveney; these photographs are good examples of the significance of the Bouligand structure.

The first reaction one has to this beetle's green color is that it has a "depth" to it. Under the microscope at ×40, this green color is found to consist of small green dots. At ×400 it has the appearance of an assembly of green bubbles, and yet a lenslike effect makes yellow light concentrate in the centers of the "bubbles," while the green surrounds the yellow spots. Replication of the surface indicates that it is planar, for all practical purposes.

Sectioning of the elytra demonstrates the brittleness of the outer layer unless very thin sections are made. Thereupon the electron micrographs (Fig. 1) display the transverse section as having four layered zones: an outer (epicuticle) zone with planoconvex lenslike structures; a second layered zone (outer exocuticle) which conforms to the convex side of the lenslike epicuticle; a third, darker, layered zone (endocuticle); and the fourth layered zone, which seems to be cellular. The layers of exocuticle show a varying periodicity inwardly of from 0.1 μm to perhaps 0.3 μm, respectively. Thus these layers could, it would seem, act as a transparent (or translucent) optical grating for visible light. This structure seems to be not only typical of these "optically active" Scarabaeidae, but also would seem to account for the particular color each species displays. However, it may be of interest that the seemingly "silver" stripes of *P. gloriosa* are associated with a very thin and nearly flat area (but not lenslike) of the epicuticle from which there is a reflection of white

Fig. 3. Beetle shell transverse section showing liquid crystal-like structure; magnification, × 100,000.

light. Thus the reflected white light dilutes the reflected green light from the exocuticle so that, by contrast to the concentration of green light effected by the lenslike areas of the epicuticle, the light appears silver-white. However, when one avoids the perpendicular reflection, the greenish color is still very pale and so seems to be associated with the thickness of the epicuticle or merely the lack of intensification of the green light by lenslike structures.

The structures of the epicuticle and exocuticle were investigated further. Sections almost parallel to the surface were made in which some of the lens bottoms were truncated and cut, so that photographs of these showed the very clear spiral Bouligand pattern associated symmetrically with each lens as it acts as a negative "tubercle," which is Bouligand's term.

Figure 2 shows the arrangement of Bouligand patterns as they appear in a plane in the epicuticle parallel to the surface but below the convex lenses of the epicuticle. As indicated by the handedness of the patterns, the left-handedness indicates a right-handedness of the pitch of the oriented layers of parallel molecules, as one proceeds down from the outer surface (epicuticle) of the beetle. This comes from the depression instituted by the lenses of the epicuticle, as was expected by Bouligand. Figure 3 shows a second manifestation of the same Bouligand structure when the section is taken at a 45-degree angle to the layers of the fourth zone.

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Decremental Conduction over "Giant" Afferent Processes in an Arthropod

Abstract. *Four "giant" mechanoreceptive cells form part of a stretch receptor organ at the base of the uropod in the sand crab,* Emerita *(Crustacea, Anomura). Injection of the fluorescent dye Procion Yellow revealed that these sensory cells are monopolar with somata located in the central nervous system. No such cells have previously been described in arthropods. These neurons are also unusual in that they do not generate propagated action potentials; rather, they mediate stretch reflexes by transmission of graded, decremental potentials.*

Four "giant" mechanoreceptors (cells I–IV) form part of a stretch receptor organ in the sand crab, *Emerita* (Crustacea, Anomura) (Fig. 1A). These sensory cells are unusual not only because of the large size of their dendrites, but also because of the location of their somata within the central nervous system, in contrast to the peripheral location of most sensory cell bodies in arthropods. Furthermore, the dendrites do not sustain self-propagating, overshooting action potentials; they thus resemble certain thoracico-coxal receptors with which they are probably serially homologous, in other decapods (*1*).

At the base of the uropod [swimming appendage on sixth abdominal segment (*2*)], an elastic strand crosses the joint from the middorsal telson to the medioventral rim of the uropod coxopodite. The four sensory neurons send dendrites to this strand through the first ventral branch of the main root from the fifth (last) abdominal ganglion (Fig. 1A). Each dendrite maintains a diameter of 45 to 50 μm in the root and receptor nerve (in a crab of carapace length 2.5 to 3.0 cm), and divides dichotomously into several

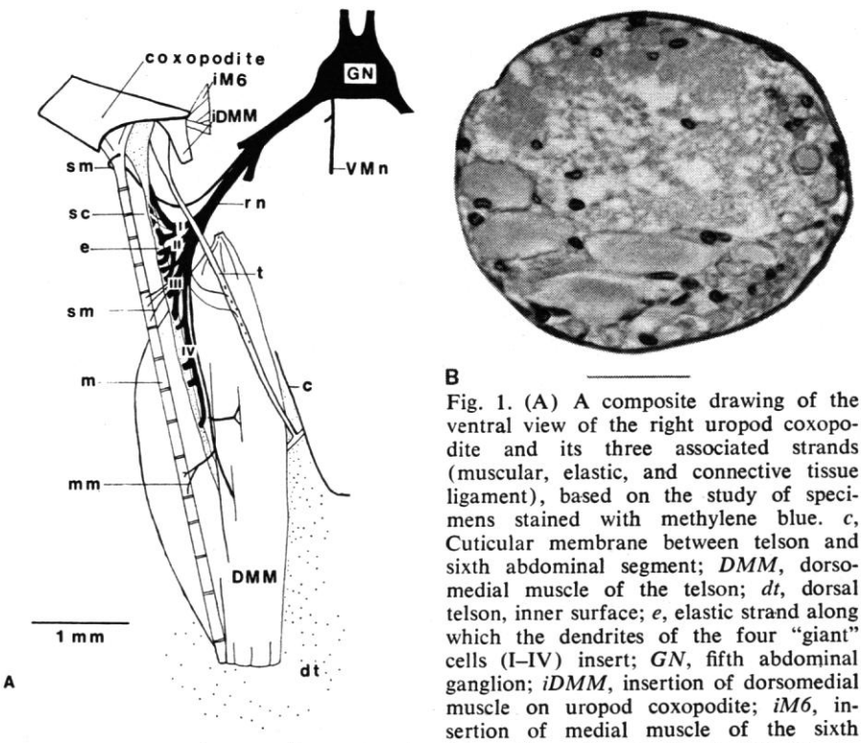

Fig. 1. (A) A composite drawing of the ventral view of the right uropod coxopodite and its three associated strands (muscular, elastic, and connective tissue ligament), based on the study of specimens stained with methylene blue. *c*, Cuticular membrane between telson and sixth abdominal segment; *DMM*, dorsomedial muscle of the telson; *dt*, dorsal telson, inner surface; *e*, elastic strand along which the dendrites of the four "giant" cells (I–IV) insert; *GN*, fifth abdominal ganglion; *iDMM*, insertion of dorsomedial muscle on uropod coxopodite; *iM6*, insertion of medial muscle of the sixth segment; *m*, muscular strand; *mm*, motor innervation of muscular strand; *rn*, receptor nerve branch of main root; *sc*, small cells of unknown function on elastic strand; *sm*, presumed sensory innervation of muscular strand; *t*, ligament between telson and uropod coxopodite; *VMn*, nerve to the ventromedial muscle, inserting on the uropod ventral to the dorsomedial muscle. (B) Cross section (silver-stained, 10 μm) of the fifth abdominal ganglion root within 1 mm of the ganglion (point of intracellular recordings). The four large profiles in the anterior-ventral quadrant are the "giant" dendritic processes; clockwise, cells IV, I, II, III, numbered according to their insertion from anterior (distal) to posterior (proximal) along the elastic strand. Marker, 40 μm.