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Crustacean Eye Fine Structure Seen with Scanning Electron Microscopy

Talbot H. Waterman and Alan S. Pooley

Summary. The internal fine structure of crustacean compound eyes has been reexamined with scanning electron microscopy. Several different preparative techniques were used in a comparative study of crab, crayfish, shrimp, and stomatopod eyes. The three-dimensional pattern of photoreceptive, dioptric, and screening components of these eyes has been directly demonstrated, and new insight has been gained into their functional organization. Particularly interesting in apposition eyes is the elaborate array of boundary membranes and protoplasmic strands linking the photoreceptive microvilli to their parent cell cytoplasm across the large intracellular vacuoles surrounding the axial rhabdom. Quantitative application of scanning electron microscopy to this system promises to advance our understanding of its proven high rate of receptor membrane turnover.

If success can be measured by the number of arthropod individuals and species dependent on compound eyes, they are the most successful light receptor organs ever evolved. Consequently, an understanding of their functional organization is important to an understanding of vision in general. Yet several critical features of their fine structure remain unresolved despite outstanding light microscopy beginning as early as the 1890's (*1*) and many subsequent light microscopic and electron microscopic studies (*2*). As a result, current research on their optics, electrophysiology, photochemistry, cell biology, and behavioral consequences is hampered by persistent morphological ambiguities. Particularly acute is the need for precise knowledge of receptor cell patterns and connectivity. These obviously determine first-order input for visual discrimination and information channeling.

To reduce such deficiencies in the field of crustacean visual physiology (*3*), we have recently turned to scanning electron microscopy (SEM) (*4*). This technique overcomes the inadequate resolution of light microscopy and the internal membrane face limitations of freeze fracture electron microscopy. It also directly demonstrates three-dimensional relationships at intermediate scale ranges usually requiring many sections and laborious reconstruction with transmission electron microscopy. Modest application of SEM has previously been made to internal structures of insect compound eyes, but little as yet to those of crustaceans (*5*). We are developing this approach specifically to apply new SEM data to quantitative experimental analyses especially of the photoreceptor membrane. The main technical problems are exposing appropriate cellular elements [like the eighth retinular cell (*6*, *7*)] and determining their precise relations (Figs. 1 and 2).

So far, we have applied a variety of well-known fixative and preparative techniques (*8*). Some eyes have been macerated in boric acid while still fresh; others, after fixation and dehydration, have been broken or cut open at room temperature. Additonal specimens were fractured while frozen in ethanol at liquid nitrogen temperatures. All were then

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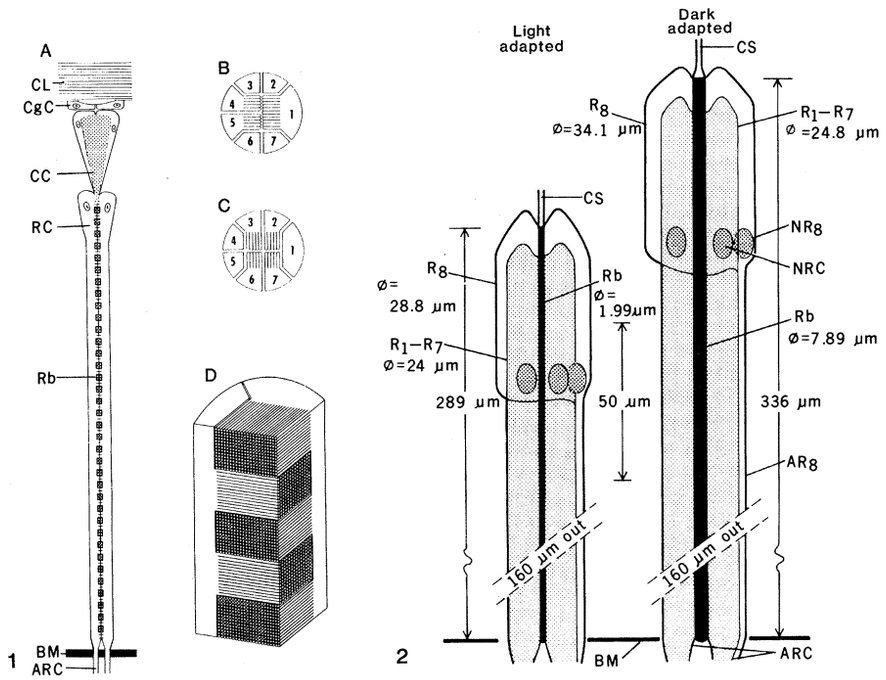


Fig. 1. The whole compound eye comprises several thousand unit structures (ommatidia) like this one from the blue crab (*Callinectes sapidus*). They are typically organized in a convex ellipsoidal radial array bounded externally by the faceted cornea. (A) Each ommatidium has optical components [*CL*, corneal lens; *CgC*, corneagenous (lens-producing) cells; *CC*, crystalline cone] that direct light from the hexagonal external facet to the deeper lying retinular (neurosensory) cells (*RC*). These receptor cells collectively constitute the retinula, which proximally rests on the perforated basement membrane (*BM*), through which the axons of the retinular cell (*ARC*) run. The banded axial rhabdom (*Rb*) is made up of microvilli contributed by all eight retinular cells. (B and C) [Modified from (*14*).] Seven regular retinular cells form the alternating orthogonal bands of microvilli in the main part of the rhabdom. The distal eighth retinular cell omitted here appears in Fig. 2. (D) Stereodiagram showing how two regular photoreceptor cells (for example, R_3 and R_4) interdigitate their respective layers of parallel microvilli. Fig. 2. The dynamic nature of retinular structure is illustrated by the massive changes in the volume of a rhabdom induced in the rock crab (*Grapsus grapsus*) by noontime light adaptation and midnight dark adaptation (*12*). The photoreceptor membrane in the dark state has an area nearly 20 times that in the light. The distal eighth retinular cell (R_8) with its nucleus (NR_8) and elongate axon (AR_8) is diagrammed along with the regular seven retinular cells (R_1–R_7), their nuclei (*NRC*) and their proximal axons (*ARC*). Abbreviations: ϕ, diameter; *CS*, crystalline cone stalk.

critical point dried, vacuum dessicated and coated with gold-palladium for examination in an SEM (ETEC Autoscan).

The organization of the compound eye differs from that of camera eyes like ours mainly in the multiple aggregate nature of its optical and sensory components. Compound eyes typically comprise an aggregate of a few hundred to a few thousand radially arranged structural and functional units, the ommatidia (Fig. 1), represented on the external corneal surface by square or hexagonal facets. Each ommatidium contains a cluster of retinular cells (Fig. 2) whose collective photoreceptor membrane, the rhabdom, contains the visual pigment in a precisely organized array of microvilli (Fig. 1).

Function critically depends on the way in which photons are collected and guided to receptor molecules, as well as on the manner in which the photoisomerization of rhodopsin leads to afferent trains of nerve impulses encoding the visual stimulus. Although fine structure alone cannot explain how this system works, such knowledge is basic to developing an explanation.

The initial challenge of analyzing fresh data of this kind is to identify the components visualized and to correlate new with old knowledge. The more novel information a new technique provides, or the less is already known from other studies, the less certain are the elements and patterns observed. Fortunately, extensive material prepared with other methods on many crustaceans (by light microscopy, transmission electron microscopy, and freeze-fracture electron microscopy) and more than two decades of related research experience (*7*, *9*) have made it relatively easy to identify many components revealed by SEM.

A more difficult objective is to perceive and define the functional implications of newly found structures or connectivity. This is already possible to a limited extent with our present material, but better fixation, dissociation, and fractionation are needed before quantitative experiments are feasible. Most of the accompanying SEM's (Figs. 3 to 12) are presented in pairs to illustrate particular points of comparison between and within the crustacean species studied. To demonstrate how effectively this technique can expose overall internal structural relations, a fragment fractured from the distal part of a *Penaeus* eye is shown at low magnification in Fig. 13.

The most striking feature of the first ten micrographs is the strong three-dimensional quality they bring to the pattern of retinular cells and their constituent intracellular organelles. The photoreceptive rhabdom, for example, is seen at two levels in cross section (Figs. 3 and 4), in longitudinal sections (Figs. 5, 6, and 12), and in three-dimensional perspective demonstrating its banding and rhabdomeric components (Figs. 7, 8, and 11) as well as its constituent microvilli (Figs. 9–12). Among the variety of pigment granules present in different retinal locations (*10*), the so-called proximal pigment in the cytoplasm of retinular cells is especially prominent (Fig. 4).

Particularly notable are the extensive intracellular vacuoles which surround the rhabdom in the apposition eyes of crabs and stomatopods (Figs. 3, 5, 6, 8, 9, and 12). The micrographs demonstrate the curious way in which the rhabdom is suspended across these vacuoles by innumerable protoplasmic strands. How these strands and vacuoles interposed between the parent cell cytoplasm and the corresponding rhabdomeric photoreceptor membrane (Fig. 1) relate to the latter's synthesis and degradation is not yet obvious. We already know that arthropod photoreceptor membranes show extraordinarily high rates of turnover (*11*).

Figs. 5 and 6 (facing page). Fig. 5. Axial longitudinal section of a retinula from a light-adapted eye of the green crab (*Carcinus maenas*) fractured in air following critical-point drying. Alternate light and dark rhabdom bands (*b*) are visible but overshadowed by conspicuous perirhabdomal vacuoles (*v*) traversed by protoplasmic strands (*s*) and bounded near the rhabdom by membranes (*m*) that were partly torn away in preparation. Abbreviation: *c*, cytoplasm of an adjacent retinular cell. Fig. 6. Longitudinal section of another *Carcinus* retinula from a dark-adapted specimen fractured while frozen in ethanol. Here most information is limited to the fracture plane, although this plane followed a periodic change of direction as it passed through alternate rhabdom bands with orthogonal microvilli. This dark-adapted rhabdom has conspicuously greater diameter than the light-adapted one in Fig. 5 (compare with Fig. 2).

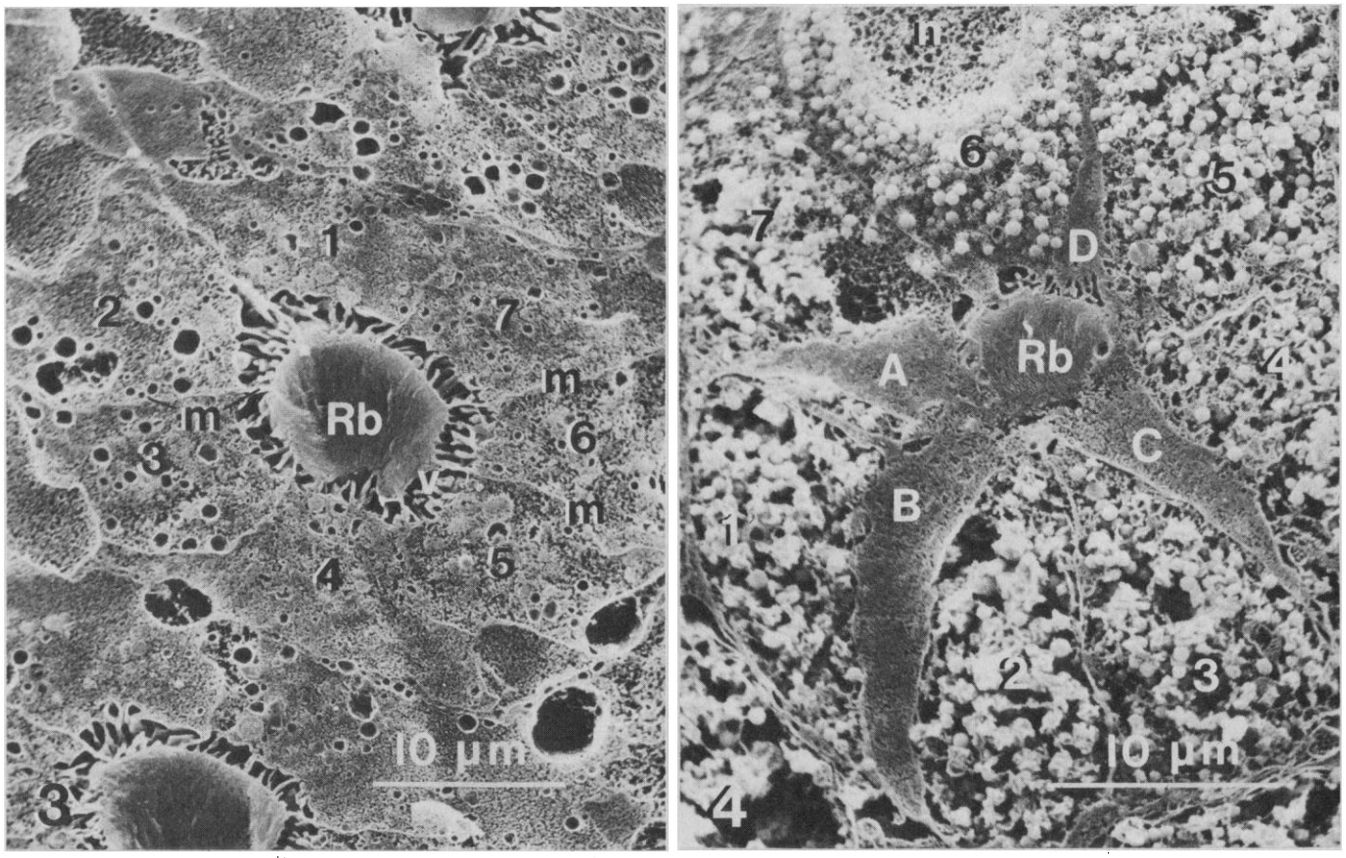
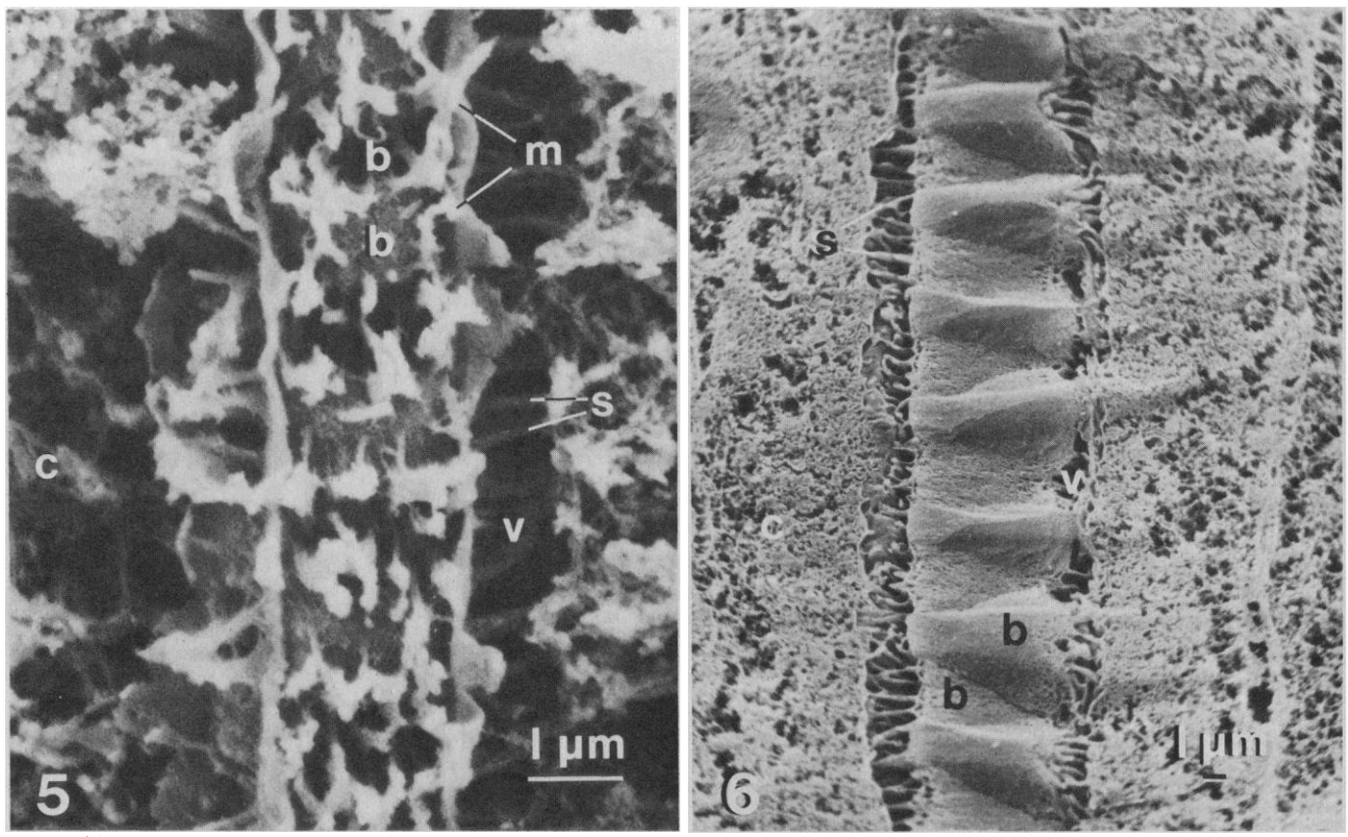
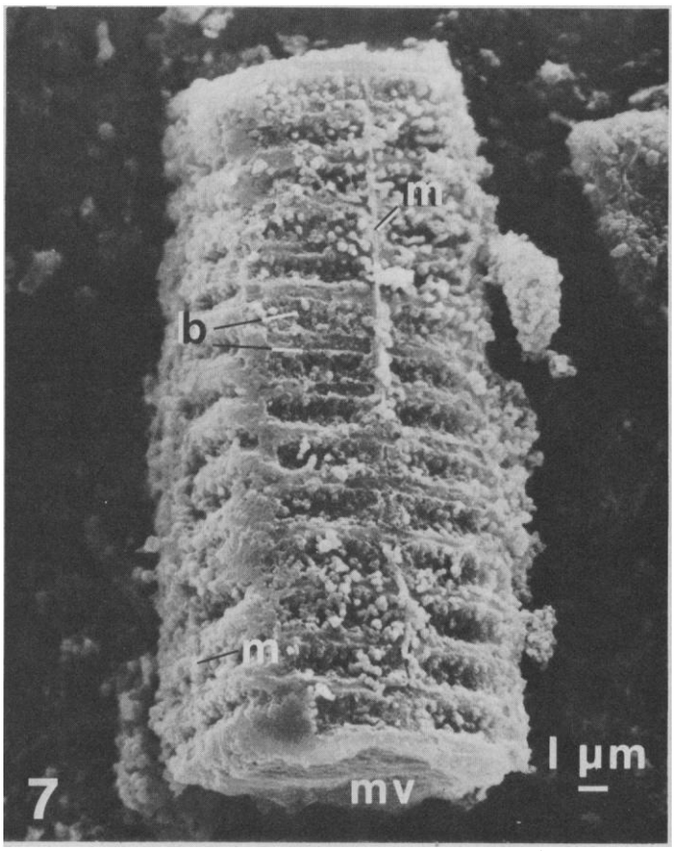


Fig. 3. Retinula from the eye of *Callinectes* cross-fractured while frozen in ethanol. Seven regular retinular cells (1 to 7), their intracellular perirhabdomal vacuoles (*v*), and the composite axial rhabdom (*Rb*) are clearly visible. Note the cell membranes (*m*) partitioning *v*. This organization pattern is typical of the proximal 80 to 90 percent of the retinula's length; that shown in Fig. 4 characterizes the more distal fraction. Fig. 4. Another *Callinectes* retinula fractured distally. The four lobes of the eighth retinular cell (*A* to *D*) are interpolated between the regular retinular cells (1 to 7), one of which contained a nucleus (*n*) at this level. Many spherical proximal pigment granules are present in the retinular cell cytoplasm.





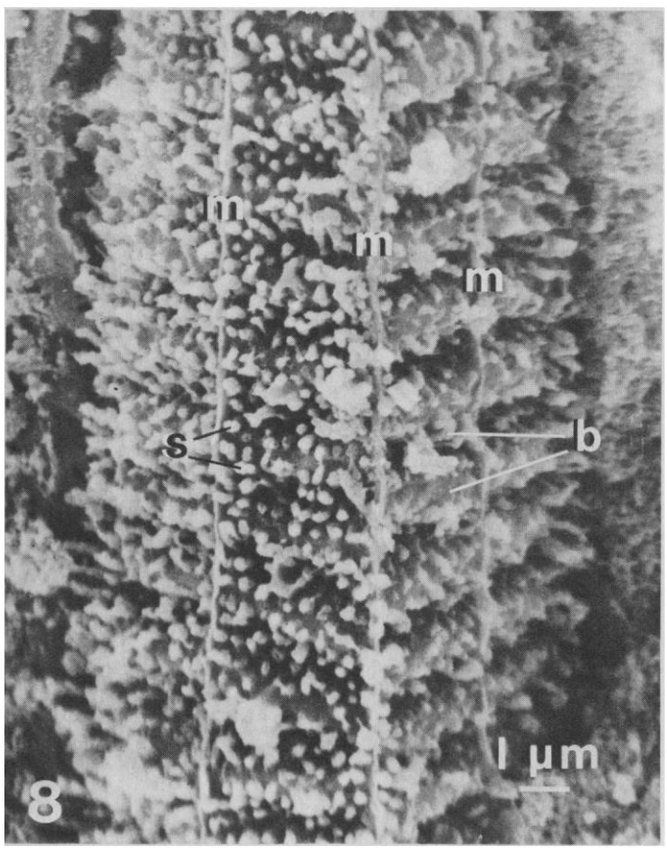
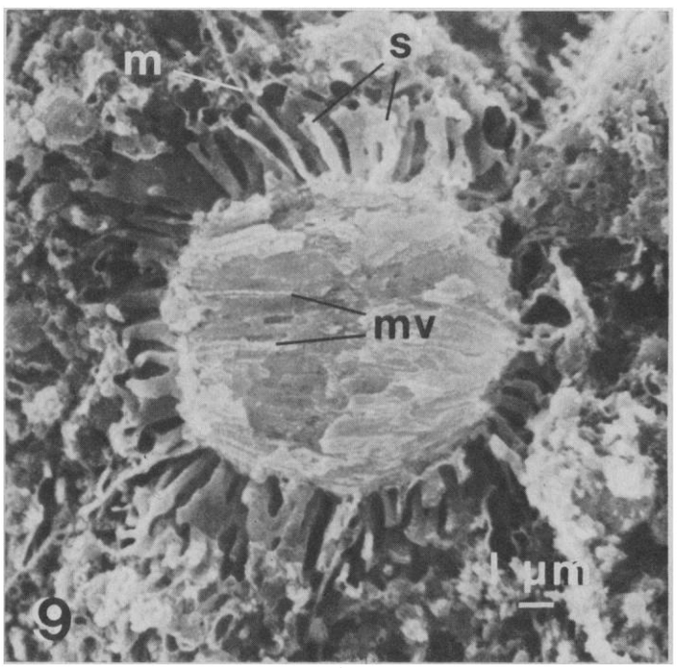


Fig. 7. Isolated rhabdom fragment from the stomatopod (*Squilla empusa*) obtained by using two strips of adhesive tape to pull apart pieces of a critical-point-dried retina in air. Abbreviations: *m*, membranes bounding retinular cells; *b*, alternating rhabdom bands; *mv*, their constituent microvilli. Fig. 8. Another *Squilla* rhabdom exposed by fragmenting retinal tissue in ethanol at room temperature followed by critical-point drying. Here the protoplasmic strands (*s*) crossing the perirhabdomal vacuoles are particularly conspicuous, as are the plasma membranes (*m*) and rhabdom bands (*b*).



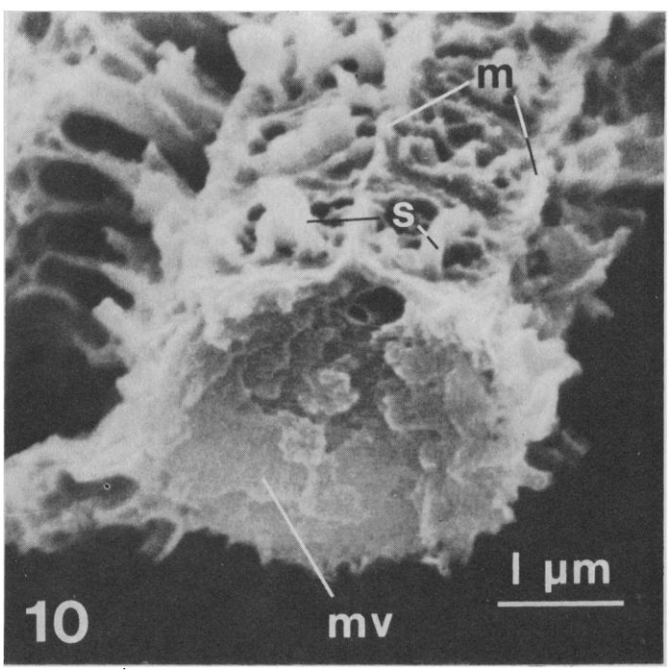


Fig. 9. In *Callinectes*, a sunburst of protoplasmic strands (*s*) traverses the vacuoles around the rhabdom of a retinula cross-fractured after critical-point drying. Microvilli (*mv*) are horizontal in the exposed rhabdom cross section and, at most, extend only halfway across its diameter. Fig. 10. *Carcinus* rhabdom projecting from a specimen fractured in air after critical-point drying. Compare with Figs. 5 and 6. The microvilli are oriented vertically and horizontally in two successive rhabdom bands.

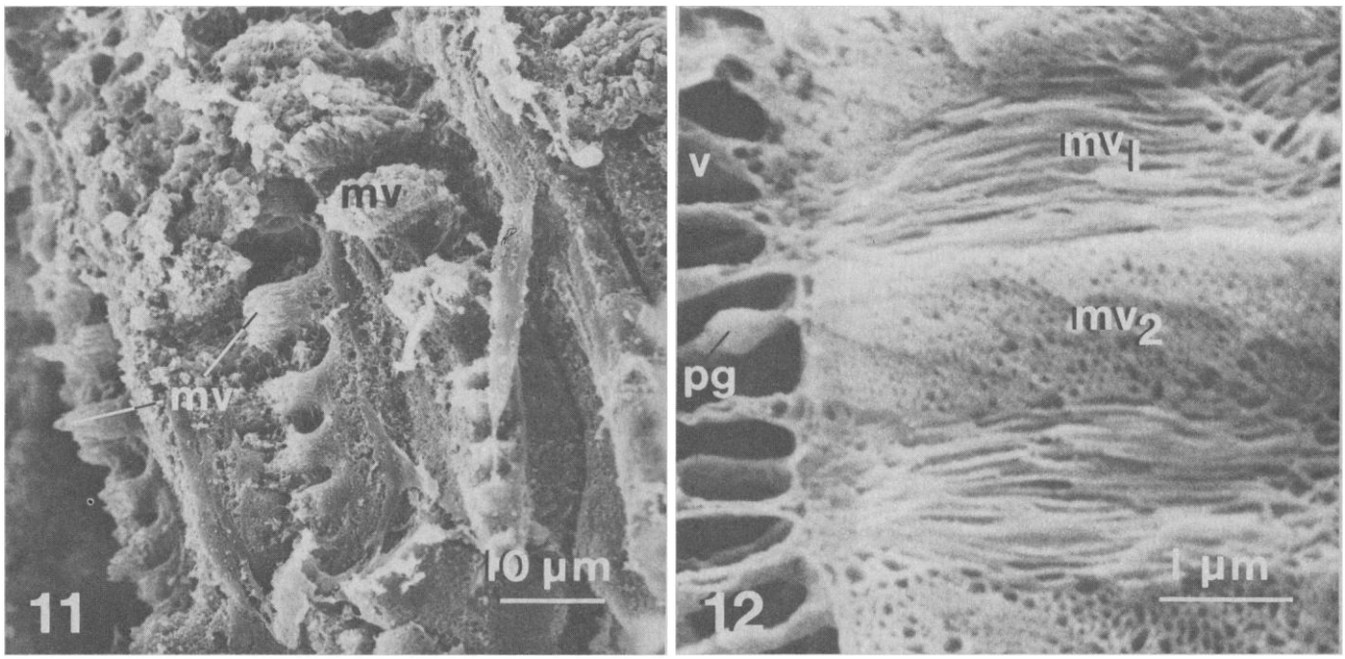


Fig. 11. Tufts of the periodically interrupted series of microvilli in individual rhabdomeres of the crayfish *Procambarus clarkii*. Each contributes parallel elements to alternate interdigitated bands of the composite photoreceptive rhabdom (Fig. 12). Microvilli originate axially from individual regular retinular cells (Figs. 1 and 3). The retina was pulled apart after the intercellular connections were softened in boric acid. Fig. 12. *Carcinus* rhabdom axially fractured while frozen in ethanol. Alternate layers of longitudinally (mv_1) and cross-fractured (mv_2) microvilli are visible in successive rhabdom bands. Protoplasmic strands [one of which contains a lysosome or pigment granule (*pg*)] traverse the perirhabdomal vacuole (*v*) at the left. Note the quite different details revealed in Figs. 5 and 10, which are also from green crab retinas.

In certain crabs (*12*), the rhabdom membrane area varies by a factor of nearly 20 between its fully light-adapted minimum and its fully dark-adapted maximum (Figs. 2, 5, and 6). Intracellular transport on a large scale is obviously necessary, yet the restriction of cytoplasmic continuity to such tenuous strands would seem hostile to the easy voluminous flow of material suggested in them by the presence of multivesicular bodies and pigment granules (Fig. 12).

Because of their documented high rate of membrane turnover, the rhabdomal systems of these crabs are particularly favorable material in which to study the basic mechanism of receptor membrane function. In addition, the direct effects of light and darkness on the rhabdom are substantially modulated either directly

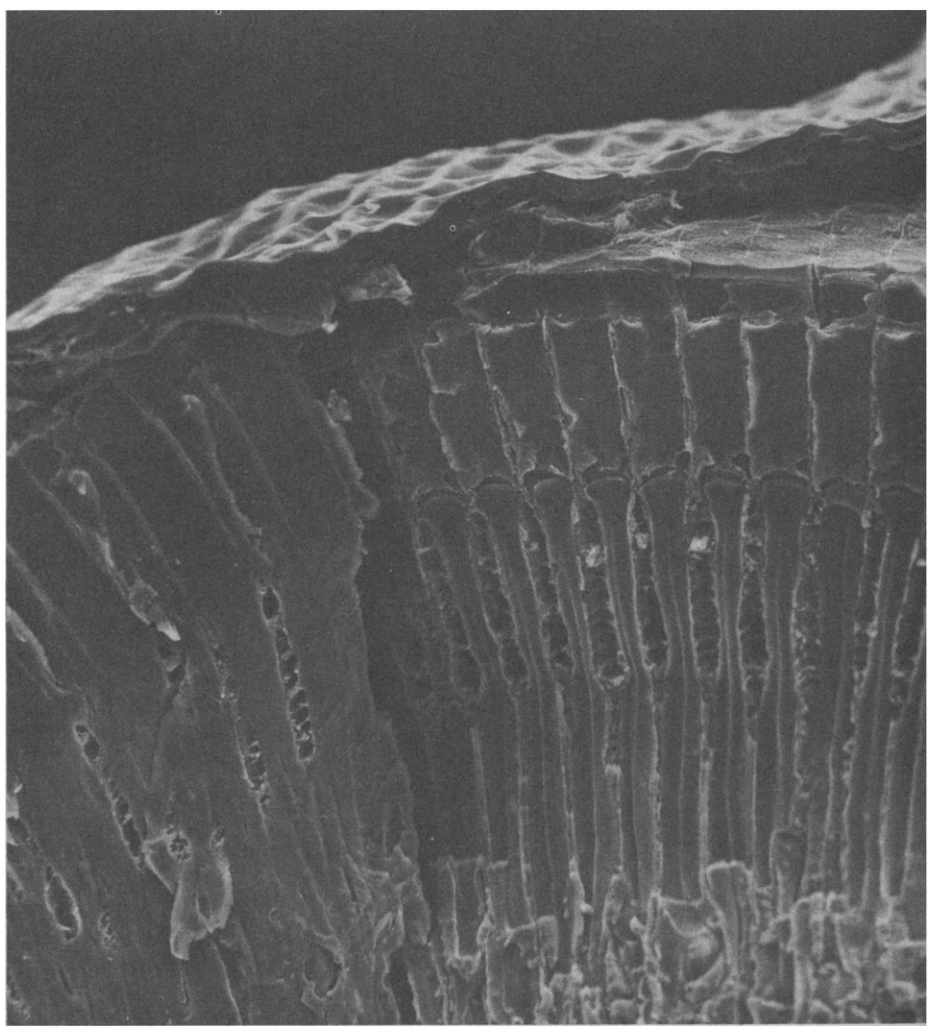


Fig. 13. Distal optical components of the superposition eye of the commercial shrimp *Penaeus setifera*. The three-dimensional organization of the elongate ommatidia characteristic of such a superposition eye appears almost diagrammatic in this fragment. Starting at the top surface, square outer facets of the cornea are followed in downward succession by the underlying corneagenous cells, the crystalline cones, and their stalks, which extend to the lower margin. Out of the frame below, and in fact not exposed on the surface of this preparation, lie the receptor cells in clusters of eight at the ends of the incoming light conductors. Eye tissue was fractured in ethanol while frozen in liquid nitrogen. Picture width, 450 μm.

or indirectly by the animal's diurnal rhythms (*12*). Both close similarities and sharp differences exist in the analogous photoreceptor membrane synthesis and shedding in vertebrate rods and cones (*13*). Hence, the effective elucidation of basic mechanisms through comparative study is pragmatically important. A substantial technique like SEM to augment our growing quantitative knowledge of these systems is most welcome.

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Pharmaceuticals: Their Role in Developing Societies

Walsh McDermott

Thirty-one years ago, President Truman in his inaugural address announced a program in which the highly valued technology of the United States would be made available for the development of the badly impoverished nations of the world. Biomedical technology, especially that related to pharmaceuticals, was just starting to flower at that time. Within a short period, medicine had greatly increased its capacity to intervene decisively in the course of a wide range of microbial diseases, including the major ones forming the disease pattern of an industrialized society. Prontosil, the first sulfonamide, was announced in 1935 (*1*) and more potent sulfonamides were rapidly developed soon afterward. Because of the rapid development of antimicrobial drugs between 1941 and 1951, I have referred to this period as the "golden decade" (*2*). In 1941, as antimicrobial drugs we had only quinine, Atabrine, the arsenicals, and the sulfonamides; but by 1951 we had available the penicillins, the streptomycins, the tetracyclines, chloramphenicol, and isoniazid. The antifungal drug, amphotericin B, was developed later; but except for that, it has been more than 25 years since a drug has been developed for a major microbial disease that was previously untreatable.

Examination of the possible usefulness of pharmaceutical technology in the management of the health problems of the developing countries is the purpose of the present article. The overall influence of these drugs has been far greater than is generally appreciated. For example, they not only transformed the disease pattern of the United States and ultimately that of the rest of the industrialized world, but they also made possible today's lung and heart surgery. They led to the development of more efficient techniques for handling viruses and cell cultures in the test tube, and thereby facilitated the production of antiviral vaccines. They also produced extensive changes in the workings of the health care delivery system. For example, fever hospitals and tuberculosis sanitoriums have disappeared, and not the least of the consequences has been the creation in the United States of an essentially new and greatly enlarged system for the nourishment of biomedical science and technology.

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Dependence of Health Care on the Delivery System

The research support system that developed after World War II in the United States involved the federal government, the pharmaceutical laboratories, and the academic laboratories, and had mixed public and private support. Theoretically, the technologies derived from this system could be applied through either (i) the public health system, in which an intervention is made that affects a number of people at once, for example, a program to reduce the incidence of goiter by putting iodine in table salt; or (ii) the personal service system, in which the intervention is applied to an individual by a

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