rabbit oral papilloma virus, but the pathogenicity studies indicate that they are distinct. The properties of the RKV virus clearly differentiate it from Virus III and rabbitpox virus.

The physical and chemical properties of the virus, the type of cytopathic effect, hemagglutination characteristics, and electron microscope findings clearly indicate the relationship of the RKV virus to the papovavirus group (*3*). Since the Shope virus belongs to this group, the possibility was considered that the RKV virus is a serologically distinct strain of rabbit papilloma virus; this possibility cannot be eliminated by present data, but seems unlikely in view of the serologic identity of all previously studied strains of rabbit papilloma virus (*4*) and the fact that RKV virus grown in tissue culture did not produce tumors.

JANET W. HARTLEY
WALLACE P. ROWE

*National Institutes of Health,
National Institute of Allergy and
Infectious Diseases, Bethesda, Maryland*

### References and Notes

1. The electron micrographic studies were done in collaboration with C. F. T. Mattern and Wendell A. Daniel, and will be reported in detail elsewhere.
2. The serologic and challenge experiments with Shope virus were done by D. O. White and R. J. Huebner (D. O. White, R. J. Huebner, W. P. Rowe, R. Traub, *Austral. J. Exptl. Biol.* **41**, 41 (1963).
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5. We thank Mrs. Joan B. Austin for invaluable assistance in developing the hemagglutination and hemagglutination-inhibition tests.

7 November 1963

## Stretch Receptor-Like Organs in the Fly Larva: Their Possible Role in Growth Regulation

Abstract. *Typical insect stretch receptors and receptor-like organs present in larvae of* Sarcophaga bullata *and other flies contain associated cells which are suspected of passing secretory products into "target" organs by way of strands of connective tissue. In the fly larva, such organs are attached to leg rudiments, tracheal discs, muscles, the genital disc and gonads, and may be concerned with the neuroendocrine control of metamorphosis of these structures.*

Throughout the insect orders there are a series of stretch receptor organs associated with the peripheral nerves (*1–5*). These organs are characterized by the presence of at least one multipolar neuron, together with a number of other cells whose nuclei are very conspicuous; all are enclosed within a common connective tissue sheath. A diagram of such an organ taken from the fly *Sarcophaga* is shown in Fig. 1. Nerves and connective tissue strands leave the organs to pass to the surrounding tissues, mainly muscles. There appears to be considerable uncertainty about the exact nature of the second type of cell, whose nuclei are arbitrarily termed "associated cell" nuclei in Fig. 1. These nuclei have been considered by Finlayson and Lowenstein (*2*) to be connective tissue nuclei, and by Osborne (*6*) to be neurilemma cell nuclei. Beckel (*7*), for the lepidopteran *Hyalophora,* described a series of "scolopophorous organs," some of which he considered to be homologous with the stretch receptor organ of Finlayson and Lowenstein (*1*). He did not find multipolar neurons within the organs and he considered that the many cells present were oenocytes.

In the fly *Sarcophaga bullata,* there are, in addition to the typical stretch receptor organs (*5*), other organs similarly attached to peripheral nerves in which there are no neurons, only associated cells and their nuclei being present. Occasionally, neurons and associated cells have also been found alongside each other, but apparently within separate connective tissue sheaths. Both of these variants suggest that there is functional independence of the neuron and "associated cell" nuclei in the typical stretch receptor.

In *S. bullata,* connective tissue strands (not nerves) from these stretch receptor-like organs have been traced not only to leg rudiments [Osborne (*4*) noted nerves passing from the stretch receptors in *Phormia*] but also to the disc of the external genitalia, and to pupal tracheal discs. It was suggested by Whitten (*5*) that rather than being neurilemma cells, the associated cells of the fly receptor organs might have a secretory function and, furthermore, that the connective tissue strands issuing from the organs may not be randomly distributed, but be in some way associated with the nuclei contained within the organ. It has since been noted that channels, apparently filled with secretory material, are present within these connective tissue strands in at least the late larva, and at the time of puparium formation. These channels are similar in appearance to those described within the epineurium of the dorsal nerves of *Sarcophaga* and other fly larvae (*8*). When observed with phase contrast optics, the channels appear as dark lines; observed with dark-field optics, they appear as opaque lines. The channels of the dorsal nerves, plus their contained material, appear to pass directly to their target organ; the channels of the receptor-like organs appear to do likewise.

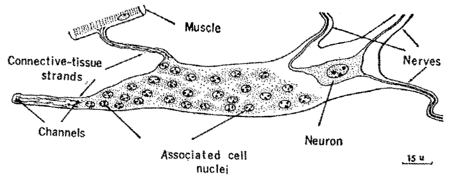

Fig. 1. Diagram of a typical stretch receptor organ from the larva of *Sarcophaga bullata* (Diptera Cyclorrhapha). Stretch receptor-like organs are similar except for the absence of the neuron and related nerves.

The receptor-like organs, as well as the stretch receptor organs themselves with their multipolar neurons, are always associated with the lateral segmental nerve branches. It has also been found that in *Sarcophaga,* a terminal branch of the last dorsal nerve connects with a stretch receptor-like organ. A receptor-like organ has even been found indirectly attached to the larval gonads. In the fly larva [for example, *Drosophila* (*9*)], the gonads have been considered to lie embedded within the fat body, unattached to other structures. However, in *Sarcophaga* it has now been found that the gonads are, in fact, attached to a fine

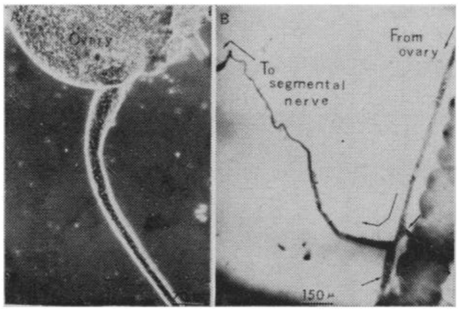

Fig. 2. (*A*) An ovary dissected from a third instar larva, showing the string of cells contained within the connective tissue sheath which is continuous with that over the ovary. (*B*) The string of cells showing attachments to a Malpighian tubule. The narrowing portion of the strand at top left passes into the ventral muscle mass and connects with a segmental nerve and receptor-like organ. Dissected in methylene blue; viewed with phase-contrast optics.

string of cells enveloped within a connective tissue membrane (Fig. 2*A*). Since the various members of the Cyclorrhapha have a very similar morphology, this finding in *Sarcophaga* will probably also apply to other members of the suborder. The connective tissue membrane is continuous with that over the gonad. The string of cells passes alongside a Malpighian tubule, to which it is attached by fusions of the respective connective tissue membranes and by short nucleated branches (Fig. 2*B*). Ultimately, the strand is traceable to the layer of ventral abdominal muscles, where it connects with a branch of the seventh lateral segmental nerve and an associated receptor-like organ. The strand has been traced repeatedly in many larvae and its position and appearance are constant. It is possible that connection is also made with the eighth segmental nerve, since it has been shown (*5*) that these receptor organs can connect nerve branches of two consecutive segments. The common sheath is traversed, at least in the prepupal stage, by channels similar to those contained within the dorsal nerves and receptor organ strands (Fig. 1). Whatever the exact histological nature of the strand, it is significant that it ultimately connects with the peripheral nervous system, so that the gonads of the larva, contrary to popular belief, have organic connection with the nervous system, and at the same time they are indirectly attached to a stretch receptor-like organ.

Thus, in the fly, the leg rudiments, pupal tracheal rudiments, the rudiments of the external genitalia, and apparently even the gonads themselves, have associated with them receptor-like organs which contain cells that are suspected of having a secretory function. Strands from such receptor-like organs also pass to various larval muscles, all of which in the fly histolyze at some time during metamorphosis. Differential histolysis could, in some way, be regulated by secretions of such cells [a similar suggestion was made for the apparent secretion by the dorsal nerves (*8*)]. Finlayson and Mowat reported recently that muscles connected with the specialized lepidopteran stretch receptors "do not degenerate when their motor innervation is severed" (*10*). This is in contrast to other muscles where "denervation in the larval stage could, in certain species, bring about the degeneration, during pupation, of longitudinal muscles that would normally have persisted" (*10*). Hitherto, no one has suggested that the intrinsic cells of insect stretch-receptor organs may be secretory cells, in some way connected with growth regulation or muscle histolysis, and possibly intimately bound up with the neuroendocrine control of metamorphosis. Circumstantial evidence, such as that given here, strongly suggests such a possibility, but verification by histochemical and experimental study is required.

JOAN M. WHITTEN
*Department of Biological Sciences,*
*Northwestern University,*
*Evanston, Illinois*

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11. Supported by NSF grant G 14544.

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## Ameiotic Alternation of Generations: A New Life Cycle in the Ferns

Abstract. *The fern* Polypodium dispersum *Evans (ined.) has a completely somatic alternation of generations. During sporogenesis the sporophyte exhibits 111 unpaired chromosomes, 16 spore mother cells, and 32 viable diplospores. The sporophyte arises by proliferation from a gametophyte lacking sex organs. This is the first completely documented report of this type of life cycle in the ferns.*

The ferns have been the classic objects for teaching the biology of the alternation of haploid and diploid generations. The regular alternation of the diploid sporophyte and the haploid gametophyte is intimately associated with several interacting biological phenomena, namely meiosis—the segregation of chromosomes in connection with reduction division and the formation of spores, and syngamy—the fusion of two haploid cells or gametes which accomplish new combinations that may be selected in evolution (Fig. 1*A*).

Since 1874, however, when Farlow (*1*) discovered apogamy, it has been realized that not all alternation of generations involve both of these phenomena. The work of Döpp (*2*), Manton (*3*), Mehra (*4*), and others has demonstrated that a considerable number of fern species reproduce by obligate apogamy, a process termed "monotonously uniform" by Manton (*3*). In these ferns the new sporophytes are produced directly by proliferation from the gametophyte, thus by-passing fertilization. The chromosome number is maintained at the same level by a process in which a doubling of chromosomes (syndiploidy) occurs prior to meiosis (Fig. 1*B*). If the chromosome number is not doubled in the sporangium, the chromosomes will not pair and only abortive spores result. The only reproductive spores, therefore, are those which have the same number as the sporophyte, and both generations accordingly possess the same 2X chromosome number. Whereas a sexual species normally has (in higher ferns) 16 spore mother cells and 64 viable spores, the obligately apogamous species has 8 spore mother cells and 32 viable spores in some sporangia and 16 spore mother cells and up to 64 aborted spores in the rest.

Until the present study, it was generally believed that in the natural state only two types of complete life cycles, with two generations participating, existed in the ferns: the classical sexual life cycle with alternating 2X and X generations, and the obligate apogamous cycle with alternating "2X" and "2X" generations and involving syndiploidy and reduction division. It is now possible to report still a third type of life cycle, in which the two generations, as in the obligate apogamous cycle described above, have the same chromosome number. But in the new cycle, there is no change of chromosome number at all, either during sporogenesis or at the time of sporophyte produc-