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The ultrastructure of the imaginal discs of *Drosophila melanogaster* was studied during their development and metamorphosis. Attention was paid to features that might be correlated with specific developmental activities. [The *SCI*® indicates that this paper has been cited in over 160 publications.]

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In the 1960s the fruitfly, *Drosophila melanogaster*, experienced a resurgence as an organism of choice for research in developmental genetics, thanks to the insightful and meticulous probing of Ernest Hadorn and his students. They focused on the development of the imaginal discs found in the body of the larvae. These discs are the primordia of adult (imaginal) structures such as legs or eyes.

The culture and bioassay of imaginal disc tissues had revealed principles of determination and regeneration as well as a puzzling change in the determined state called transdetermination. Genetic and physical mosaics were employed to decipher rules of pattern formation and intercellular communication. We needed to understand the detailed anatomy of imaginal disc tissues to build a conceptual framework to explain the experimental observations. We undertook our study of the ultrastructure of the developing leg imaginal disc to fill that need.

The paper has been widely cited mainly for two reasons. It was the first comprehensive and well-documented ultrastructural study of an imaginal disc. Thus, it explored a number of aspects of development, summarized below, that have been carried further by many subsequent studies. Second, its timely appearance provided a bridge between the experimental work and the explanations of the underlying cell biology.

We reaffirmed that the precursor of the adult integument is a single-layered, secretory epithelium. I say reaffirmed because the same conclusion had been reached in histological studies of similar structures from houseflies and blowflies some 80 years earlier. However, the high resolution of electron microscopy can also lead to a myopic view, and pioneering ultrastructural studies had depicted the imaginal discs as multilayered. This distinction is important because patterning of a single-layered structure can be viewed as a problem of ordering differentiations in two dimensions rather than three.[1] A comparison of the disc through the early stage of metamorphosis (the prepupal period) suggested that morphogenesis is accompanied by and perhaps driven by a change in cell shape from tall columnar to cuboidal. Dianne Fristrom extended this finding to show that cells not only change shape but also undergo a limited rearrangement during this morphogenesis.[2]

Using improved methods of preserving cellular ultrastructure, we revised earlier notions that the disc was a syncytium and described the specialized junctions that connect cells and presumably facilitate intercellular communication. The quality of tissue preservation was such that we could say with some assurance that there was no morphological correlate to the determined state of the cells within the disc epithelium. We described a population of adepithelial cells and suggested, as had several earlier workers, that they are the precursors of adult muscles.

Writing the paper, which was my first as a graduate student, was a long and arduous ordeal. Much of the descriptive portion of the work was completed at Case Western Reserve University in Cleveland, although the actual writing was done while I was a visitor at the University of California, Irvine. The paper went through 10 drafts over the course of nine months. I had, of course, hoped that each was a final product. Since I continued to do experiments while writing, the manuscript grew proportionately with time. After such a long gestation period and after assembling 42 plates (in triplicate), my major concern in mailing it to the journal editor was not how it would be reviewed, but whether it would be lost in the mail. The manuscript was accepted without revision, which is a tribute to the patience, good taste, and judgment of my coauthor and mentor, H.A. Schneiderman.

Imaginal discs continue to provide an important model system to study the unsolved mysteries of determination, epimorphic regeneration, and pattern formation.[3] A new generation of methods must be employed to unravel the cellular and molecular details behind these intriguing problems. The single-layered, secretory property is shared by all glandular tissues, such as the mammary, for example. Therefore, principles revealed through studies of imaginal discs of *Drosophila* should apply broadly to the development, regeneration, and growth control of many vertebrate tissues.

1. **Bryant P J, Girton J R & Martin P M.** Physical and pattern continuity in the insect epidermis. (Locke M & Smith D S, eds.) *Insect biology in the future*. New York: Academic Press, 1980. p. 517-42.
2. **Fristrom D.** The mechanism of evagination of imaginal discs of *Drosophila melanogaster*. III. Evidence for cell rearrangement. *Develop. Biol.* 54:163-71, 1976. (Cited 55 times.)
3. **Larsen-Rapport E W.** Imaginal disc determination: molecular and cellular correlates. *Annu. Rev. Entomol.* 31:145-75, 1986.

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