

## Cestode Ultrastructure Research Across the Decades: Past Successes, Present Trends, Future Challenges

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Shortly after the introduction of electron microscopy into biological research in the mid 1900's, parasitologists began using this powerful new technology to uncover aspects of cestode biology that previously had been unapproachable. The earliest ultrastructural studies on cestodes in the 1960's were applied to the fully formed eggs and the primary tegument and musculature of adults. In the 1970's this was extended to the ultrastructure of early embryos, including macromeres, which pose still unresolved questions regarding phylogeny of the triploblastic condition. This relates to loss of macromeres to form the outer embryonic envelopes, which is unique to neodermatans as a difference from other protostomes. The early work focused primarily on medically important groups such as the taeniids, and standard laboratory models such as hymenolepidids. In the 1980's new work on reproductive system epithelia and other aspects of reproductive systems commenced, with growing emphasis on the diversity and functionality of uterine epithelia across various taxa. These studies extended the neodermatan structural plan beyond the tegument and into other cestode epithelia. Comparative studies of spermatozoa also expanded during this period, with phylogenetic implications emerging from the sperm studies. More comprehensive studies on the musculoparenchymal system followed, including elucidation of the first examples of apoptosis implicated in the morphogenesis of epitheliomesenchymal organs. This was the first elucidation of developmental mechanisms associated with phylogenetic aspects of programmed

selective cell death and tissue senescence in these most primitive triploblastic bilaterians. In the 1990's through the 2020's, work in many of these areas has expanded to include a much wider range of cestode taxa, thus exploring potential phylogenetic trends. Currently, work along these lines continues in many laboratories around the world, with each lab tending to emphasize certain developmental stages, processes, or cell types.

Many questions remain that ultrastructural research can address in the future. Among the most important proposed here include examining across diverse cestode taxa more detailed aspects of:

- 1) the processes of oogenesis;
- 2) the process of synvitellogamy in neooporans (as distinct from syngamy of most animals), resulting in the capsule-enclosed zygote;
- 3) metamorphosis of the hexacanth larvae into diverse metacestode juveniles, which have adult somatic features;
- 4) the maturation process from metacestode to adult, resulting in gonads, genitalia, with the addition of strobilation in polyzoic taxa;
- 5) cellular senescence as it variously contributes to morphogenesis as well as atrophy of gravid and post-gravid forms;
- 6) malignant transformation, including hypertrophy, shape changes, and neoplastic interactions of tegumental and excretory epithelia as reported in the metacestodes of some taxa; and
- 7) functional, developmental, and phylogenetic aspects of extracellular vesicles and multivesicular bodies.