Ultrastructure and Differentiation of Ascidian Muscle

I. Caudal Musculature of the Larva of Diplosoma macdonaldi *

Michael J. Cavey** and Richard A. Cloney

Department of Biology, University of Calgary, Calgary, Alberta, Canada
Department of Zoology, University of Washington, Seattle, Washington, USA

Summary. The larval caudal musculature of the compound ascidian Diplosoma macdonaldi consists of two longitudinal bands of somatic striated muscle. Approximately 800 mononucleate cells, lying in rows between the epidermis and the notochord, constitute each muscle band. Unlike the caudal muscle cells of most other ascidian larvae, the myofibrils and apposed sarcoplasmic reticulum occupy both the cortical and the medullary sarcoplasm.

The cross-striated myofibrils converge near the tapered ends of the caudal muscle cell and integrate into a field of myofilaments. The field originates and terminates at intermediate junctions at the transverse cellular boundaries. Close junctions and longitudinal and transverse segments of nonjunctional sarcolemmata flank the intermediate junctions, creating a transverse myomuscular (TMM) complex which superficially resembles the intercalated disk of the vertebrate heart.

A perforated sheet of sarcoplasmic reticulum (SR) invests each myofibril. The sheet of SR spans between sarcomeres and is locally undifferentiated in relation to the cross-striations. Two to four saccular cisternae of SR near each sarcomeric Z-line establish interior (dyadic) couplings with an axial analogue of the vertebrate transverse tubular system. The axial tubules are invaginations of the sarcolemma within and adjacent to the intermediate junctions of the TMM complex.

Send offprint requests to: Dr. Richard A. Cloney, Department of Zoology NJ-15, University of Washington, Seattle, Washington 98195, USA

* This investigation was supported by Developmental Biology Training Grant No. 5-T01-HD00266 from the National Institute of Child Health and Human Development, National Institutes of Health, by National Research Service Award No. 1-F32-GM05259 (M.J.C.) from the National Institute of General Medical Sciences, National Institutes of Health, and by Research Grant No. BMS 7507689 (R.A.C.) from the National Science Foundation. A portion of this study was carried out at the Friday Harbor Laboratories of the University of Washington, and the authors gratefully acknowledge the cooperation and advice extended by the former Director, Dr. Robert L. Fernald

** Research facilities were provided in part by Douglas E. Kelly, Professor and Chairman, Department of Anatomy, University of Southern California School of Medicine, Los Angeles, California 90033, USA. The provisions and counsel are warmly acknowledged.
The caudal muscle cells of larval ascidians and the somatic striated muscle fibers of lower vertebrates bear similar relationships to the skeletal organs and share similar locomotor functions. At the cellular level, however, the larval ascidian caudal musculature more closely resembles the vertebrate myocardium.

Key words: Ascidian larva – Striated muscle – Intercellular junctions – Sarcoplasmic reticulum – Interior couplings.

Introduction

Somatic striated muscle cells of the ascidian larva are disposed in paired caudal bands lying lateral to the notochord. The caudal musculature lacks myocommata and consists of mononucleate cells joined by intricate myomuscular junctions. Motor axons from the visceral ganglion extend along the dorsal nerve cord and associate with a small percentage of the muscle cells (Tannenbaum and Rosenbluth, 1972). Specialized intercellular junctions may mediate electrical coupling between the incompletely innervated cells of each muscle band (Cavey and Cloney, 1972).

The fine structure of the caudal muscle cells has been examined in only a few ascidian larvae: the polycitorid *Distaplia occidentalis* (Cavey and Cloney, 1972), the cionid *Ciona intestinalis* (Castellani et al., 1972; Pucci-Minafra, 1965), the perophorid *Perophora orientalis* (Terakado, 1972), and the styelids *Dendrodoa grossularia* (Berrill and Sheldon, 1964) and *Botryllus schlosseri* (Schiaffino et al., 1974, 1976). These species represent four of the fourteen families in the three orders of ascidians (Monniot and Monniot, 1972).

The distributions of organelles and inclusions in the caudal muscle cells are quite similar among the ascidian larvae studied. The myofibrils and associated sarcoplasmic reticulum are usually confined to the cortical sarcoplasm. The emergence of the myofibrils near the tapered ends of each cell establishes a field of myofilaments which originates and terminates at intermediate junctions at the transverse cellular boundaries.

The sarcoplasmic reticulum (SR) in larval ascidian caudal muscle cells is morphologically diverse, ranging from a diffuse system of ramifying tubular cisternae to compact fenestrated sheets deployed in single and double arrays. A transverse (T) tubular system is absent in cells where the myofibrils lie close to the sarcolemma. Numerous peripheral couplings between the sarcolemma and subsarcolemmal cisternae of SR occur on all cellular surfaces. The subsarcolemmal cisternae are confluent with the network of SR appressed to the myofibrils (Castellani et al., 1972; Cavey and Cloney, 1972, 1973, 1974).

Myofibrils within the larval caudal muscle cells of *Botryllus schlosseri* are not restricted to the cellular periphery but are distributed throughout the sarcoplasm. A lamellar analogue of the transverse tubular system has been described in these cells, as well as numerous interior (dyadic) couplings between the lamellar tubules and cisternae of sarcoplasmic reticulum (Schiaffino et al., 1974, 1976). The caudal muscle cells of *Diplosoma macdonaldi* also contain myofibrils residing