A Note on the Structural Organization of the Cardiac Myofiber in

*Nautilus pompilius*¹

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ABSTRACT: The ultrastructure of the cardiac myofiber in *Nautilus* resembles that of bivalves more than the decapod cephalopods. The fiber is nonstriated, the mitochondrial density is relatively small and the cristae poorly developed, and the sarcoplasmic tubule system is either sparse or absent. These features suggest that the *Nautilus* heart is not highly adapted to enhance the transport of large volumes of oxygen to the tissues and that the adaptations found in the decapods arose within the class Cephalopoda.

¹This research was conducted as part of the Alpha Helix Cephalopod Expedition to the Republic of the Philippines, supported by National Science Foundation grant PCM 77–16269 to J. Arnold.

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METHODS AND MATERIALS

The ventricle was excised and fixed for 1 hr in 2.6% gluteraldehyde in seawater (osmo-
FIGURE 1. Transmission electron micrographs of *Nautilus pompilius* myocardium. A, intercellular space (IS) surrounded by serpentine sarcolemma (arrows), note number of open areas. B, cross section of intercalated disk (ID) and longitudinal section of dense bodies (DB). Bar indicates 1 μm.
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lality 1003 mOsm, pH 7.2). Following a 1-hr rinse in filtered seawater, the tissue was post-fixed in 1% OsO₄ (pH 7.0). The tissue was embedded in Epon 812, cured at 60°C, sectioned, and stained with lead citrate (0.3% for 30 sec). The sections were examined with Zeiss 9S-2 and Phillips EM-201 electron microscopes.

**RESULTS AND DISCUSSION**

The *Nautilus* myocardium more closely resembles the bivalve myocardium than that of decapod cephalopods. As in the bivalves (Hayes and Kelly 1969; Irisawa, Irisawa, and Shigeto 1973; Rutherford 1972), the ventricle is composed of loosely organized molluscan nonstriated muscle with dense, or Z, bodies scattered throughout the sarcoplasm (Figure 1). In contrast, the decapod cardiac myofiber is obliquely striated, with Z bodies stacked linearly (Dybens and Mangum 1979, Jensen and Tjønneland 1977, Schipp and Schäfer 1969). The dense bodies are slightly larger (0.4-0.6 μm) in *Nautilus* than in the bivalve *Mercenaria mercenaria* (0.08-0.12 μm), and they do not form the attachment plaques seen in both *M. mercenaria* (Hayes and Kelly 1969) and the decapod *Rossia macrosoma* (Jensen and Tjønneland 1977, Schipp and Schäfer 1969). The dense bodies are slightly larger (0.4-0.6 μm) in *Nautilus* than in the bivalve *Mercenaria mercenaria* (0.08-0.12 μm), and they do not form the attachment plaques seen in both *M. mercenaria* (Hayes and Kelly 1969) and the decapod *Rossia macrosoma* (Jensen and Tjønneland 1977, Schipp and Schäfer 1969). The *Nautilus* myocardia are smaller (0.6-0.9 μm diameter), and they usually contain less than ten poorly developed cristae, features that also resemble bivalves. As in most mollusks, although the mitochondria are distributed throughout the myofiber, they typically occur in groups that tend to concentrate in the core of the cell or directly beneath the sarcolemma (Figure 2).

As reported earlier (Hochachka et al. 1978), the tissue is characterized by numerous open areas that resemble vacuoles. These spaces range in diameter from 0.1 to 0.5 μm, and they occur most densely in the mitochondrial clusters. Partially disrupted mitochondria were observed in several of these “vacuoles,” suggesting that they are artifacts of unknown origin formed during fixation. The normal appearance of other structures, however, such as the cell nuclei, Golgi apparatus, and endoplasmic reticulum, suggests that the vacuoles may not be due to osmotic imbalance. Their presence complicates the identification of a sarcoplasmic reticular system. Tubulelike structures with patent lumina of 0.01-0.10 μm diameter are scattered throughout the myofilaments (Figure 1). In both Figures 1 and 2 and in the micrographs of the cardiac myofiber shown by Hochachka et al. (1978), these tubulelike structures could represent a tangential section of a round vacuole, made at
FIGURE 2. *Nautilus pompilius* myocardium. *A*, higher magnification of intercalated disk; *B*, longitudinal section of intercalated disk; *C*, open areas scattered throughout myofilaments and mitochondrial core of cell (M). Bar indicates 1 μm.
the top so that the diameter would appear to be small. Sarcoplasmic reticulum is clearly present in the muscles of the funnel that leads to the gills and the mantle cavity of *Nautilus* (Hochachka et al. 1978). We suggest, however, that neither their study nor ours unequivocally demonstrates a sarcoplasmic reticulum in the cardiac myofiber. More important to the present point, the density of the tubulelike structures is low relative to the density of sarcoplasmic reticulum in decapods (Dykens and Mangum 1979); even if they do prove to be components of a sarcoplasmic reticular system, the system is not highly developed in the *Nautilus* heart.

While the sarcoplasmic reticulum is highly developed in all the decapods studied, the transverse tubule system either may (Jensen and Tjønneland 1977, Kawaguti 1963, Schipp and Schäfer 1969) or may not (Dykens and Mangum 1979) be present. There is no indication of a transverse tubule system in *Nautilus*.

Thus, the organization of the cardiac myofiber in *Nautilus* resembles the decapod myofiber in virtually no feature of relevance to the cardiovascular or metabolic performance of the system, and it does not appear to be specially adapted to sustain an exclusively aerobic and also highly mobile way of life. In addition, it is clear from the present results that the adaptations that permit contraction frequencies in excess of 250 beats/min (20°C) in squids occurred within the class Cephalopoda. Whether they are found only in the decapods or whether they also occur in the octopods is not known.

**LITERATURE CITED**


