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Ultrastructural changes in the autotomy tissues of *Eupentacta quinquesemita* (Selenka) (Echinodermata: Holothuroidea) during evisceration

MARIA BYRNE
Smithsonian Marine Station at Link Port, Fort Pierce, Fla., USA

ABSTRACT: Evisceration in the dendrochirote holothurian Eupentacta quinquesemita (Selenka) is associated with the sudden breakdown of three autotomy tissues. These tissues were examined before, during and after evisceration to investigate the presence of autotomy related specializations and to elucidate the morphological events associated with autotomy. The tissues are characterized by a preponderance of connective tissue and also contain muscle and nerve. Axon-like processes containing large electron-dense vesicles (LDVs) are found in the connective tissue and in association with muscle cells. These processes are similar to the neurosecretory-like processes described for other echinoderm autotomy tissues. Autotomy is part of the general phenomenon of variable tensility in echinoderm connective tissues and involves a change in the connective tissue matrix. During autotomy, the matrix loses its structural integrity causing collagen fibril disarray and disorganization of associated cells. Some axon membrane and basal lamina disruption occurs, but the vesicles contained in axons and the LDVs appear to remain in tact. The vesicles contained in locally distributed axons do not appear to be the source of agents that effect connective tissue breakdown; an alternate source is discussed.

1 INTRODUCTION

The autotomy of body parts through a sudden reduction in the tensility of connective tissue structures is characteristic of the Phylum Echinodermata (Emson & Wilkie 1980) and appears to be unique to the group. Echinoderm autotomy differs from autotomy in other invertebrates where body parts are cast off through rupture of muscle tissue specializations (McVean 1975). The sudden breakdown of connective tissue during autotomy is part of the general phenomenon of variable tensility of echinoderm connective tissues (Motokawa 1984; Wilkie 1984). Another aspect of the phenomemon is the reversible stiffening/softening changes demonstrated by echinoderm catch ligaments. The changes associated with variable tensility have attracted attention because they occur in an extracellular tissue and are considered by many workers to be under neutral control (Jordan 1914,1919; Serra-von Buddenbrock 1963; Wilkie 1978,1983, 1984; Holland & Grimmer 1981a,b; Motokawa 1981,1982a,1984; Byrne 1982; Hilgers & Splechtna 1982; Hidaka & Takahashi 1983).

Autotomy is usually associated with anatomical specializations that facilitate ejection of body parts (McVean 1975). This aspect of variable tensility has received relatively little attention, although there are several ultrastructural studies of echinoderm catch ligaments (Holland & Grimmer 1981b; Smith et al 1981; Motokawa 1982b; Hidaka & Takahashi 1983; Wilkie 1983). Thus far, the fine structure of ophiuroid and crinoid arm autotomy tissues has been described (Wilkie 1979; Holland & Grimmer 1981a).

The presence of axon-like processes, filled with large electron-dense vesicles (LDVs), appears to be characteristic of echinoderm connective tissues (Wilkie, 1979,1984; Holland & Grimmer 1981a,b; Smith et al 1981; Byrne 1982; Hilgers & Splechtna 1982; Motokawa 1982b,1984; Hidaka & Takahashi 1983). The LDVs resemble neurosecretory vesicles found in firmly established neurosecretory neurons (Maddrell & Nordmann 1979) and, based on their morphology, LDVs have been suggested to be involved in the control of variable tensility (Wilkie 1979, 1984; Holland & Grimmer 1981 a,b; Smith et al 1981; Motokawa 1982b, 1984; Hidaka & Takahashi 1983).

Holothurian evisceration results in autotomy of the digestive tract and tentacular crown (Kille 1935; Smith & Greenberg 1973; Byrne 1982). In the dendrochirote

holothurian Eupentacta quinquesemita (Selenka) evisceration is associated with the irreversible breakdown of three structures, (1) the introvert (the anterior extensible portion of the body wall), (2) the tendon (P-L tendon) that connects the pharyngeal retractor muscle (PRM) to the longitudinal body wall muscle (LBWM), and (3) the intestine-cloacal junction. The fine structure of the intact P-L tendon has previously been reported (Byrne 1982) and will be described here briefly. The ultrastructure of the introvert and intestine-cloacal junction is also described. Particular emphasis is placed on the changes that occur in the three structures during evisceration and for evidence of neural involvement in the connective tissue change.

2 MATERIALS AND METHODS

Specimens of E. quinquesemita were collected using S.C.U.B.A. near Victoria, British Columbia. Evisceration was induced in freshly-collected specimens by squeezing the body transversely with forceps. For transmission electron microscopy, intact and eviscerating specimens were injected with 3% glutaraldehyde in 0.2M cacodylate buffer (pH 7.4). The autotomy tissues were dissected and placed in fresh fixative for one hour at room temperature. The tissues were then rinsed in the same buffer, post-fixed in 1% OsO_4 in cacodylate for one hour at 4°C, decalcified in ascorbic acid (Dietrich & Fontaine, 1975), dehydrated, and embedded in Epon 812. Thick sections were stained with Richardson's stain (Richardson et al 1960) for light microscopic examination. Thin sections were stained with uranyl acetate and lead citrate and viewed with a Philips EM 300.

3 RESULTS

3.1 Structure of intact introvert

The introvert is predominantly dermal connective tissue with the cuticle and epidermis on the outside and the musculature, nerve plexus and peritoneum on the coelomic side (Figs. 1-3). The dermal connective tissue has three layers, the superficial dermis, a dense connective tissue (DCT) layer and a loose connective tissue layer (LCT). The superficial dermis contains ossicles, cross striated collagen fibrils and connective tissue matrix (Fig. 1). The DCT contains abundant collagen fibrils varying in diameter from 20-160nm associated with an interfibrillar matrix, Fig. 4,

Fig. 1. One micrometer cross section of the epidermis (E) and superficial dermis (S). The ossicles (O) are surrounded by collagen fibrils (CF). Scale=1.0μm.

Fig. 2. Cross section of the dense connective tissue (D) and the loose connective tissue (L). M, muscle fibres; Arrow, DCT-LCT interface. Scale=1.0μm.

Fig. 3. Cross section of the 'transparent' LCT (L). M, muscle fibres MC, morula cells; P, peritoneum. Scale=1.0μm.

Fig. 4. LDV-filled process and muscle fibre bundle (M) in the DCT. BL, basal lamina; CF, collagen fibrils. Scale=2.0μm.

Fig. 5. LDV-filled process in LCT (L). The LCT is electron-lucent and contains a few unstriated fibrils (UF). BL, basal lamina. Scale=1.0μm.

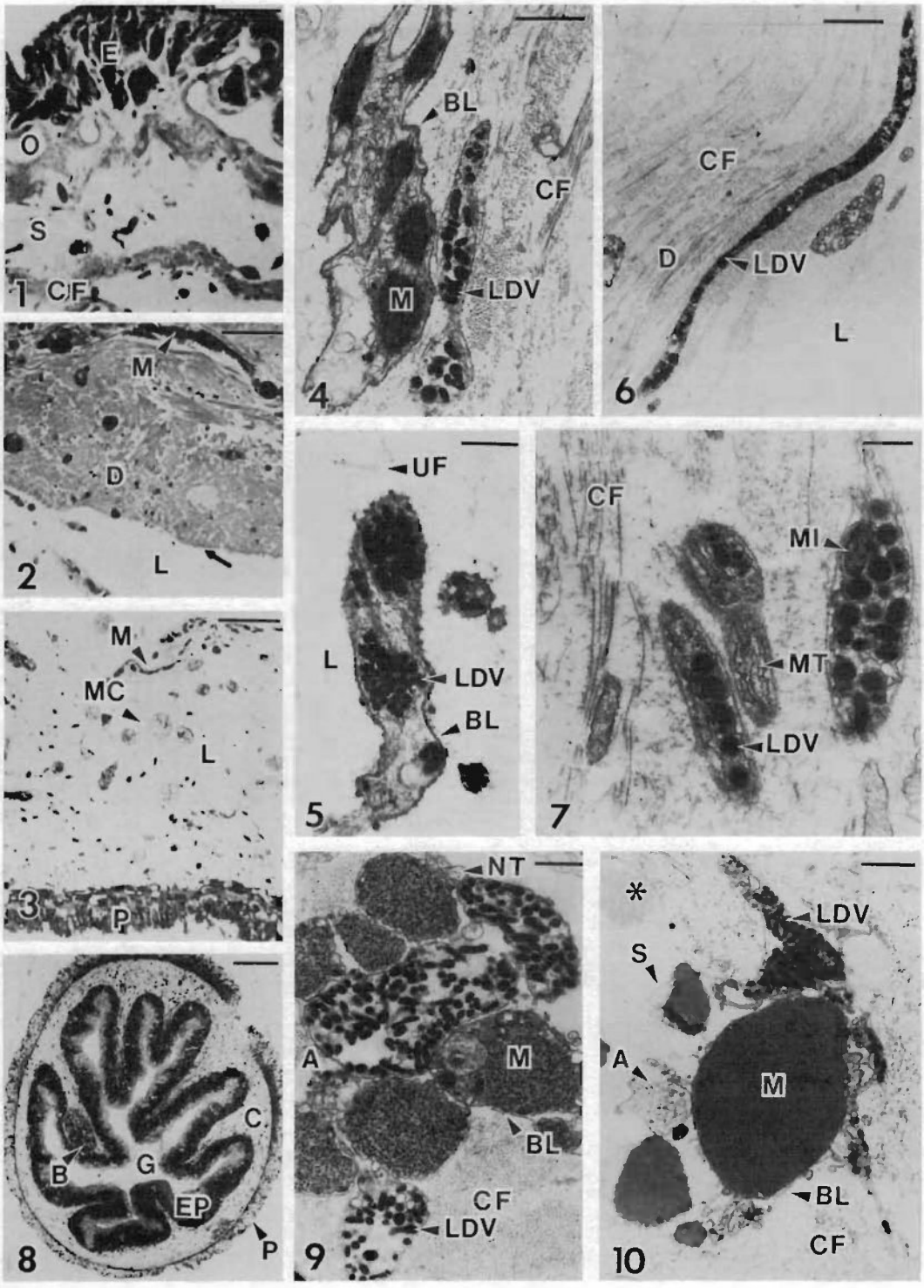
Fig. 6. Elongate LDV-filled process in autotomizing introvert near the DCT-LCT interface. CF, collagen fibrils; D, DCT; L, LCT. Scale=2.0μm.

Fig. 7. LDV-filled processes in the gut connective tissue contain axial microtubules (MT) and occasional mitochondria (MI). CF, collagen fibrils. Scale=0.5μm.

Fig. 8. One micrometer cross section of the intestine adjacent to the intestine-cloacal junction. B, brown body; C, connective tissue; EP, intestinal epithelium; G, gut lumen; P, peritoneum. Scale=0.1mm.

Fig. 9. Cross section of a PRM bundle surrounded by P-L tendon collagen fibrils (CF). LDV-filled processes and axons (A) are found with the muscle fibres (M). BL, basal lamina, NT, neurotubules. Scale=1.0μm.

Fig. 10. Cross section of autotomized P-L tendon. An intact LDV-filled process is alongside a dispersed PRM bundle. The muscle fibres (M) lack thick filaments, and the contractile elements disperse (asterisk). The collagen fibrils (CF) are in disarray, and the sarcolemma (S) has lifted away. An axon-like profile (A) has an irregular membrane profile and contains few vesicles. BL, basal lamina. Scale=2.0μm.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6,11,12). Many of the collagen fibrils have unstriated fibrils (10-14nm in diameter) attached. Bundles of muscle cells surrounded by a basal lamina are scattered through the DCT (Figs. 4,11). Axons are present in the DCT in association with muscle fibres and also surrounded by connective tissue. The axons are ensheathed in a basal lamina and contain neurotubules, occasional mitochondria and two types of vesicles, clear vesicles (70-80nm) and dense-core vesicles (90-140nm). The DCT also contains axon-like processes (Figs. 4, 5) filled with large, electron-dense vesicles (LDVs) that vary in shape from round (150-300nm) through ellipsoidal to sausage-shaped (180-550nm X 125-220nm). Axial microtubules and occasional mitochondria are present in the processes (Fig. 7). These LDV-filled processes are found beside muscle bundles along with axons and are scattered throughout the connective tissue (Figs. 4,6).

The LCT is an amorphous electron-lucent layer of connective tissue matrix with occasional collagen fibrils (40-60nm in diameter) and more common, small diameter (7-12nm), unstriated fibrils (Figs. 3,5,6) Muscle fibres, morula cells, axons and LDV-filled processes are also present in the LCT.

3.2 Structure of intact P-L tendon

The P-L tendon is comprised of a collagenous connective tissue layer surrounding a central muscle region containing the tapered ends of PRM cells and is overlain by peritoneum (Figs. 9,13). Connective tissue ramifies throughout the interior of the tendon so the PRM fibres are completely embedded in connective tissue. The tendon contains abundant small diameter collagen fibrils (30-40nm) and unstriated fibrils (10-15nm) in an interfibrillar matrix. Axons and LDV containing processes similar to those described for the introvert are present in the tendon in association with muscle and connective tissue (Fig. 9).

3.3 Structure of intact intestine cloacal junction

The intestine cloacal junction is the posterior end of the intestine where it joins with the cloaca. It contains a thick connective tissue layer with the gut musculature and peritoneum on the coelomic side and the epithelium on the luminal side (Figs. 8,15), The connective tissue is largely matrix and contains small diameter (4-10nm) unstriated fibrils (Fig. 7). A diffuse layer of collagen fibrils (20-40nm in diameter) is found along the basal lamina near the gut musculature (Fig. 15). Axons are rarely found in the intestinal connective tissue but LDV-filled processes are encountered, especially near the basal lamina (Fig. 7). Morula cells and brown bodies are common in the connective tissue (Figs. 8,15).

3.4 Structure of autotomizing introvert

During evisceration the introvert changes from a solid, opaque structure to one that is soft and translucent. Introvert thickness decreases as it distends, with the viscera and coelomic fluid propelled for-

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Figs. 11-16. Similar fields of intact and automized tissues.

Fig. 11. Intact introvert DCT. The muscle fibres (M) are contracted and sarcolemmal extensions (S) lie within basal laminar (BL) folds. CF, collagen fibrils. Scale= 2.0µm.

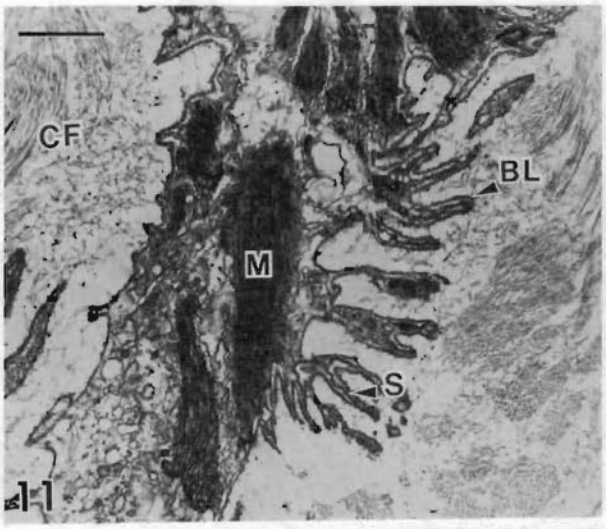
Fig. 12. Autotomizing DCT. The muscle fibres (M) are extended. The sarcolemmal extensions and basal laminar folds have straightened out and the basal lamina (BL) is disrupted (arrows). CF, collagen fibrils. Scale=2.0µm.

Fig. 13. Intact P-L tendon. The peritoneum (P) overlies the relatively compact collagenous connective tissue of the tendon. CF, collagen fibrils; M, muscle; MV, microvilli. Scale=3.0µm.

Fig. 14. Automized P-L tendon. The peritoneum (P) is disrupted (arrow), and the collagen fibrils (CF) are dispersed. M, muscle; MV, microvilli. Scale=2.0µm.

Fig. 15. Intact intestine-cloacal junction. The peritoneum (P), nerve plexus (NP) and muscle (M) layers cover the intestinal connective tissue. Collagen fibrils (CF) are particularly abundant along the basal lamina (BL). B, brown body; MC, morula cell. Scale=5.0µm.

Fig. 16. Autotomized intestine-cloacal junction. The peritoneum (P), nerve plexus and muscle layer are disrupted (arrow), and the collagen fibrils (CF) are dispersed. Scale-5.0µm.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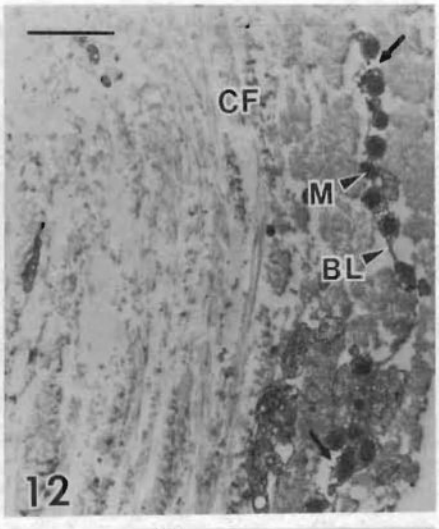
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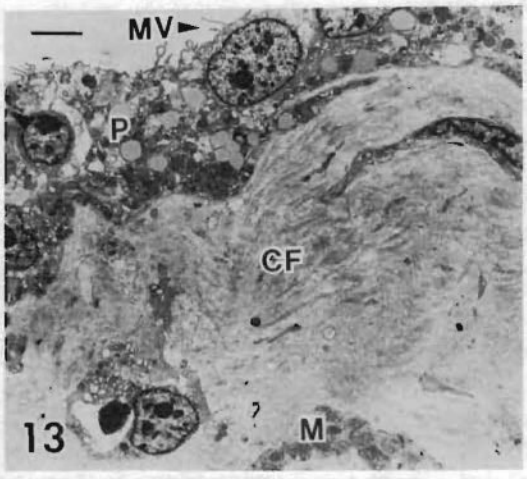
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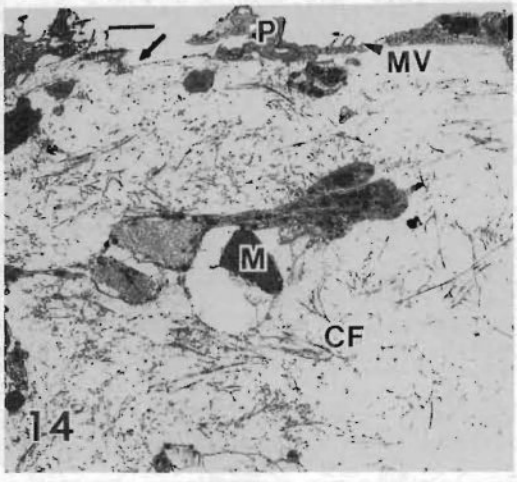
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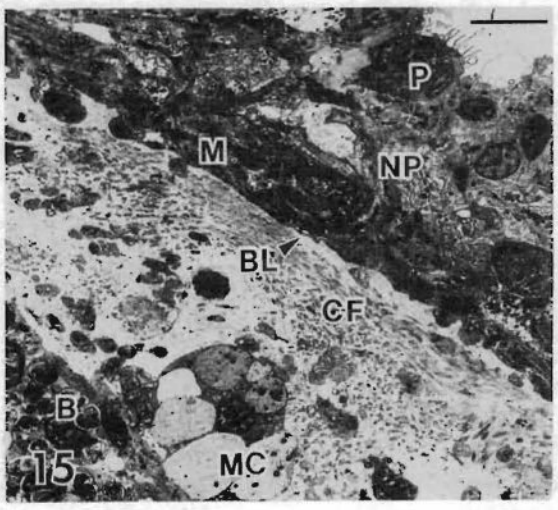
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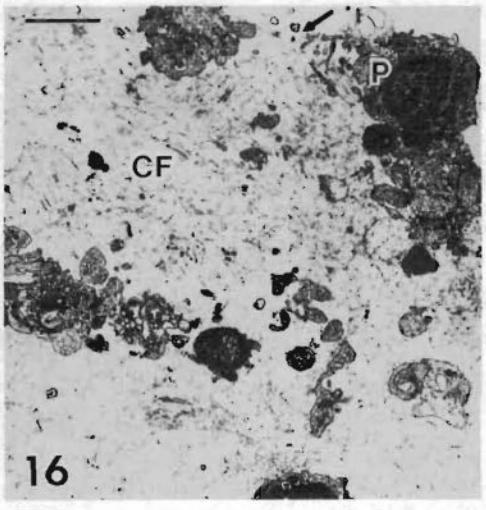
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ward by body wall muscle contraction. As the introvert autotomizes, the superficial dermis and epithelium delaminate from the underlying DCT, and the ossicles embedded within it become visible to the eye. Changes are evident when similar fields of normal and autotomizing DCT are compared (Figs. 11,12). The muscle fibres extend as the introvert distends, and the basal lamina surrounding the muscle fibres is disrupted. Structural examination reveals that the collagen fibrils remain intact and that they appear to slide across and away from each other. This suggests that changes occur in the interfibrilar matrix. Axons and LDV-filled processes also appear to extend, with some damage to axon membranes and the basal lamina, but their vesicular contents appear intact (Fig. 6). The peritoneal cells, muscle fibres and nerve plexus axons dissociate into the coelom, and the LCT is infiltrated by coelomic fluid. Collagen fibrils and unstriated fibrils in the LCT also remain intact, but the matrix loses its structural integrity and the cells embedded in it become disorganized. LDV-filled processes in the LCT and among the dissociated plexus axons retain their vesicles during autotomy.

3.5 Structure of autotomized P-L tendon

During autotomy, the P-L tendon changes from a relatively compact collagenous tissue, to one comprised of disorganized fibrils. Similar fields of normal and autotomized tendon show the increase in interfibril distance and fibril disarray resulting from autotomy (Figs. 13,14). After autotomy, the peritoneum is disrupted, and portions dissociate from the basal lamina. Although the collagen fibrils remain intact, it appears that the associated matrix undergoes a structural change. This results in fibril disorganization and a marked increase in the interfibril distance. The PRM muscle bundles are disrupted, and the contractile filament organization is lost with a disappearance of the thick filaments (Figs. 10,14). Sarcolemmal disruption is evident, and eventually the muscle cell contents are dispersed. Axons and LDV-filled processes also disperse and show membrane irregularity, but for the most part retain their vesicles. Some axon-like profiles devoid of vesicles may represent axons which have lost vesicles during autotomy (Fig. 10). The LDV-filled processes remain surprisingly intact (Fig. 10), although some vesicular loss through mechanical damage might be expected.

3.6 Structure of autotomized intestine-cloacal junction

As for the other autotomy tissues, the intestinal peritoneum, muscle layer and nerve plexus dissociate during autotomy, and the underlying connective tissue is infiltrated with coelomic fluid (compare Figs. 15,16). The collagen fibrils are disorganized, but remain intact. Some axons in the dissociated nerve plexus and connective tissue have an irregular contour, and their basal lamina is disrupted. Vesicles are present in most axons. However, some axons completely surrounded by coelomic fluid contain few or no vesicles, suggesting that the vesicles may have been lost during autotomy.

4 DISCUSSION

Previous examination of echinoderm catch and autotomy tissues revealed that they are collagenous connective tissues (Takahashi 1967; Wilkie 1979; Holland & Grimmer 1981a, b; Smith et al 1981; Motokawa 1982b; Hidaka & Takahashi 1983) and the ultrastructure of the P-L tendon and introvert dense connective tissue is similar. The structure of the introvert loose connective tissue and the intestine differ by having a high matrix content relative to fibril content. The collagen fibrils and unstriated fibrils of the autotomy tissues are characteristically of small diameter and are similar to those observed in other echinoderm connective tissues (Junqueira et al 1980; Holland & Grimmer 1981a,b; Smith et al 1981; Motokawa 1982b; Hidaka & Takahashi 1983). Unlike ophiuroid and crinoid autotomy structures that are comprised entirely of connective tissue (Wilkie 1979; Holland & Grimmer 1981a), the autotomy tissues of E. quinquesemita also contain muscle cells.

Axons and LDV-containing processes are present in the autotomy structures of E. quinquesemita. They are surrounded by connective tissue as well as in association with muscle cells and the nerve plexus. The axons and their vesicular contents appear to be typical of echinoderm neurons. The clear vesicles may be cholinergic, while the dense-core vesicles may be monoaminergic, as suggested elsewhere (Prosser & Mackie 1980; Byrne 1982; Pentreath & Cobb 1982). The LDV-filled processes resemble axons in containing axial microtubules and vesicles, and in their association with muscle fibres. Based on their morphology, the LDV-filled processes of E. quinquesemita are considered to be axons.

The LDVs are similar to the neurosecretory-like vesicles in other echinoderm connective tissues that are typically large, electron-dense and of variable shape. The LDV-containing processes appear characteristic of echinoderm connective tissues and are thought to play a role in connective tissue variable tensility (Wilkie 1979, 1984; Holland & Grimmer 1981a,b; Hilgers & Splechtna 1982; Motokawa 1982b,1984; Hidaka & Takahashi 1983).

The sudden breakdown of the autotomy tissues during evisceration involves a change in the connective tissue matrix, as occurs in arm autotomy in ophiuroids and crinoids (Wilkie 1979; Holland & Grimmer 1981a). During autotomy the fibrillar elements of the autotomy tissues remain intact, but they disperse as the matrix loses its structural integrity. Although it is difficult to describe change in the electron-luscent matrix, the fibril disarray suggests that the matrix has undergone a physical and chemical change, perhaps a sol-gel-like change.

In the autotomy tissues of ophiuroids and crinoids, the LDV-filled processes appear to be the only potential source of autotomy-inducing agents that can be detected microscopically within the connective tissue (Wilkie 1979; Holland & Grimmer 1981a). The contents of the LDVs have been suggested to be proteolytic enzymes or chelating agents that when secreted, effect connective tissue change (Wilkie 1979; Holland & Grimmer 1981a). Axon profiles without vesicles and LDV exocytosis observed in the autotomized crinoid syzygy have been suggested to be part of a massive vesicle exocytosis that plays a role in effecting autotomy (Holland & Grimmer 1981a). However, it is not clear whether these profiles are a cause or a result of autotomy.

During evisceration in E. quinquesemita, the LDVs appear to remain intact. The disruption of axon membranes and basal lamina observed in autotomized tissues may be mechanical rupture occurring during autotomy. Swollen axons devoid of vesicles were observed adjacent to intact vesiculated axons and are likely to be a result rather than a cause of autotomy. Evisceration and autotomy in E. quinquesemita appear to be neurally controlled (Byrne 1983) but, based on morphological evidence, the vesicles contained in locally distributed neurons do not appear to be the source of agents that effect connective tissue breakdown. Numerous neurons and LDV-filled processes are found in association with muscle fibres, especially in the P-L tendon. In ophiuroid and crinoid autotomy tissues, LDV-processes are found only with connective tissue (Wilkie 1979; Holland & Grimmer 1981a); perhaps the LDV-processes of E. quinquesemita are not homologous to those of ophiuroid and crinoid autotomy tissues.

Coelomic fluid factors that alter connective tissue tensility have been isolated from several echinoderms (Motokawa 1981, 1982a,c). There is evidence for the presence of an autotomy-inducing factor in the eviscerated coelomic fluid of E. quinquesemita (Byrne 1983), as found in another dendrochirote holothurian, Sclerodactyla briareus (Smith & Greenberg 1973). The peritoneal disruption, followed by coelomic fluid infiltration into the connective tissues during evisceration, may be important to the autotomy process of E. quinquesemita. The three autotomy tissues are partially or completely bathed in coelomic fluid and in this respect, differ from the arm autotomy tissues of ophiuroids and crinoids. The autotomy tissues of these groups are not associated with a large coelomic fluid medium and so ophiuroid and crinoid arm autotomy may depend on locally distributed cells. In contrast, cells involved in holothurian evisceration may be located at some distance from the autotomy tissues and effect the change through the medium of the coelomic fluid.

Introvert and P-L tendon autotomy was mimicked in vitro by altering the ionic composition of test solutions (Byrne in press). The results suggest that the mechanism of autotomy involves a change in the ionic interations within the proteoglycan matrix. How this is brought about is not known. Although echinoderm autotomy appears to be neurally controlled, the morphological basis for neural mediation has not been established.

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