THE FUNCTIONAL MORPHOLOGY OF THE UROPOD STRETCH RECEPTOR OF THE SAND CRAB *EMERITA ANALOGA* INCLUDING A COMPARISON WITH THE UROPOD STRETCH RECEPTOR OF THE SQUAT LOBSTER *MUNIDA QUADRISPINA*.

by

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ABSTRACT:

While much is known about the response characteristics and the central connections of crustacean primary afferents, the mechanism of stimulus transduction in stretch receptors remains enigmatic. I studied the morphology of a basal joint proprioceptor in two Anomura (Hippidae, Galatheidae) in order to better understand the mechanical aspects of the transduction process (the other aspects depend on the electrochemical properties of the membrane).

The uropod stretch receptor (USR) complex in the sand crab *Emerita analoga* (Stimpson 1857) consists of an elastic strand innervated by four giant, nonspiking, mechanoreceptive neurons (NSRs) with central somata and a separate, parallel muscular strand innervated by two groups of neurons of unknown modality (Paul, 1972).

Each of the NSRs has three morphologically distinct zones in the periphery. The Zone of Dendrite Entry for each NSR begins outside the strand at the first bifurcation of the dendrite into two primary branches which enter the strand at acute to right angles as thick (40 to 60μm) cylinders and immediately turn rostrally and caudally along the long axis of the strand and extend into the strand where further branching occurs. The Zone of Branching consists of 4 to 15 m diameter dendritic branches within the strand. Tiny (0.1-0.5 μm) cylindrical processes (dendritic tips) arise directly from all levels of this zone so that even the largest branches appear to be covered in the fine dendritic "hairs" of the Zone of Dendrite Termination.

Each pair of branches is divided by a rod of extracellular matrix (ECM) running parallel to the long axis of the strand. These vacuolated strings are fusiform in shape and extend for the length of the dendritic branch with which each string is associated. Dendritic tips project into the strings and are probably the site of mechanosensory transduction because they are in direct contact with the ECM of the vacuolated string which is compressed by strand-stretching. Fibres in the ECM of the capsule and vacuolated strings of the elastic strand appear to belong to

a special class of 'invertebrate elastic fibres' described by Elder and Owen (1967) and give the strand its resilience.

Cross-sectional profiles of dendritic tips are significantly larger but significantly less numerous in stretched than in relaxed receptors. I propose a model in which distal tips are compressed until they are too small to be recognized in stretched strands. The large profiles are the proximal tip regions which have expanded by hydrostatic pressure.

Like *Emerita*, the squat lobster, *Munida quadrispina* (Benedict 1902) has a USR complex consisting of parallel elastic and muscular strands. The strands are closely opposed to one another and lie in a single, ventral plane rather than running dorso-ventrally as they do in *Emerita*. The receptor complex receives its innervation from the receptor nerve which contains 10-13 profiles whose signal characteristics are unknown. Two of the smallest appear to innervate the receptor muscle, the remainder the elastic strand. The one or two largest profiles (10-20 μm), upon entering the strand transversely, turn longitudinally, and become associated with vacuolated strings into which they send tips as do the four NSRs in *Emerita*. Homologies between the two USRs and other basal joint proprioceptors are suggested and some functional and evolutionary consequences of USR morphology are discussed.

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

LIST OF ABBREVIATIONS

ATU-	anterior telson uropodalis
ECM-	extracellular matrix
EM-	electron microscope
NSR-	nonspiking mechanosensory cell
SR-	stretch receptor

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INTRODUCTION

Walking and swimming are the two major forms of locomotion in decapod crustaceans. Proprioceptive feedback about limb position and velocity is required to coordinate these behaviors, to ensure that antagonistic muscles contract alternately and not synchronously (resistance reflex) (e.g., Davis, 1969a,b, 1973), to ensure interlimb coordination (Evoy and Ayers, 1982), to entrain locomotory rhythms (Sillar *et al.*, 1986a, 1986b), to enable the locomotory system to respond appropriately to changing loads (Evoy and Fourtner, 1973a, 1973b; Barnes, 1977; Clarac, 1977; Grote, 1981), to change the phase relationships of power and return strokes (Paul, 1976; Miyan and Neil, 1986a) and to produce different gaits (e.g., Ayers and Davis, 1979). With the exception of tailflipping, which is accomplished by flexing and extending the abdomen and is monitored by abdominal muscle receptor organs, crustacean locomotion depends on limb movement. Walking consists of repetitive cycles of movement of pereiopods (walking legs) and these appendages are used by some crabs for swimming (Evoy and Ayers, 1982). Other crustaceans swim by rhythmically beating the pleopods (swimmerets, e.g., *Homarus*, Davis, 1968), thoracic setaceous appendages (e.g., larval *Homarus*, Neil *et al.*, 1976) or uropods (Paul, 1971a, 1971b, 1971c). There are specific proprioceptors which respond to angular changes in limb position, joint position, muscle tension and cuticular deformation during locomotion and others which are involved in postural adjustments (Evoy and Ayers, 1982).

Homologous Proprioceptors

A proprioceptor spans the basal joint of each of the locomotory appendages. These stretch receptors (SRs) share some properties which are rare among crustacean sense organs. They all have innervated elastic strand(s) often with a parallel muscular strand, sensory neuron somata in the central nervous system, relatively large diameter afferent fibres and nonspiking (or dual signal) primary sensory neurons (Bush, 1976). The similarities of their positions and morphological and physiological properties (Table 1) suggest that the oval organ, thoracico-coxal, crayfish swimmeret and anomuran uropod stretch receptors are

Table 1: Innervation of the strands of decapod basal joint proprioceptors.

PROPRIOCEPTOR COMPLEX	LOCATION	TYPE OF STRAND	TOTAL INNERVATION	STRAND INNERVATION IDENTIFIED CELLS	VACUOLATED STRINGS
OVAL ORGAN[1]	base of 2nd maxilliped	many elastic	3 DSNs	3 DSNs innervate all strands	Absent
THORACICO-COXAL	base of periopods	muscle-proximal tendon	1 NSR	T fibre	Present[10]
Brachyura[2]		flanking elastic- dorsal	1 NSR	S_d branch	Present[10]
Anomura[3]		flanking elastic- ventral	2 NSRs	S_v branch + P fibre	Present[10]
		levator elastic	2 NSRs + 1 UM		Present[10*]
		depressor elastic[4]	1 NSR	D fibre	Present[10*]
Astacura[2]		muscular	2 NSRs	S and T fibres	Absent[10]
Palinura[5]		additional elastic levator elastic	4+ UMs	3 stout/1 fine UMs	Unknown
SWIMMERET	base of pleopods	S_1 elastic	1 NSR + 1 UM	NSSR-A	Unknown
crayfish[6]		S_2 elastic	1 NSR + 4-6UMs	NSSR-P	Unknown
lobster[7]		elastic (S_1 homolog)	2 SSRs	unnamed	Present
UROPOD	base of uropods	elastic	4 NSRs	NSRs I-IV	Present[11]
Emerita[8]		muscular	2+ UMs	MNs?	Absent[11]
Galathea[9]		elastic	11 UMs	3 NSRs?/8 SSRs?	Unknown
		muscular	1+ UM		Unknown

[1] Pasztor, 1979
[2] Alexandrowicz and Whitear, 1957
[3] Alexandrowicz, 1958
[4] Cannone, 1987
[5] Alexandrowicz, 1967
[6] Heitler, 1982
[7] Miyan and Neil, 1986
[8] Paul, 1972
[9] Maitland *et al.*, 1982
[10] Whitear, 1965.
[11] this study.

DSN- dual signal neuron
NSR/NSSR- nonspiking stretch receptor neuron
UM- neuron of unknown modality
SSR- spiking stretch receptor neuron
MN- motoneuron
* - in Brachyurans.

serial homologs (Paul, 1988). Although it is not associated with a locomotory appendage, the oval organ is included in this group because the second maxilliped does move rhythmically during respiration and feeding (Pasztor and Bush, 1983a) and the oval organ has the properties typical of the group (Pasztor, 1979). The twisting muscle receptor of the lobster may be homologous with the crayfish swimmeret receptor (Miyan and Neil, 1986b), and thus be entitled to a place in this list. However, since its afferents are spiking, it has been omitted from Table 1 (see discussion).

The sensory portion of the proprioceptor complex consists of (an) innervated strand(s) linking the basal segment of the limb to the body. Branches of the afferent neurons lie within the strand(s) and are depolarized when the strand is stretched by movemement of the limb in a specific direction (strand-stretching direction). Table 1 shows that the nonspiking (or dual signal, see discussion) receptor neurons (NSRs) innervate only the elastic portion of all the basal joint proprioceptors. The thoracico-coxal stretch receptors of Brachyurans and the one Anomuran which has been studied (Alexandrowicz, 1958), commonly classified as "muscle receptor organs" have flanking elastic strands and a proximal tendon into which branches of the NSRs insert. In the astacuran thoracico-coxal SR the branches of the NSRs are also embedded in connective tissue although the latter lies within the muscle bundle (Whitear, 1965). The structure of these coxal organs is thus quite different from the true muscle receptor organs.

The NSRs are multiterminal and their peripheral processes elude the usual classification into axons and dendrites. The large, cylindrical processes which join the cell bodies in the central nervous system to the receptor strands resemble axons in morphology (length, diameter, peripheral branching). However, I will adhere to the convention of Shepherd (1988) and refer to them as dendrites because they conduct impulses toward the soma, although this designation is not universally accepted (Bush, 1981).

The finest periperal branches (dendritic termini) of most NSRs studied so far (Table 1) are embedded in vacuolated strings. These are electron-dense rods of extracellular matrix (ECM) which lie within the receptor strand parallel to its long axis.

Along with the elastic sensory strand, the uropod and thoracico-coxal SRs have a receptor muscle which maintains receptor sensitivity in the thoracico-coxal SR by contracting along with the muscles whose contractions cause the strand to slacken (antagonists to the strand-stretching muscles). This ensures that the parallel, elastic, sensory strand is never slack but always maintains a certain tautness at minimum length. This has been demonstrated in the thoracico-coxal SR (Bush, 1976) where the receptor muscle shares innervation with the muscle which moves the limb in the anti-strand stretching direction (promotion); co-contraction of antagonistic muscles prevents slackening of tension in the sensory strand and a resultant decline in sensitivity. The role of the receptor muscle is clear only in the thoracico-coxal SRs where it contains sensory endings (Astacura) or is attached along its length to the flanking elastic, sensory strands (Brachyura). The elastic and muscular strands in the uropod SRs of both *Munida* and especially *Emerita* are quite separate from each other, and, the function of the muscular strand is uncertain. No structural connections have been seen and no shared innervation with the antagonists of the strand-stretching muscles has been demonstrated. Furthermore, the swimmeret stretch receptor and the oval organ lack receptor muscles altogether. Clearly the elastic receptor strands, and the NSRs which innervate them, are functionally the most important part of the basal joint proprioceptor complex and are the component which has been conserved throughout the evolutionary specialization of segmental appendages for different functions.

The first member of this class of unusual proprioceptors to be described (Alexandrowicz and Whitear 1957) was the thoracico-coxal stretch receptor. A stretch receptor function for it based on purely morphological criteria was proposed by Alexandrowicz (1958). Subsequently Paul (1971a, 1971b, 1971c, 1972) described the uropod stretch receptor, Pasztor (1979) the oval organ and Heitler (1982) the swimmeret stretch receptor.

The novel physiological properties of the thoracico-coxal SR were first demonstrated in *Carcinus* and *Potamon* by Ripley, Bush and Roberts (1968) who showed that the afferents are normally nonspiking and, further, that the graded response is active in a resistance reflex (Bush and Roberts, 1968). Stretching the

receptor produces a receptor potential which spreads to the ganglion and evokes a reflex discharge in the motor axons to the coxal promotor muscle (Bush and Roberts, 1968). Since the receptor is stretched by limb remotion, the net effect of this reflex is to counteract strand stretching. Subsequently it was shown that T fibres of *Carcinus* make connections to the promotor motoneurons (Cannone and Bush, 1980) and that thoracico-coxal SR input is required for "normal" leg positioning in forward and backward walking in the crayfish *Procambarus* (DiCaprio and Clarac, 1981). Similar reflexes are elicited by the NSRs of the swimmeret receptors and uropod SRs. The reflex mediated by *Emerita*'s uropod SRs is outlined below. The S_1 elastic strand of the swimmeret receptor in the crayfish *Pacifastacus leniusculus* is stretched by swimmeret retraction; this action depolarizes the two NSRs innervating the strand which excites or inhibits several of the swimmeret motoneurons (Heitler, 1982). If swimmeret retraction (powerstroke) is mimicked by injection of depolarizing current into an NSR then powerstroke motoneurons are inhibited; injection of hyperpolarizing current excites them in a negative feedback resistance reflex (Heitler, 1986).

Stretch Receptor Ultrastructure

My first objective was to describe the ultrastructure of *Emerita*'s uropod SR. Understanding the ultrastructure of a stretch receptor can aid in understanding the results of physiological studies (Pasztor, 1979). The oval organ (Pasztor, 1979, Pasztor and Bush, 1987) and thoracico-coxal SRs (Whitear, 1965; Krauhs and Mirolli, 1975) have been examined but until now uropod stretch receptors (and nonspiking swimmeret receptors) have not.

The mole or sand crab *Emerita analoga* (family Hippidae) swims by beating its uropods. A stretch receptor, consisting of an elastic strand innervated by the dendrites of four giant nonspiking mechanosensory neurons (NSRs) with central somata, senses the return stroke of the uropod (Paul, 1972). Like the nonspiking neurons innervating the thoracico-coxal SR, the NSRs are active in a resistance reflex. One of the effects of stretching the uropod SR is to excite powerstroke motoneurons, initiating the next powerstroke via reciprocal reflexes in antagonistic muscles, during a swimming behavior known as 'treading water'. Proprioceptive

input from the NSRs is essential for this behavior in which powerstroke follows return stroke at a uniform latency. Deprived of this sensory input, *Emerita* cannot tread water. Reafference from the uropod SRs during the true 'swimming' behavior appears to modulate the excitability of the swimming circuit by reinforcing centrally-initiated powerstroke bursts during high frequency locomotion (Paul, 1976).

The uropod stretch receptor in *Emerita* is an excellent preparation in which to study mechanisms of mechanosensory transduction using physiological, morphological and combined techniques. This is because it has "giant" dendrites which are accessible to intracellular recording techniques, is innervated by only four cells and some of their connections are known (Paul, 1971c, 1972, 1976, 1985).

Some of the ultrastructural characteristics of the uropod SR (this study), and other stretch receptors, which may be physiologically significant are compared in Table 2. Two types of stretch receptor which are not basal joint stretch receptors are included because they are strand receptors and, although sharing some morphological features, have interesting differences. The most important differences are the proximity of the dendritic endings to muscle fibres and the junctional densities, which are specializations for attachment to the connective tissue of the intercalated tendinous region or to a muscle fibre sarcolemma (Nadol and de Lorenzo, 1969, Euteneur and Winter, 1979). These features are absent from the basal joint stretch receptors. Including the abdominal cord receptor and the abdominal muscle receptor organs in Table 2 highlights the unity of the homologous set of basal joint proprioceptors as a distinctive class of receptor.

The structure of the dendritic termini is probably the most important ultrastructural feature since the stretch stimulus is converted there to a membrane depolarization (mechanosensory transduction; reviewed in Bush, 1981). The termini of the basal joint receptors, including *Emerita*'s, are parallel to the axis of the strand and, therefore, to the vector of the strand-stretching force. All are unsheathed and have few organelles (Table 2). All the true coxal receptors (basal joint proprioceptors excluding the oval organ) examined so far have "vacuolated strings" into which the dendritic termini insert. Vacuolated strings (named by

Table 2: Comparison of functionally important ultrastructural features of decapod strand proprioceptors.

Receptor	Genus	Connective Tissue	Orientation of Large Dendrites	Terminal Orientation	Terminal Shape	Term. Diam.(μm)	Organelles in Termini	Glial Sheath
Basal Joint Stretch Receptors:								
Oval Organ	*Homarus*1 *Palinurus*1 *Callinectes*1 *Orconectes*1	longitudinal c.t. strands in cone-shaped array	run along strands parallel, branch to 2°/3° twigs clusters of termini	longitudinal or oblique to strands, 1 direction	bulbous	0.15-2.5	large,central mito. no MTs DCVs/CVs	NO
TCSR	*Cancer*2	ECM vacuolated strings	entry transverse, short 2° branches at right angles to entry	longitudinal in vacuolated strings,1 or 2 directions	blunt cylinders	0.08-0.17	vesicles, no mito. +MTS vesicles	NO
Brachyura	*Carcinus*3 *Pagurus*3					≥0.1		
	--------	----------						
Astacura	*Astacus*3 *Homarus*4	no discrete vaculoated strings				≤0.1		
USR	*Emerita*5 *Munida*5	ECM vacuolated strings inside capsule	entry transverse at acute-right angle,turns longitudinally 2°/3° branches	longitudinal in vacuolated strings,1 or 2 directions parallel to long axis of strand	blunt cylinders	0.1-0.5	occasional MTs, fuzzy material no mito.	NO
Other Stretch Receptors:								
Nerve Cord	*Pacifastacus*6	amorphous c.t. with "macaroni" spaces/ fibre bundles	entry transverse branches at 90° 1° dendr. irregularly oriented	longitudinal in dense ECM	varicose	0.4	MTs,-MFs fuzzy material, laminar cores	NO
MRO	*Orconectes*7	thin strands project outward from around muscle fibres	entry transverse branches irreglarly arranged in strand		varicose	0.48-0.6#		NO
						0.05-0.3		
	*Procambarus*8 9 10 11	tendinous intercalated zone where dendrites insert	entry transverse turn and run oblique or parallel to long axis	parallel to long axis in ECM	varicose	0.1-0.2	Vs,+MTs, SER,-mito. JDs	NO
-slow	*Homarus*12	dendrites branch parallel to long axis		no glomeruli, parallel to long axis	varicose		few Vs, most CVs, JDs	NO
-fast		short branches ramify to glomeruli		glomeruli			many Vs most CVs, JDs	NO
	*Astacus*13	no intercalated tendon region	entry transverse turn and run oblique to long axis	curled		Unknown	Unknown	Unknown

1 Pasztor, 1979
2 Krauhs and Mirolli, 1975
3 Whitear, 1965
4 Alexandrowicz & Whitear,1957
5 this study
6 Cobb and Heitler, 1985
7 Bodian and Bergman, 1962
8 Peterson and Pepe , 1961
9 Komuro, 1981a, 1981b
10 Tao-Cheng *et al.*, 1981a
11 Kosaka, 1969
12 Nadol and de Lorenzo, 1969
13 Florey and Florey, 1956

measured from Fig. 9, ref 7
MT- microtubule
MF- microfilament
mito.- mitochondria
DCV,CV,V- dense core, clear vesicle
JD- junctional density (with muscle)

Whitear, 1965) are dense rods of extracellular matrix, running parallel to the long axis of the receptor strand.

Morphological Responses of Proprioceptors to Stretch

My second objective was to search for morphological correlates of stretch in the uropod SR of *Emerita*. Comparison of the structures of receptors fixed in different physiological "states" can reveal the morphological foundation underlying receptor potential production. Invertebrate examples are provided by Bodian and Bergman, 1961; Komuro, 1981b; Moran and Varela, 1971; Krauhs and Mirolli, 1975; Tao-Cheng *et al.*, 1981a, and vertebrate examples by Bendeich *et al.*, 1978; Karlsson *et al.*, 1971.

Evolution of Basal Joint Proprioceptors

Unlike the thoracico-coxal SRs which are common to all decapods, uropod SRs appear to belong only to members of the infraorder Anomura (Paul *et al.*, 1985). Macrurans may never have developed homologous structures during their evolution or they may have lost them. *Emerita*'s NSRs are the terminal members of a set of serially homologous coxal proprioceptors. I judged that comparing them to their serial and interspecific homologs could reveal how stretch receptors change as the structure and function of limbs are modified during evolution. Therefore, I studied the structure of the uropod SR of an anomuran from another family, the squat lobster *Munida quadrispina* (family Galatheidae), which swims by tailflipping. This behavior resembles the macruran non-giant tailflipping (Wilson and Paul, 1987) from which *Emerita*'s novel swimming behavior is thought to have been derived (Paul, 1981). The external structure of *Munida*'s tailfan is also macruran-like and, therefore, the tailfan and uropod SR might be considered to be less specialized than *Emerita*'s. The uropod SR of a closely related squat lobster, *Galathea strigosa*, is innervated by both spiking and nonspiking cells (Maitland *et al*, 1982) and it is likely that *Munida*'s uropod SR also receives both types of innervation.

A third (subsidiary) objective of my study was to search for ultrastructural characteristics of nonspiking neurons in order to predict which, if any, of the cells in the *Munida* receptor might be nonspiking.

Analog versus Digital Signal Transmission:

The NSRs of the coxal proprioceptors which have been well characterized, including those of *Emerita*, have giant fibres. These large processes must be metabolically costly to maintain, yet there may be an evolutionary sequence from spiking to nonspiking sensory neurons in uropod SRs (see discussion).

Is there a functional advantage for a proprioceptor which monitors limb position to send information via analog signalling? Nonspiking transmission is favoured by basal joint proprioceptors on the true locomotory limbs: uropods, pleopods and periopods (Table 1). The premier advantage of nonspiking signalling in a mechanoreceptor is that it allows the neuron to follow limb movement with great precision and sensitivity. Nonspiking impulse conduction is favoured if a sensory structure is innervated by only one or a small number of afferents (Bush, 1981). The evolutionary modification of a galatheid-like tailfan to the hippid tailfan, which is adapted for swimming with the uropods, may have been accompanied by a shift in impulse conduction from mixed spiking and nonspiking innervation to a smaller number of nonspiking neurons.

Pearson (1976) used a computer model to show that there will necessarily be discontinuities in the post-synaptic response to the output from a single spiking input; at very low firing frequencies post-synaptic potentials appear as discrete events and the graded nature of the original stimulus is lost. This is not a problem in galatheid uropod SRs since they are innervated by several afferents and multiple spiking inputs can transmit precisely graded information to a post-synaptic cell (Pearson, 1976). However, *Emerita*'s uropod SRs and decapod thoracico-coxal SRs escape this problem by having afferent neurons which are nonspiking. Furthermore, there is a time and, potentially, an information loss when the analog sensory signal corresponding to limb movement is encoded into a frequency-modulated spike train and subsequently when it is decoded to a post-synaptic membrane depolarization (Bush, 1981).

The fidelity of the signal may be greater over long distances in spiking than in nonspiking cells and cells which produce action potentials may be more independent of temperature and osmotic perturbations, direct current and fluctuating field potential or other electrical noise (Bullock, 1981). However, the fact that non-decremental, spiking conduction probably transmits information more faithfully over long distances is probably not relevant to the functioning of the basal joint stretch receptors since Bush (1981) has demonstrated that nonspiking impulses evoke a post-synaptic effect in 9mm long dendrites. One of the other possible disadvantages of non-impulse neurons is that the large diameter fibre needed to produce the large space constant required for transmission of graded signals over long distances is metabolically costly. Moreover, a high membrane resistance is required to produce the long length constant and is accompanied by a high time constant which theoretically limits the cell to transmitting low frequency events. However, this does not appear to be a problem for basal joint proprioceptors since *Emerita*'s NSRs can follow the uropods even when they are beating at frequencies up to about 13 Hz (Paul, 1976, 1988).

In this paper I first describe the ultrastructure of *Emerita*'s uropod SR. Next, I compare the ultrastructure of the uropod SRs which were fixed in stretched and relaxed positions and propose a model for stretch-induced dendritic tip deformation. Finally, I describe the ultrastructure of the uropod SR of *Munida* and identify two putative nonspiking cells innervating it. Based on these results I propose some evolutionary relationships between the coxal stretch receptors.

METHODS AND MATERIALS-

Emerita analoga:

Animals:

Female *E. analoga* were collected from Monterey Bay, California, and maintained in aquaria in a circulating seawater system at the University of Victoria. Animals were chilled to anesthesia on ice then pinned "non-invasively" in Sylgard dissecting dishes, ventral side up with pins through the tergal flaps of the gill covers. They were then perfused with seawater or pH 7.4-7.5 crab saline, introduced through a 20 gauge needle inserted into the meropopodite-carpopodite joint of the first walking leg. An incision through the ventral arthroidial membrane of the telson and the rostrocaudal vein under the strand allowed saline to flow through the animal. After perfusion was complete (10-20 minutes), the arthroidial membrane of the telson and last abdominal segment was removed. Muscles were dissected away, or their insertions cut as necessary, to view the gross layout and structure of the uropod SRs. uropod SRs were observed *in situ* in "abdomen/telson" preparations which consisted of the abdomen and tailfan (telson and uropods). "Uropod SR" preparations were those in which the receptor strand (with attached piece of coxopodite and dorsal telson for grasping with forceps), receptor nerve and sixth abdominal ganglion were removed from the animal and pinned flat on Sylgard.

In some preparations 0.5% methylene blue was added to the saline and the preparation was left at 4° C for from 4 to 24 hours. Camera lucida drawings of abdomen/telson preparations were made with a Wild M5 stereomicroscope (Fig. 1); other preparations were photographed with a Zeiss Ultraphot microscope (Fig. 2).

Cell Filling:

NSRs were exposed as for gross morphological study. The connectives just rostral to the fifth abdominal ganglion were cut. A Sylgard platform was maneuvered underneath the sixth abdominal ganglion and pinned in place. I made wells with a Vaseline-filled syringe fitted with a plastic suction electrode over the

end of the needle. The sixth abdominal ganglion remained inside the well while the receptor nerve protruded through the vaseline. The seawater was drained from the dissecting dish. Using a pipette with a drawn tip I removed the seawater from inside the well and replaced it with 400mM $CoCl_2$. In some preparations I cut 2 or 3 of the NSRs just before they entered the strand or ligatured them with fine cotton threads to obtain outfills of individual NSRs (Fig. 2). The dissecting dish was re-filled with seawater and the preparation was left at 4° C for 20-28 hours (shorter times produced incomplete fills) (rate = 84 μm/hr). I then removed the well and platform and dissected the abdomen and telson from the animal, pinning them in a small "fix" dish. The metal was precipitated with 2% ammonium sulfide $(NH4)_2S$ (Pitman *et al*, 1972) in saline or pH 7.4 Millonig's phosphate buffer (2-10 minutes) then rinsed with buffer or crab saline (3 x 5 minutes) and fixed in 10% crab saline for 1-2 hours. Preparations were dehydrated; then the uropod SRs were dissected free and cleared in methyl salicylate on a depression slide and viewed and photographed in wholemount.

Transmission Electron Microscopy (Transmission EM):

Both abdomen/telson and uropod SR preparations were made for transmission EM. When making abdomen/telson preparations I pinned one uropod so that the uropod SR was stretched (in a position corresponding to the start of the swimming powerstroke) while the other was left in the animal's natural resting position (=relaxed) as in Fig. 1. In order to ensure that the relaxed receptors were physiologically relaxed (the telson and uropod muscles contract when fixative is added), I cut all accessible nerves to the telson and uropod muscles; then the preparation and fixative were chilled. No movement was observed when this was done. Receptors were fixed in 2.5% glutaraldehyde in pH 7.4 Millonig's phosphate buffer (Millonig, 1961) for two hours at room temperature, rinsed in a buffer rinse solution (1 part Millonig's buffer to 1 part 0.6M NaCl- 3 x 5 minutes) then post-fixed in 1% OsO4 at 4° C for one hour. Specimens were dehydrated in a graded series of ethanol (a./t. preparations) or acetone (uropod SR preparations) and embedded in Luft's Epon 812 (Luft, 1961,

1963). Some specimens were stained *en bloc* for 5 hours in 2% uranyl acetate in 70% ethanol.

Section Preparation for Transmission Electron Microscopy:

Sections of receptors were cut (with glass knives on a Reichert UM 2 ultramicrotome) parallel, perpendicular and oblique to the long axis of the elastic strand. Sections were cut in the same orientation from the pair of receptors from each crab. Silver-grey or light gold sections were collected on uncoated copper grids and grids from preparations which had not been stained *en bloc* were stained conventionally with uranyl acetate and Reynold's lead citrate (Reynolds, 1960). Serial 0.5-1.0 μm sections were cut throughout each block. Semi-thick sections were stained with Richardson's stain (Richardson, 1960). From some blocks very thick (2.5-5.0 μm) sections were collected and mounted on plastic coverslips to be reembedded and sectioned at right angles to the original plane of section (e.g., Fig. 6.).

Both abdomen/telson and uropod SR preparations were examined using the Philips 300 transmission EM. uropod SR preparations were embedded pinned to Sylgard which was removed from the block prior to cutting sections. When embedded this way the receptor strand was visible in the block allowing precise alignment of the plane of section.

Sections of some blocks included RM so I could use sarcomere length as an index of stretch magnitude.

Photographs of vacuolated strings were taken at magnification step 12 and printed to obtain a total enlargement of 100,000x. Areas and diameters of transverse sections of dendritic terminals were measured using a Numonics Model 2210 Digitizing Tablet and Sigma-Scan Measurement System (Jandel Corp., Sausalito, CA).

Scanning Electron Microscopy (Scanning EM):

Uropod SR preparations (telson/abdomen preparations had too great a depth of field to be informative) were fixed as for transmission EM, dehydrated in

ethanol, critical point dried, coated with gold and viewed with a JEOL JSM 35 Scanning EM.

Histological Staining:

Abdomen/telson preparations were fixed in cold seawater Bouin's fixative (Humason,1967) for 24 hours at 4° C, dehydrated in ethanol, cleared in toluene and embedded in Tissue Prep II. Serial 3-5 μm sections of the entire preparation were cut in either transverse or longitudinal orientation and mounted on subbed slides. Paraffin sections were stained with one of the following: Masson's trichrome stain (Humason, 1967), Verhoeff's elastic connective tissue stain (Mallory, 1944), Cason's Mallory-Heidenhain stain (Cason, 1950) or potassium-permanganate Spirit blue stain (Elder and Owen, 1967).

Munida quadrispina:

Animals:

Munida quadrispina (both sexes) were collected from Saanich inlet by otter trawl from the MSSV John Strickland and maintained in aquaria in a circulating seawater system at the University of Victoria. Animals were chilled, pinned and perfused in the same manner as *Emerita* except that the caudal incision was made through the ventral arthroidial membrane of the sixth segment, not the telson. uropod SRs were exposed and stained with methylene blue (see above). All work was done on abdomen/telson preparations of *Munida* because the receptors lie in a single plane *in situ* (Fig. 28), making it possible to orient blocks accurately for cutting sections and to observe the uropod SRs with the stereomicroscope.

Cell Filling:

Receptor nerves were outfilled with 400mM $CoCl_2$ as described above with the following modifications. In *Munida* the receptor nerve was left intact for outfilling because the cells innervating the receptor are not well separated ouside the strand as are *Emerita*'s NSRs (compare Figs. 1 and 28). Preparations were left at 4° C for 20-28 hours (fill rate = 150 μm/hr), and processed as described above, except that the uropod SRs were not dissected free from the telson but instead,

entire abdomen/telson preparations were examined in tiny dishes containing methyl salicylate.

Transmission Electron Microscopy:

Only abdomen/telson preparations were made for transmission electron microscopy (transmission EM). One uropod was pinned so that the uropod SR was stretched in an arrangement corresponding to the flared position which characterizes the start of the abdominal flexion (swimming powerstroke) while the other was left in the position typical for a resting animal (=relaxed). Except for the receptor nerve, all nerves to the telson, uropods and sixth segment were cut. Fixation, dehydration and embedding were carried out as outlined above.

Because the uropod SRs lie in the same plane along the telson/sixth segment joint (Fig. 28), I could embed both uropod SRs in one block and cut transverse sections sequentially from the same block. Receptors were sectioned parallel, perpendicular and oblique to the long axis of the elastic strand. Serial 0.5-1.0 μm sections were cut throughout each block and stained with Richardson's stain.

Histological Staining:

Abdomen/telson preparations of *Munida* were fixed, dehydrated, cleared in toluene and embedded in paraffin as described above. Serial 3-5 μm transverse sections were cut, mounted on subbed slides and stained as above with one of Masson's trichrome, Cason's Mallory-Heidenhain, potassium permanganate Spirit blue or Verhoeff's elastic connective tissue stain.

RESULTS-

Emerita analoga:

Gross Morphology:

The uropod stretch receptor complex in *Emerita* consists of an elastic strand innervated by four giant, nonspiking mechanoreceptive neurons (NSRs) and a separate, parallel muscular strand innervated by two groups of neurons of unknown modality. The elastic strand arises from the hypodermis inside the dorsal telson, in the middle of the origin of the anterior telson uropodalis (ATU) muscle, runs anteroventrally, and inserts near the medial edge of the uropod coxopodite just dorsolateral to the tendon of ATU (Fig. 1). The muscle receptor arises from the dorsal telson lateral to the origin of ATU and inserts just lateral to the elastic strand insertion.

The elastic strand is an elliptical cylinder 20-60 μm in diameter near the uropod coxopodite. It becomes crescent shaped in cross-section in the region where the NSRs enter, then it tapers as it passes into the ATU. The elastic strand is not birefringent under polarised light in wholemount. Nevertheless, it contains refractile strands running lengthwise which can be seen under phase contrast (Fig. 2A). Its outer surface is quite smooth (Fig. 2B,C).

Dendrites of the four giant NSRs leave the sixth abdominal ganglion in a large nerve containing all the innervation of the lateral telson and uropod from which, accompanied by the two ATU motoneurons, they diverge ventrally toward the elastic strand as the receptor nerve (Paul, 1972; Paul et al.,1985). The four NSRs fan out as they approach the strand from a dorsomedial direction and enter the strand separately (Figs. 1,2D-G). NSR I enters the end of the strand nearest the coxopodite (Fig. 2D); NSR IV enters the strand most posteriorly Fig. 2G). NSRs II and III divide the intervening region (Figs. 2E,F). Usually the NSRs divide into two primary branches before entering the strand. NSR I enters the strand about one tenth of the way along the strand from the coxopodite (0.5 mm in a crab with a carapace length of 26 mm). The zones of entry (see below) of the NSRs (I through IV) occupy the next one quarter of the strand (1.3 mm).

Posterior to NSR IV the strand, accompanied by the ATU motoneurons, merges with the connective tissue of the ATU muscle.

Morphological Zones of the Peripheral Dendrites:

Each of the NSRs has three morphologically distinct zones in the periphery (Fig. 3). The Zone of Dendrite Entry for each NSR begins outside the strand at the first bifurcation of the dendrite into two primary branches and extends into the strand where higher-order branching occurs. The Zone of Branching consists of 4 to 15μm diameter dendritic branches within the strand. Tiny cylindrical processes (dendritic tips) form the Zone of Dendrite Termination. Tips arise directly from all levels of the Zone of Branching so that even the largest branches in the Zone of Branching appear to be covered in fine dendritic "hairs" (Fig. 3- inset).

Dendritic processes in the Zone of Dendrite Entry (20 to 30μm) both outside and inside the strand are nearly indistinguishable from motoneurons in their ultrastructure (Fig. 4). Both have abundant neurofilaments and neurotubules, many peripheral mitochondria, multilamellar glial wrapping and sparse, collagenous extracellular matrix (ECM)(Fig. 4). The only specialization of the NSR is a thickened plasma membrane (Fig. 4F- inset) - a characteristic of large crustacean neurons (Hama, 1961; Whitear, 1965).

Within the strand, in the Zone of Branching, between large branches and dendritic endings, secondary dendritic branches divide further into 10 to 15μm tertiary and 4 to 12μm quaternary and higher-order processes. Dendritic tips arise from all of these branches. ECM in this region consists of electron-dense ground substance in which are embedded wavy fibres (Fig. 5).

The structure of bifurcations of NSRs within the strand is unlike the type of branching which produces dendritic arbours in ganglia (Figs. 3,8). The branches of the primary dendrite enter the strand at acute to right angles as thick (40 to 60μm) cylinders and immediately turn rostrally and caudally along the long axis of the strand (Figs. 6,7). At the level of dendrite entry the strand is almost filled by dendritoplasm. The remainder of the volume ofthe strand is occupied by glial cells and ECM. The ventral aspect of the strand is surrounded by a connective tissue capsule which extends about two thirds of the distance around the strand

circumference (Figs. 3,6). Complex glial-ECM structures extend inwards from the capsule radially dividing the dendritic branches into two (Fig. 8) That is, a dendritic process, which is irregularly ovoid in cross section, divides by becoming horseshoe-shaped and finally separating into two branches between which is the radial intrusion of ECM from the capsule (Fig. 8). Further branching occurs in the same manner by radial intrusions of ECM extending inward from the capsule (Fig. 3,8).

The ECM which divides each pair of branches forms a rod which runs parallel to the long axis of the strand for a short distance (10-15μm); none of the ECM rods extend along the entire length of the strand. Whitear (1965) observed structures which are morphologically almost identical in the presumptive homologous, thoracico-coxal organs in other decapods (*Carcinus*, Pagurus and Astacus) and called them 'vacuolated strings' because in cross-section they appear to have 0.3-0.7 μm "holes". I have retained this term for the dense, rodlike structures that separate branches of the NSR dendrites in *Emerita*'s uropod SR (Fig. 5). The vacuolated appearance of the strings is produced by the tiny (0.3 to 0.7 μm diameter) dendritic termini (Fig. 5- insets). Strings are fusiform in shape. Their flattened axis extends radially inward from the capsule; their long axis is parallel to the long axis of the strand. Each vacuolated string arises at a branch point and spans the entire length of the dendritic branches with which it is associated (see above, Fig. 3). Thus, vacuolated strings are of unequal lengths. Where a new string arises, it is usually attached to the base of the adjacent string (Fig. 5).

Dendritic branching is usually unequal. For example, the first division of 60 μm primary branches produces two process of 35 μm and 25 μm diameter (Fig. 3). After dividing four to seven times, the resultant irregularly shaped processes end bluntly as 4 to 10 μm processes. Dendritic termini, or tips, arise from all higher levels of Zone of Branching branches. These tips are the tiny (0.3 to 0.7 μm) cylindrical processes which are embedded in the vacuolated strings (Figs. 3,5-insets); they run parallel to the long axis of the strand for 3 to 20μm. Tips arise from the large (secondary, tertiary, quaternary, etc.) processes via very short 'stubs' (Fig. 9). Tips may project in one or both directions (Figs. 9,10). Tips, like higher-

order branches terminate bluntly with rounded ends; they neither taper nor end in a bulbous expansion as do the termini in other receptors (see Table 1; Figs. 3,10 C,D).

Stubs and tips are in direct contact with the ECM of the vacuolated string (Figs. 5- inset, 9,10). There are usually mitochondria in the dendritic process from which the stubs arise and dense vesicles and neurotubules often occur in the stubs (Fig. 11). Tips often contain 'dense cores' and sometimes neurotubules (Figs. 9B,11). Fuzzy material lies on the inside of the tip membrane (Fig. 11 H,I). This may be a specialization associated with possible attachment to the ECM, although the ECM is too dense to allow recognition of any corresponding specialization on the outside of the tip membrane or in the string material (Fig. 11 H,I).

Neuroglia:

The glial wrapping of the Zone of Dendrite Entry resembles that of motoneurons (Figs. 4 and 12A). Glial cells interdigitate extensively with each other and send "fingers" into the dendritoplasm (e.g., Fig. 12B). Some of these glial fingers, which run parallel to the long axis of the dendrite, appear to contain dense rods which, because of their morphology and orientatation, may be structural supports providing longitudinal stiffening to the dendrite (Fig. 12 C,D,E). Glial nuclei in this zone are flattened (Fig. 12 A).

Glial cells are associated with the vacuolated strings, their nuclei located in the troughs between dendritic branches and at the ends of branches (Fig. 13A,B). These glial cells probably secrete the ECM of the adjacent vacuolated string (in which the tips of the adjoining dendritic branches are embedded). Strings are surrounded by a single, thin layer of glial cytoplasm except where they are attached to the capsule and where dendritic tips enter them (Fig. 14). In the lateral part of some regions along the strand, where smaller dendritic processes predominate, there are large numbers of glial cells (Fig. 13 C). There is little glial cytoplasm and there are no glial nuclei near the capsule and at the bases of the vacuolated strings where the latter are continuous with the capsule (Figs. 5,6,13B). Shapes of glial cells vary with their location within the strand (Fig. 13). Cells in the lateral part of the strand and those at the ends of strings have larger volumes of perinuclear

cytoplasm (Fig. 13 C,D) while those whose nuclei lie in the troughs between dendritic branches are crescent-shaped (Fig. 13A). The association between the glial cells and ECM of the vacuolated strings is complex (e.g., Figs. 11,14). Most strings appear to be associated with a single glial cell. Glial and dendritic profiles can be distinguished from one another by their shape and orientation in transverse sections of the strand, as well as by their cytoplasmic characteristics (Figs. 14-16). I have observed no gap junctions between glial cells or between glia and dendrites. Cytoplasmic connections between glial cells (Fig. 16E) are rare.

Dorsal and lateral branches in the Zone of Dendrite Entry and Transition Zone contain infoldings of glial cytoplasm (Fig. 14). These may give rise to the multilamellar vesicles which are abundant in the dendritoplasm (e.g., Fig. 11).

Glial cytoplasm contains mitochondria, Golgi stacks, rough (and smooth) endoplasmic reticulum and many vesicles in the region surrounding the nucleus whereas other parts of the cell may be nearly devoid of organelles (Fig. 15). Some cells contain dark granules which resemble the pigment granules of other crustacean nervous systems (Fig. 14 E,F,G).

Extracellular Matrix of the Elastic Strand

The ventrolateral surface of the elastic strand is composed of a 0.3-0.7 μm capsule made of electron-dense extracellular material in which are embedded "wavy" fibres (Fig. 5). The latter are arranged radially in the capsule and do not have the appearance of collagen fibres (see below).

The ECM is associated with, and probably secreted by, glial cells (Figs. 5,13,14). Dorsal, lateral and medial edges of transition zone dendritic branches are often covered by up to twelve alternating layers of glial cytoplasm and ECM.

The ECM of the vacuolated strings and the capsule is continuous and is composed of the same substance, although there are more fibres in the capsule. The strings are shaped like irregularly flattened cigars attached to the capsule along their outer side. Where two strings are attached and where strings abut the capsule, the ECM must be a mixture of the product of at least two different glial cells.

Staining Characteristics of the Elastic Strand:

Tests with specific connective tissue stains on paraffin sections of abdomen/telson preparations from *Emerita* have shown the distribution of collagen and invertebrate elastic fibres in the telson (Fig. 17; Table 3).

Table 3: Staining reactions of the uropod SR elastic strand in *Emerita*.

Stain	Elastic Tissue	Collagen
Mallory-Heidenhain	N.A.	None
Masson's Trichrome	N.A.	None
Potassium Permanganate Spirit Blue (invertebrate elastin)	Strong	N.A.
Verhoeff's Elastin (vertebrate elastin)	Weak*	N.A.

*Portions of the strand were brown but not as dark as vertebrate elastin fibres would be.

The ECM fibres stained in the uropod SR by potassium permanganate Spirit Blue appear to belong to a special class of 'invertebrate elastic fibres' described by Elder and Owen (1967) as having: 1) a distinctive appearance under the electron microscope, 2) physical elasticity and 3) a deep blue staining reaction with potassium permanganate spirit blue. The only structures in the telson (a./t. preparation) to share the staining properties of the uropod SR elastic strand were blood vessels (Fig. 17). Elder and Owen also found this type of fibre in the walls of crustacean blood vessels. These invertebrate elastic fibres seem to be composed of

a substance other than vertebrate elastin, according to Elder and Owen, and this explains the negative reaction with Verhoeff's stain, which is specific for vertebrate elastin (Mallory, 1944).

The Spirit Blue positive fibres lack the 25nm banding pattern of collagen, are more electron-dense and are wavy rather than straight (Fig. 18).

The sheaths of nerves and muscles show staining characteristics typical of collagen (intense blue with Mallory-Heidenhain, green with Masson's Trichrome) but not of elastic tissue (i.e., potassium permanganate Spirit Blue and Verhoeff's elastin stains gave negative reactions)(Fig. 17).

Characteristics of Individual NSRs

While the branching pattern of each NSR varies between NSRs and from individual to individual, there are some major features of the branching pattern which are consistent (Figs. 19-23). NSRs I and II have very similar, asymmetric branching patterns. NSR I: the primary process enters medially and sends about seven large branches rostrally in the strand. Its caudal branch divides into two or more branches. NSR II enters laterally as a large process which divides immediately into about eight branches caudally and two large branches rostrally. NSR III is characteristically different. Each of its two caudal and two rostral dendritic processes divides into two major branches, one medial and one lateral, in the strand. NSR IV enters the dorso-lateral part of the strand and divides into two to four large processes (2°) which continue to divide then end bluntly in the connective tissue (glial cells and ECM) just rostral to the entry of the elastic strand between the fibres of ATU (Fig. 22,23). The caudal portion of the strand is not innervated by the NSRs.

Aside from certain recognizable forms of their higher- order branching, specific details of the branching patterns vary both between the bilateral pair of receptors in a crab and between crabs. However, the general mechanism of branching (see above) is the same for all NSRs. Since the receptor potential is probably generated in the dendritic tips, the precise arrangement of higher-order branches may be relatively unimportant if they are just conducting fibres. The uniform size and arrangement of the tips, on the other hand, probably is

functionally important for optimizing sensitivity to stretch. Each μm^2 of Zone of Branching dendritic membrane gives rise to about 10.6 μm^2 of dendritic tip membrane.

Morphological Changes Associated With Stretch:

I have compared light and electron micrographs of receptors fixed in stretched and relaxed positions. The elastic strand changes shape from roughly circular in transverse section to a flattened elipse, as it is stretched (Fig. 24). Because the vacuolated strings are attached to the capsule, they must be deformed by strand stretching; and, because the tips are embedded in the capsule and string ECM, it is likely that the mechanism for transferring the force of the strand-stretching stimulus to the tips to produce a receptor potential involves either the surrounding ECM compressing the tips or pulling them lengthwise, if they are attached to the ECM (see below). The vacuolated strings are farther apart along the inside of the capsule in stretched than in relaxed receptors (Fig. 25). Because I was unable to identify bilaterally homologous vacuolated strings, and because string shape is so variable in cross-section, I could not quantify changes in vacuolated strings upon stretching. However, strings often appear to become taller and thinner with strand stretching and some stretched strings have a basal constriction (Fig. 25).

I measured cross-sectional area and smallest linear dimension of dendritic tips in relaxed receptors. Tip size does not appear to be correlated with crab size or with the position of the string within the receptor although I did not study this systematically. I then compared tip cross-sectional areas in electron micrographs of stretched and relaxed receptors in abdomen/telson preparations. Cross-sectional profiles of tips are significantly larger and significantly less numerous in stretched than in relaxed receptors (Figs. 25,26; Table 4).

Table 4: Dendritic tip profiles of crab A.

	Stretched n=226	Relaxed n=383	Difference
Mean Area ± S.E. μm^2	3.25x10-3 ±3.6x10-4	1.45x10-3 ±1.6x10-4	S > R p<0.001
Mean SLD* ± S.E. μm	4.40x10-1 ±4.8x10-2	5.41x10-1 ±4.1x10-2	S > R p<0.01

* Smallest linear dimension

In order to reduce the chance that the difference in area was due to a slight difference in the plane of section of the receptors, I compared the mean smallest linear dimensions of stretched and relaxed receptors. The smallest linear dimension should reflect the true cross-sectional diameter even had the stretched receptor been cut slightly obliquely leading to overestimation of the tip area. For three out of four crabs, change in smallest linear dimension was in the same direction as the change in cross-sectional area (Table 5), *i.e.*, stretched larger than relaxed.

Failure to obtain the same result for crab 4, in which relaxed smallest linear dimensions were larger than stretched, could have been the result of contraction of muscles causing the "relaxed" uropod to move and stretch the receptor. This would mean that both uropod SRs were actually stretched at the instant of fixation.

Alternatively, this receptor could have been anomalous. The second possibility seems more likely since no uropod movement was observed.

Table 5: Mean smallest linear dimension for receptors from four crabs [m±SE (n=)].

	Stretched	Relaxed
Crab A	0.44±0.005	0.35±0.003
	(226)	(383)
Crab B	0.46±0.011	0.40±0.012
	(134)	(84)
Crab C	----	0.32±0.009
		(101)
Crab D	0.44±0.007	0.54±0.009
	(139)	(191)

Model for Differential Tip Deformation:

The smaller number and larger cross-sectional area of dendritic tips in stretched compared to relaxed receptors may be due to differential compression of distal and proximal portions of the tips (Fig. 24-26). In relaxed receptors, tips are cylinders of uniform diameter. Stretch-induced compaction of vacuolated string ECM may compress only the distal tips; their cross-sectional areas may become so reduced that some tips are no longer recognizable or are not resolved clearly enough to be measured (Fig. 27). Hydrostatic forces would then cause expansion of the proximal tip. Water may also move into the dendrite from the extracellular space in response to the influx of cations which accompanies the generator potential (Tao-Cheng *et al.*, 1981a).

Dendritic tips have been found to change shape in the thoracico-coxal SR (Krauhs and Mirolli, 1975) and abdominal muscle receptor organs (Euteneur and Winter, 1979). It seems likely that the dendritic tips are the sites of mechanosensory transduction. Tip membranes may be susceptible to stretch because the low concentration of microtubules makes the tips less rigid than the Zone of Dendrite Entry and Zone of Branching processes. Sparsity of organelles is also characteristic of dendritic tips in abdominal muscle receptor organs (Tao-Cheng *et al.*,1981a) and thoracico-coxal SRs (Whitear, 1965; Krauhs and Mirolli, 1975).

Figure 1: Gross morphology of the telson. A. Line drawing of an *Emerita* with uropods in the position corresponding to the end of the return stroke with the receptor stretched. Arrow- direction of return stroke. B. Ventral view of sixth abdominal segment, telson and uropods (abdomen/telson preparation). All muscles, except the receptor muscle, have been removed from the left side of the crab, the ATU and powerstroke muscles were left on the right side. The elastic and muscular strands arise from the dorsal surface of the telson, run antero-ventrally amid the fibres of ATU and insert on the uropod coxopodite. The 4 NSRs have somata in the sixth abdominal ganglion (G_6) and dendrites in the receptor nerve. Scale bars: 5mm.

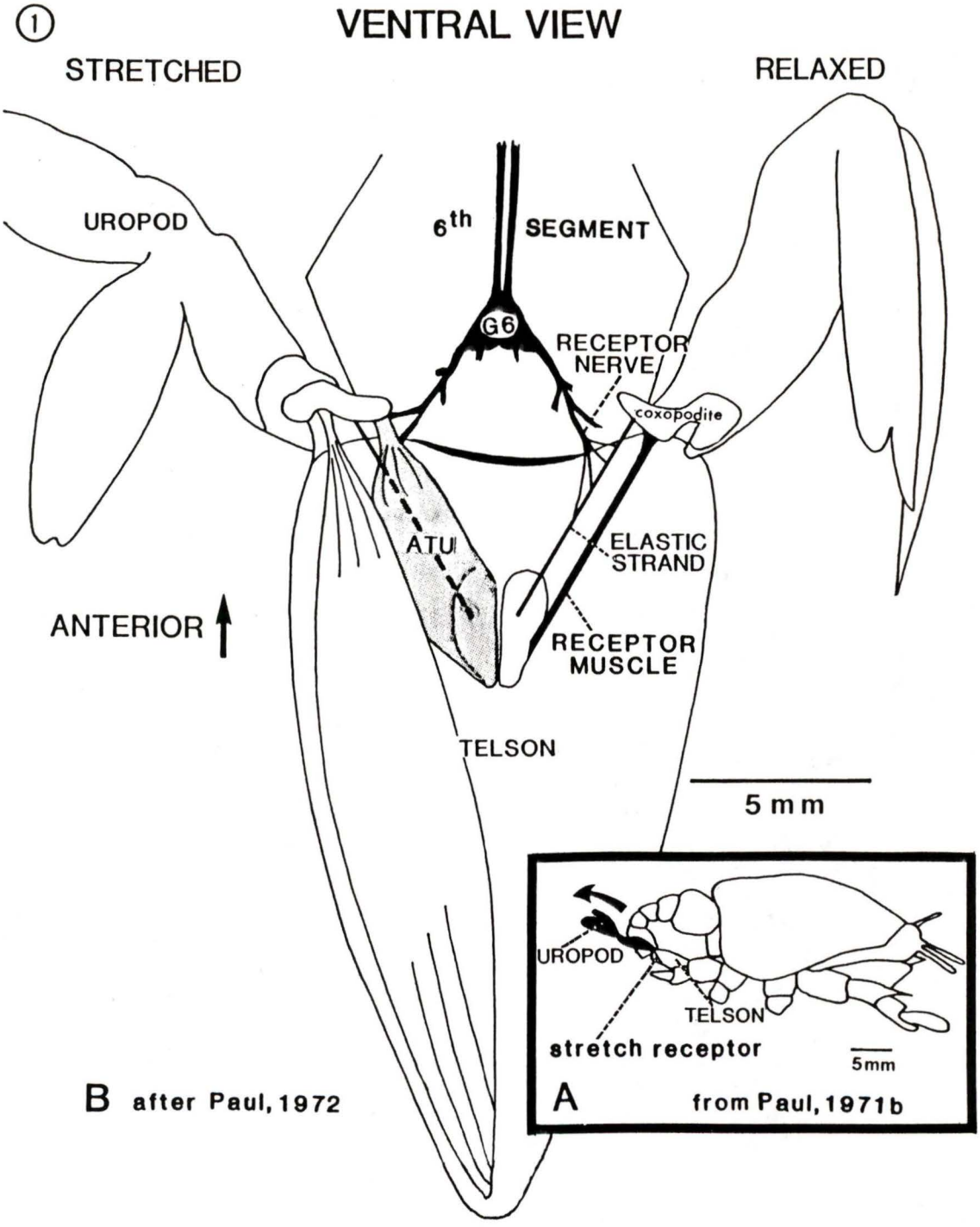

①
VENTRAL VIEW
STRETCHED
RELAXED
UROPOD
6th SEGMENT
G6
RECEPTOR NERVE
coxopodite
ATU
ELASTIC STRAND
ANTERIOR
RECEPTOR MUSCLE
TELSON
5 mm
UROPOD
TELSON
stretch receptor
5mm
A from Paul, 1971b
B after Paul, 1972

Figure 2: Details of elastic strand morphology. A. Phase contrast light micrograph of the longitudinally oriented refractile strands in the elastic strand. B. Scanning electron micrograph of the elastic strand and the 4 NSRS. Region of stand and NSR IV at arrow shown enlarged in C. C. the surface of the elastic strand is smooth. D-G. $CoCl_2$ outfills of individual NSRs. Note that each NSR has a distinct domain in the strand. Scale bars: A- 50 μm, B- 100μm, C- 5μm, D,E,F,G- 200μm.

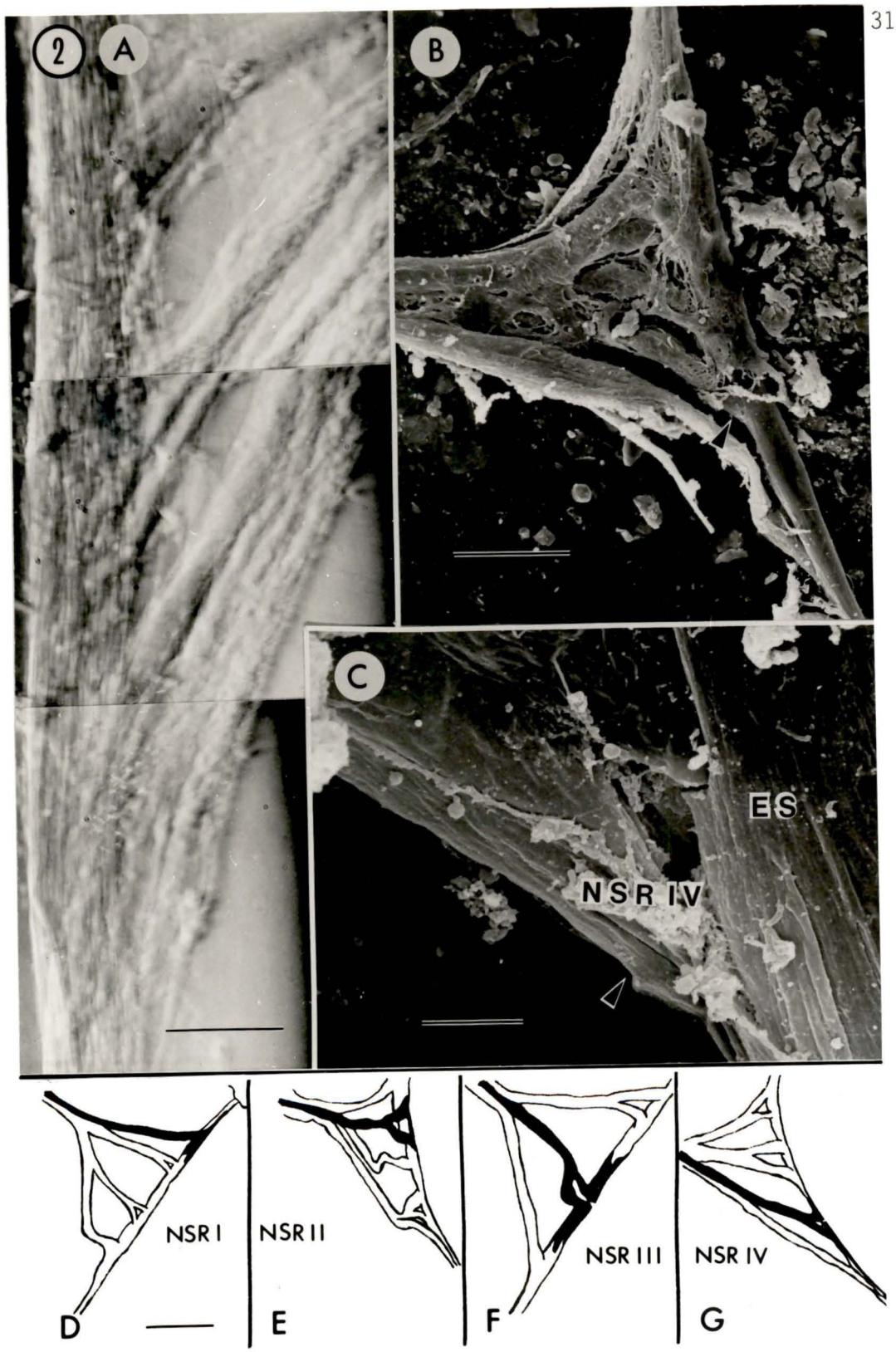
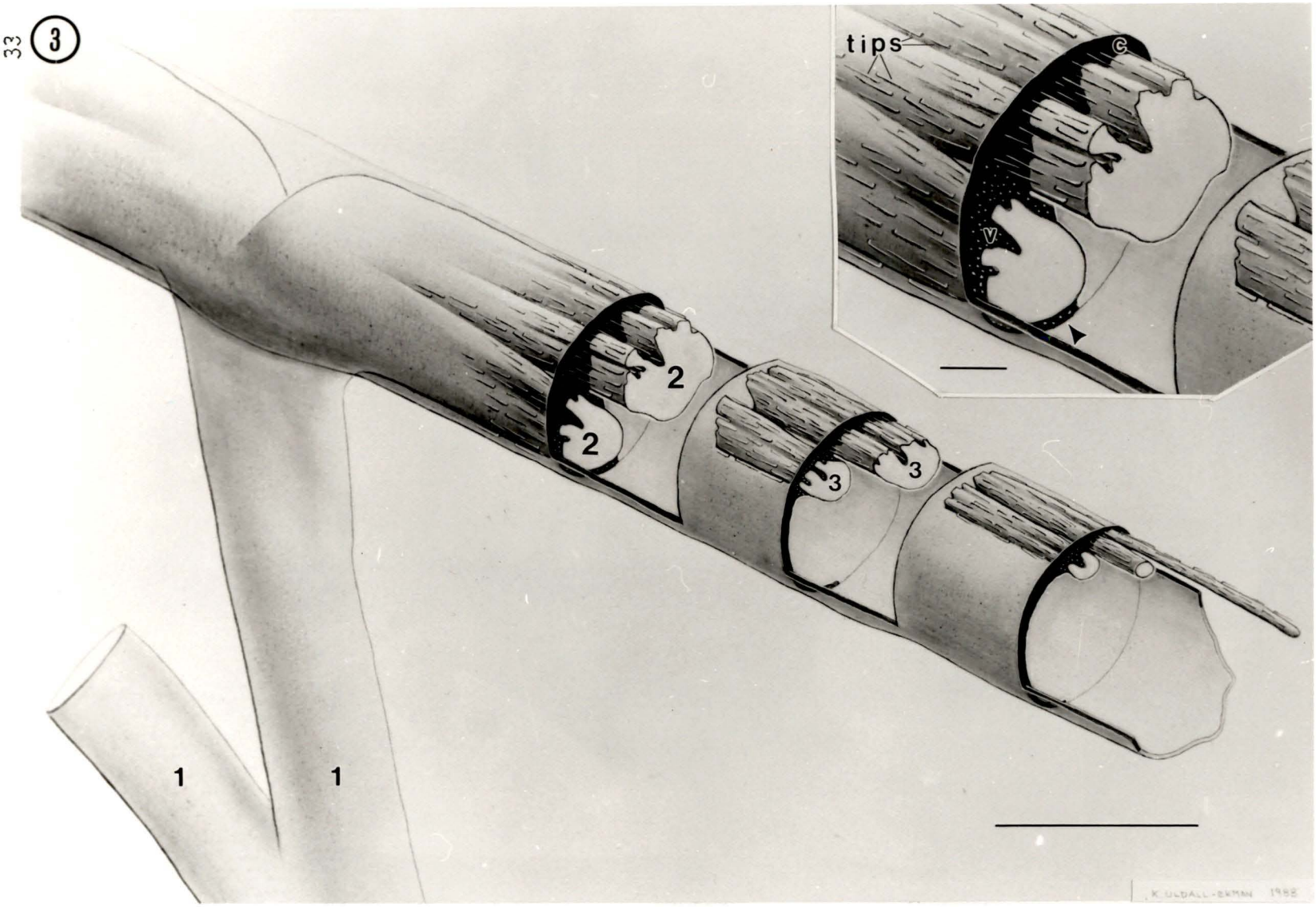

2
A
B
C
ES
NSR IV
NSR I
NSR II
NSR III
NSR IV
D
E
F
G

Figure 3: Artist's representation of dendritic branching pattern of one primary process of an NSR. The NSR dendrite divides into 2 primary processes (1) outside the strand (=Zone of Dendrite Entry (ZDE)). The capsule (c-inset) covers about two thirds of the ventrolateral aspect of the strand; primary dendritic processes enter dorsomedially. Each NSR enters the strand, turns rostrally and caudally. The cylindrical dendritic process is made horseshoe-shaped and is finally split into 2 unequal branches (secondary processes- 2) by the vacuolated string (v). Secondary processes are then divided further, by the vacuolated strings, into tertiary processes (3). Secondary, tertiary and higher-order branches form the Zone of Branching (ZB). N.B. Although only one branch is illustrated at each bifurcation (the other is cut off for clarity), all branches are divided this way and the capsule at each level is filled with dendritic processes (endings), vacuolated string ECM, and glia. Inset- dendritic tips arise from 2° to 5° processes and are embedded in the vacuolated string (v) and in the capsule - e.g., at arrow. Dendritic tips form the Zone of Dendrite Termination (ZDT). Scale bar: 50 μm, inset: 15μm.


3
tips
C
V
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1
1
K. ULDALL-ERMAN 1988

Figure 4: Comparison of the ultrastructure of an NSR 1° process (B,D,F) and a motor axon (ATU motoneuron, A,C,E). The unbranched dendrite and its primary processes outside the strand (e.g., B) resemble motoneurons(e.g., A). A,B. Glial cells (g) and collagenous ECM (e) surround the neurites. Both neurites contain neurotubules, neurofilaments and peripheral mitochondria. Fingers of glial cytoplasm extending into the dendritoplasm are common in the Zone of Dendrite Entry just outside the uropod SR strand (arrow). C,D.Parallel, longitudinal collagen fibres adjacent to the neuron. E,F. The sheath of the receptor nerve (=ATU motoneurons and NSRs) contains spiralling collagen fibres (E); the sheath of the elastic strand contains radial elastic fibres (F). F- inset: thickened neuronal membrane characteristic of NSR dendrites, arrow- electron-dense material associated with the cytoplasmic side of the dendritic membrane. Scale bars A,B- 5 μm, C,D- 0.1 μm, E,F- 0.5 μm.

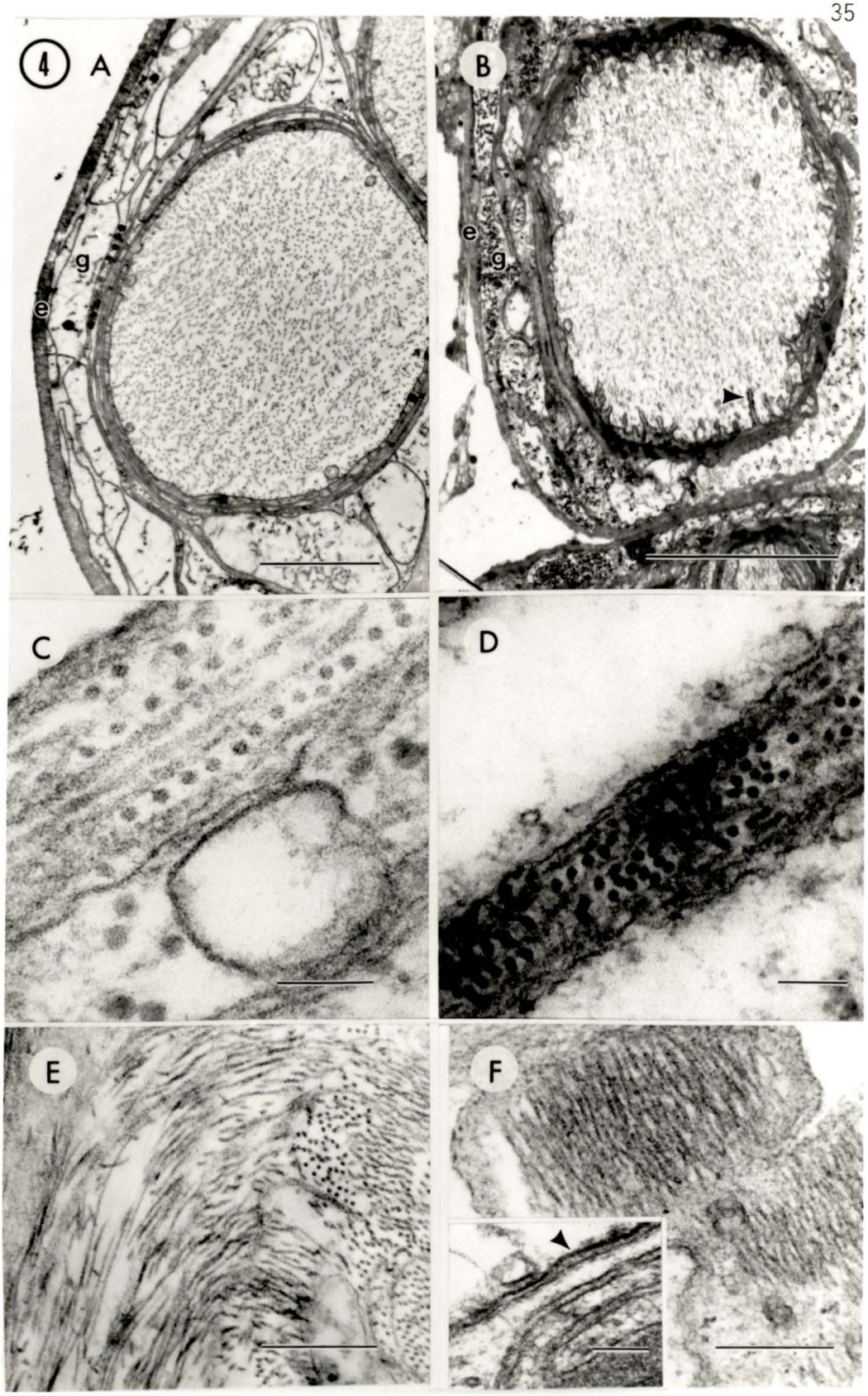
4
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Figure 5: Ultrastructure of vacuolated strings and dendritic tips. Vacuolated strings (vs) are contiguous with the capsule (c) of the elastic strand and are associated with glial cytoplasm (g). The 0.1 to 0.7 μm holes in the strings contain dendritic endings (tips) (top inset- arrows) which are in direct contact with the ECM. Larger dendritic processes are rare (arrows- bottom inset) and may contain organelles. Scale bars: 1.0 μm.

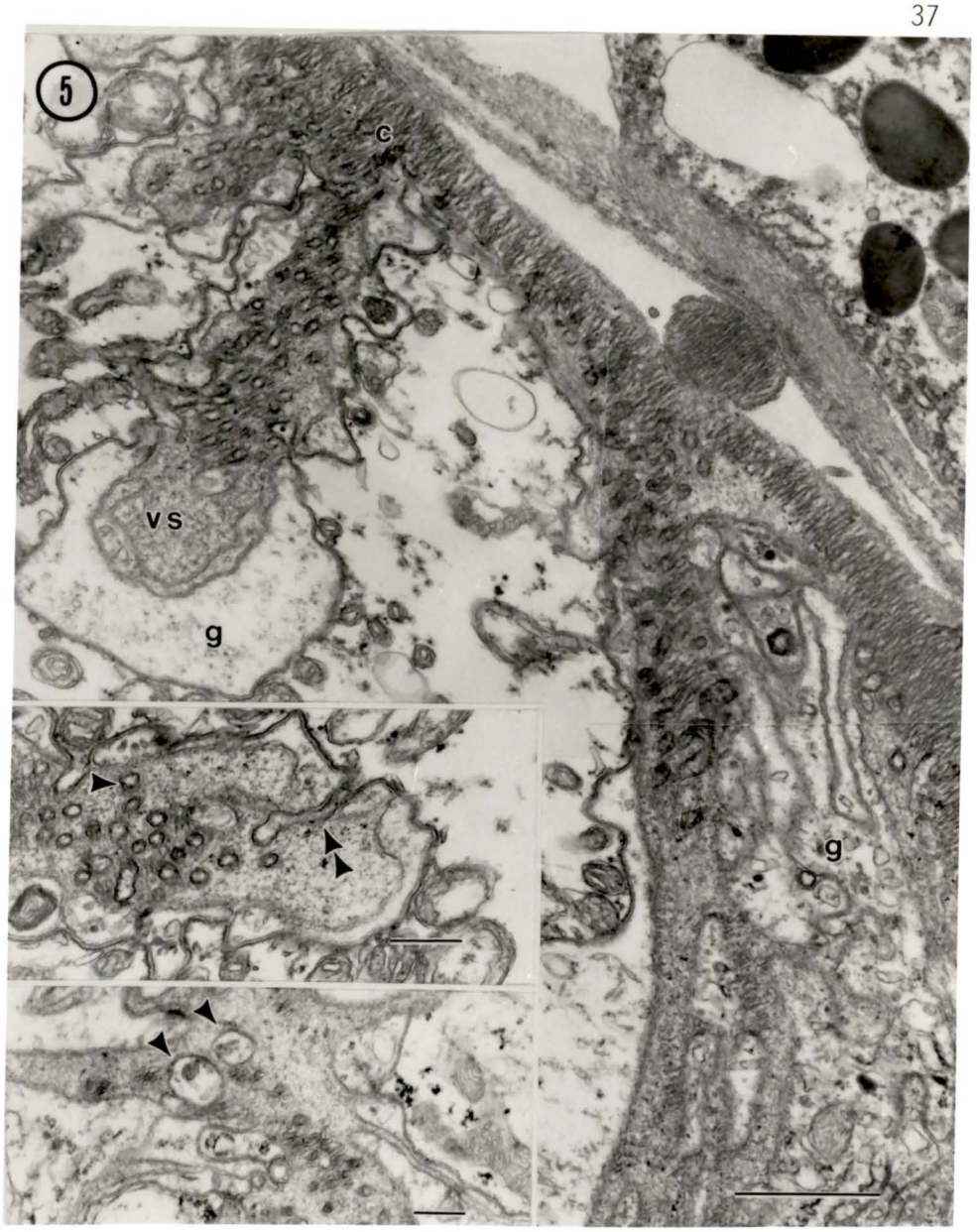
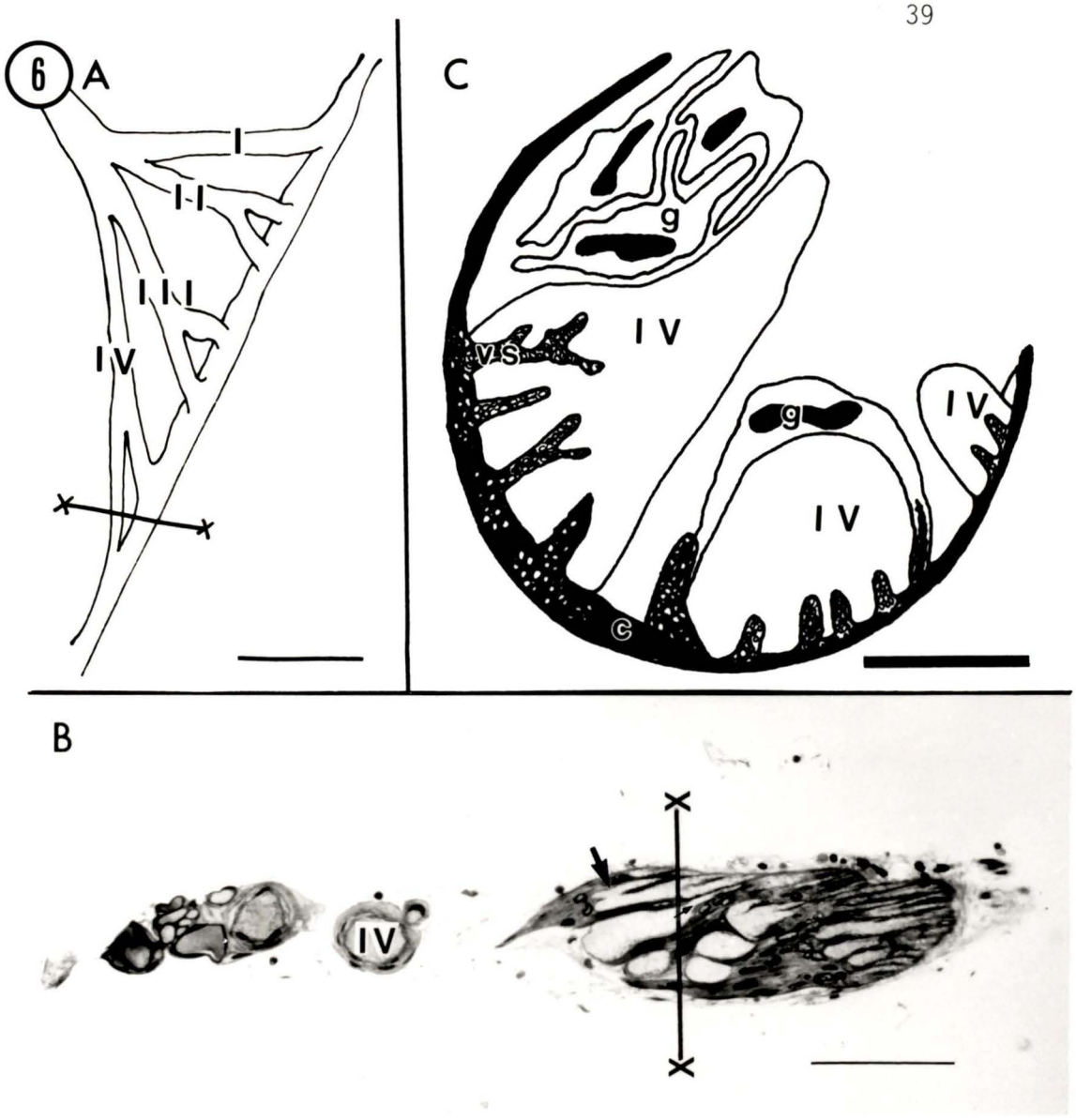

5
c
vs
g
g

Figure 6: Relationship of capsule, vacuolated strings and dendritic branches. A. Camera lucida drawing of elastic strand and the 4 NSRs (I-IV). B. Oblique section of elastic strand and NSR IV at the level indicated in A. Dendritic branches are parallel to the long axis of the strand. Note that dendritic branches narrow abruptly rather than tapering (small arrow) and that some branches extend both rostrally and caudally (large arrow). C. Line drawing traced from an electron micrograph of a transverse section of the elastic strand at the level indicated in B. (The section illustrated in B was mounted on a coverslip, reembedded and sectioned for transmission EM- see methods). All dendritic branches at this level belong to NSR IV (g- glial cell, vs- vacuolated string, c- capsule). Scale bars: A- 200 μm, B- 100 μm, C- 10 μm.


6
A
I
II
III
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C
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V.S.
g
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IV
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IV
g

Figure 7: Higher-order dendritic branches in the elastic strand. A. Camera lucida drawing of NSRs I, II, III and IV fanning out from the receptor nerve to the strand (anterior is up). B-J: Light micrographs of oblique sections of the elastic strand at the levels indicated in A showing the branching of NSR III. NSR IV remains opposed to the other neurons of the receptor nerve (e.g., B). Scale bars: A- 200 μm, B-J- 50 μm.

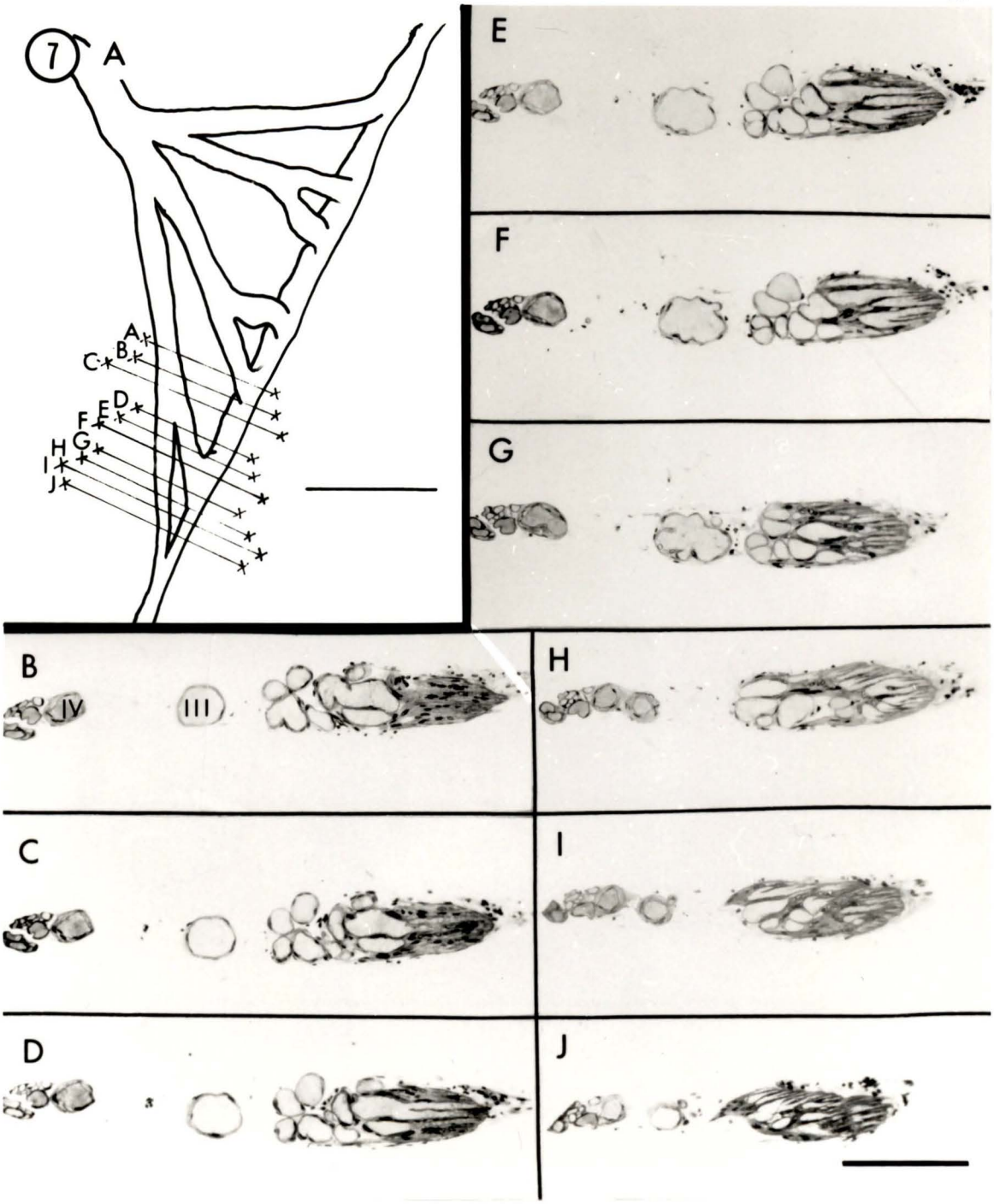
7
A
A
B
C
D
E
F
G
H
I
J
E
F
G
B
IV
III
H
C
I
D
J

Figure 8: Morphology of dendritic branching within the strand. Left: light micrographs of 3 transverse sections 2μm apart. Right: Tracings of these sections. Stippling indicates how a vacuolated string in the centre of the process in A extends further into the dendritoplasm in B and finally divides the process into two in C. Scale bars: 10 μm.

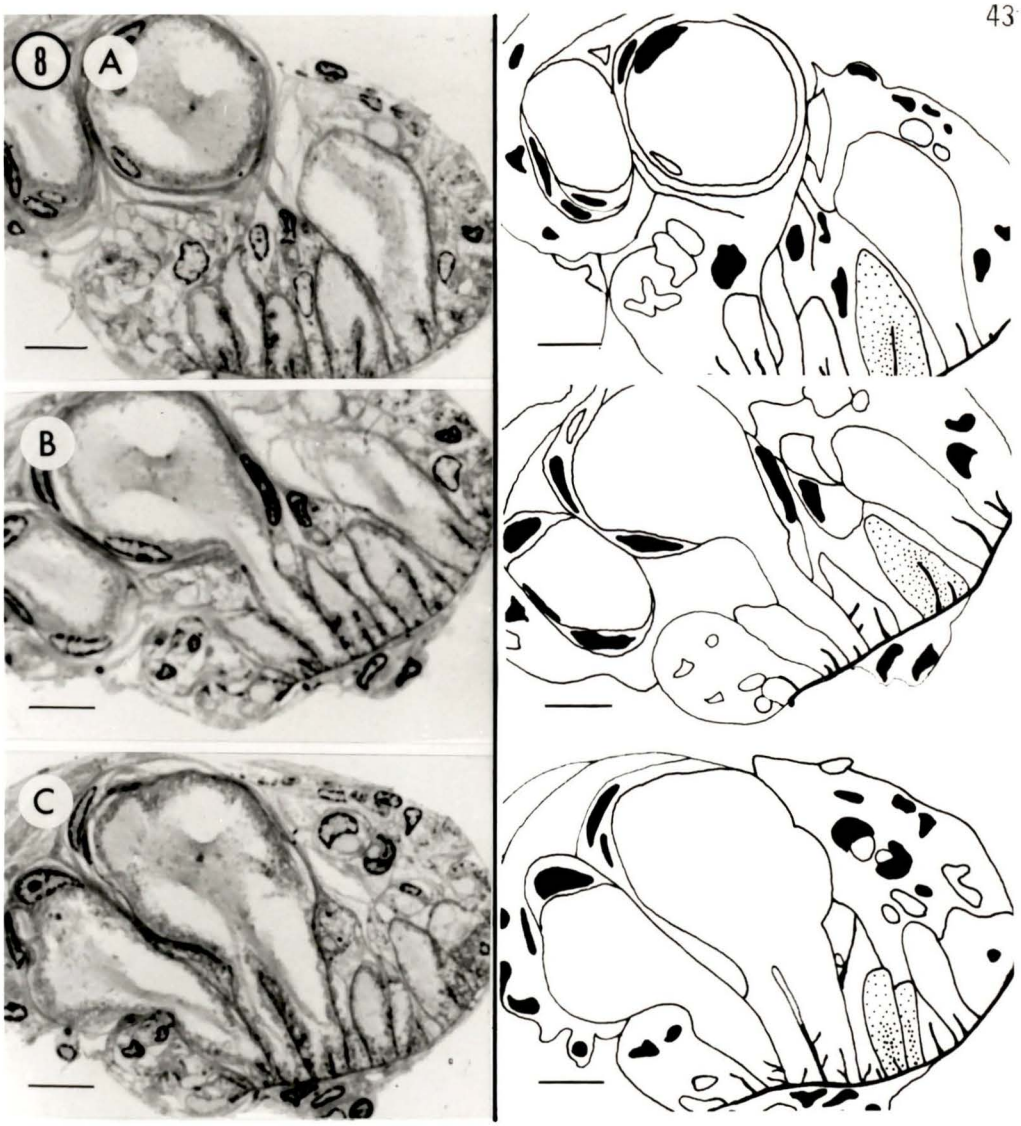
8
A
B
C

Figure 9: Morphology of dendritic stubs. A. Electron micrograph showing the relationship of a vacuolated string to the dendrite. Note the concentration of mitochondria in the dendritoplasm and the many alternating layers of glial cytoplasm (g) and ECM at the end of the string (arrow). Dendritic tips arise from the large dendritic proces via "stubs" (B,C). B,C,D- enlargements of the areas labelled "B","C":,"D" in panel A. B. A stub enters the vacuolated string at the left and gives off tips which run rostrally and caudally (up and down in this photograph). Note the neurotubule in one of the tips, arrow. C. A stub enters from the right and sends tips rostrally and caudally. Note the mitochondrion in the stub. D. oblique section of dendritic tips. E. A dendritic process (d) within the end of a vacuolated string. Scale bars: A,E- 1 μm, B-D- 0.25 μm.

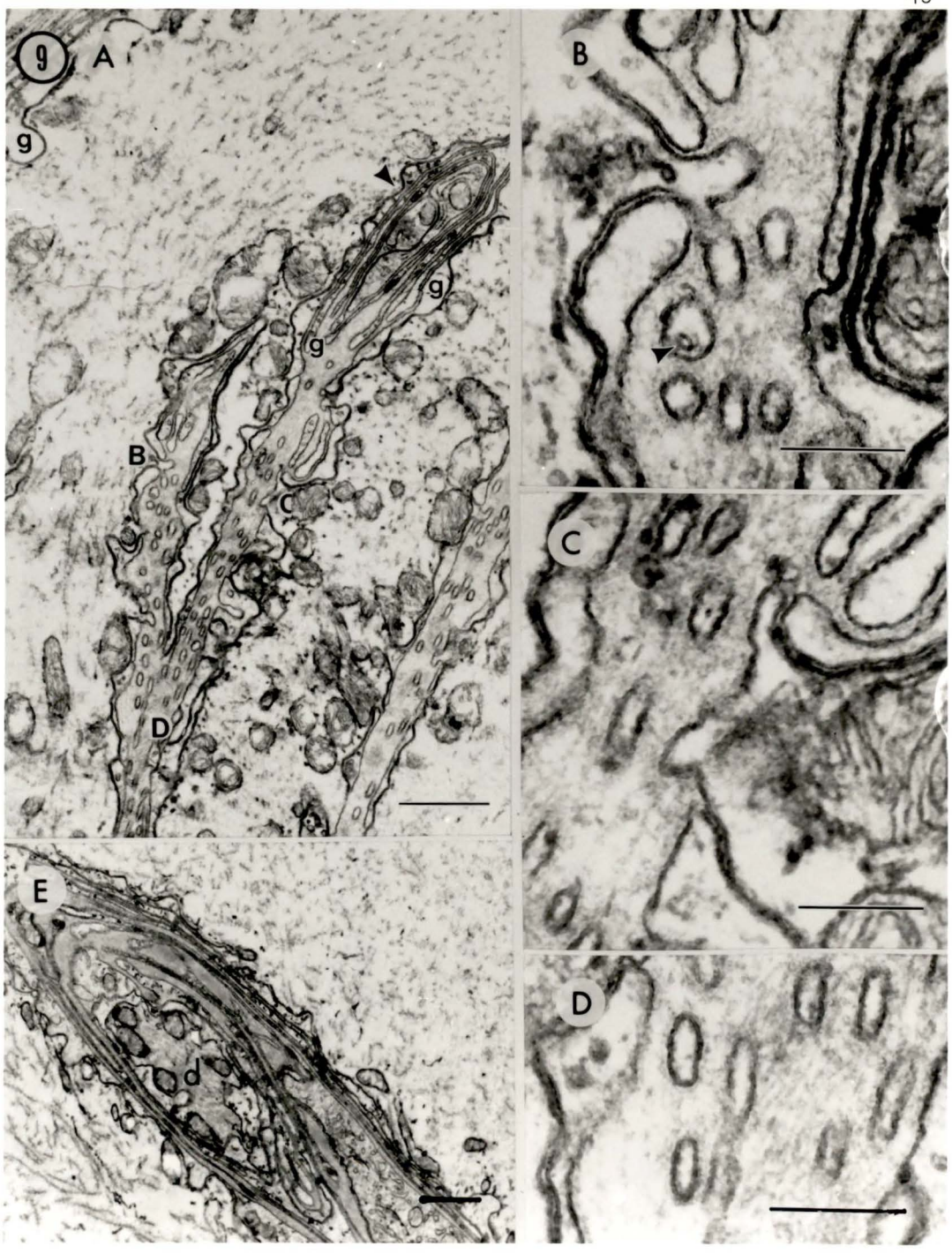
A
g
g
g
g
B
C
D
B
C
D
E
d

Figure 10: Longitudinal profiles of dendritic tips from a relaxed receptor. A,B. Electron micrographs of oblique sections of vacuolated strings with the two common configurations of dendritic tips and stubs. A. Short vacuolated string with dendritic tip arising from a tertiary process (arrow) and turning caudally (not shown). B. Dendritic tips extending both rostrally and caudally (arrows). C,D. Longitudinal profiles of dendritic tips. C. Double arrow-tip in vacuolated string (vs) extending rostrally (arrow- another tip). D. Arrow- caudal portion of a dendritic tip which extends both rostrally (not shown) and caudally in the capsule (c). Scale bars: A,B- 0.2 μm, C,D- 0.5 μm.

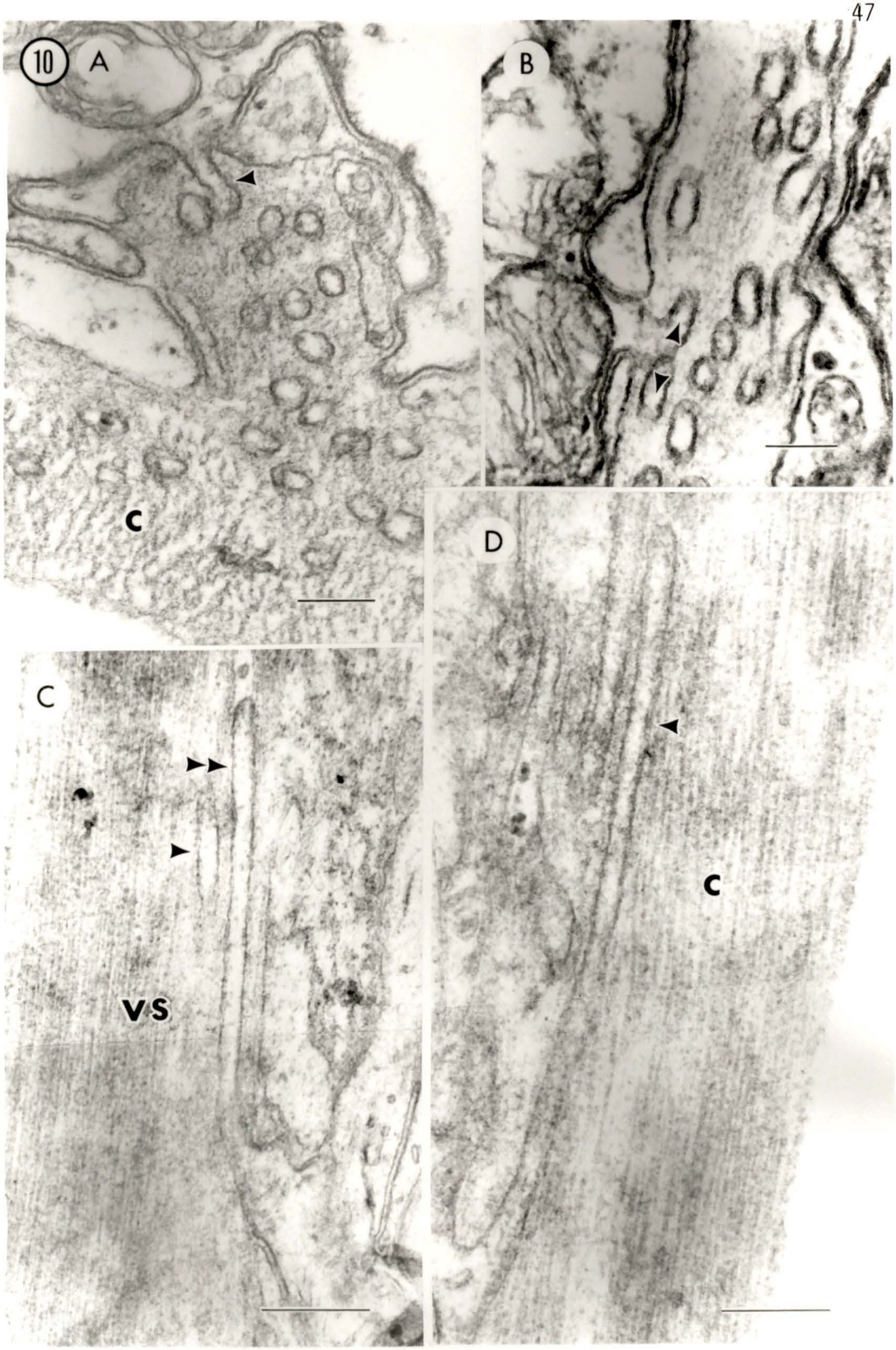
10
A
B
C
D
C
VS
C

Figure 11: Ultrastructure of the dendritoplasm. A. NSR cytoplasm in the Zone of Branching appears relatively empty and is characterized by peripheral mitochondria (m) and vesicles (e.g., arrow). B. Transverse section of the elastic strand. Neurofilaments and neurotubules run parallel to the dendritic process which enters the strand transversely from the bottom left and turns to run parallel with the long axis of the strand at the level of the arrow. C,D. Neurofilaments and neurotubules in longitudinal (C) and transverse (D) section. E. Multilamellar vesicles characteristic of processes in the Zone of Branching (e.g., arrow). F,G. Dense-core vesicles. H. Densities in dendritic tips (e.g., arrow). I. Arrow- fuzzy material lining dendritic tip. Scale bars: A- 1 μm, B- 2 μm, C,D,F,G,H,I- 0.1 μm, E- 0.2 μm.

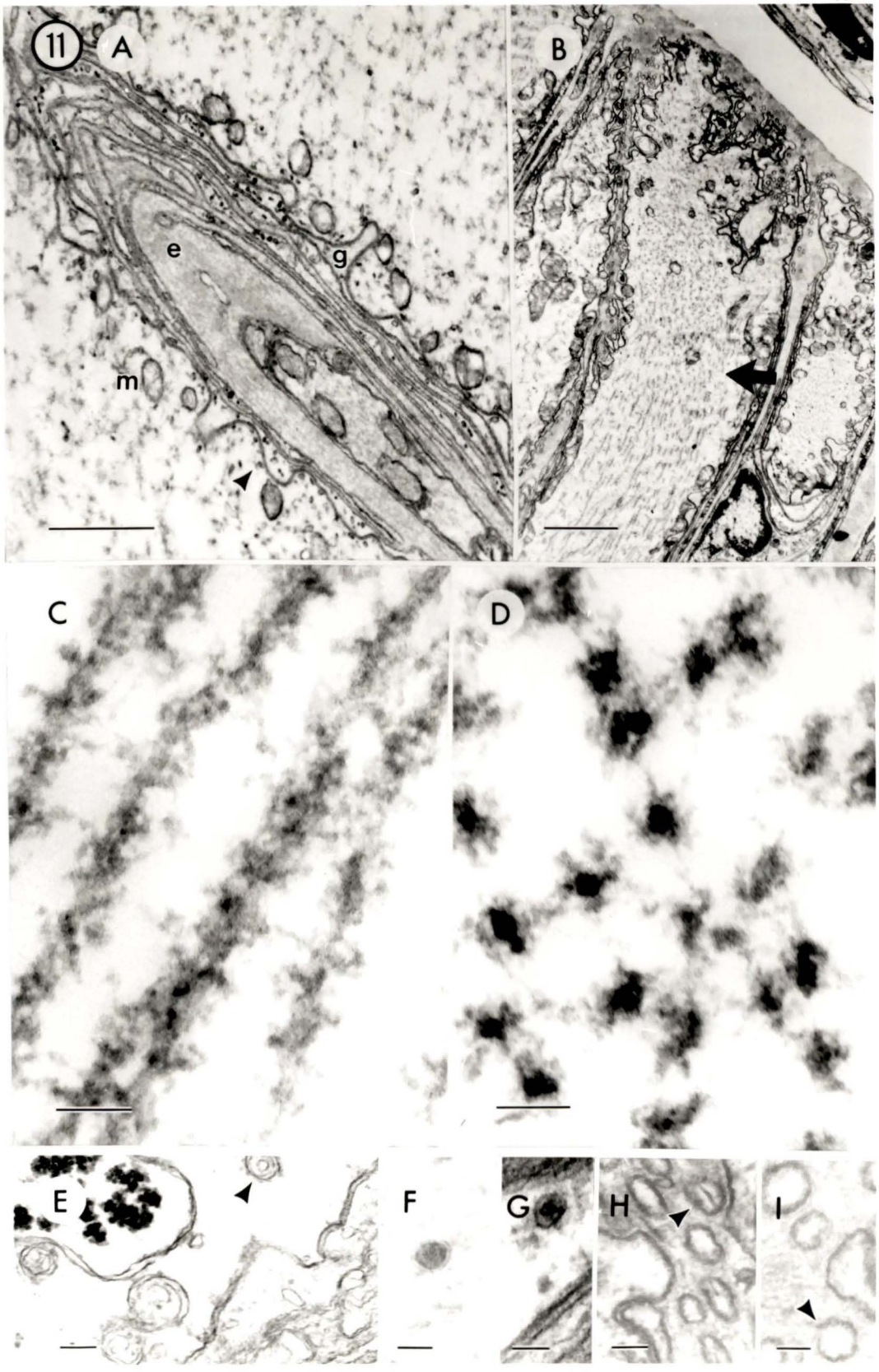
11
A
e
g
m
B
C
D
E
F
G
H
I

Figure 12: Glial structures of the Zone of Dendrite Entry. A. Large dendritic processes entering the strand are surrounded by layers of highly folded glial cytoplasm alternating with ECM. Arrow: glial cell cytoplasm folds back on itself to enclose ECM (Skinner, 1985). B. Arrow- glial microtubules are parallel to the long axis of the primary dendritic process in the Zone of Dendrite Entry. Note ECM in regions where the intercellular space between glial cells is expanded. V- clear vesicle in the glioplasm. C. Edge of primary process. Glial projection into the dendrite with a dense core (probably of ECM). D. Enlargement of the glial process in C (transverse section). Arrow indicates a membrane expansion. E. Longitudinal section of dense-cored glial finger in primary dendritic process. F. Glial fingers extending into the dendritoplasm. G. Glial nuclei are crescent-shaped in the region of the strand where NSR dendrites enter. Scale bars: A, E- 0.2 μm, B- 0.1 μm, C- 2 μm, D- 0.5 μm, F- 3.3 μm, G- 2 μm.

1
2
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12

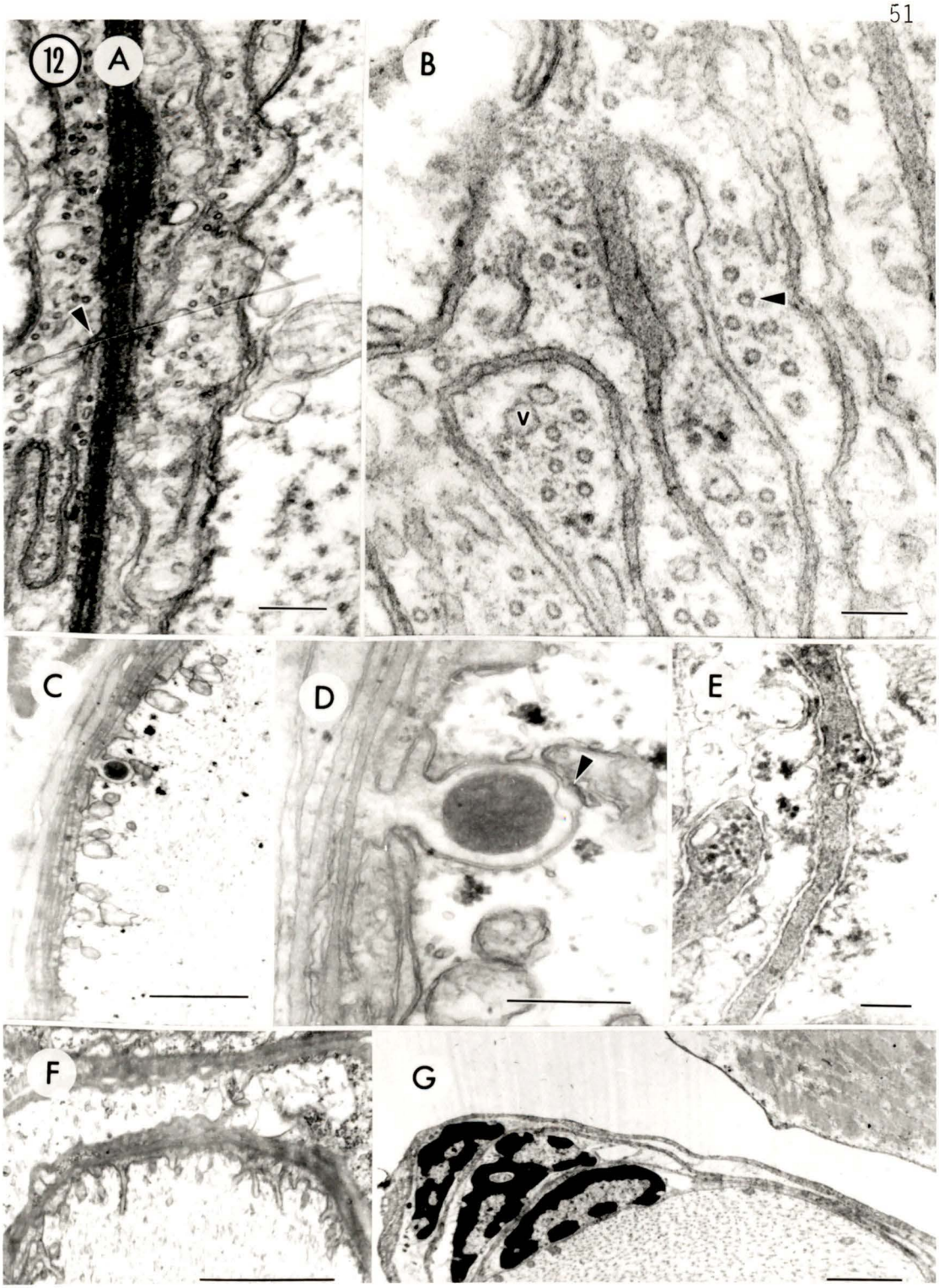

12
A
B
v
C
D
E
F
G

Figure 13: Glial cells within the elastic strand Left: Electron micrographs. Right: Shapes of glial cells whose nuclei are in the plane of section are stippled. A. In the region of entry of a primary branch of NSR II, glia wraps over the dorsal apexes of secondary, tertiary and quaternary dendritic branches and is associated with the ECM of the vacuolated strings. Many glial nuclei are located in the troughs between higher-order dendritic branches. B. The glial cell associated with the vacuolated string which divided a secondary process into two tertiary processes (arrow). C. A more caudal section from the same receptor where there is a larger number of higher-order dendritic branches, especially in the lateral portion of the strand (to the right). Glial cells occupy proportionally more of the strand in this region. D. Interdigitation of a glial cell in the lateral strand with other glial processes and with ECM. The ECM may have been produced by this cell. Scale bars: A,C- 5 μm, B- 3 μm, D. 1 μm.

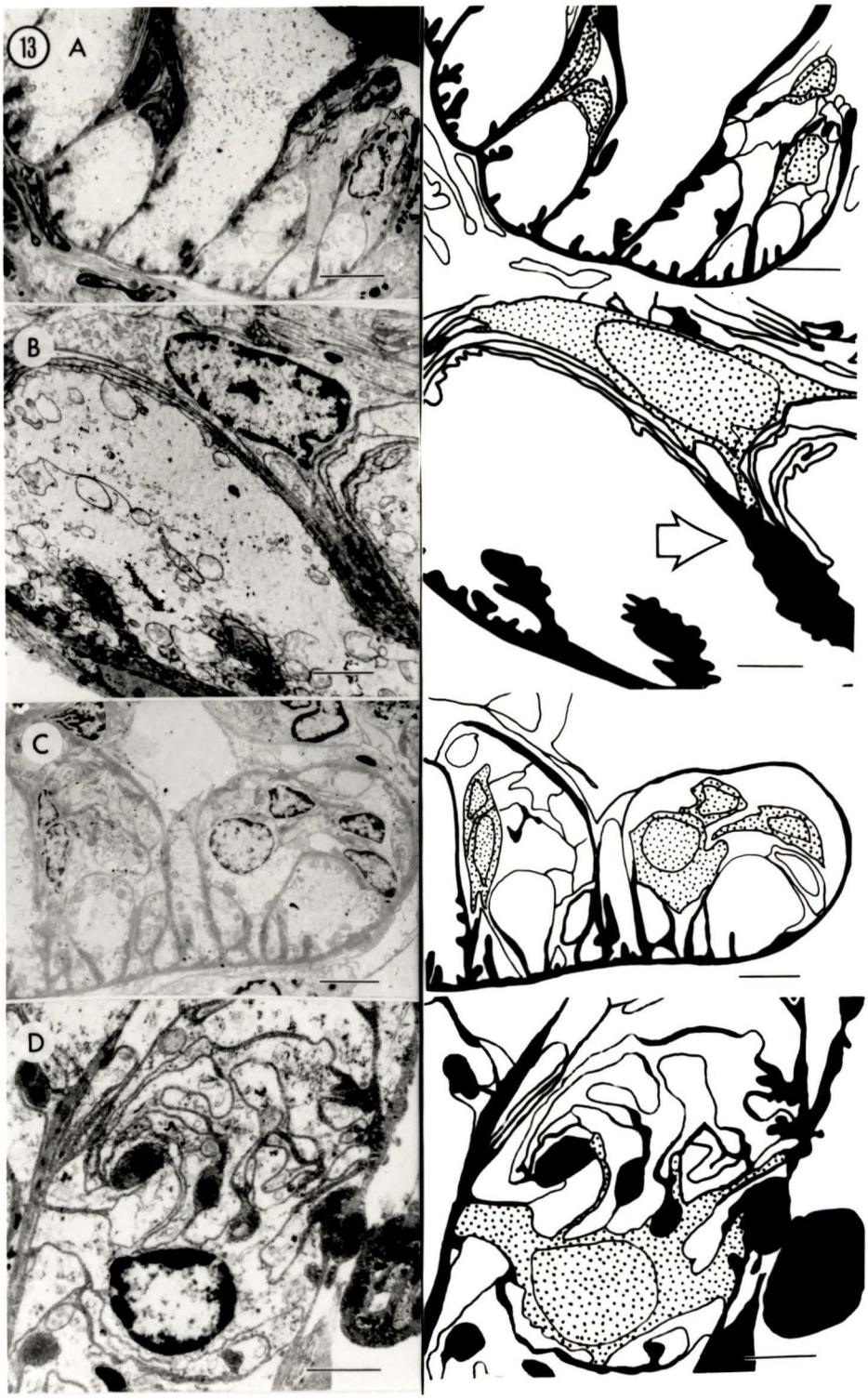

13
A
B
C
D

Figure 14: Association of glial cells with dendrites and vacuolated strings. Glial cytoplasm forms complex sheets and folds in the vacuolated string ECM. A. Along with microtubules, certain glial cells of some crabs contain electron-dense pigment granules (p) which are more abundant in cell processes than near the glial nuclei. B. Pigmented glial "fingers" are found in the dendritoplasm of higher-order branches. C. Even very narrow sheets of glial cytoplasm may contain pigment. D. Processes of the Zone of Branching often have complex glial infoldings (gi; g- glioplasm, e- ECM). E. Glial infoldings and a multilamellar vesicle (arrow). F. Complex interdigitation of glial processes (e.g., g) and vacuolated string ECM (arrow- tip entering vacuolated string). Glial nuclei (gn) have peripheral, clumped chromatin. G. Unusual association of one glial cell with 3 vacuolated strings (1,2,3). Scale bars: A- 2 μm, B,C- 0.5 μm, D,E- 0.2 μm, F- 0.25 μm, G- 2 μm.

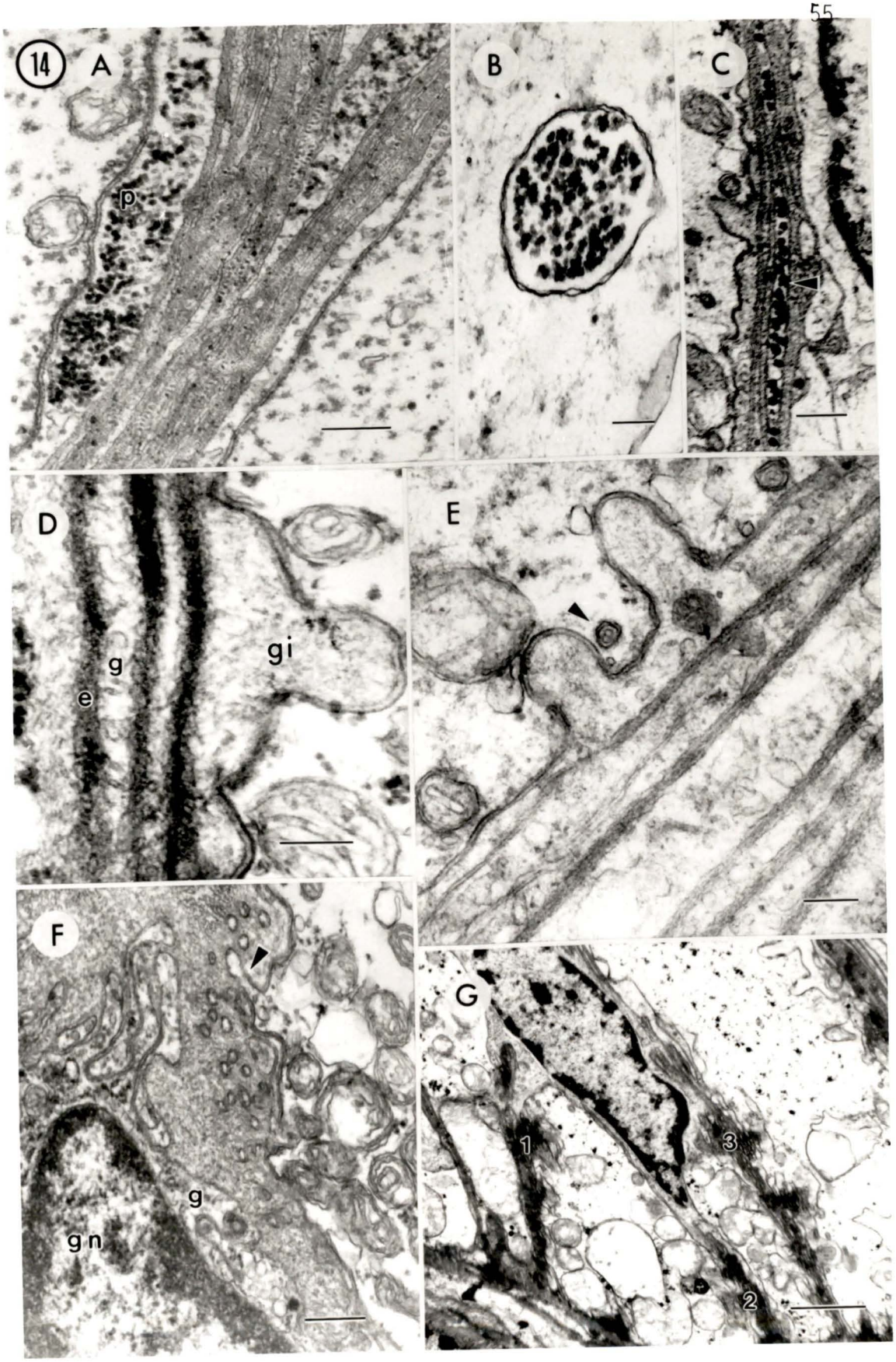

14
A
p
B
C
D
g
e
gi
E
F
g
gn
G
1
2
3

Figure 15: Ultrastructure of the glioplasm: organelles. A,B. Abundant organelles in the perinuclear cytoplasm of glial cells near vacuolated strings (A) and in the lateral strand (B). C. Rough endoplasmic reticulum is abundant. D. Mitochondria and smooth endoplasmic reticulum cisternae. E. Golgi stacks in the perinuclear region of a glial cell. F. Mitochondria and smooth endoplasmic reticulum. Scale bars: A- 3 μm, B- 1 μm, C-F- 0.25 μm.

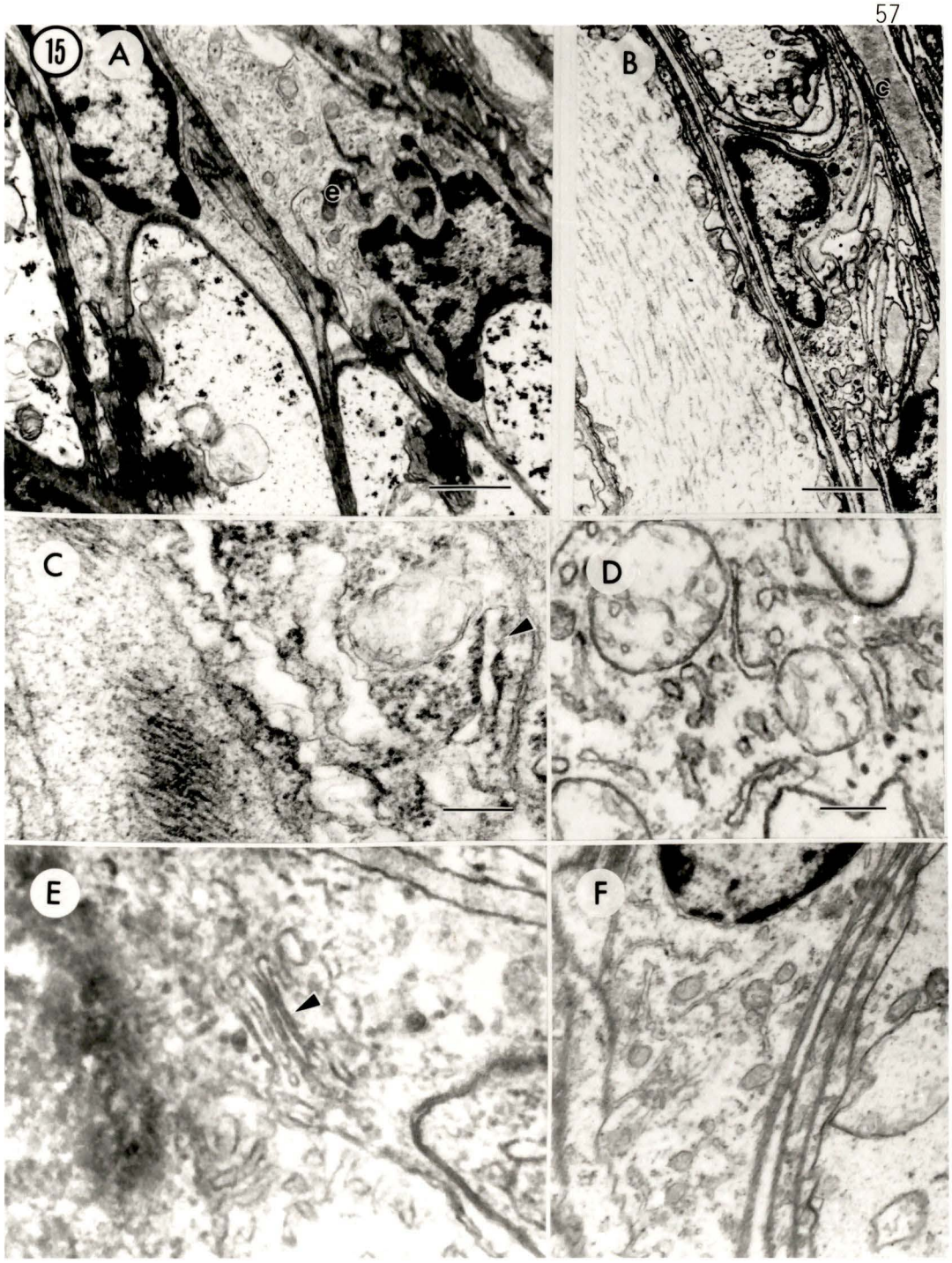

15
A
e
B
c
C
D
E
F

Figure 16: Ultrastructure of the glioplasm. A. Glial cell in the lateral strand. B. Enlargement of A: Rough endoplasmic reticulum, mitochondria and ECM within the glioplasm (e). C. Interdigitation of glial processes and ECM (e). Arrow: ECM extending into glioplasm. D. Glial nuclei have a single nucleolus (nu), peripheral chromatin and lobes created by inward projections of cytoplasm (arrows). E. Arrow: apparent cytoplasmic continuity between adjacent glial processes. Scale bars: A- 2.5 μm, B,C- 1 μm, D- 0.5 μm, E- 0.1μm.

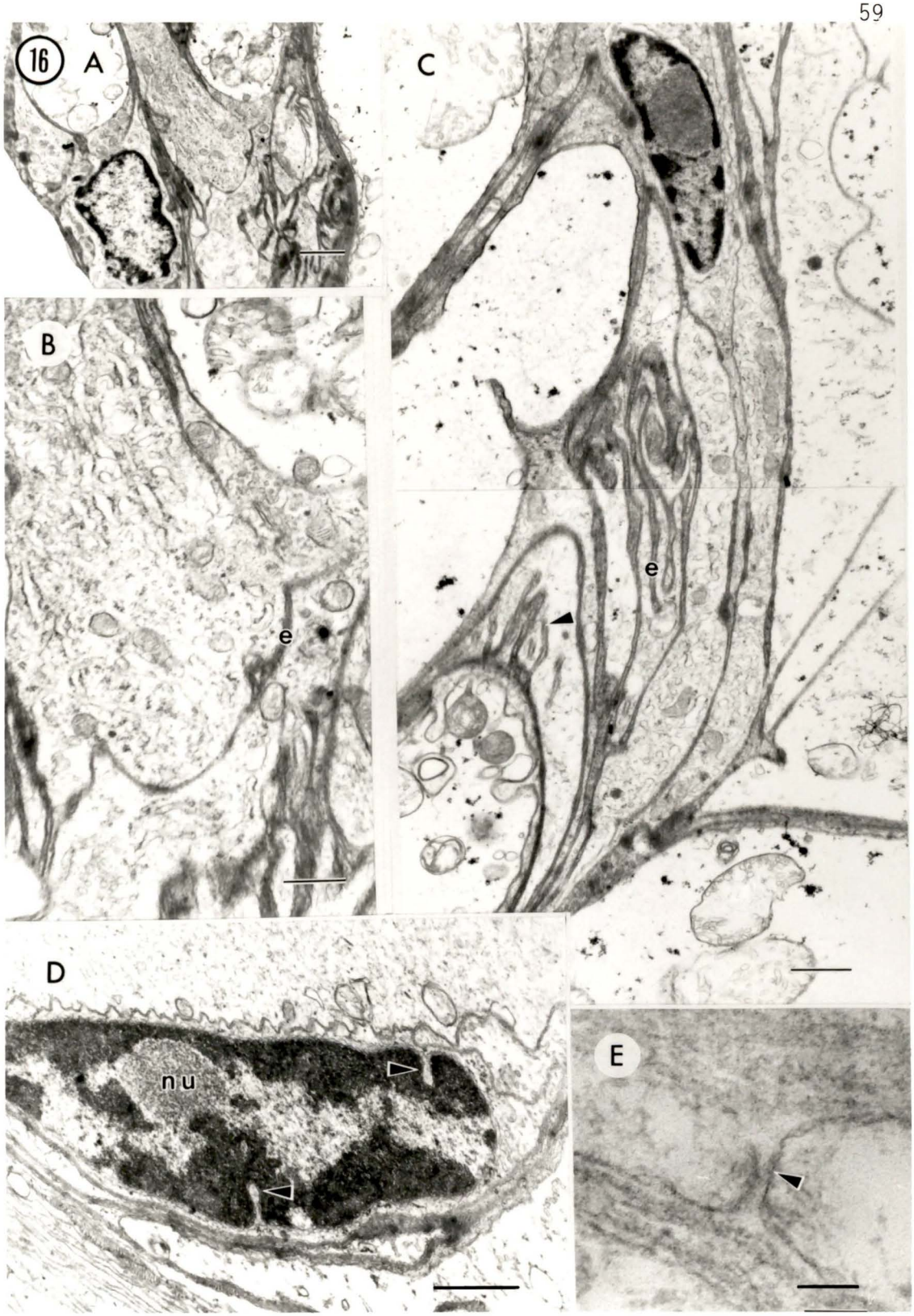

16
A
B
e
C
e
D
nu
E

Figure 17: Results of histological staining of paraffin sections of the uropod SR. A. Masson's trichrome stain. B. Potassium permanganate-Spirit Blue stain. BV- blood vessel, c- receptor capsule, N- ATU nerve, RM- receptor muscle, RN- receptor nerve, s- blood vessel sheath, ES- elastic strand, vs- vacuolated string. Scale bars: both parts, 20 μm.

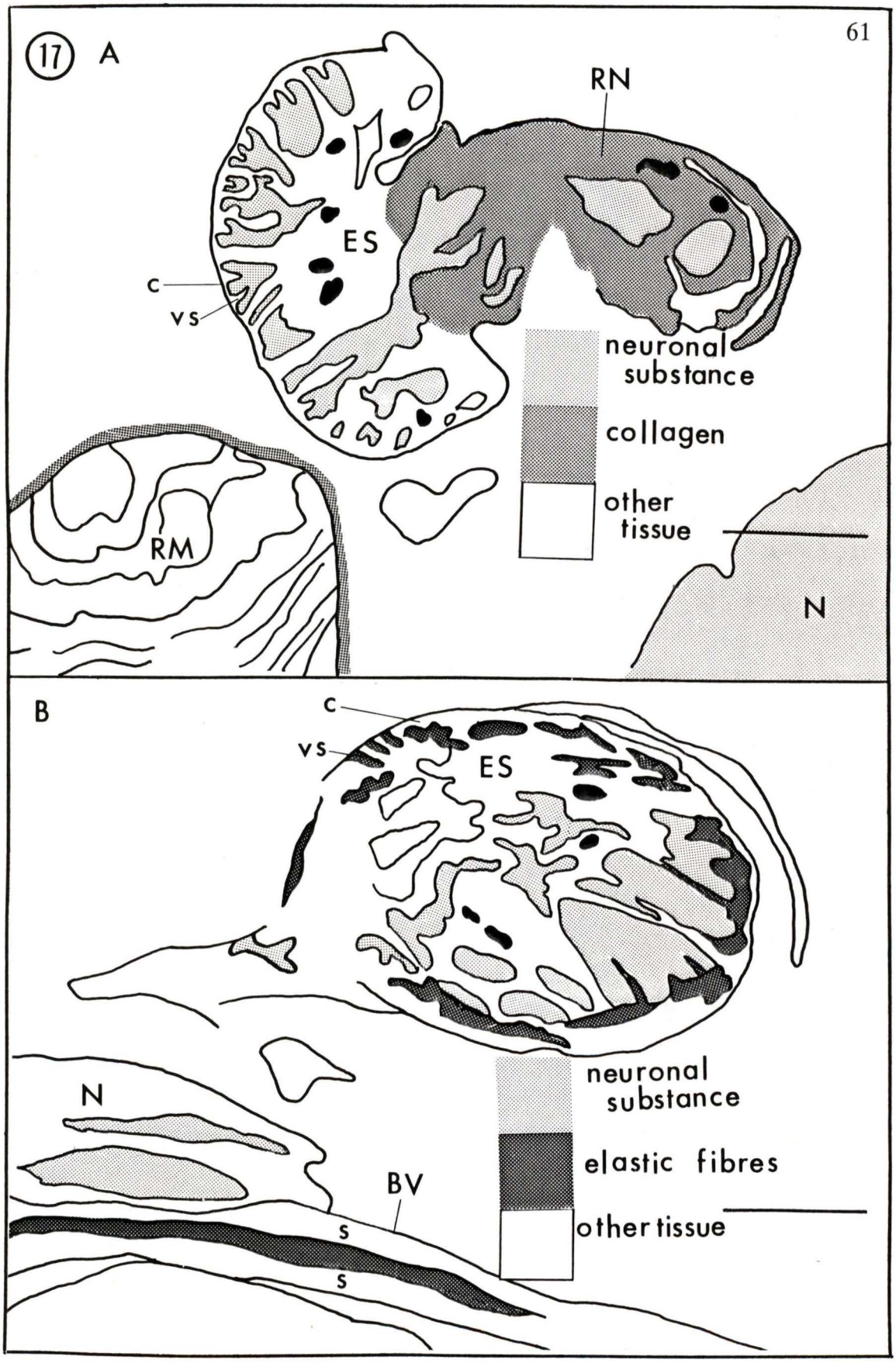

17
A
RN
ES
C
VS
neuronal substance
collagen
other tissue
RM
N
B
C
VS
ES
neuronal substance
N
elastic fibres
BV
other tissue
S
S

Figure 18: Comparison of elastic fibres in the elastic strand (B,D,F) with collagen fibres in the sheath around a primary process of an NSR (A,C,E). A. Collagen fibres spiral around the neurons. B. Elastic fibres are arranged parallel to each other in the strand. C,D. Elastic fibres (D) are narrower than collagen fibres (C). E. Collagen fibres have 20-23 nm banding, (resembling collagen in insect nervous systems; Ashhurst, 1968) circular cross-sectional profiles (inset) and regular spacing. F. In cross-section uropod SR fibres appear "fuzzy" and are irregularly arranged. Scale bars: A,B- 0.25 μm, C-F- 0.1 μm, E-inset- 0.05 μm.

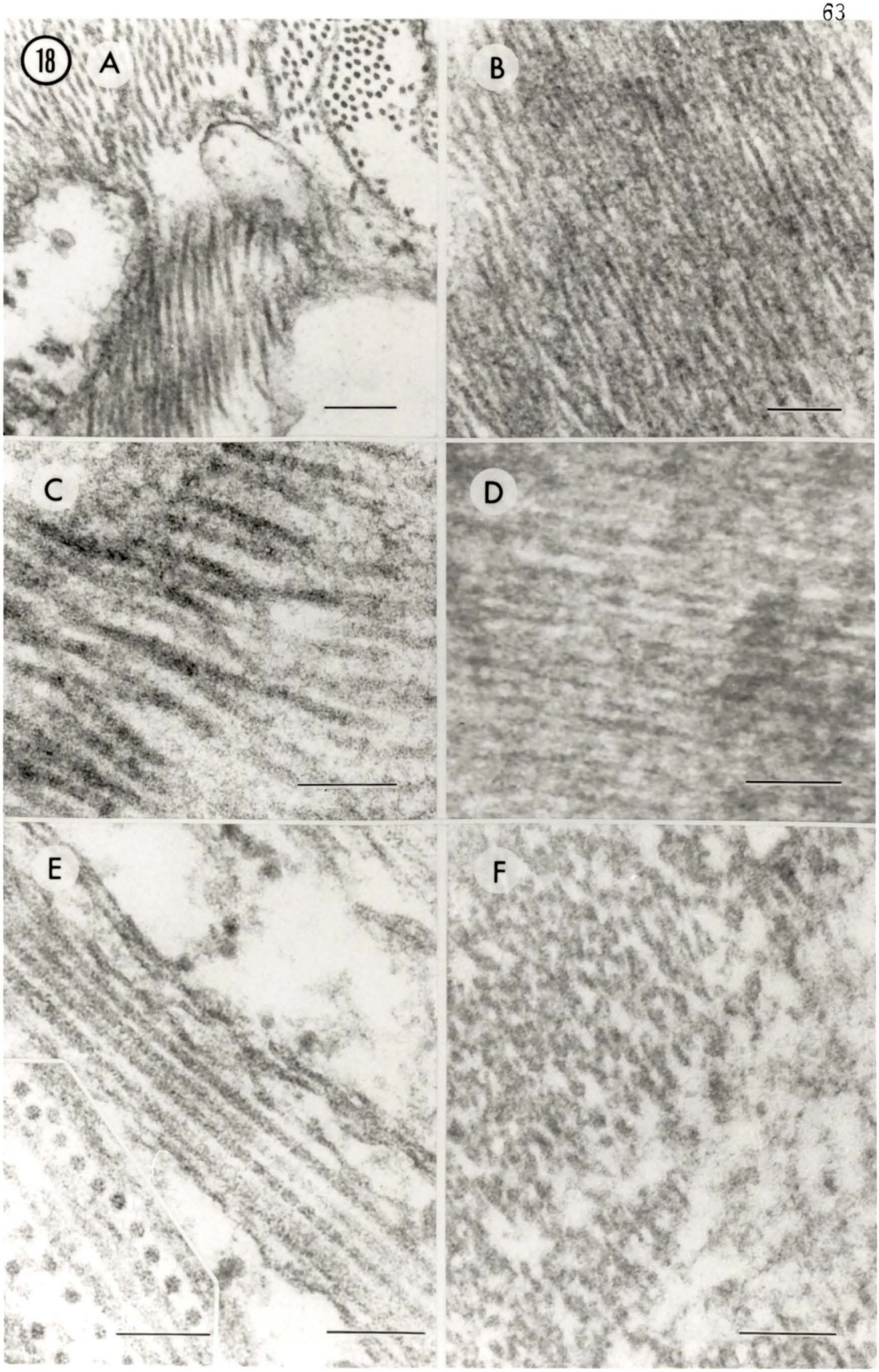

18
A
B
C
D
E
F

Figure 19: Branching of individual NSRs. Figs. 19-23 are light micrographs of sections taken from the levels indicated in the camera lucida drawing at the right. On the left side of each of these figures is a series of sections taken from a single receptor; on the right side are equivalent sections from other receptors to show the characteristic arrangements of the larger branches. Sections are oriented ventral-side up, lateral is to the left. A,B. The coxal portion of the strand resembles an elastic tendon. C,D,E. Characteristic branching of NSR I. Scale bar for Figs. 19-23- 10 μm.

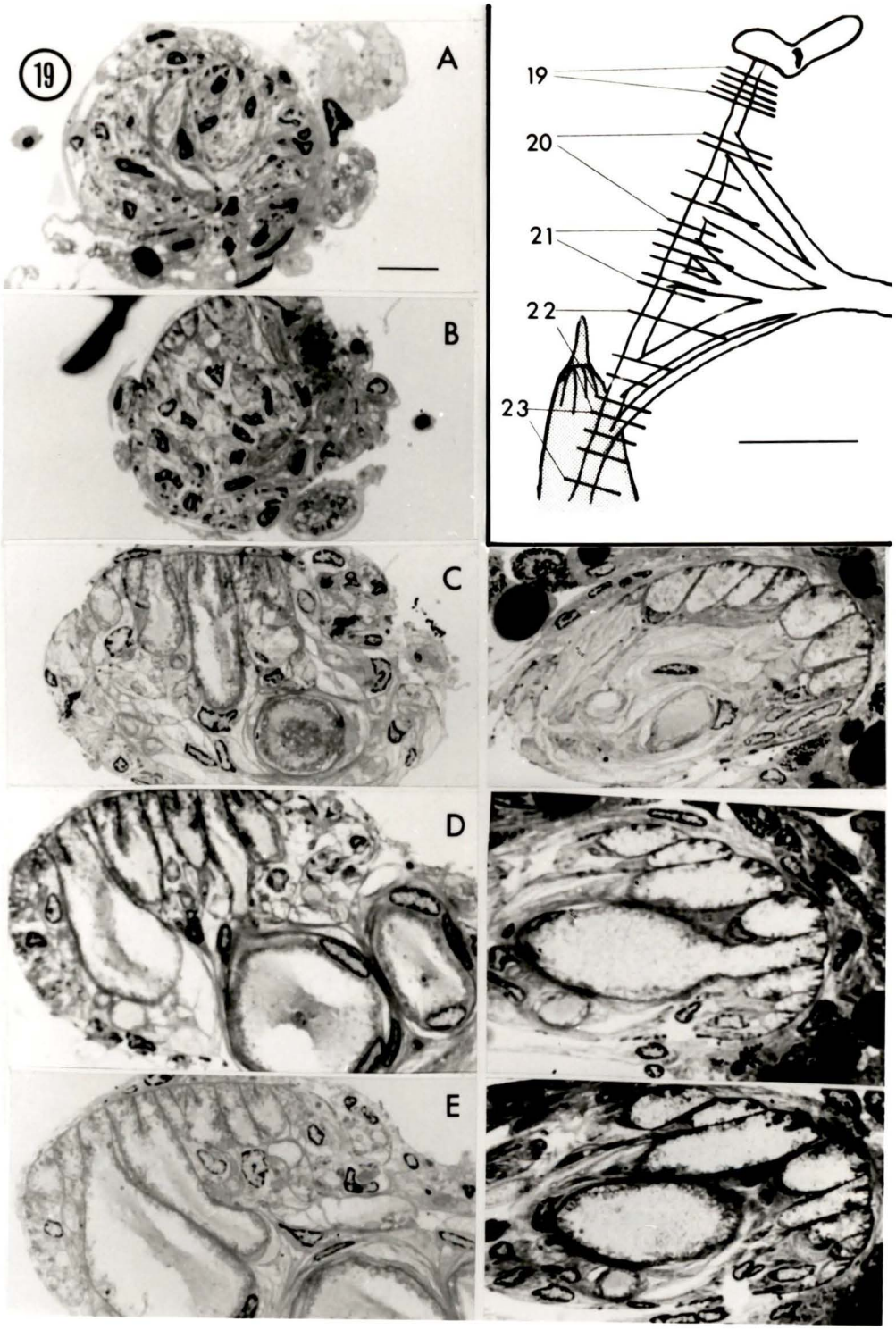

19
A
B
C
D
E
19
20
21
22
23

Figure 20: Branching of individual NSRs. A,B. Large dendritic processes in the region of entry of NSR I. C. Region of the strand between NSRs I and II. D. NSR II entering the strand. E. Characteristic lateral branch of NSR II.

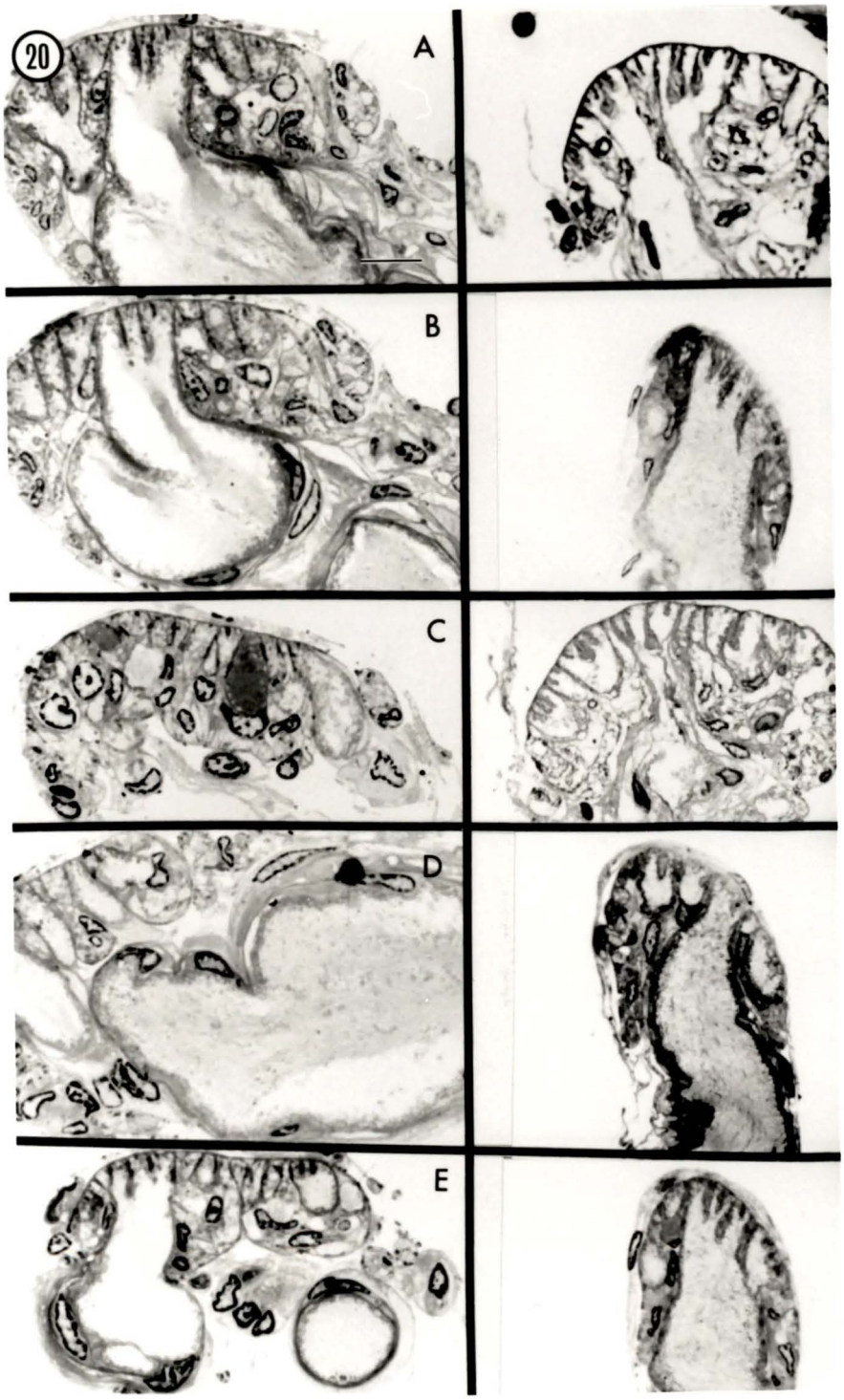

20
A
B
C
D
E

Figure 21: Branching of individual NSRs. A. Rostral branches of NSR III. B. Primary process of NSR III enters the strand. C. Two large processes of NSR III which run caudally. D. Part of the lateral, caudally-directed process and the medial part of the strand containing small branches of NSR III. E. NSR III processes in the region of the strand between NSRs III and IV.

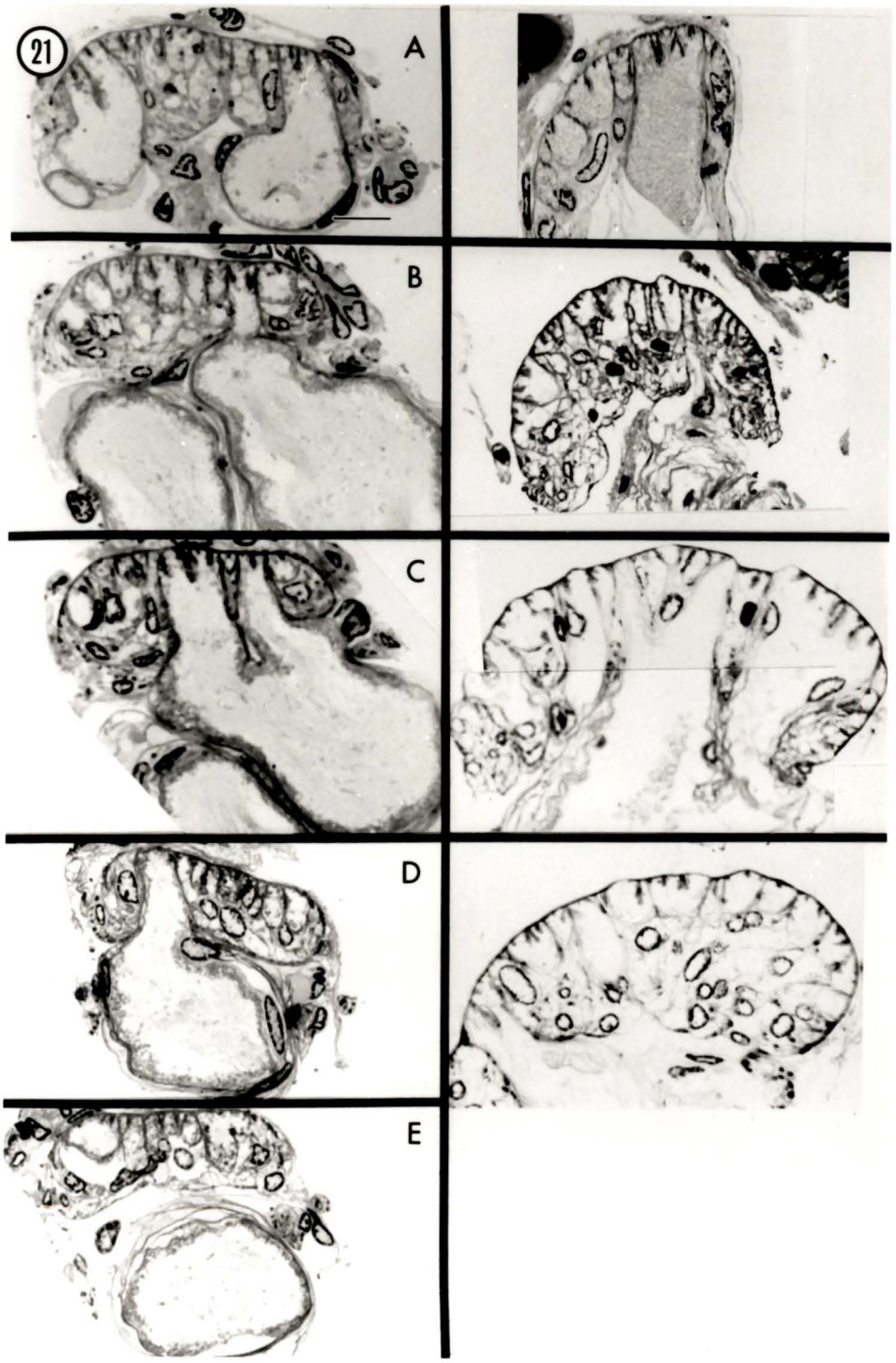

21
A
B
C
D
E

Figure 22: Branching of individual NSRs. A. NSR IV entering the strand. B. Characteristic medial branch of NSR IV. C,D. Branches of NSR IV within the strand accompanied by the other neurons of the receptor nerve outside the strand.

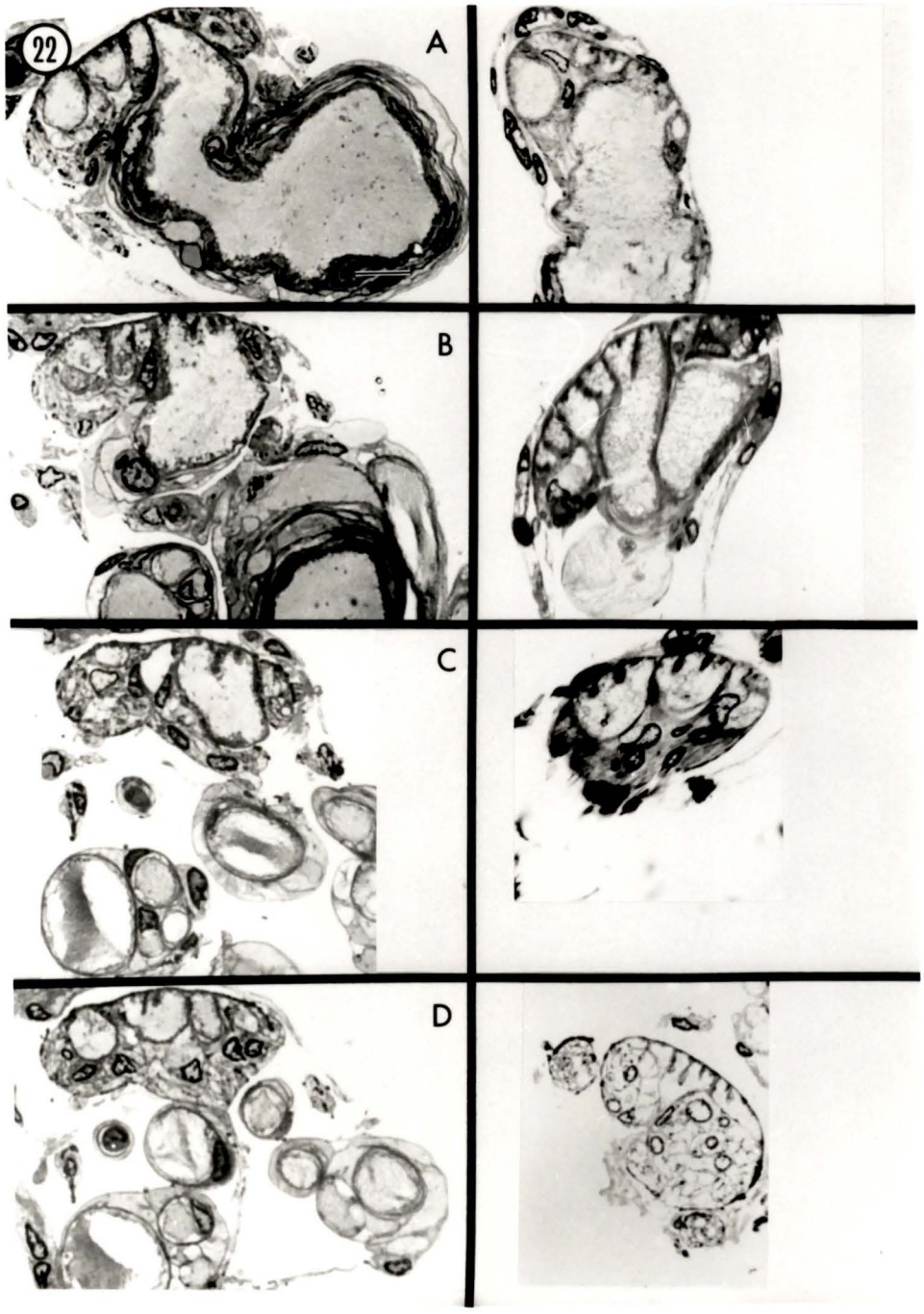

22
A
B
C
D

Figure 23: A. Caudalmost branches of NSR IV. B,C. Elastic strand connective tissues merges with the sheath of the telson nerve.

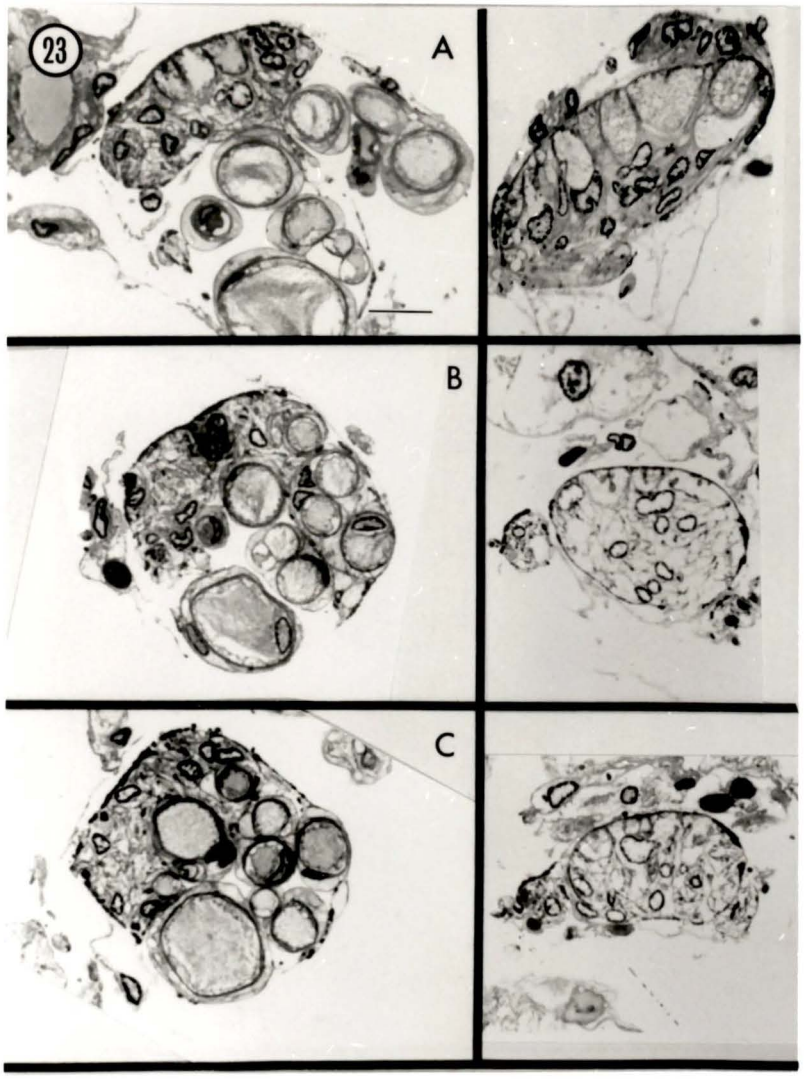

23
A
B
C

Figure 24: Stretch-induced changes in the shape of the elastic strand. A,B. Camera lucida drawings of methylene blue stained uropod SR preparations when stretched (B) and relaxed (A). Light micrographs of stretched (D) and relaxed (C) receptors from the same crab at the levels indicated in A and B show that vacuolated strings are farther apart in a stretched than a relaxed receptor. The overall cross-sectional shape of the strand becomes broader and flatter with stretch. Scale bars: A,B- 100 μm, C,D- 20 μm.

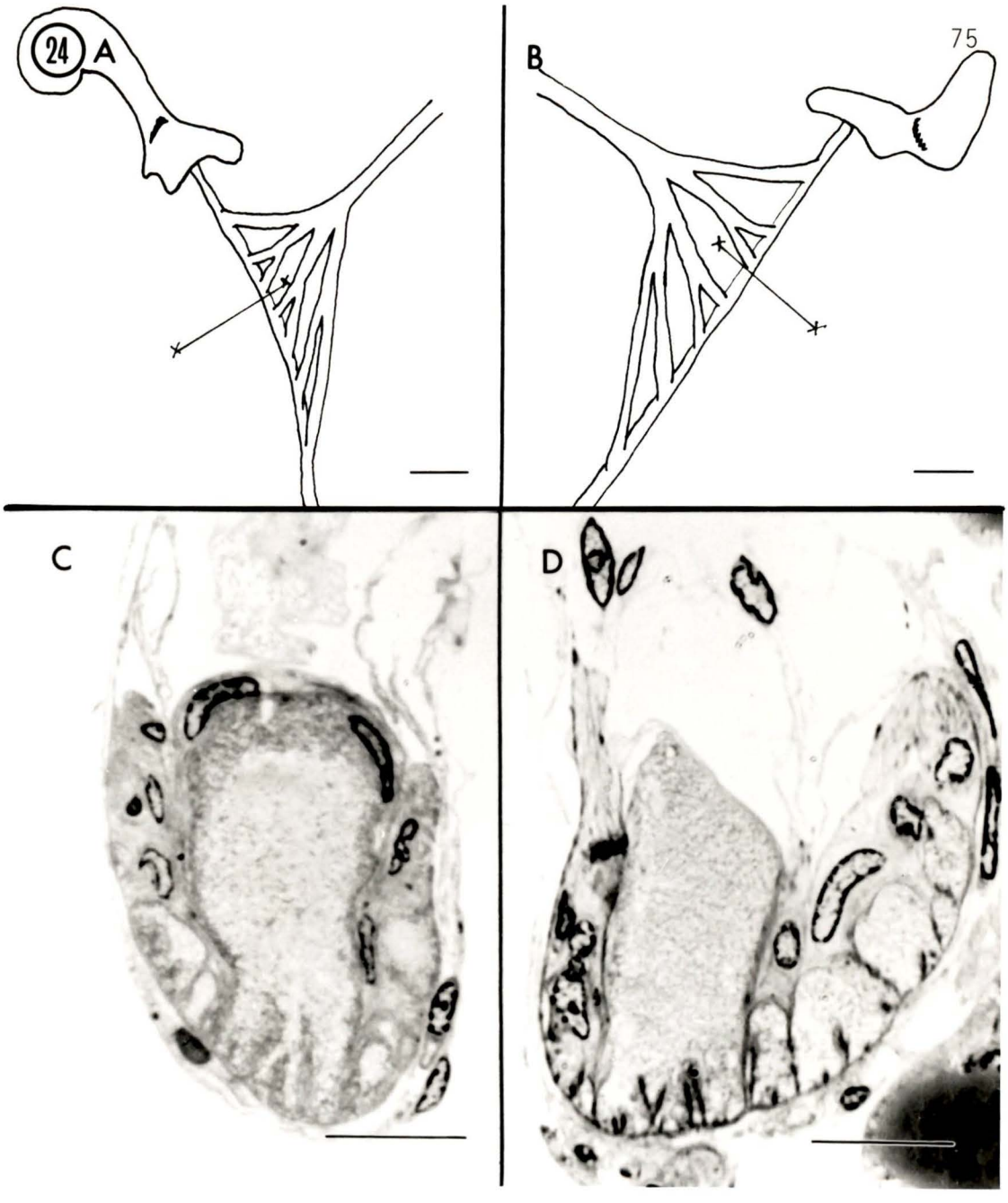

24
A
B
C
D

Figure 25: Stretch-induced changes in vacuolated strings and dendritic tips. Electron micrographs of the region between NSRs III and IV in crab A (Tables 3 and 4). Vacuolated strings are farther apart in stretched (B) than in relaxed (A) receptors. The cross-sectional area of dendritic tips is larger in stretched (D) than in relaxed (C) receptors although there are fewer tip profiles in the stretched receptor (i.e., their density decreases). Scale bars: A,B- 2 μm, C,D- 0.2 μm.

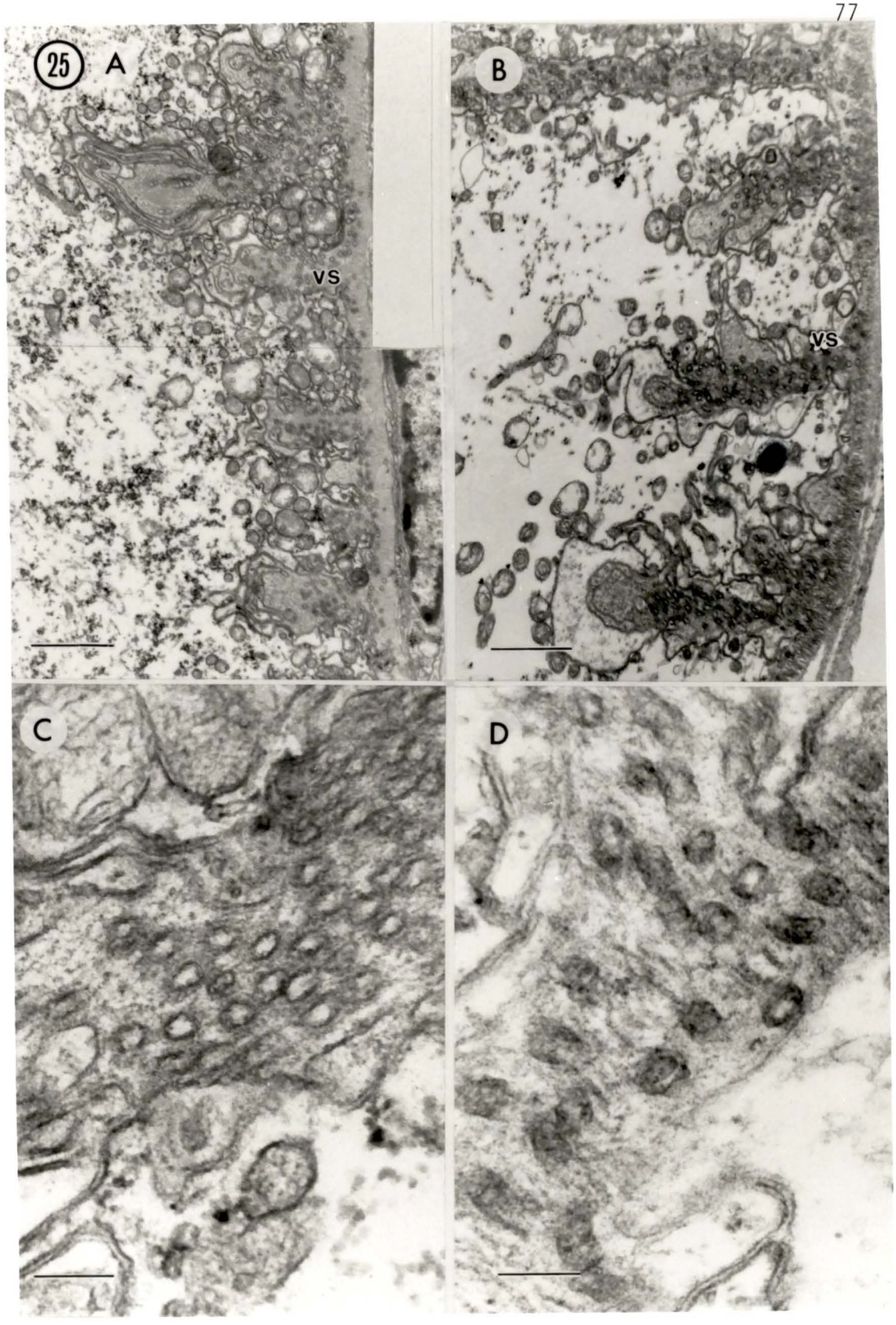

25
A
VS
B
VS
C
D

Figure 26: Transverse sections of dendritic tips from stretched (A,C,E) and relaxed (B,D,F) receptors. A,B. Tips are less numerous in stretched (A) than relaxed receptors (B). (g- glial cell, *- mitochondrion in stub). C. Arrows- dense spots in the ECM may be compressed distal dendritic tips. D. Arrows: microtubules in tips. E,F. Dendritic stubs (*) and glial processes at the edges of vacuolated strings. Scale bars : 0.2 μm.

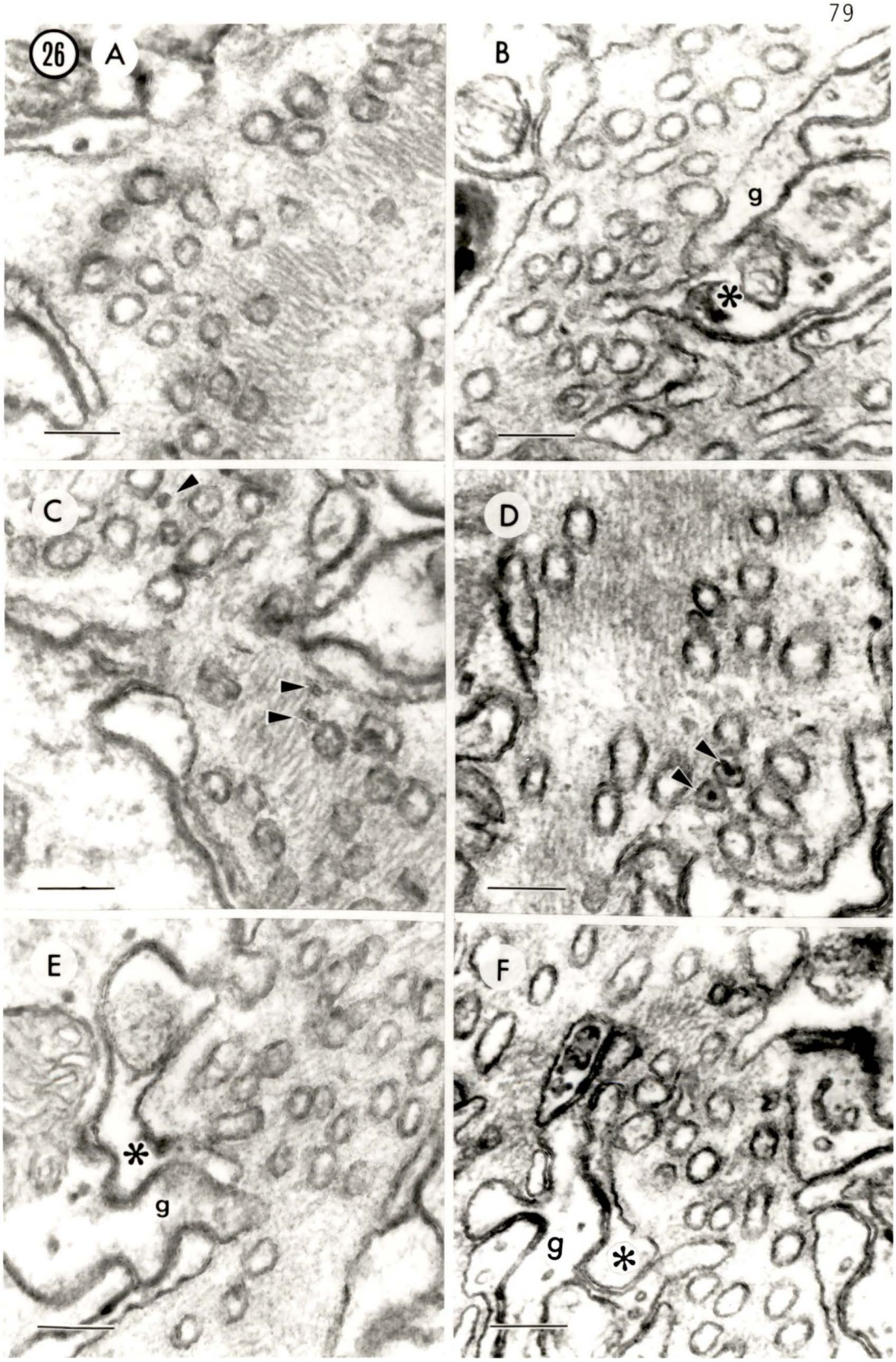
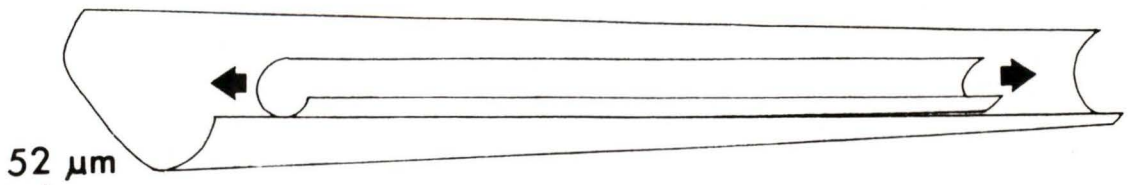

26
A
B
g
*
C
D
E
*
g
F
g
*

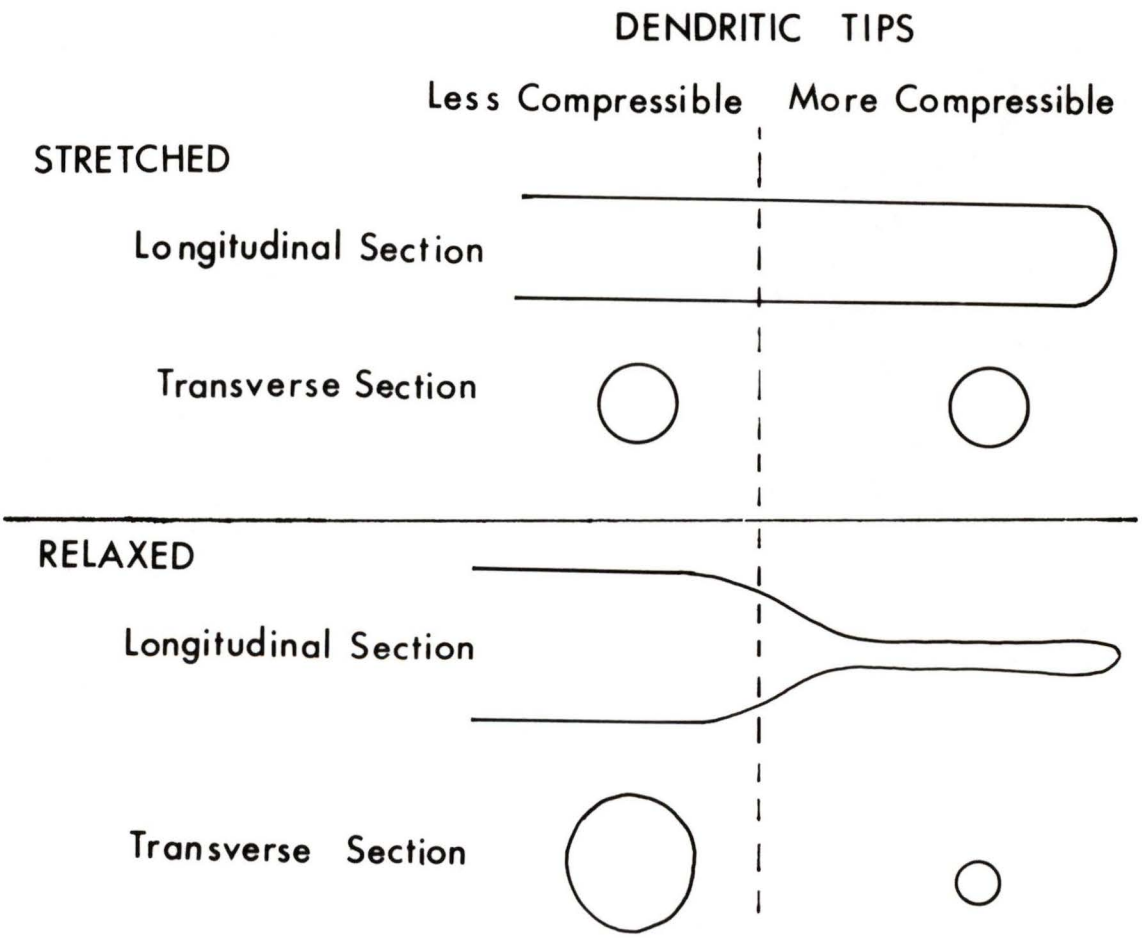
Figure 27: A. Cartoon of the shape change of the entire receptor. Receptor dimension changes are those of a crab with a carapace length of 26 mm. B. Model for differential tip deformation.



52 µm → 66 µm
+27%

55 mm → 65 mm
+18%

B Model for Differential Tip Deformation



RESULTS-

Munida:

Gross Morphology and Ultrastructure:

Like *Emerita*, *Munida* has a uropod SR complex consisting of parallel elastic and muscular strands. In *Munida* both the muscular and elastic strands arise from a lip on the dorsal, rostral edge of the telson and insert on the uropod coxopodite ventral to the insertion of the ATU muscle (Fig. 28). The strands are closely opposed to one another running almost medio-laterally in the very flattened telson (compare Figs 28, *Munida* and Fig.1, *Emerita*).

The receptor muscle consists of two bundles of fibres, and the elastic strand lies ventrally in the cleft between them (Figs. 29,30). The elastic strand is widest in the central region, where the neurons enter, and tapers toward its origin and insertion. The elastic strand is an elongated elipse in transverse section (30-100 μm) and has a much more variable cross-sectional shape than in *Emerita*.

The receptor complex receives its innervation from the receptor nerve which contains 10-13 profiles (Fig. 29). Two of the smallest appear to innervate the receptor muscle, the remainder the elastic strand.

The smaller neurons turn at the level of the strand to run parallel with its long axis but remain ensheathed in glial wrapping which is contiguous with that of the receptor nerve (Fig. 29). Except at the EM level the strand appears to be a single structure. In thin sections, the large and small neurons within it are separated by glia and ECM, implying that the strand may actually contain two functional units.

The one or two largest profiles (10-20 μm), upon entering the strand transversely, turn longitudinally, and become associated with vacuolated strings into which they send tips (Fig. 30) as do the four NSRs in *Emerita*.

Strings are not arranged peripherally inside the capsule, as they are in *Emerita*, but they are contiguous with the ECM of the capsule. The capsule of the *Munida* uropod SR is a combination of glial cells and ECM (Fig. 30) which, like Brachyuran thoracico-coxal SR's (Whitear, 1965), but unlike the acellular capsule of *Emerita*'s uropod SR, extends around the entire perimeter of the strand.

Staining Characteristics of the Elastic Strand:

The elastic strand contains Spirit blue fibres and no collagen.

Figure 28: Gross morphology of the telson of *Munida*. A. Line drawing of a *Munida* with uropods in the position corresponding to the end of the return stroke with the receptor stretched. B. Ventral view of sixth abdominal segment, telson and uropods (abdomen/telson preparation). All muscles have been removed from the left side of the crab. The elastic and muscular strands arise from a ridge on the rostral edge of the telson, run medially and insert on the uropod coxopodite. The uropod SR complex (=receptor muscle and elastic strand) is innervated by the receptor nerve. Scale bars: 5 mm.

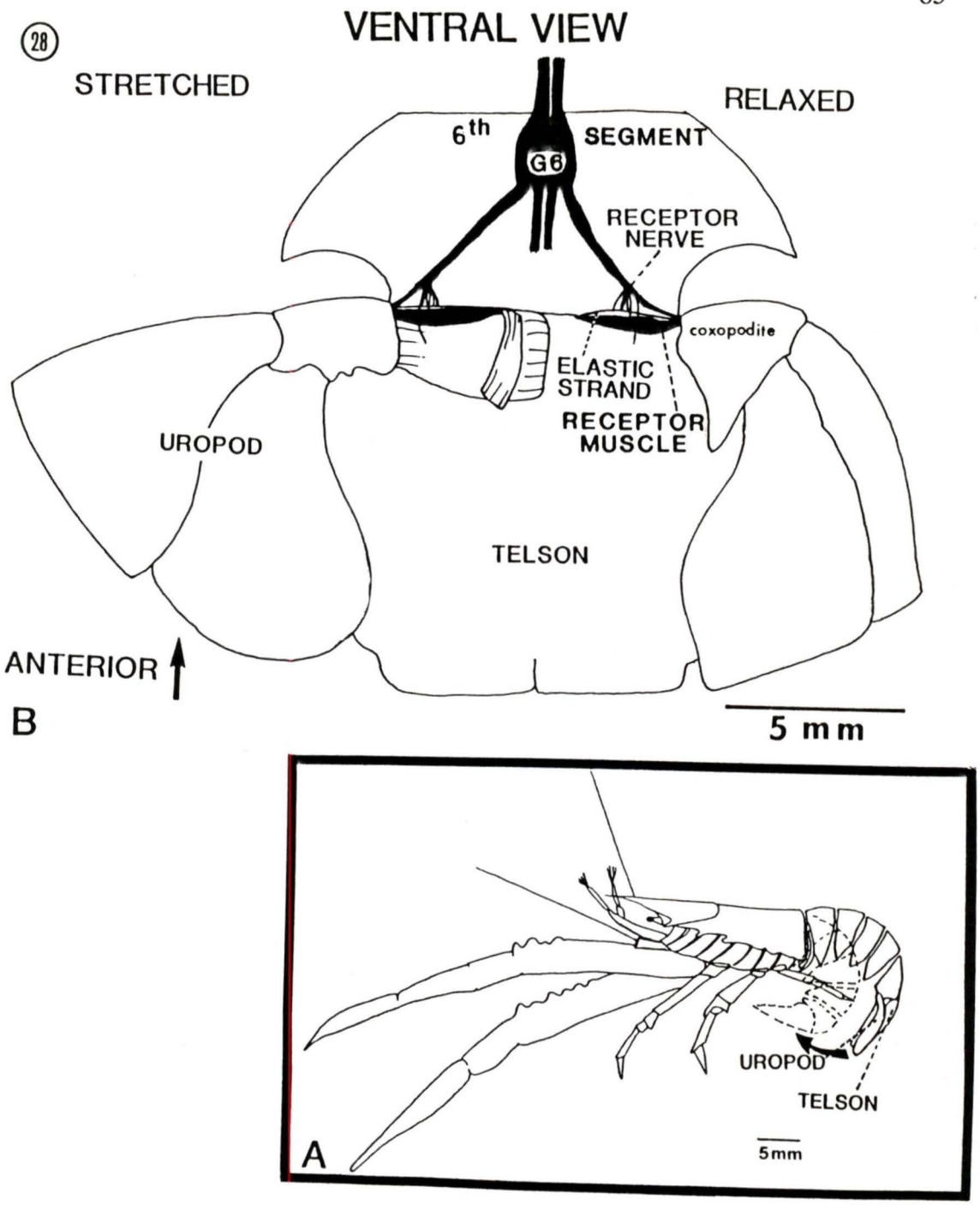
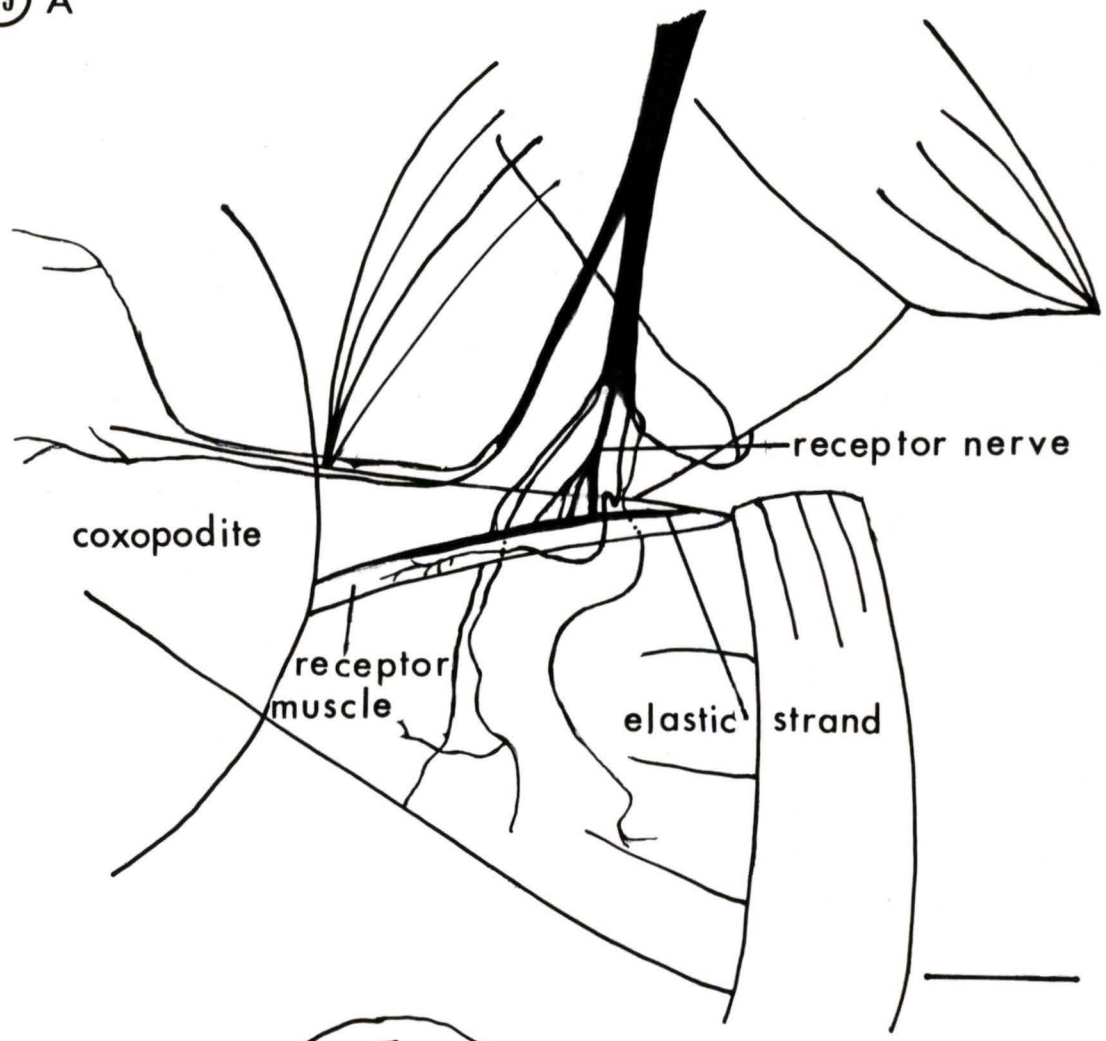

28
VENTRAL VIEW
STRETCHED
RELAXED
6th SEGMENT
G6
RECEPTOR NERVE
coxopodite
ELASTIC STRAND
RECEPTOR MUSCLE
UROPOD
TELSON
ANTERIOR
B
5 mm
UROPOD
TELSON
A
5mm

Figure 29: Details of uropod SR morphology. A. Camera lucida drawing of uropod SR complex. B. Cross-section of receptor nerve at the level indicated in A. Scale bars: A- 500 μm, B- 50 μm.

(29) A


receptor nerve
coxopodite
receptor muscle
elastic strand

B

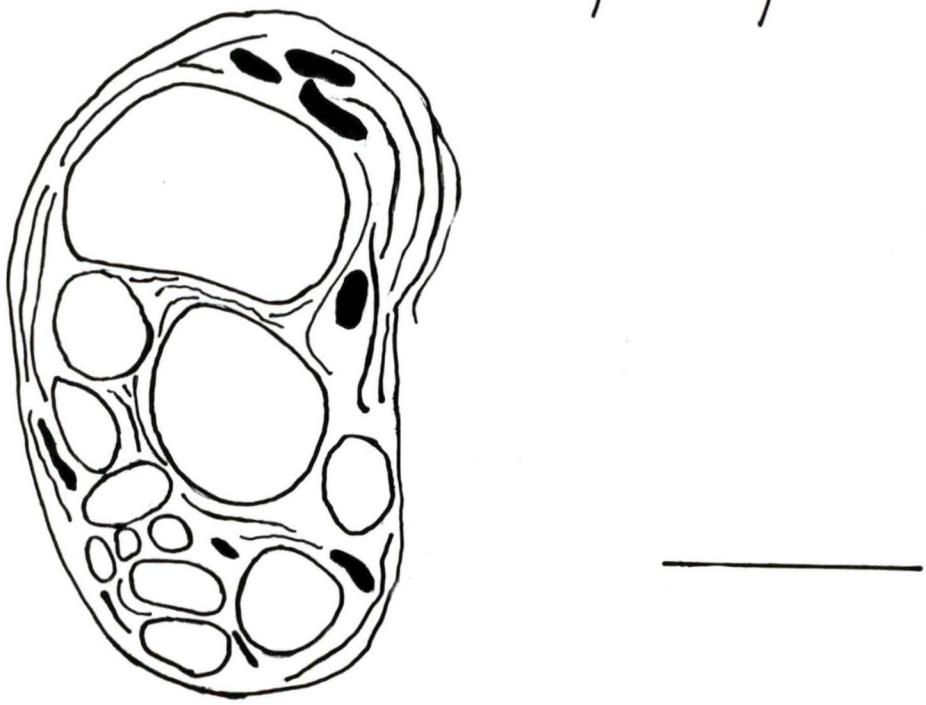
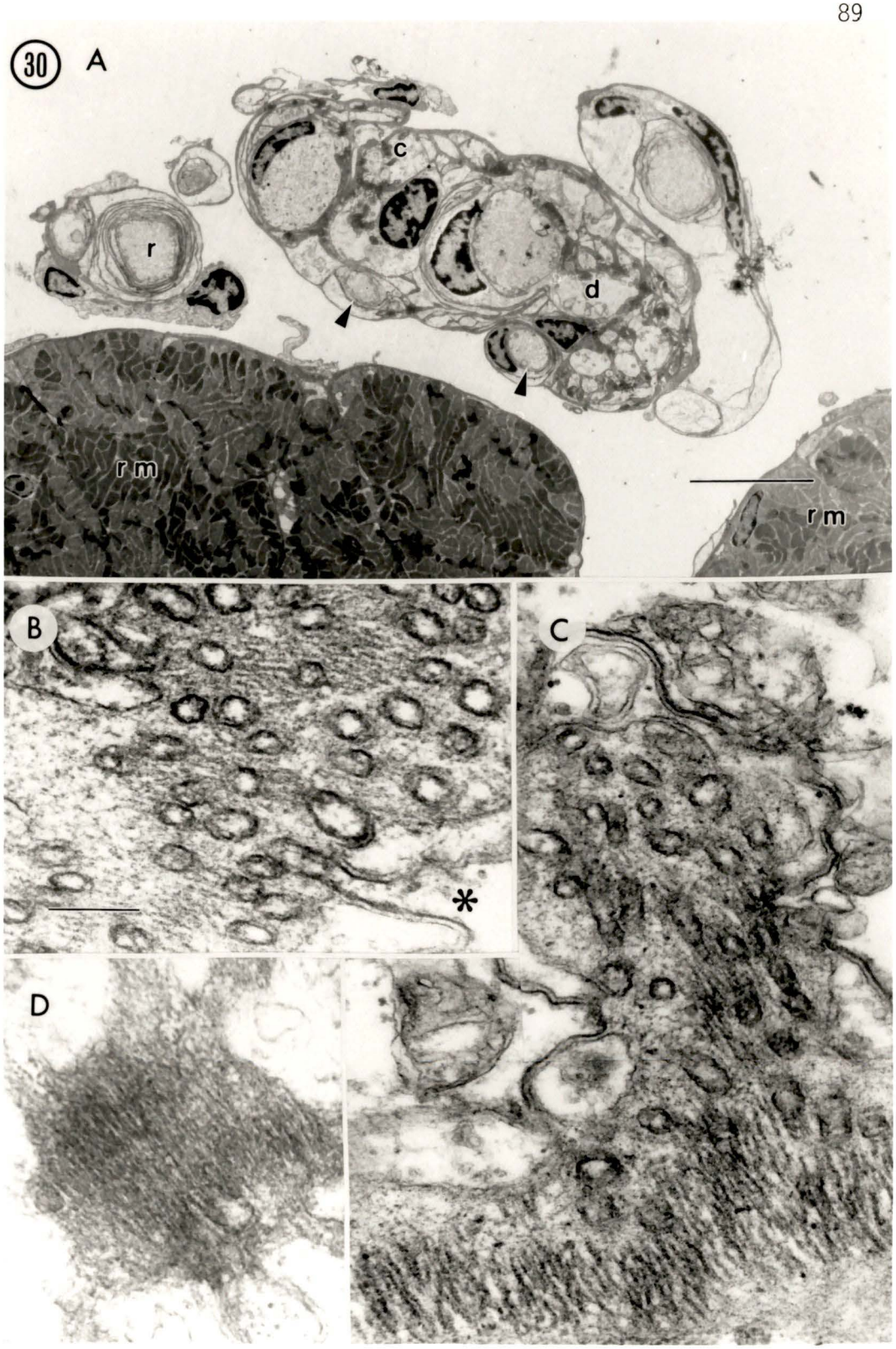


Figure 30: Ultrastructure of the uropod SR. A. Low-power electron micrograph of the uropod SR complex. The elastic strand lies rostral and ventral to the two lobes of the receptor muscle (rm) (r- innervation of the receptor muscle). Arrows: branches of small neurites which are not associated with vacuolated strings. B. Vacuolated string with tip entering (*). C. Vacuolated string in the region indicated (c) in A. D. Dense ECM rod from the region indicated (d) in A. Scale bars: A- 10μm, B,C,D- 0.25μm.


30
A
c
r
d
r m
r m
B
C
*
D

DISCUSSION:

Mechanosensory Transduction:

The variability in the pattern of NSR branching in the elastic strand (between and within crabs), which is due to the ECM arrangement, is similar to the variability in the connective tissue region (intercalated tendon zone) of the abdominal muscle receptor organs where the sensory dendrites lie. The arrangement of this zone in muscle receptor organs is very variable, even between segments in a single animal (Euteneur and Winter, 1979). Such variability suggests that the arrangement of the large dendritic branches may not be critical to the mechanosensory transduction process. On the other hand, the consistency of the arrangements of the dendritic termini within a group of receptors (e.g., thoracico-coxal SRs, uropod SRs) implies that this feature is important. That is, a specific plan of dendritic termini is characteristic of a given class of receptors (e.g., parallel: uropod SRs, thoracico-coxal SRs, some muscle receptor organs; oblique: other muscle receptor organs: see Table 2) probably because this arrangement is effective in transmitting a physiologically useful stimulus to the neurons given the specific position and structure of the strand. The conservation of dendritic terminal orientation reconfirms the concept (Euteneur and Winter, 1979) that the termini are the sites of conversion of the mechanical stimulus to an electrical event (=mechanosensory transduction).

Although they are morphologically indistinguishable, stretch receptor afferents may have different response characteristics. The fact that I was unable to find any differences in the structure of the dendritic tips between the four NSRs in *Emerita*'s uropod SR does not suggest that they necessarily respond to strand-stretching in the same way. There are no ultrastructural differences in the morphology and arrangement of the termini of the three dual signal afferent fibres of the oval organ (Pasztor, 1979; Pasztor and Bush, 1983b) yet they differ in threshold, sensitivity and proportion of spiking and nonspiking signals (Pasztor and Bush, 1982, 1983a, 1983b).

The low threshold of the fast compared to the slow abdominal muscle receptor organ is probably due to differences in the arrangement and length of the connective tissue into which the dendrites insert (Euteneur and Winter, 1979). This could not explain the differences in the oval organ because, unlike the muscle receptor organs, there are no morphological differences in the connective tissue surrounding the termini of the three cells (Pasztor, 1979). The differences between the oval organ afferents (and any differences which may exist between *Emerita*'s four NSRs) must be due to differences in their membrane properties (Pasztor and Bush, 1983b).

Given that the dendritic termini deform with stretch, (Krauhs and Mirolli, 1975; Tao-Cheng *et al.*, 1981a; this study) two questions arise. 1) How are dendritic termini deformed? and 2) How is terminal deformation "translated" into a receptor potential?

Dendritic tips in uropod SRs may be deformed in one or a combination of ways. When the strand is stretched tips may be compressed by the vacuolated string ECM or, if the tips are attached to the ECM, they may be pulled lengthwise. No attachments of dendritic tips to ECM have been described in any coxal receptor.

The nonuniformity of tip deformation (see below) may be a result of heterogeneities in either the ECM or the dendrite. Tao-Cheng *et al.* (1981b) suggest that the beadlike deformations of the dendritic tips of the stretched slow muscle receptor organs imply that there are membranes with different properties in this region. The cylindrical tips of the relaxed receptor have an even distribution of particles on the P membrane face, but when the receptor is stretched, the resultant swollen regions have a decreased particle density, while the shrunken regions have an increased particle density with particle-free patches; the particle composition does not change and there is no formation of aggregates. This may mean that there is compression and expansion of the lipid bilayer (Tao-Cheng *et al.*, 1981b).

There are three theories about how mechanosensory transduction occurs (Nadol and de Lorenzo, 1969). The first, chemical transmission, first proposed by Wiersma and others (1953) to explain the responsiveness of the vertebrate muscle

spindle to acetylcholine, is unlikely because the latency of transduction is considerably less than that of a chemical synaptic delay. According to the second theory, the dendritic membrane becomes thinner and increases in area with stretch, thereby increasing the membrane capacitance. This leads to charge redistribution and depolarization (Katz, 1950). However, no changes in membrane thickness have been noted in either thoracico-coxal SRs (Krauhs and Mirolli, 1975) or uropod SRs (this study). The third theory is that stretching the dendritic membrane leads to membrane permeability changes (Nadol and de Lorenzo, 1969). The permeability hypothesis seems most likely, especially in light of the discovery of stretch-activated ion channels (see below).

There are no changes in the cytoplasmic contents of stretch receptor dendrites associated with stretch. The size, density and distribution of mitochondria and vesicles are the same in stretched and relaxed uropod SRs (this study), thoracico-coxal SRs (Krauhs and Mirolli, 1975) and abdominal muscle receptor organs (Tao-Cheng *et al.*, 1981a). The vesicles, therefore, do not appear to be synaptic vesicles but may contain neuromodulators. Proctolin-like immunoreactivity has been demonstrated in the dense core vesicles in the oval organ and proctolin has been shown to enhance the discharge of the afferents (Pasztor and Bush, 1987a, 1987b).

Mitochondria may be involved in the restoration of ionic equilibrium after depolarization, they may absorb and store cations and may "mop up" the ions which caused the generator potential (Nadol and de Lorenzo, 1969). The peripheral location of mitochondria in the dendrites of the thoracico-coxal SRs (Whitear, 1965; Krauhs and Mirolli, 1975), the oval organ (Pasztor, 1979) and uropod SRs (this study) is suggestive of this role. The absence of mitochondria in the dendritic termini of thoracico-coxal SRs and uropod SRs implies that the electrogenic components in the transducing membranes do not rely on oxidative phosphorylation as their source of energy (Krauhs and Mirolli, 1975). The clumps of mitochondria found at the branch points of the thoracico-coxal SR secondary dendrites may provide energy for the maintenance of a standing gradient between the dendritic termini (more depolarized) and the larger branches (less depolarized). According to this model the dendritic termini are permeable to

sodium ions (=constant voltage source) while the secondary dendrites have an energy requiring sodium pump (=constant current source) (Krauhs and Mirolli, 1975). Physiological evidence exists for this in the thoracico-coxal SRs (Mirolli, 1979, 1981, 1983). *Emerita*'s NSRs also lack mitochondria in their termini and have a high concentration of these organelles in the larger branches in the strand so a similar mechanism may operate in uropod SRs.

Differential Tip Deformation:

Evidence from the study of at least two different proprioceptors supports the hypothesis that differential deformation of afferent processes can occur in a mechanoreceptor. The frog muscle spindle is similar to the uropod SR in that the afferent endings are in contact with ECM and are arranged in parallel with the long axis of the receptor (Bendeich *et al.*,1978). The frog muscle spindle differs from the uropod SR by having two morphologically distinct ECM zones which change shape and size upon stretching; the reticular zone is more viscoelastic and may be more subject to compression than the compact zone (Karlsson *et al.*,1971). (If there are any differences in the ECM of *Emerita*'s vacuolated strings they are subtle.) Differences in these zones are postulated to account for the presence of two phases in muscle spindle response. Oscillations in the more extensible reticular zone may produce the dynamic phase, while extension of both zones probably contributes to the static phase (Bendeich *et al.*, 1978). *Emerita*'s receptor has only a single phase response (Paul, 1987; pers. comm.), which corresponds to the static phase of muscle spindle action, and if there are two zones in the tips/vacuolated strings presumably they are both involved in the production of the nonspiking signal. Furthermore, two zones can be distinguished in the afferent endings of the frog muscle spindle which change dimensions differentially upon stretching; links decrease in diameter while the adjacent bulbs in the compact zone decrease in diameter and increase in length (Bendeich *et al.*, 1978). The links are compressed, as are the distal tips of the NSR, while the adjacent bulbs increase in volume as do the proximal tips of the NSR.

Cylindrical tips in the tonic abdominal muscle receptor organ in the crayfish deform differentially when the receptor muscle is stretched; regions of shrinkage

alternate with bulbous swollen regions (Tao-Cheng *et al.*, 1981a). In this organ, the deformation persists after generator potential production has stopped so it is more likely that deformation is a result rather than a cause of the generator potential (Tao-Cheng *et al.*, 1981a).

Neuroglia:

The glial cells within the elastic strands of the uropod SRs of both *Emerita* and *Munida* have the appearance of typical peripheral glia, characterized by sparse perinuclear cytoplasm containing rough endoplasmic reticulum, smooth endoplasmic reticulum, ribosomes, mitochondria, Golgi and microtubules (Cuadras and Marti-Subriana, 1985; Lane, 1981, Peracchia, 1981). Microfilaments are rare in peripheral glia in general (Lane, 1981) and absent in the uropod SR glia. Typically, thin processes ramify with one another and wrap neuronal processes (Lane, 1981). This is true of the glia of the Zone of Dendrite Entry of the uropod SRs; the glial cells within the strand also have long processes which attenuate distally. The distinctive peripheral, clumped chromatin in the glial nuclei is also characteristic of crustacean glia (Cuadras and Marti-Subriana, 1985). In contrast to the glia of the thoracico-coxal SRs, where sheath and string cells can be differentiated (Whitear, 1965), the glia of the uropod SRs appears to be a homogeneous population; sheath cells are missing because the uropod SR capsule is acellular and the variability in the uropod SR glia is in cell shape and not cytoplasmic contents.

It seems likely that the glia within the strand is responsible for secreting the ECM of both the capsule and vacuolated strings. Whether it also serves a nutritive function is unclear.

The glial processes which project into the dendritoplasm ("trophospongia") both inside and outside of the strand may either be sites of metabolic exchange or may couple an intracellular activity (e.g., protein synthesis) to the neuronal electrical activity (Lane, 1981). If, as Krauhs and Mirolli (1975) suggest for the S fibre of the thoracico-coxal SR, a standing potential gradient exists in the NSRs, these trophospongia might help supply energy for an electrogenic pump needed to maintain the gradient. These glial infoldings are most common in the large

processes of the Zone of Dendrite Entry (Fig, 12). In insects the trophospongia might be a site for the transfer of glucose from glia to nerve cells (Lane, 1981) and it would not be unreasonable to propose that this mechanism helps to meet the metabolic costs of maintaining the huge NSR dendrites.

The ECM produced by insect glia has been found to contain mucopolysaccharides and to play a buffering role; in areas where hyaluronic acid is present, the ECM may be a cation reservoir (Lane, 1981). ECM may help maintain and regulate membrane excitability by binding ions (Cuadras and Marti-Subirana, 1987; Lane, 1981).

The glial layers of the receptor nerve and the Zone of Dendrite Entry resemble those of the roots of the sixth ganglion of crayfish because there are many spiral layers of attenuated cytoplasm alternating with layers of extracellular matrix (Shivers and Brightman, 1976). In many arthropods, the sheath formed by the glia and ECM has been shown to act like myelin, to insulate the neurite and to speed impulse conduction; it also forms a permeability barrier (reviewed in Lane, 1981). Whether the glial cells play a trophic role is uncertain (Peracchia, 1981) but they definitely provide mechanical support and protection for the neurites (Lane, 1981).

The ramifications of glial processes are complex and variable, and despite examining semi-serial sections with the transmission EM, I was unable to reconstruct the three- dimensional structure of glial cells within the strand. Single glial cells may form several layers around crayfish axons and several glial cells may contribute to the axonal sheath (Cuadras and Marti-Subriana, 1985). This appears to be true of the Zone of Dendrite Entry of *Emerita*'s uropod SR. The 30nm microtubules which run parallel to the long axis of the dendrites, in the Zone of Dendrite Entry and in dendritic branches within the strand, have also been seen in crayfish adaxonal glial cells (Cuadras and Marti-Subriana, 1985).

Extracellular Matrix:

The physical properties of the ECM of a coxal proprioceptor are crucial to its function. Morphologically elastic tissue is characterized by 11 nm fibrils embedded in an amorphous matrix (Ross and Bornstein, 1971). The ECM into

which the dendritic termini of the thoracico-coxal SRs, oval organ and uropod SRs insert, appears to be composed of this tissue. The physical properties of elastic tissue resemble those of lightly vulcanized natural rubber: both are stretchable, have moderate tensile strength and return rapidly to their original dimensions upon the release of the stress (Ross and Bornstein, 1971). However, these properties probably arise from different structural characteristics in these two materials (Ross and Bornstein, 1971). Until specific staining properties were discovered, the elastic tissues of invertebrates could only be distinguished by their rubberlike characteristics (Elder, 1973). While it is clear that the elastic fibres are not identical to vertebrate elastin (Elder and Owen, 1967) their viscoelastic properties are unknown. Until these are described, it is impossible to predict the mechanical characteristics which may be important in transferring the stretch to the dendritic termini because the known elastic molecules have different properties. For example, resilin (a protein rubber in insect cuticle), abductin (a protein rubber in bivalve hinges) and elastin all differ considerably in both resilience, (=capacity to absorb and release energy) and in the frequency-dependence of resilience-damping (Wainwright *et al.*, 1976). Furthermore, tissue traits may vary, reflecting regional requirements, as in the case of invertebrate collagenous tissue (Adams, 1978). Therefore, it is imprudent to extrapolate properties from one elastic tissue to another even within a species.

Possible Ionic Mechanisms of NSR Function

It seems likely that the dendritic membranes of the NSRs of the basal joint proprioceptors have at least two functionally distinct regions: a stimulus-transducing zone where the receptor potential is generated (dendritic tips in the uropod SR of *Emerita* and *Munida*) and a connecting segment to the ganglion which is specialized for conduction of the membrane depolarization back to the synaptic neuropil. The ionic characteristics of each of these three regions would be expected to differ, reflecting their functions.

The stimulus transducing region of the distal dendrite (dendritic tips) is inaccessible to patch-clamp analysis because it is embedded in dense ECM.

However it has been demonstrated indirectly that the resting potential of both the T and S fibre is dependent on external potassium (Roberts and Bush, 1971) and sodium ions (Mirolli, 1979b). The receptor potential is unaffected by application of tetrodotoxin so the sodium component must be mediated by tetrodotoxin-insensitive sodium channels (Roberts and Bush, 1971).

Regardless of whether the action of mechanosensory transduction in the dendritic tips is caused by a lengthwise stretching of the tips or by a differential compression leading to proximal tip expansion (see below), stretch-sensitive ion channels are probably involved. These channels are opened by a small increase in membrane area, as little as two per cent for channels in chick skeletal muscle (Guharay and Sachs, 1984). This corresponds well with the magnitude of the estimated increase of tip area in *Emerita*.

One function of stretch-sensitive channels is in osmoregulation and the control of cell volume (Kullberg, 1987). Nerves in most animal change their length with body movements (Koike, 1987) and squid giant axons increase in volume when conducting impulses (Hill, 1950); uropod beating may produce shape changes in the conducting portions of the uropod SRs. The Zone of Dendrite Entry, Zone of Branching and the long dendritic segment between the elastic strand and the ganglion might be stretched during uropod beating and this osmotic mechanism might enable the cell to maintain a constant volume or to change its volume during stretch of the elastic strand. Stretch-sensitive channels in the conducting portion of the dendrite (Zone of Dendrite Entry, Zone of Branching and especially the proximal dendritic tips) could compensate for changes in cell volume which may occur with stretch. Furthermore, the expansion and subsequent return to resting volume of the proximal tips, expanded by stretch, may be mediated by stretch-sensitive channels in the following way. When the strand lengthens, membrane distention in the proximal tips could open stretch-sensitive channels. The influx of cations would create an osmotic gradient causing water to enter the cell to reinflate the distal tips.

Channel properties of the proximal conducting region(s) of both the S (Mirolli, 1979a) and T (Lowe *et al.*, 1978; Mirolli, 1979a, 1979b, 1983) dendrites have been studied by patch clamping. Lowe *et al.* (1978) demonstrated that the

sodium channels in this part of the cell differed from those in the transducing region because they were tetrodotoxin- sensitive if they were first opened by veratridine. Blight and Llinàs (1980) reported on a tetrodotoxin- sensitive calcium channel in the pre-synaptic portion of T fibres which was not found by the other investigators in the proximal dendrite. Clearly the pre-synaptic, proximal and distal dendritic portions of the cell each have specific channel properties which differ from one another.

Since the non-transducing membrane of crab coxal receptors contains classical (fast, voltage-gated, inward) sodium channels (Lowe *et al.*, 1978; Mirolli, 1979a, 1979b, 1981) there must be some other difference between this and the membrane of spiking sensory neurons. These sodium channels appear to be fully differentiated and to possess the usual voltage-gating characteristics (Mirolli, 1981). If so then, why are these cells (and those in *Emerita* and *Munida*) nonspiking?

Mirolli provides evidence that the inability of the NSRs of the thoracico-coxal SR to generate action potentials is a result of an outward current shunt in the form of sodium channels (transient current 1981; longer-lasting current 1983) and he speculates that the membranes may also contain a very low density of typical, fast inward sodium channels, which would further lower the ability to produce action potentials. Transient outward currents in the spiking sensory cells of marine gastropods (Connor and Stevens, 1971) and two species of nudibranch (Aldrich *et al.*, 1979a, 1979b) regulate the firing characteristics of these neurons (most significantly they cause spike broadening (Aldrich *et al.*, 1979b)), so their prominence in these sensory neurons may be a specialization to suppress spiking completely (Mirolli, 1981).

Moreover, occasionally a few graded, active membrane responses were recorded in the T fibres of receptors from some individual *Carcinus*, *Portunus*, *Potamon* and *Birgus* (Bush, 1976). This response indicates that the membrane properties required for spike generation are present in membranes of at least some "nonspiking" neurons. In addition, the 9DL local interneurons of the terminal ganglion of crickets, which are usually nonspiking, can be made to spike by injecting hyperpolarizing current while simultaneously giving the primary

afferents their typical stimulus (wind) (Bodnar *et al.*, 1988). There are enough similarities between the characteristics of known ionic channels of thoracico-coxal SRs and other nonspiking neurons and cells which produce spikes to suggest that there may be some plasticity in the membrane response; *i.e.*, a cell may not be committed to being nonspiking by structural constraints but rather by the particular balance of inward and outward channels of each cell which acts to produce an analog response under the normal operating conditions of the receptor. The channel properties may be such that when the normal stimulus is applied to the cell a graded response is produced even though the cell might produce a spike when stimulated differently. Any change in the usual sensory stimulus (e.g., type, duration, frequency, etc.) during evolution could lead to changes in the signal coding properties of the receptor.

Burrows and Siegler (1978) found that graded synaptic potentials in nonspiking interneurons elicit graded postsynaptic responses in motoneurons by the "stepwise" release of chemical transmitter and they suggest that graded changes in membrane potential are responsible for transmitter release even in spiking cells. The distinction between spiking and nonspiking cells probably reflects only the usual mode of internal signal transmission and not a dichotomy of synaptic mechanisms (Burrows and Siegler, 1978). Bullock (1981) predicts that many neurons will be found that are capable of spiking but need not spike to produce physiological effects.

Of special significance to the uropod SR of *Emerita* is the evidence that the long, stout, nonspiking dendrites in the thoracico-coxal SR act as signal filters and enhancers which accentuate the high-frequency component of the signal (Mirolli, 1983). During fast swimming the uropods beat at frequencies approaching 13 Hz (Paul, 1971a, 1976), a rate which probably exceeds the walking speed of any decapod! (1.5 Hz for single leg movement in lobster walking; from Fig. 22, Macmillan, 1975). Therefore a system which can faithfully transmit information about high-frequency uropod movement is essential. Comparison of the membrane channel properties of the connecting segment of an *Emerita* dendrite with those of thoracico-coxal SR fibres might reveal that the tetraethyl ammonium and 4- aminopyridine-sensitive outward channels responsible for this filtering

effect are more abundant in *Emerita*'s NSRs or are distributed specifically in a way which allows the nonspiking neurons to exploit this filtering property optimally.

Evidence for Homology of Basal Joint Proprioceptors

It is misleading to classify the stretch receptor at the base of the decapod walking leg as a muscle receptor organ. There are many more similarities with the uropod SRs of *Emerita* and *Munida*, which are entirely non-muscular than there are with the dorsal muscle receptor organs. Although the receptor complex in *Carcinus* contains a central muscle, the vacuolated strings and accompanying sensory dendrites (S fibres) are located in the dorsal and ventral flanking strands, separated from the muscle bundle by layers of connective tissue; most strings are found within the flanking strand on the side away from the muscle (Whitear, 1965). Except for a few cases where the muscle and vacuolated strings of the T fibre are in contact (Fig. 6; Whitear, 1965) the dendritic endings are sequestered away from the muscle; they are always in direct contact only with ECM and never with muscle fibres. Therefore, while muscle tension would affect strand length, and thus the receptor potential, the sensory and muscular parts of the receptor are separate. The separation is even more striking in *Pagurus* (Whitear, 1965).

The morphological separation of muscle and neuronal elements within the strand is probably functionally important for two reasons. First, the connective tissue divider which can have as many as twelve layers and be as wide as 13.5 μm (measured from Fig. 5; Whitear, 1965) precludes local ionic changes which result from muscle contraction from contributing to the thoracico-coxal SR mechanosensory transduction process, as has been proposed for abdominal muscle receptor organs (Nadol and de Lorenzo, 1969). It is reasonable to suppose that transduction is similar in thoracico-coxal SRs and uropod SRs. Second, the similarity between thoracico-coxal SRs and uropod SRs is more apparent when thoracico-coxal SRs are not confused with true muscle receptor organs. Without the central muscle the thoracico-coxal SR of *Carcinus* resembles *Emerita*'s uropod SR quite remarkably (compare Fig. 5; Whitear, 1965 with Fig. 6C; this study). The similarity with the thoracico-coxal SR of *Pagurus* is even more striking (compare Fig. 7, Whitear, 1965 with Fig. 6C, this study). Vacuolated strings in all three

receptors are not distributed around the entire circumference of the strand but are confined to the part opposite the entry point of the NSRs: the anteroventral surface in the *Carcinus* thoracico-coxal SR (Whitear, 1965), the anterior margin of the thoracico-coxal SR of *Pagurus* (Whitear, 1965), the ventrolateral arc of *Emerita*'s uropod SR (Figs. 3,6C).

The arrangement of large dendritic branches, dendritic termini and vacuolated strings with their associated glial cells is identical in uropod SRs and thoracico-coxal SRs. There are only two differences between the ultrastructural plan of the two receptors. Firstly, the capsules of the thoracico-coxal SR in *Carcinus* (Whitear, 1965) and *Cancer* (Krauhs and Mirolli, 1975) are cellular and continuous with the glial sheath of the NSRs outside the strand, whereas the capsule of the receptor strand of *Pagurus*' thoracico-coxal SR and *Emerita*'s uropod SR is composed of ECM and is completely acellular.

The second difference is undoubtedly of functional importance. The vacuolated strings in *Carcinus* are not attached along their length to the capsule of the receptor strand but attach at their ends to muscle fibres in the proximal tendon region and "merge with the connective tissue of the flanking strands" (Whitear, 1965; p. 448). Although Whitear (1965) does not describe the attachments of the vacuolated strings in *Pagurus*, she states that they have a higher fibre content and "do not stand out as well from the general connective tissue" (p. 448). Most strings in Fig. 7 (Whitear, 1965) abut the capsule and appear to be attached to its inside edge as they are in the uropod SR of *Emerita*.

Evolution of Uropod Stretch Receptors

NSRs may have evolved from motoneurons (Bush,1976). There are at least five similarities which support this scenario. First, like motoneurons and unlike most crustacean sensory neurons, the NSRs have centrally located cell bodies. Although there are a few exceptions, conservation of developmental patterns is the rule in invertebrate central nervous systems (Thomas *et al.*, 1984). Sensory neuroblasts are usually located peripherally and send axons into the ganglion, while motoneuroblasts are in the primordial ganglion and send axons out to the muscles. It is unlikely that during the course of evolution the ontogeny of a

sensory neuron would be altered such that its neuroblast would move from the periphery to the ganglion.

Besides the strand receptors (and presumably the nerve cord stretch receptor), there is another example in crustaceans of primary afferents without peripheral somata. Cell bodies of the neurons innervating the soft, ventral cuticle of crayfish are located in the main trunks of first and second nerve roots of all the abdominal ganglia (Pabst and Kennedy, 1967). These cells are bi- or more often tripolar, with thick dendrites and extensive, peripheral dendritic trees; there may be other cells with similar peripheral (dendritic) structures whose somata lie in a "spectrum" of positions from the ganglion to near the terminals (Pabst and Kennedy, 1967). These cells may be intermediate stages in an evolutionary transition series between the more common afferent type with peripheral somata and the unusual type with central cell bodies. It is more likely that these cells, which differ in morphology, in the structures they innervate and in the type of stimulus they monitor, are members of another class of mechanoreceptive neurons, distinct from the basal joint NSRs.

Second, the muscular part of the thoracico-coxal SR complex is actually a specialized portion of the leg promotor muscle (Whitear, 1965). Furthermore, although it has lost all qualities of muscle tissue, the elastic strand of *Emerita*'s uropod SR may have arisen from the ATU muscle or the ATU connective tissue; its insertion is adjacent to the insertion of ATU and caudally the elastic strand of the uropod SR is closely apposed to the connective tissue of ATU. The receptor muscle and elastic strand of *Munida*'s uropod SR form a single bundle at the level of gross dissection, originating and inserting together. *Munida*'s elastic strand, which is much less robust than *Emerita*'s (compare Figs. 2 and 26), might easily be a specialization of the muscle, its connective tissue or the nerve supplying the motor innervation.

Third, afferent processes are usually smaller in diameter than motor axons. The cell bodies and sensory processes of the neurons innervating the oval organ have dimensions resembling motoneurons (Pasztor, 1979) and the diameters of the NSR dendrites are within the size range characteristic of motor axons.

Fourth, the NSRs in *Emerita* have a spreading arbour in the ganglion, which is more typical of motoneurons than of individual primary afferents which usually terminate in a discrete sensory neuropil, often in a glomerulus (Paul, 1972, pers. comm.; Liese *et al.*, 1987). The central projections of the NSRs are located with those of the telson motoneurons in a region of motor neuropil (Paul, pers. comm.). The branching structure of the S,T and D neurons of the thoracico-coxal SR closely resembles that of the ipsilateral promotor motoneurons of the same segment (Bush, 1976).

Finally, each afferent innervating the oval organ signals by both spiking and nonspiking conduction (Pasztor and Bush, 1983a, 1983b, 1987). There is a difference in the relative contributions of the two modes of signalling in the response of each of the three afferents. The largest fibre has the largest graded response, the smallest has the highest spike frequency (Pasztor and Bush, 1983a). With some exceptions nonspiking neurons are usually of large diameter (reviewed in Pearson, 1976). There may be a spectrum of neurons with response characteristics ranging from wholly spiking to dual signalling to wholly nonspiking. A change during evolution in the ionic channel properties of the membrane would change the signal response of the neuron (*e.g.*, an increase in the number of inward sodium channels might cause a cell to change from nonspiking to spiking, see above). The uropod SR of *Galathea strigosa* signals stretch using both types of signal; it is unknown whether individual afferents exhibit dual signalling or if there are separate populations of spiking and nonspiking neurons (Maitland *et al.*, 1982). These authors proposed, using size as the criterion, that the three largest afferents may be nonspiking (Maitland *et al.*, 1982). Comparison of the uropod SRs of *Munida* and *Galathea* suggests that some of the neurons of *Munida*'s uropod SR (probably the two largest, Fig. 29) may also be nonspiking. These two are the cells which have tips embedded in vacuolated strings.

The hypothetical history of the decapod tailfan proposed by Paul *et al.* (1985) suggests that the transition from macruran-like tailflipping, (as performed by *Munida*), to *Emerita*'s swimming by uropod beating was accompanied by the emergence of features characteristic of segmental appendages including the

(re)appearance of the basal joint stretch receptor associated with the modern anomuran uropod. Some specific suggestions about how stretch receptors may have evolved in the overall pattern of tailfan specialization emerge from the comparison of uropod SR structure in the two species of crab as well as with their serial homologs in other decapods.

The coxal stretch receptors may have arisen as specializations of muscles (Whitear, 1965). The following "changes" would be required for the transformation to a proprioceptor, although they need not occur exactly in the order described. Either a motoneuron changed its direction of axonal impulse - conduction, or one of its dendrites, elongated out to the muscle (followed or accompanied by regression of the axon). Given the general stretch-sensitivity of neuronal membranes any neuron could act as a proprioceptor if a mechanism existed to transfer the stretch stimulus to the cell. (Branches of the sensory fibres might be compressed when the muscle contracts.) This would produce a muscle receptor organ similar to those in the abdominal segments (but with central somata). The ECM would then have become organized into vacuolated strings. The result would have been a stretch receptor like the lobster twisting swimmeret coxal receptor with spiking afferents with central somata and endings in vacuolated strings (Miyan and Neil, 1986).

The modality of some of the neurons might then change from spiking to nonspiking, possibly through the intermediate of dual signalling (see above). A thoracico-coxal-SR-like receptor would be the result: nonspiking sensory endings embedded in vacuolated strings within a strand with both muscular and elastic components (see above discussion of thoracico-coxal SRs) which may also retain some spiking innervation. From this ancestral structure, *Munida*'s receptor might arise by separation of the muscular from the elastic element. *Emerita*'s uropod SR would be the result of both processes. The muscle in the uropod SR receptor complex of *Emerita* and *Munida* is probably homologous with the thoracico-coxal SR receptor muscle which has separated from the elastic connective tissue. There are no homologs of the elastic or muscular strands in the macruran tailfan; they appear to be associated with the specialization of the tailfan in anomurans (Paul *et al.*, 1985; Paul, 1988).

Conclusion:

This description of the ultrastructure of the uropod SRs in *Emerita* and *Munida* reconfirms the homology between the coxal proprioceptors and provides a basis for predictions about how mechanosensory transduction may occur in crustacean stretch receptors. Moreover, this study inspires specific physiological questions such as: Do *Emerita*'s four NSRs have the same response characteristics? What are the membrane properties of the three functional regions of the NSRs?, Are the two largest cells innervating the uropod SR of *Munida* nonspiking? Thus, the uropod stretch receptor appears to be an excellent preparation in which to study many aspects of proprioception and to compare the physiology and morphology of spiking and nonspiking mechanosensory afferents.

LITERATURE CITED:

Adams, E. 1978. Invertebrate collagens. Science, 202: 591-598.

Aldrich,R.W., P.A. Getting and S.A. Thompson. 1979a. Inactivation of delayed outward current in molluscan neurone somata. J. Physiol 291: 507-530.

Aldrich,R.W., P.A. Getting and S.A. Thompson. 1979b. Mechanism of frequency-dependent broadening of molluscan neurone soma spikes. J. Physiol 291: 531-544.

Alexandrowicz, J.S. 1958. Further observations on proprioceptors in Crustacea and a hypothesis about their function. J. Mar. Biol. Assocn. 37: 379-396.

Alexandrowicz, J.S. 1967. Receptor organs in the coxal region of *Palinurus vulgaris*. J. Mar. Biol. Assocn. 47: 415-432.

Alexandrowicz, J.S. and M. Whitear, 1957. Receptor elements in the coxal region of decapod Crustacea. J. Mar. Biol. Assocn. 36: 603-628.

Ashhurst, D.E. 1968. The connective tissues of insects. Ann. Rev. Entomol. 13: 45-74.

Ayers,J. and W.J. Davis. 1979. Neuronal control of locomotion in the lobster *Homarus americanus*. I. motor programs for forward and backward walking. J. Comp. Physiol. A, 115A: 1-27.

Barnes,W.J.P. 1977. Proprioceptive influences on motor output during walking in the crayfish. J. Physiol (Paris) 73: 543-563.

Bendeich, E.G., W.M. Hooker and U.L. Karlsson. 1978. Sensory nerve deformation in the stimulated frog muscle spindle. J. Ultrastr. Res. 62: 137-146.

Berger, C.S. and B.M.H. Bush. 1979. A non-linear mechanical model of a non-spiking muscle receptor. J. Exp. Biol. 83: 339-343.

Blight, A.R. and R. Llinás. 1980. The non-impulsive stretch- receptor complex of the crab: a study of depolarization-release coupling at a tonic sensorimotor synapse. Phil. Trans. Roy. Soc. B, 290: 219-276.

Bodian, D. and R.A. Bergman. 1961. Muscle receptor organs of crayfish: functional anatomical-correlations. Bull. Johns Hopkins Hosp. 110:78-106.

Bodnar, D., G. Jacobs and J. Miller. 1988. Characterization of local interneurons of the cercal afferent system of the cricket *Acheta domesticus*. J. Comp. Physiol. (in preparation).

Bullock T.H. 1981. Spikeless neurones: where do we go from here? In: Neurones without impulses. Edited by A.Roberts and B.M.H. Bush, Cambridge Press, Cambridge. pp. 269-284.

Burrows, M. and M.V.S. Siegler. 1978. Graded synaptic transmission between local interneurones and motor neurones in the the metathoracic ganglion of the locust. J. Physiol. (London) 285: 231-255.

Bush, B.M.H. 1976. Non-impulsive thoracic-coxal receptors in crustaceans. In: Structure and function of proprioceptors in the invertebrates, Edited by P.J. Mill. Chapman and Hall, London. pp. 115-151.

Bush, B.M.H. 1977. Nonimpulsive afferent coding and stretch reflexes in crabs. In: Identified neurons and behavior of arthropods. Edited by G. Hoyle. Plenum Press, New York. pp. 439-460.

Bush, B.M.H. 1981. Non-impulsive stretch receptors in crustaceans. In: Neurones without impulses. Edited by A. Roberts and B.M.H. Bush, Cambridge Univ. Press, Cambridge. pp. 147-176.

Bush, B.M.H. and A.J. Cannone. 1973. A stretch reflex in crabs evoked by muscle receptor potentials in nonimpulsive afferents. J. Physiol. (London), 232: 95-97P.

Bush, B.M.H. and A.J. Cannone. 1974. A positive feed-back reflex to a crustacean muscle receptor. J. Physiol. (London), 236: 37-39P.

Bush, B.M.H and A. Roberts. 1968. Resistance reflexes from a crab muscle receptor without impulses. Nature, 218: 1171-1173.

Bush, B.M.H. and A. Roberts. 1971. Coxal muscle receptors in the crab: the receptor potentials of S and T fibres in response to ramp stretches. J. Exp. Biol. 55: 813-832.

Cannone, A.J. 1987. Crustacean elastic strand receptors that function without impulses. I. the depressor receptor in the shore crab, Carcinus maenas. J. Comp. Physiol. 160: 599-611.

Canonne A.J. and B.M.H. Bush. 1980. Reflexes mediated by nonimpulsive afferent neurones of thoracic-coxal muscle receptor organs in the crab, *Carcinus maenas* I. receptor potentials and promotor motorneurone responses. J. Exp. Biol. 86: 275-303.

Cason, J.E. 1950. A rapid one-step Mallory-Heidenhain stain for connective tissue. Stain Technology, 25: 225-226.

Clarac, F. 1977. Motor coordination in crustacean limbs. In: Identified neurons and behavior of arthropods. Edited by G. Hoyle, Plenum, New York. pp. 167-186.

Cobb, J.L.S. and W.J. Heitler. 1985. Ultrastructure of the phasic stretch receptor in the crayfish abdominal nerve cord. J. Neurocytol. 14: 413-426.

Connor, J.A. and C.F. Stevens. 1971. Inward and delayed outward membrane currents in isolated neural somata under voltage clamp. Voltage clamp studies of a transient outward membrane current in gastropod neural somata under voltage clamp. J. Physiol. (London), 213: 1-19, 21-30.

Cuadras, J. and A. Marti-Sibirana. 1985. Glial cells in abdominal ganglia of crayfish. Acta Zoologica. 66: 217-228.

Cuadras, J. and A. Marti-Sibriana. 1987. Elements other than neurons or glia of nervous abdominal ganglia of crayfish (Decapoda, Astacidea). Crustaceana, 52: 187-193.

Davis, W.J. 1968. The neuromuscular basis of lobster swimmeret beating. J. Exp. Zool. 168: 363-378.

Davis, W.J. 1969a. Reflex organization in the swimmeret system of the lobster. I. intrasegmental reflexes. J. Exp. Biol. 51: 547-563.

Davis, W.J. 1969b. Reflex organization in the swimmeret system of the lobster. II. reflex dynamics. J. Exp. Biol. 51: 565-573.

Davis, W.J. 1973. Neuronal organization and ontogeny in the lobster swimmeret system. In: Control of posture and locomotion. Edited by R.B. Stein, K.G. Pearson, R.G. Smith and J.B. Redford, Plenum, New York. pp. 437-455.

DiCaprio, R.A. and F. Clarac. 1981. Reversal of a walking leg reflex elicited by a muscle receptor. J. Exp. Biol. 90: 197-203.

Elder, H.Y. 1973. Distribution and functions of elastic fibers in the invertebrates. Bio. Bull. 144: 43-63.

Elder, H.Y. and G. Owen. 1967. Occurrence of "elastic" fibres in the invertebrates. J. Zool. (London), 152: 1-8.

Euteneuer, C. and C. Winter. 1979. The abdominal muscle receptor organ in *Astacus leptodactylus* (Crustacea). A fine structural analysis. Cell Tissue Res. 202: 41-61.

Evoy, W.H. and J. Ayers. 1982. Locomotion and control of limb movements. In: The biology of crustacea v.4. Edited by D.C. Sandeman and H.L. Atwood, Academic Press, New York. pp. 61-105.

Evoy, W.H. and C.R. Fourtner. 1973a. Nervous control of walking in the crab *Cardisoma granhumi*. III. proprioceptive influences on intra- and intersegmental coordination. J. Comp. Physiol. 83: 303-318.

Evoy, W.H. and C.R. Fourtner. 1973b. Crustacean walking. In: Control of posture and locomotion. Edited by R.B. Stein, K.G. Pearson, R.G. Smith and J.B. Redford, Plenum, New York. pp. 477-493.

Eyzaguirre, C. and S.W. Kuffler. 1955. Processes of excitation in the dendrites and in the soma of single isolated sensory nerve cells of the lobster and crayfish. J. Gen. Physiol. 39: 87-119.

Florey, E. and E. Florey. 1956. Microanatomy of the abdominal stretch receptors of the crayfish (*Astacus fluviatilis*). J. Gen. Physiol. 39: 69-85.

Grote, J.R.. 1981. The effect of load on locomotion in crayfish. J. Exp. Biol. 92: 277-288.

Guharay. and Sachs. 1984. Stretch-activated single ion channel currents in tissue-cultured embryonic chick skeletal muscle. J. Physiol (London), 352: 685-701.

Hama, K. 1961. A photoreceptor-like structure in the ventral nerve cord of the crayfish *Cambarus virilus*. Anat. Rec. 140: 329-336.

Heitler, W.J. 1982. Non-spiking stretch-receptors in the crayfish swimmeret system. J. Exp. Biol. 96: 355-366.

Heitler, W.J. 1986. Aspects of sensory integration in the crayfish swimmeret system. J. Exp. Biol. 120: 387-402.

Hill, D.K. 1950. The volume change resulting from stimulation of a giant nerve fibre. J. Physiol. 111: 304-327.

Humason, G.L. 1967. Animal tissue techniques. 2nd ed. W.H. Freeman, San Francisco.

Karlsson, U.L., W.M. Hooker and E.G. Bendeich. 1971. Quantitative changes in the frog muscle spindle with passive stretch. J. Ultrastr. Res. 36: 743-756.

Katz, B. 1950. Depolarization of sensory terminals and the initiation of impulses in the muscle spindle. J. Physiol. 111: 261-282.

Koike. 1987. The disturbance of the fast axonal transport of protein by passive stretching of an axon in *Aplysia*. J. Physiol. 390: 489-500.

Komuro, T. 1981a. Fine structural study of the abdominal muscle receptor organs of the crayfish (*Procambarus clarkii*). Fast and slow receptor muscles. Tissue Cell, 13: 79-92.

Komuro, T. 1981b. Fine structural differences between inhibitory and excitatory synapses in crayfish stretch receptor organs prepared by rapid freezing. Anat. Rec. 199: 180A.

Kosaka, K. 1969. Electrophysiological and electron microscopic studies on the neuromuscular junction of the crayfish stretch receptors. Japanese J. Physiol. 19: 160-175.

Krauhs, J.M. and M. Mirolli. 1975. Morphological changes associated with stretch in a mechano-receptor. J. Neurocytol. 4: 231-246.

Kullberg, R. 1987. Stretch-activated ion channels in bacteria and animal cell membranes. T.I.N.S. 10: 387-388.

Lane, N.J. 1981. Invertebrate neuroglia- junctional structure and development. J. Exp. Biol. 95: 7-33.

Leise, E.M., W.M. Hall and B. Mulloney. 1986. Functional organization of crayfish ganglia: I. the flexor systems. J. Comp. Neurol. 253: 25-45.

Lowe, D.A., B.M.H. Bush and S.H. Ripley. 1978. Pharmacological evidence for 'fast' sodium channels in nonspiking neurones. Nature, 274:289- 290.

Luft, J.H. 1961 . Improvements in epoxy resin embedding methods. J. Biophys. Biochem. Cytol. 9: 409-414.

Luft, J.H. 1963. Embedding media- old and new. In: Biological electrical microscopy. Edited by J.D. Koehler. Springer-Verlag, New York. pp. .

Macmillan, D.L. 1975. A physiological analysis of walking in the American lobster, *Homarus americanus*. Phil Trans. Roy. Soc. London B, 270: 1-59.

Maitland, D.P., M.S. Laverack and W.J. Heitler. 1982. A spiking stretch receptor with central cell bodies in the uropod coxopodite of the squat lobster Galathea strigosa (Crustacea,anomura). J. Exp. Biol. 101:221-231.

Mallory, F.B. 1944. Pathological technique. W.B. Saunders, Philadelphia.

Millonig, G. 1961. Advantage of a phosphate buffer for OsO_4 solution in fixation. J. Appl. Physiol. 32: 1637.

Mirolli, M. 1979a. The electrical properties of a crustacean sensory dendrite. J. Exp. Biol. 78: 1-27.

Mirolli, M. 1979b. Electrogenic Na^+ transport in a crustacean coxal receptor. J. Exp. Biol. 78: 29-45.

Mirolli, M. 1981. Fast inward and outward current channels in a non-spiking neurone. Nature, 292: 251-253.

Mirolli, M. 1983. Inward and outward currents in isolated dendrites of crustacea coxal receptors. Cell. and Molec. Neurobiol. 3: 355-370.

Miyan, J.A. and D.M. Neil. 1986a. Phase-dependent modulation of auxilliary swimmeret muscle activity in the equilibrium reactions of the Norway lobster, *Nephrops norvegicus* L. J. Exp. Biol. 126: 157-179.

Miyan, J.A. and D.M. Neil. 1986b. Swimmeret proprioceptors in the lobsters *Nephrops norvegicus* L. and *Homarus gammarus* L. J. Exp. Biol. 126: 181-204.

Moran, D.T. and F.G. Varela. 1971. Microtubules and sensory transduction. Proc. Nat. Acad. Sci. 68: 757-760.

Nadol, J.B., Jr. and A.J.D. de Lorenzo. 1969. Observations on the organization of the dendritic processes and receptor terminations in the abdominal muscle receptor organ of *Homarus*. J. Comp. Neurol. 137: 19-58.

Neil, D.M., D.L. Macmillan and M.S. Laverack. 1976. The structure and function of thoracic exopodites in the larvae of the lobster, *Homarus gammarus*. Philos. Trans. Roy. Soc. London B, 274: 53-68.

Pabst, H. and D. Kennedy. 1967. Cutaneous mechanoreceptors influencing motor output in the crayfish abdomen. Z. Vergl. Physiol. 57: 190-208.

Pasztor. 1979. The ultrastructure of the oval organ a mechanoreceptor in the second maxilla of decapod crustacea. Zoomorphologie, 193: 171-191.

Pasztor, V.M. and B.M.H. Bush. 1982. Impulse-coded and analog signaling in single mechanoreceptor neurons. Science, 215: 1635- 1637.

Pasztor, V.M. and B.M.H. Bush. 1983a. Graded potentials and spiking in single units of the oval organ, a mechanoreceptor in the lobster ventilatory system I. characteristics of dual affferent signalling. J. Exp. Biol. 107: 431-449.

Pasztor, V.M. and B.M.H. Bush. 1983b. Graded potentials and spiking in single units of the oval organ, a mechanoreceptor in the lobster ventilatory system II. individuality of the three afferent fibres. J. Exp. Biol. 107: 451-464.

Pasztor, V.M. and B.M.H. Bush. 1987. Modulation of the receptor potential in crustacean mechano-sensitive afferent neurons by proctolin, serotonin and octopamine. Neurosci. Abstr. 13: 143.

Paul, D.H. 1971a. Swimming behavior of the sand crab, *Emerita analoga* (Crustacea, Anomura). I. analysis of the uropod stroke. Z. Vergl. Physiol. 75: 233-258.

Paul, D.H. 1971b. Swimming behavior of the sand crab, *Emerita analoga* (Crustacea, Anomura). II. morphology and physiology of the uropod neuromuscular system. Z. Vergl. Physiol. 75: 259-285.

Paul, D.H. 1971c. Swimming behavior of the sand crab, *Emerita analoga* (Crustacea, Anomura). III. Neuronal organization of uropod beating. 286-302. Z. Vergl. Physiol. 75: 233-302.

Paul, D.H. 1972. Decremental conduction over "giant" afferent processes in an arthropod. Science, 176: 680-682.

Paul, D.H. 1976. Role of proprioceptive feedback from non-spiking mechanosensory cells in the sand crab, *Emerita analoga*. J. Exp. Biol. 65: 243-258.

Paul,D.H. 1981. Homologies between body movements and muscular contractions in the locomotion of two decapods of different families. J. Exp. Biol. 94: 159-168.

Paul, D.H. 1981. Homologies between neuromuscular systems serving different functions in two decapods of different families. J. Exp. Biol. 94: 169-187.

Paul, D.H. 1985. Intracellular analysis of uropod stretch receptor input in the terminal ganglion of the crab *Emerita analoga*. Neurosci. Abstr. 11:1023.

Paul, D.H. 1987. Proprioceptive and tactile integration by identified interneurons in the sand crab *Emerita*. Neurosci. Abstr. 13: 142.

Paul, D.H. 1988. A neurophylogenist's view of decapod crustacea. Bull. Mar. Sci. (in press).

Paul, D.H., A.M. Then and D.S. Magnuson. 1985. Evolution of the telson neuromusculature in decapod crustacea. Biol. Bull. 168: 106-124.

Pearson, K.G. 1976. Nerve cells without action potentials. In: Simpler networks and behavior. Eidted by J.C. Fentress. Sinauer, Sunderland, Mass. 99-110.

Perrachia, C. 1981. Direct communication between axons and sheath cells in crayfish. Nature, 290: 597-598.

Peterson, R.P. and F.A. Pepe. 1961. The fine structure of inhibitory synapses in the crayfish. J. Biophys. Biochem. Cytol. 11: 157-169.

Pitman, R.M., C.D. Tweedle and M.J. Cohen. 1972. Branching of central neurons: intracellular cobalt injection for light and electron microscopy. Science, 176: 412-414.

Poppele, R.E. and D.C. Quick. 1985. Effect of intrafusal muscle mechanics on mammalian muscle spindle sensitivity. J. Neurosci. 5: 1881-1885.

Reynolds, E.S. 1963. The use of lead citrate at high pH as an electron-opaque stain in electron microscopy. J. Cell. Biol. 17: 208.

Richardson, K. C., L. Jarett and E.H. Finke. 1960. Embedding in epoxy resins for ultrathin sectioning in electron microscopy. Stain Tech. 35: 313-323.

Ripley, S.H., B.M.H. Bush and A. Roberts. 1968. Resistance reflexes from a crab muscle receptor without impulses.Nature, 218: 1170-1171.

Roberts, A. and B.M.H. Bush. 1971. Coxal muscle receptors in the crab: the receptor current and some properties of the receptor nerve fibres. J. Exp. Biol. 54: 515-524.

Ross, R. and P. Bornstein. 1971. Elastic fibers in the body. Sci. Amer. 224: 44-52.

Shepherd, G. 1988. Neurobiology (2nd ed.) Oxford University Press, Oxford. p. 63.

Shivers, R.R. and M.W. Brightman. 1976. Trans-glial channels in ventral nerve roots of crayfish. J. Comp. Neurol. 167: 1-26.

Sillar, K.T. and R.C. Elson. 1986a. Slow active potentials in walking-leg motor neurones triggered by non-spiking proprioceptive afferents in the crayfish. J. Exp. Biol. 126: 445- 452.

Sillar, K.T., P. Skorupski, R.C. Elson and B.M.H. Bush. 1986b. Two identified afferent neurones entrain a central locomotor rhythm generator. Nature, 323: 440-443.

Skinner, K. 1985. The structure of the fourth abdominal ganglion of the crayfish, Procambarus clarki(Girard). II. Synaptic neuropils. J. Comp. Neurol. 234: 182-191.

Tao-Cheng, J.H., K. Hirosawa and Y. Nakajima. 1981a. Ultrastructure of the crayfish slowly-adapting stretch receptor in relation to its function. J. Comp. Neurol. 200: 1-21.

Tao-Cheng, J.H., K. Hirosawa , Y. Nakajima and H. Peng. 1981b. A freeze-fracture study of the crayfish stretch receptor. J. Comp. Neurol. 200: 23-38.

Thomas, J.B.. M.J. Bastiani, M. Bate and C.S. Goodman. 1984. From grasshopper to *Drosophila*: a common plan for neuronal development. Nature, 310: 203-207.

Wainwright, S.A., W.D. Biggs, J.D. Currey and J. M. Gosline. 1976. Mechanical design in organisms. Edward Arnold, London. p. 118.

Whitear, M. 1965. The fine structure of crustacean proprioceptors. II. The thoracico-coxal organs in *Carcinus*, *Pagurus* and *Astacus*. Phil. Trans. Royal Soc. B, 248: 437-456.

Wiersma, C.A.G., E. Furshpan and E. Florey. 1953. Physiological and pharmacological observations on muscle receptor organs of the crayfish, *Cambarus clarkii* girard. J. Physiol. 30: 136-150.

Wilson, L.J. and D.H. Paul. 1987. Tailflipping of *Munida quadrispina* (Galatheidae): conservation of behavior and underlying musculature with loss of anterior contralateral flexor motoneurons and motor giant. J. Comp. Physiol. 161: 881-890.

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WILSON, L.J. and D.H. PAUL. 1987. Functional Morphology of nonspiking uropod stretch receptors in the sand crab (*Emerita analoga*) Neuroscience Abstracts 13:142.

WILSON, L.J. and D.H. PAUL. 1986. Swimming of a galatheid crab: tailflipping behavior and the flexor motoneurons. First International Congress of Neuroethology Proceedings page 80.

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The Functional Morphology of the Uropod Stretch Receptor of the Sand Crab *Emerita analoga* Including a Comparison With the Uropod Stretch Receptor of the Squat Lobster *Munida quadrispina*.

Linda J. Wilson

15 June 1988