

A COMPARATIVE STUDY OF PROPRIOCEPTION IN
THE APPENDAGES OF DECAPOD CRUSTACEANS

William Wales

A Thesis Submitted for the Degree of PhD
at the
University of St Andrews



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A Comparative Study of Proprioception in the
Appendages of Decapod Crustaceans

by

William Wales

Gatty Marine Laboratory,
University of St. Andrews

1971

A thesis submitted for the degree of
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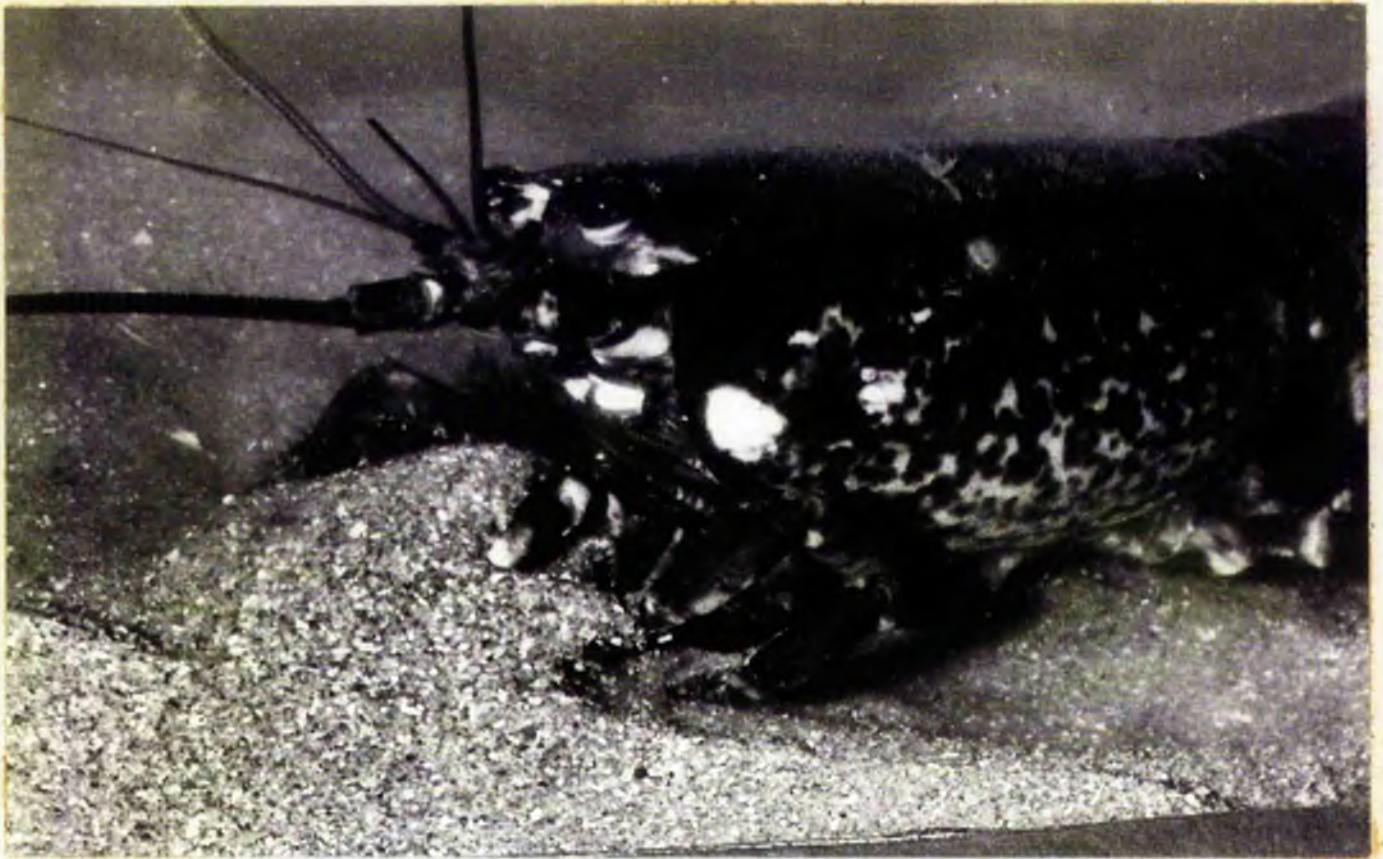
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FRONTISPIECE. The common lobster, Homarus gammarus, using its 3rd maxillipeds and 2nd and 3rd pereopods as a scoop to excavate sand. The large chelae are not normally involved in this process and have been removed by induced autotomy so that the other appendages may be seen more clearly.



SUPERVISOR'S CERTIFICATE

I certify that William Wales has fulfilled the conditions laid down under Ordinance No. 16 of the University Court, St. Andrews, and is accordingly qualified to submit this thesis for the degree of Doctor of Philosophy.

DECLARATION

I declare that the work reported in this thesis is my own and has not previously been submitted for any other degree.

VITAE

I was educated at Grove Academy, Broughty Ferry, Angus and subsequently at Tay Street College for Further Education, Dundee, Angus. I attended the University of St. Andrews as an undergraduate from October, 1964 to June, 1968 and graduated in Zoology. The work reported in this thesis was carried out between September, 1968 and March, 1971.

ACKNOWLEDGEMENTS

I wish to express my gratitude to Professor M.S. Laverack for his encouragement and helpful discussion given freely throughout this study. I am also grateful to the technical and administrative staff of the Gatty Marine Laboratory for willing assistance amiably rendered and am particularly grateful to Roland Jack, Charles Roemméle and John Stevenson.

I am indebted to my wife who typed this manuscript and to Mrs. W.M. Grace both of whom have tolerated and consoled me in times of despondency.

CONTENTS LIST

	<u>Page</u>
<u>SUMMARY</u>	i
<u>INTRODUCTION</u>	1
<u>EXPERIMENTAL</u>	
Section 1. PROPRIOCEPTION IN THE PEREPIOPOD	
Part 1.1. Introduction	8
1.2. Materials and Methods	10
1.3. Morphology of the Limb Joints and Associated Proprioceptors of <u>Homarus</u>	13
1. Thorax-Coxopodite and Coxopodite- Basipodite Joints (T-C, C-B)	14
2. Basipodite-Ischiopodite Joint (B-I)	15
3. Ischiopodite-Meropodite Joint (I-M)	16
4. Meropodite-Carpopodite Joint (M-C)	17
5. Carpopodite-Propodite Joint (C-P)	18
6. Propodite-Dactylopodite Joint (P-D)	20
7. Cuticular Articulated Peg Sensilla (CAP)	21
1.4. Receptors of the Basi-ischiopodite Region and Autotomy Plane of Reptantian Decapods	23
1. Brachyura	23
2. Anomura, Superfamily Galatheidae	29
3. Macrura, Superfamily Nephropsidae	30
4. Macrura, Superfamily Scyllaridae	34
1.5. Responses of the Limb Joint Proprioceptors	37
1. Response of CP2 and Rotation of the C-P Joint	37
2. Response of CAP Sensilla to Mechanical Stimulation	38

1.6.	Cuticular Stress Detection in the Basi-ischiopodite of the Reptantian Decapods	39
1.	Responses of the CSD Receptors to Different Modes of Stimulation	39
1.a.	Response to Waterborne Vibrations	39
1.b.	Response to Substrateborne Vibrations	40
1.c.	Stimulation of the Soft Cuticle	40
1.d.	Response to Increased Tension in the Tendons of the C-B Joint Muscles	42
1.e.	Responses of the CSD receptors to Joint Movement	43
2.	Responses of the CSD Receptors During Autotomy	45
3.	Post Autotomy Responses in CSD.1	47
3.a.	Stimulation of the Soft Cuticle	47
3.b.	Stimulation of the Breakage Plane Membrane	47
3.c.	Movement of the Regenerating Limb Bud	48

Section 2. PROPRIOCEPTION IN THE 3RD MAXILLIPED

Part	2.1. Introduction	49
	2.2. Materials and Methods	51
	2.3. Morphology of the Limb Joints and Associated Proprioceptors of <u>Homarus</u>	52
	1. Thorax-Coxopodite and Coxopodite-Basi-ischiopodite Joints (T-C, C-B)	53
	2. Basipodite-Flagellum Joint (B-F)	54
	3. Basipodite-Ischiopodite Joint (B-I)	55
	4. Ischiopodite-Meropodite Joint (I-M)	55
	5. Meropodite-Carpopodite Joint (M-C)	56
	6. Carpopodite-Propodite Joint (C-P)	56
	7. Propodite-Dactylopodite Joint (P-D)	57
	8. Cuticular Articulated Peg Sensilla (CAP)	58
	2.4. Receptors of the Basi-ischiopodite Region and Autotomy Plane of <u>Homarus</u>	59

2.5. Responses of the Limb Joint Proprioceptors.	61
1. C-B Joint Receptor	61
2. I-M Joint Receptors	61
3. M-C Joint Receptor	62
4. C-P Joint Receptor	63

Section 3. PROPRIOCEPTION IN THE MANDIBLE

Part 3.1. Introduction	65
3.2. Materials and Methods	66
3.3. Morphology of the Mandible and its musculature	68
1. Skeletal Anatomy	68
2. Musculature	69
2.a. The Ventral Muscle Group	70
2.b. The Anterior Muscle Group	71
2.c. The Posterior Muscle Group	71
2.d. Muscles of the Mandibular Palp	72
3.4. The Mandibular Innervation	74
1. Inner Mandibular Nerve (imn)	74
2. Outer Mandibular Nerve (omn)	75
3.5. The Mandibular Muscle Receptor Organ	78
1. Mandibular MRO Morphology	78
1.a. The Receptor Muscle	78
1.b. Afferent and Efferent Innervation	80
1.c. The Sensory Cells	82
2. Responses of the Mand. MRO to Mechanical Stimuli	83
2.a. Afferent Activity on Direct Stimulation of The Receptor Muscle	83
2.b. Afferent Responses to Mandibular Movements	84
2.c. Sensory Unit Types	85
3.6. The Posterior Stomach Nerve (omn 4)	88
1. Afferent Activity in the PSN	89

DISCUSSION

Part 1. The Definition of a Proprioceptor	91
2. The Connective Chordotonal Organs of the limb joints	92
3. The C-P Joint and its Additional Muscle	96
4. The CAP Sensilla	98
5. The Cuticular Stress Detector (CSD) Organs	100
5.a. Determination of the Normal Stimulus	102
5.b. Classification of Unit Types	105
5.c. The Autotomy Mechanism and the Association of the CSD Organs with the Breakage Plane	107
5.d. Receptor Function	111
6. The Evolution of the Crustacean Connective Chordotonal Organs	118
7. Proprioception in the Nephropsidae Mandible	119
7.a. Muscle Receptor Organs of the Decapod Crustacea	123
7.b. A Comparison of the Multiterminal Muscle Receptor Organs of Decapods	124
7.c. Afferent Unit Activity in Muscle Receptor Organs	128
7.d. Muscle Receptor Organ Function	135

<u>CONCLUSIONS</u>	138
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<u>SUGGESTIONS FOR FURTHER WORK</u>	141
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<u>APPENDIX I</u>	144
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<u>APPENDIX II</u>	152
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<u>REFERENCES</u>	154
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SUMMARY

1. The number and structure of the chordotonal organs present at all joints between the coxopodite and dactylopodite of the pereopods and 3rd maxilliped of the macruran Homarus gammarus L are described. As the form of the receptors depends to some degree upon the structure of the joint I have included details of musculature, planes of movement and degrees of freedom at each joint.
2. The 3rd maxilliped has a smaller number of chordotonal organs than the pereopod, in particular at the mero-carpopodite and carpo-propodite joints where only one organ is present. The response of these receptors shows considerable differences from the corresponding receptors in the pereopod.
3. The structure of the carpo-propodite joint of both limbs is discussed in detail as this joint differs greatly from that of the Brachyura as a third muscle is present. In the pereopod this joint is capable of rotation about the longitudinal axis but the additional muscle does not appear to produce this rotation. A small number of units in the CP2 receptor respond to rotation.
4. Cuticular sensilla (CAP organs) are described at the mero-carpopodite and carpo-propodite joints in both limbs and at the I-M joint of the pereopod.
5. Situated in the basi-ischiopodite of the brachyuran Carcinus maenas are two receptors which resemble the

chordotonal receptors of the limb articulations but are obviously not part of the series associated with the joints. The receptors have large numbers of bipolar neurones with their dendrites embedded in distinct connective tissue strands which insert onto discrete areas of thin or soft cuticle. The receptor strands do not span a limb joint nor do they attach to a muscle or its tendon. The receptors are referred to as cuticular stress detectors (CSD). CSD.1 lies proximal to the preformed breakage plane and the area of cuticle, onto which the strand inserts, lies close to the attachment of the anterior levator muscle tendon (autotomiser muscle). CSD.2 which lies distal to the breakage plane is located in the ventral ischiopodite.

6. Because of the proximity of the receptors to the preformed breakage plane the external cuticular features of the basi-ischiopodite and the musculature of the coxo-basipodite joint are described in some detail.
7. Comparative details are given for representative species of the Macrura and Anomura. The nephropsideans, Macrura, are particularly interesting as only the 1st pereopod, chela, exhibits true autotomy but both receptors are present in all the pereopods.
8. A third group of bipolar neurones is described in Palinurus vulgaris where they innervate the membrane that seals the aperture after breakage.

9. The dual role of the two levator muscles in both posture control and autotomy and possible functions of the CSDs are discussed at length.
10. The CSD organs respond to pressure applied to the basi-ischiopodite and upon deformation of the discrete areas of soft cuticle onto which the connective tissue strands of the receptors insert. The CSDs exhibit a wide range of unit activity and both receptors have a similar population of unit types. Some units are active only on application or removal of a force applied to the soft cuticle but a large number of phaso-tonic and tonic units respond to a constant pressure applied to the soft cuticle. The majority of the units respond during application of the stimulus (ON units) but a small proportion of the units increase activity on removal of the stimulus (OFF units).
11. Passively produced tension in the anterior levator (autotomiser) muscle and depressor muscle tendons of the C-B joint is a potent stimulus to both receptors.
12. Both receptors respond to movement of the B-I joint of the Nephropsidae walking leg and to movement of the I-N joint in the pereopods of other reptantian decapods where the basipodite and ischiopodite have fused. The degree of activity is not directly related to the joint position or direction of movement.
13. During autotomy both receptors respond strongly, particularly CSD.1. CSD.2 also shows increased

activity but as the receptor is located distal to the breakage plane the receptor nerve is severed when breakage occurs.

14. After autotomy CSD.1 responds normally to deformation of the soft cuticle but manipulation of the breakage plane membrane or of the regenerating limb bud produces low levels of activity even though the stimulus is gross.
15. The possible functional roles of the CSD receptors are discussed.
16. The skeletal anatomy, innervation and complex musculature of the mandible of Homarus gammarus are described.
17. The proprioceptors of the mandible are primarily based on multiterminal sensory neurones. There are two main proprioceptive inputs 1) the mandibular muscle receptor organ 2) the posterior stomach nerve.
18. The mandibular muscle receptor organ (Mand. MRO) consists of a ribbon of muscle innervated at its ventral insertion by 10-20 multiterminal sensory neurones. The sensory cells have a small number of dendritic processes. The receptor muscle exhibits some structural properties of both fast and slow muscle.
19. The Mand. MRO sensory units respond to receptor muscle contraction and to passive stretch indicating the adequate stimulus to be receptor muscle tension.

The receptor monitors the degree and rate of change of muscle tension. The units which are tonic are largely alike but some aberrant units are described.

20. The possible function of the Mand. MRO is discussed with reference to other muscle receptor organs.
21. A number of cells in the posterior stomach nerve (omn 4) overlying the lateral mandible articulation innervate the hypodermis of this region. These cells are multiterminal and in some cases the processes innervate widely separated sensory fields. The sensory neurones appear to be position sensitive rapidly adapting units.
22. An interesting group of cells is described (omn 2/3/4 connective) which may prove to have some sensory function.

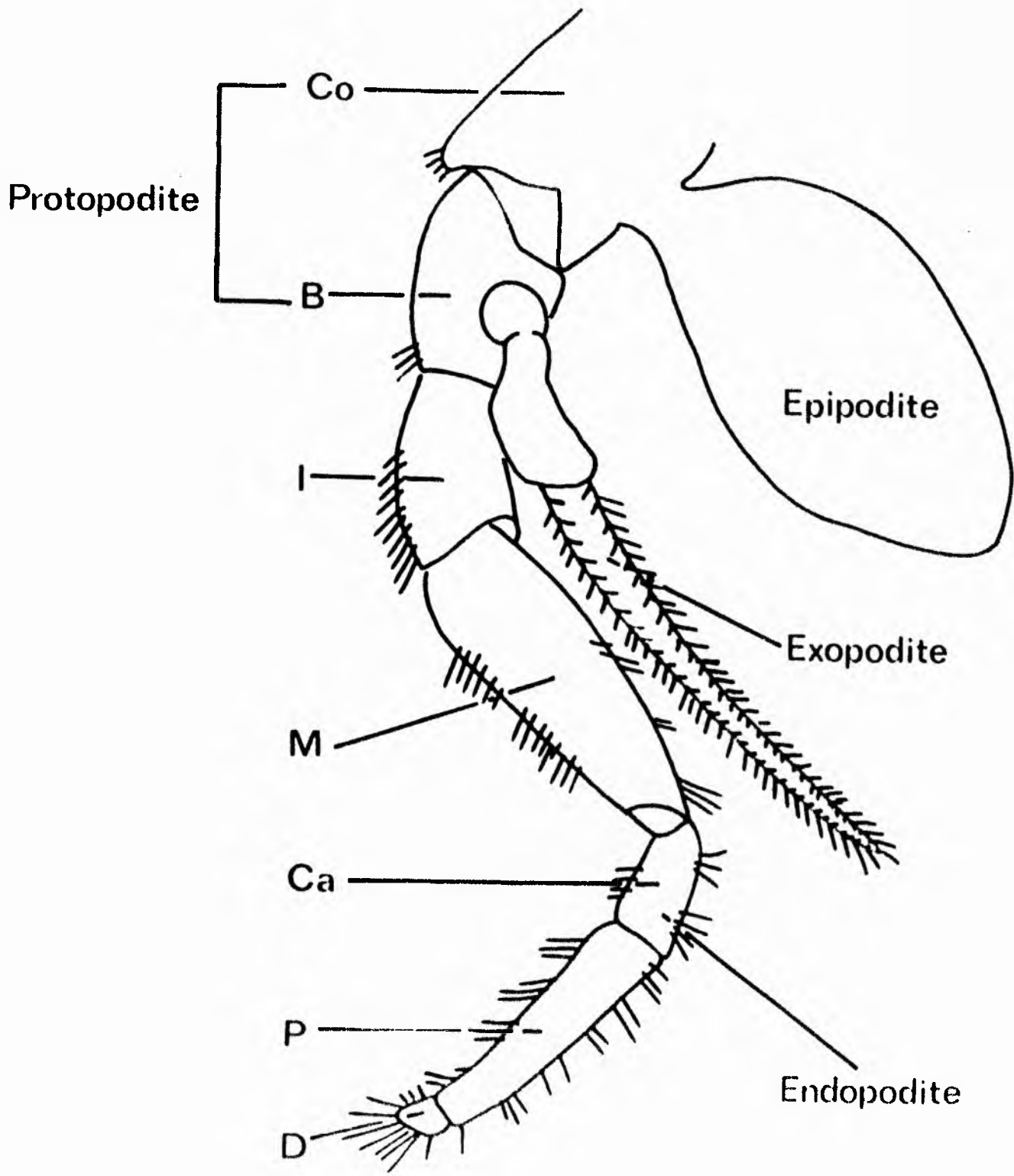
INTRODUCTION

INTRODUCTION

It is generally accepted that the post-antennular limbs of primitive crustaceans were alike (Borradaile, 1917; Snodgrass, 1950). This conjecture has been formed, in the absence of fossil evidence, by analogy with the Trilobites, which, though they are not ancestral to the extant arthropods are considered to give indications as to what the anatomy of the ancestral forms may have been (Snodgrass, 1952). All the trilobite appendages, with the exception of the filamentous antennae, were uniramous ambulatory limbs consisting of eight (Snodgrass, 1952) or possibly nine segments (Stormer, 1944). Stormer's argument that the proximal rim of the coxa is a separate segment is difficult to uphold in the absence of evidence demonstrating that it was at some stage articulated with the coxa and had a separate musculature. The trilobite limb carried an epipodite on the coxa but was uniramous.

Most authors agree that the appendages of the ancestral crustacea were biramous though there is some dispute as to whether they were phyllopodial, swimming, or stenopodial, ambulatory, limbs. The pereopods of the syncaridian, Anaspides tasmaniae may be considered to represent the generalised form of the crustacean appendage (Snodgrass, 1952; Waterman and Chase, 1960). This limb (Fig. 1) consists of a protopodite which is divided into two podomeres, a coxopodite and basipodite. The coxopodite bears one or more epipodites and the basipodite bears two rami, the exopodite and endopodite. It is the endopodite which forms the walking leg of the reptantian decapods and typically it consists of five segments, the ischiopodite, meropodite, carpopodite, propodite and dactylopodite.

FIG. 1. The generalised malacostracan appendage as typified by the pereopod of the syncardian, Anaspides tasmaniae. This illustration is of the right 5th pereopod. (After Waterman and Chace, 1961).
Segments: coxopodite (Co), basipodite (B), ischiopodite (I), meropodite (M), carpopodite (Ca), propodite (P), dactylopodite (D).



Thus the walking leg of the decapods has seven podomeres, one less than trilobites. This apparent anomaly is due to "The coincidental occurrence of a patella and of two segments in the trochanteral region" (Snodgrass, 1952), a situation which also occurs in the Pycnogonida and some arachnids. As the segmental appendages of the decapod crustacea are developed from the same ancestral appendage it is possible in most cases to identify the homologous parts of the limbs.

The common lobster, Homarus gammarus (L), was chosen for this study because of its large size and because its appendages are much more accessible than those of the other decapod groups. It was, however, necessary to expand the study to include other decapods when studying the preformed breakage plane which is not well developed in the walking legs of the nephropsidean decapods. The cephalothorax of Homarus has thirteen appendage bearing segments but only four pairs of these appendages are ambulatory. None of the abdominal appendages are used in walking. The posterior three cephalic appendages, the mandible, 1st and 2nd maxilla and the anterior three thoracic appendages, the 1st, 2nd and 3rd maxillipeds, are jointly described as the "mouthparts" (Borradaile, 1917, 1922). This is something of a misnomer as the primary function of the 2nd maxilla and 1st maxilliped is the production of a respiratory current and there is little evidence that they are involved in feeding. The remaining appendages, however, are clearly functional in the feeding process as are the first three pairs of pereiopods.

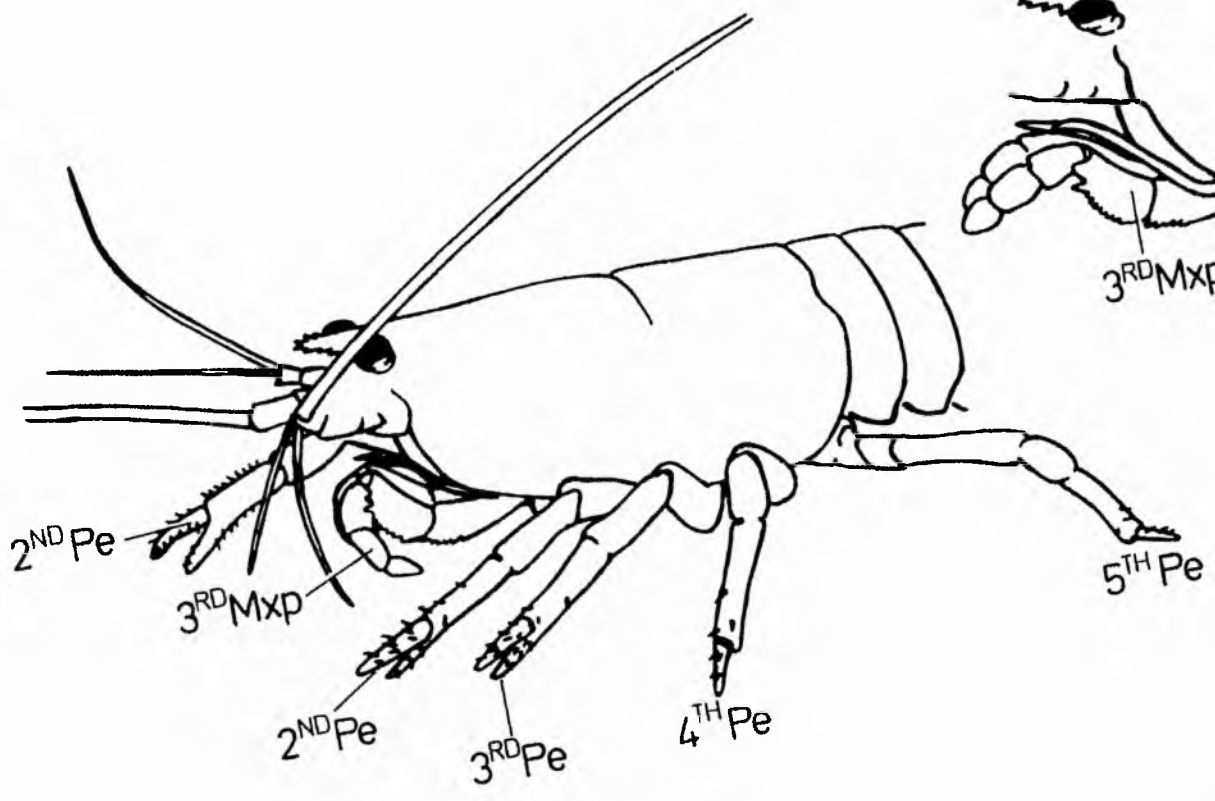
The appendages chosen for this comparative study were the walking leg, as typified by the 2nd pereiopod,

the 3rd maxilliped and the mandible. The pereopod (Figs. 2, 3 and 4) is the standard limb of which most is known (see Appendix 1). It is an elongate cylindrical uniramous appendage, the exopodite being absent, which bears no close resemblance to the pereopod of Anaspides. The 3rd maxilliped (Figs. 2, 33 and 34) is structurally similar to the generalised crustacean limb and may be considered to be morphologically the most primitive of the three limbs studied. However, this appendage has become specialised for a function other than walking and cannot be said to be functionally primitive. The third of the three appendages, the mandible, is reduced in its number of podomeres to such a degree that it is difficult to identify it with the limb from which it is believed to have developed. The most leg-like mandible occurs in the ostracod Philomedes globosa (Snodgrass, 1950) but it has the reduced number of podomeres corresponding to that of the Homarus mandible. As shown by Snodgrass (1950), the small exopodite borne by the second segment of the mandible in some species identifies this segment as the basipodite and hence the main body of the mandible is a coxopodite. The mandible and the first segment of the palp in Homarus form the protopodite, the epipodite and the exopodite are absent and the endopodite is represented by the two distal segments of the palp.

The proprioceptive systems in the appendages of higher crustaceans are based upon the connective chordotonal organ. The chordotonal organs of Arthropods have received considerable attention by anatomists and electrophysiologists alike. In the Insecta, chordotonal sensilla are associated with a wide variety of accessory structures and are found

FIG. 2. A. An outline drawing traced from a photograph of Homarus gammarus (L) in a normal resting stance. The 1st pereopods, chelae, have been removed by autotomy to allow the 3rd maxillipeds (Mxp) and other pereopods (pe) to be seen more clearly. See text for descriptions of limb usage. B. Demonstrates the 3rd maxillipeds held in the extended position.

A.



B.



in large numbers forming complex organs such as the subgenual organ and crista acoustica in the walking legs of tettigonids or Johnston's organ of the Culicid mosquitoes (Bullock and Horridge, 1965). The chordotonal organs of the reptantian decapods, which provide excellent experimental preparations by virtue of their larger size and accessibility, have remained relatively morphologically unspecialised. With the exception of the flagellar chordotonal organ, FCO, of the antenna (Taylor, 1967a) and possibly the myochordotonal organ, MCO, of the walking leg (Clarac, 1968a), the crustacean chordotonal organs consist of strands or sheets of connective tissue in which the scolopidia of the chordotonal sensilla are embedded (Whitear, 1962). These connective chordotonal organs are either associated with the muscles or their tendons, at the limb joints or have strands which span the limb joints. They have not been described in association with other accessory structures.

Howse (1968) has proposed that the term "connective chordotonal organ" be restricted to those organs in which the scolopidia are contained in a connective tissue strand and which span body segments. However, such a definition is not suitable for application to the crustacean chordotonal organs as several of the connective chordotonal organs in the appendages of the decapods do not actually span the joint as is the case with the BI, IM1, MC1 and CP1 receptors of the walking leg (see Fig. 4). I have therefore used the term to include all chordotonal receptors which have a distinct connective tissue strand.

Our knowledge of crustacean limb proprioceptors is, with few exceptions, limited to the brachyuran walking leg.

The series of chordotonal receptors for the three peripheral joints in the antennule is described by Wyse and Maynard (1965) in the macruran Panulirus argus and for the two proximal joints by Sandeman (1963) in the stomatopod Squilla mantis, but it is not possible to make comparisons between this cephalic appendage and the walking leg (Snodgrass, 1950). The proprioceptors of the 2nd maxilla have been investigated in a number of macruran species by Pasztor (1969) and no chordotonal organs of the type found in the pereopods have yet been described.

At some articulations the connective chordotonal organs are supplemented or replaced by muscle receptor organs (MRO), e.g. at the thoracic-coxopodite joint of the pereopod, or a connective chordotonal organ may have become associated with a muscle at the limb joint. The MROs of the decapod crustacea are diverse in their structure and location. MROs have been described in the thorax, abdomen and pereopods (Alexandrowicz, 1967a,b; Alexandrowicz and Whitear, 1957; Clarac, 1968a; Clarac and Masson, 1969; Wiersma and Pilgrim, 1961). The myochordotonal organ of the pereopod is the only known receptor innervated by uniterminal bipolar cells similar to those of the chordotonal organs at the other limb joints (Clarac, 1968a). The MROs of the thorax and abdomen are innervated by small numbers of multipolar or bipolar multidendritic cells, one cell innervating each muscle. The median thoracic MRO of Leander serratus is an exception in that it is innervated by 4 cells but this has been attributed to the regression of the MROs of the 5th to 8th thoracic segments (Alexandrowicz, 1956). The total number of sensory cells innervating the thoracic-

coxopodite MRO is uncertain but only two sensory fibres (S & T) have so far been shown to respond to muscle stretch (Ripley, Bush and Roberts, 1968).

Elastic strands innervated by multiterminal sensory neurones have been described in the coxopodite (Alexandrowicz and Whitear, 1957; Alexandrowicz, 1958) and in the terminal region of the oesophagus overlying the mandible and paragnatha (Dando and Laverack, 1968; Laverack and Dando, 1968). The latter receptors, though possibly important in monitoring mandibular movement, do not respond to mandibular movement alone (Laverack and Dando, 1968; Moulins, Dando and Laverack, 1970).

The work described in this thesis was undertaken for a number of reasons:-

- 1) Pringle (1961) rightly contends that analysis of the co-ordination of arthropod movements requires that the catalogue of proprioceptors needs extending. It would also seem profitable to learn as much as possible of proprioception in the decapod crustaceans which, by virtue of their size and simple joint musculature generally innervated by a small number of motoneurons, lend themselves admirably to the electrophysiological analysis of walking (Atwood and Walcott, 1965; Barnes, private communication; Clarac and Wales, 1970; Spirito, Evoy and Barnes, unpublished). Dando (private communication) has recently discovered tension sensitive receptors in the apodeme of a crustacean leg muscle. Thus, although our knowledge of the joint movement and position sensitive connective chordotonal organs may be well advanced there are most probably other forms of proprioceptor not yet described.
- 2) It was hoped to learn something of the degree to which

proprioceptor morphology is related to the structure, function and relative importance of the limb joint at which it is located by comparing the proprioceptors at the same joint in different appendages. Details have therefore been given of the anatomy of each limb including the musculature, cuticular structure and degrees of freedom of the limb joints.

3) The work of Pasztor (1969) has shown that the proprioceptive organs of the 2nd maxilla are not of the same type as found in the pereopod. It was therefore of interest to see how the proprioceptive requirements of the three anatomically and functionally different limbs had been met.

Functional analysis of proprioceptors located in the basipodite and ischiopodite of the common lobster, required that for these receptors the study be extended to include the other sections of reptantian decapods but otherwise this thesis remains a comparative study of the proprioceptors present in the mandible, 3rd maxilliped and pereopod of Homarus gammarus (L). In some places, however, reference is made to the brachyuran pereopod as this is the limb which has been best described (see Appendix 1).

EXPERIMENTAL

1. PROPRIOCEPTION IN THE PERIPOD

1.1. Introduction

The walking leg, as typified by the 2nd pereopod, is the largest and most accessible appendage of the decapod crustaceans and the connective chordotonal organs of the brachyuran walking leg form one of the best described proprioceptive systems in the invertebrates (Finlayson, 1968). The proprioceptive organs of the corresponding macruran limb are incompletely known and are described here. Appendix 1 summarises the literature published on the proprioceptive systems of decapod appendages to the end of 1970.

The 2nd pereopod is mainly concerned with support and locomotion and lobsters can progress equally well in any direction, unlike the crabs which are more proficient in lateral movement. The pereopods of the lobster are also involved in gathering food particles, which they pass forward to the maxillipeds and in cleaning of the cephalothorax and abdomen. The pereopods are capable of actions requiring flexibility and precision such as cleaning of the upper carapace and rostral area. They have retained a remarkable degree of flexibility despite the comparative rigidity required for walking.

The walking leg of the brachyuran, Carcinus, on the other hand, has become specialised for lateral rapid movement, and is less flexible than the macruran pereopod having lost the facility to rotate at the C-P joint. It is not chelate. Hence the typical brachyuran pereopod is less effective in manipulative tasks such as cleaning and food handling.

In most reptantian decapods the B-I joint is absent, the basipodite and ischiopodite having fused to form a

single entity with a single line of separation, the preformed breakage plane. Because of its role in autotomy the basi-ischiopodite received some attention in the last two decades of the 19th century and the first two decades of the 20th century (Fredericq, 1883, 1891; Demoor, 1891; Paul, 1915). The work published on autotomy was reviewed by Wood and Wood (1932). Since then only one major work on the mechanism of autotomy has appeared (McVean, 1970). Bliss (1960) summarises the work done on autotomy but the mechanism postulated is largely that of Wood and Wood (1932). To the best of my knowledge only one description of receptors which may be involved in autotomy has appeared (Brousse-Gaury, 1958) and this was in the cricket, Acheta domestica.

The joints of the limbs and the receptors present at these joints will be referred to by the initials of the names of the limb segments between which the joint occurs. For example, the joint between the carpopodite and the propodite is the C-P joint and the receptors present at this joint are CP1 and CP2. The crustacean classification scheme adopted is that of Waterman and Chace (1960).

1.2. Materials and Methods

The species examined in the course of this study were the macrurans Homarus gammarus, Nephrops norvegicus, Astacus leptodactylus and Palinurus vulgaris; the anomurans Pagurus bernhardus and Galathea strigosa; and the brachyurans Carcinus maenas and Hyas araneus. All the species save Astacus and Palinurus were provided by the Gatty Marine Laboratory. The animals were caught locally and maintained in tanks of circulating sea water until required. Astacus and Palinurus were examined during a European Science Exchange Programme study visit to the C.N.R.S. Laboratory in Marseille. I was also able to observe some fixed specimens of the pereiopods of Homarus americanus which were supplied by courtesy of the Fisheries Research Board of Canada.

The external cuticular features of the limb were best observed in fresh preparations but the musculature of the joints was examined by fixing the limb in Bouins fixative (Pantin, 1948) and then dissected in water. The receptors and their innervation were examined by methylene blue staining techniques (see Appendix 2) and in serial wax sections stained in Heidenhains Azan stain (Pantin, 1948).

Electrical activity in the afferent fibres of CP2 was detected via platinum wire electrodes, amplified differentially and recorded by conventional means. Movement of the C-P joint was produced by a micromanipulator-potentiometer system (Shelton and Laverack, 1968).

All experiments on the Cuticular Stress Detectors (Experimental 1.6) were performed on the isolated pereiopod which was removed by cutting through the thoracic

articulation. The extirpated limb was then sectioned through the meropodite and the proximal portion placed in a bath of cold sea water. It was necessary that the method of attachment of the limb in the bath should be rigid, cause a minimum degree of stress in the cuticle of the basi-ischiopodite region and prevent all movement or restrict it to a single joint as required. This problem was overcome by embedding portions of the limb in modelling clay and attaching the clay by pins to the wax-bottomed bath. The effectiveness of this method of attachment and its influence upon the results is discussed at length later.

When stimulating the soft cuticle, on which the receptor strand inserts, the limb was orientated with the soft cuticle approximately normal to the probe of the stimulator. This procedure was adopted to prevent the probe from sliding on the surface of the cuticle. Thus for CSD.1 the limb was placed dorsal surface uppermost, and for CSD.2 either anterior or posterior surface uppermost. The coxopodite was then opened accordingly to expose the nerves from which the recordings were made. The dissection normally necessitated the removal of the anterior levator muscle and tendon to allow recording from CSD.1 but some experiments were performed with the tendon intact to ensure that the method of dissection was not influencing the results. Cuticular hairs lie near the soft cuticle of the receptors and it was necessary to remove these to ensure that the activity recorded was not the response of the hairs to the movement of the probe in the bath.

I-M or B-I joint movement was achieved by embedding the limb in modelling clay so that the ischiopodite or meropodite projected freely above the surface. At all

times it was ensured that the other joints were embedded in their normal resting positions.

Movement of the B-I and I-M joints was produced in a similar manner to that used for the C-P joint. Tension was passively produced in the tendons of the levator and depressor muscles by means of artery forceps mounted on the micromanipulator.

Stimulation of the soft cuticle was achieved by means of a blunted fine insect pin mounted on the moving plate of a miniature 6 v. D.C. relay so that when the circuit was closed the probe moved a distance of approximately 2mm. A diode was connected across the coil of the relay to reduce the switch artefact, and the apparatus was mounted on a Prior micromanipulator to allow accurate positioning of the probe. In practice the probe was positioned so that it was just touching the soft cuticle but not eliciting a response, thence during the period of closure of the switch a reasonably constant pressure was applied via the probe.

Electrical activity of the afferent fibres was detected and recorded as detailed above for CP2.

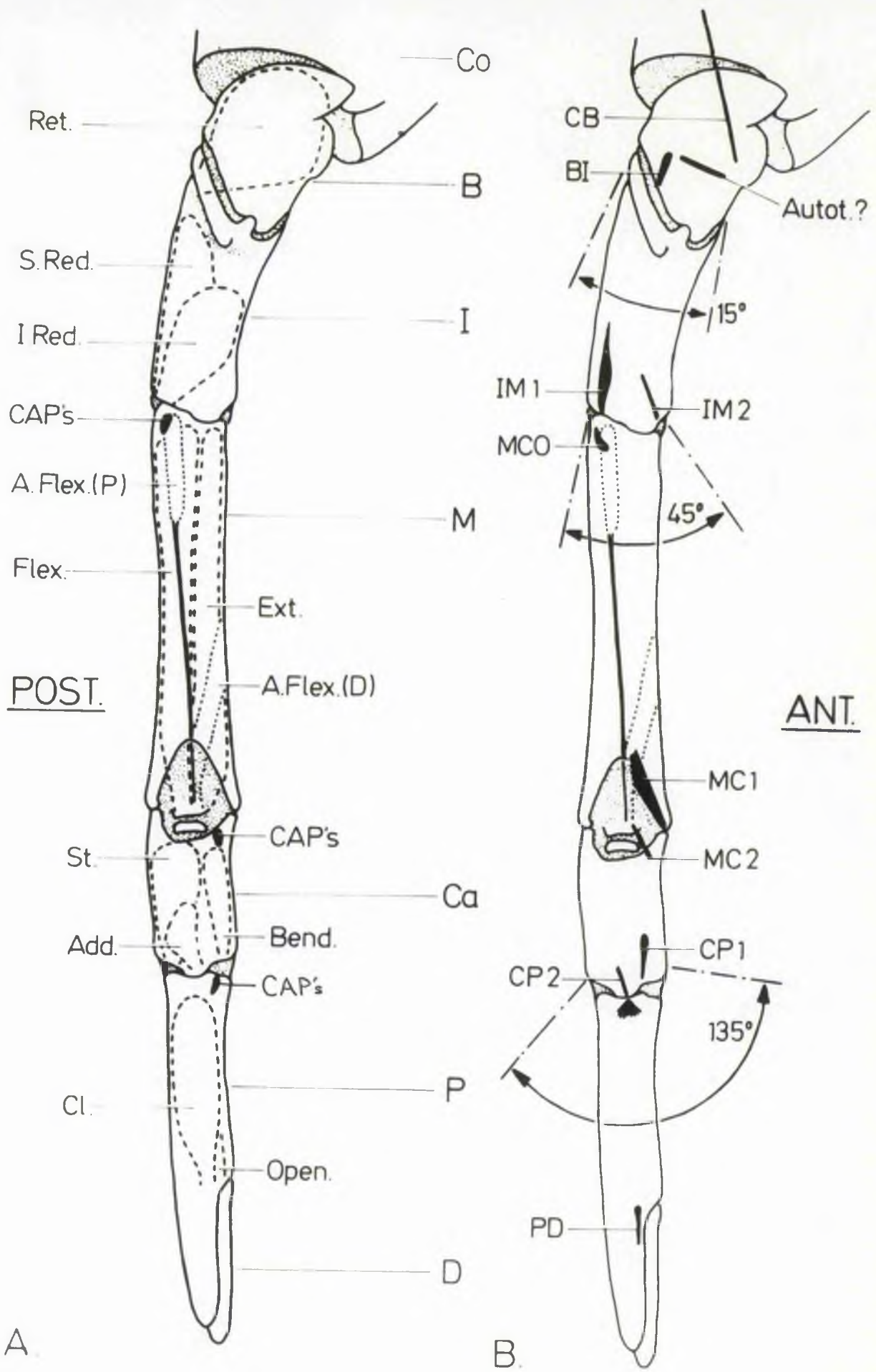
1.3. Morphology of the Limb Joints and Associated Proprioceptors of Homarus

The Homarus walking leg as typified by the second pereopod (Figs. 2, 3 and 4) is different in several ways from the equivalent limb in the brachyuran Carcinus (see Whitear, 1962, Fig. 1). The most striking difference lies in the chelate nature of the P-D joint. In this it differs from the fourth and fifth pereopods of Homarus itself as well as from the brachyuran walking leg. In both groups the first pereopod, of course, forms the great claw.

With the exception of the most proximal segments, the leg of Homarus is ovoid in cross section and of similar width throughout its length. The legs of Carcinus are flattened laterally and are broader at the base, tapering towards the distal extremity. In Carcinus the basipodite and ischiopodite have fused but in Homarus these two segments remain separate. The ischiopodite is of greater length relative to the other leg segments in Homarus (where it is 15-20% of the total leg length) than in Carcinus (where it is only 8-10% of the total length).

The joints of the second pereopod of Homarus allow greater flexibility than occurs in the crab leg. The degrees of movement possible at the respective joints and the planes in which the movements occur are shown in Figs. 3B and 4B. The degree of movement indicated is the maximum possible, not necessarily the movement achieved by the animal and the plane of movement is not always exactly in the plane of the paper. The greatest degrees of freedom in Homarus legs occur at the M-C and C-P joints which permit movement in the dorsal-ventral and anterior-posterior plane respectively. As described later, the

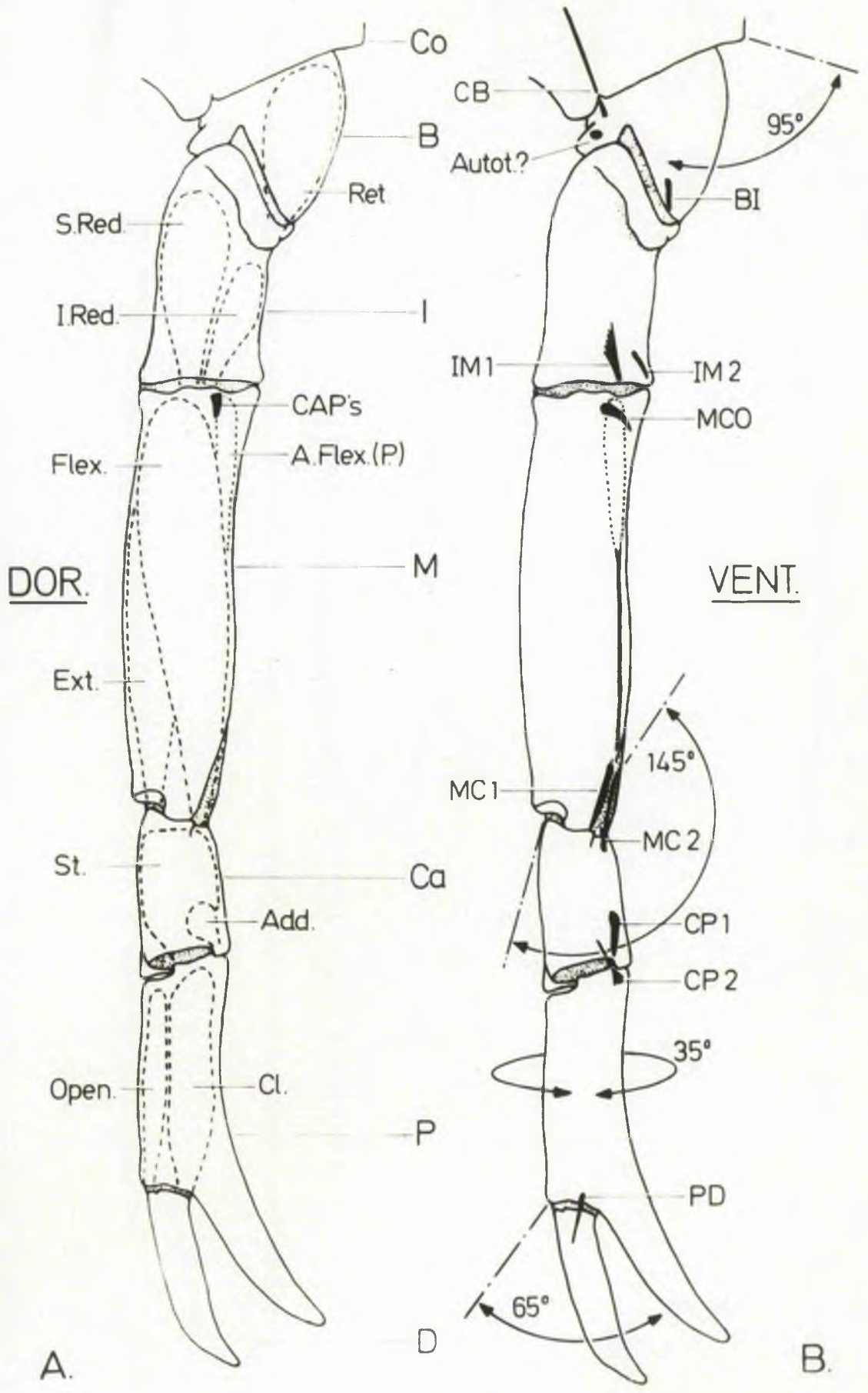
FIG. 3. A and B. Ventral views of a left walking leg of Homarus gammarus with the relevant parts of the internal anatomy shown in transparency. A. To show the musculature and the position of the externally located cuticular articulated peg sensilla (CAPs). B. To show the position of the internal chordotonal organs and the extent of movement possible at each of the joints. Segments: coxopodite (Co), basipodite (B), ischiopodite (I), meropodite (M), carpopodite (Ca), propodite (P), dactylopodite (D). Muscles: retractor (Ret.), superior reductor (S. Red.), inferior reductor (I. Red.), flexor (Flex.), extensor (Ext.), accessory flexor proximal head (A. Flex. (P.)) and distal head (A. Flex. (D.)), stretcher (St.), bender (Bend.), additional muscle (Add.), closer (Cl.), opener (Open.). Receptors: The receptors are named by the initials of the limb segments which constitute the joint at which they are situated. An exception to this rule is the myochordotonal organ (MCO) which responds to movement of the M-C joint although the sensory cells are situated close to the I-M joint. Autot? indicates the position of CSD.1. For the orientation shown, posterior (POST.) and anterior (ANT.) relate to the position of the limb in its normal attitude (see Fig. 2).



A.

B.

FIG. 4. A and B. Posterior views of the left walking legs of Homarus gammarus with the relevant parts of their internal anatomy shown in transparency. A. To show the musculature and the position of the externally located cuticular peg sensilla (CAPs). B. To show the position of the internal chordotonal organs and the extent of movement possible at each of the joints. The lettering is the same as for Fig. 3.



A.

B.

C-P joint is so constructed that the propodite is able to rotate about the longitudinal limb axis. Rotation is not possible at the C-P joint of the chela of Homarus or at any joint of any pereopod of Carcinus. The high degree of freedom at the M-C joints is of value when the animal walks sideways as this joint is responsible for most of the stride. The C-P joint, however, moves only slightly when the animal walks regardless of the direction of movement. Walking in an anterior or posterior direction is achieved by movement at the more proximal joints. Although the basipodite and ischiopodite are not fused, movement at the joint is restricted.

Figures 3 and 4 summarise the anatomy of the walking leg in Homarus gammarus (L). The chordotonal organs and the cuticular articulated peg (CAP) organs lie close to one another and are illustrated on separate diagrams so that their positions may be clearly seen. The muscles of the macruran limbs were named by Schmidt (1915) but where possible I have followed the nomenclature of Bush, Whitear and Wiersma in recent papers on the decapod walking leg.

1.3.1. Thorax-Coxopodite and Coxopodite-Basipodite Joints (T-C, C-B)

The joint primarily responsible for moving the limb in an anterior-posterior direction is the T-C joint and it is largely the muscles of the C-B joint which raise the limb (levators) or apply the limb to the substrate and hence bear the animal's weight (depressors). The coxopodite is moved mainly by the remotor muscle and its antagonist the promotor (see Schmidt, 1915) but, as indicated later, heads of the levator muscles also traverse the T-C joint

and will effect movement of the joint.

Because of their involvement in the production of autotomy the muscles of the C-B joint are described in Section 1.6.

The anatomy of the proprioceptors at the T-C joint has been described by Alexandrowicz and Whitear (1957) for Homarus vulgaris (Milne Edwards) (= Homarus gammarus L.) and some brachyurans. There are two types of receptors present at the T-C joint, a chordotonal receptor and a muscle receptor. They lie parallel to each other and proximally both are attached to the same cuticular projection. There is also a pair of innervated elastic strands which insert proximally in the thorax and attach distally to the tendons of the levator and depressor muscles of the basipodite. Thus, these receptors traverse the T-C and C-B joints and must be affected by movement of either joint.

The chordotonal receptor at the C-B joint is described along with the innervated elastic strands by Alexandrowicz and Whitear (1957). The strand of this receptor does not attach proximally to a peg as in Carcinus but divides into a number of strands which insert separately into the hypodermis.

1.3.2. Basipodite-Ischiopodite Joint (B-I)

This joint is present only in the 2nd to 5th pereopods of the Nephropsidae. It has a single muscle (retractor) which inserts posteriorly and moves the limb in a posterior-lateral direction with respect to the body. An antagonistic muscle is absent and the counter movement is produced by elasticity and the disposition of body

weight. The amount of movement possible at this joint is small.

The anatomy of the chordotonal organ present at this joint is closely similar to that in Astacus leptodactylus as described by Clarac and Masson (1969). The receptor is situated in the posterior basipodite between the retractor tendon and the hypodermis.

1.3.3. Ischiopodite-Meropodite Joint (I-M)

The movement possible at the I-M joint in Homarus is greater than that of Carcinus but the musculature is very similar in both limbs. Movement is produced by two synergistic muscles, the superior and the inferior reducers, which pull the meropodite in an anterior-ventral direction. There is no antagonist. The heads of the reductor muscles insert on the posterior and ventral surfaces of the ischiopodite and occupy much of the space in this segment. The proximal ischiopodite is largely occluded by connective tissue save for a cavity through which the main leg nerve and blood vessels pass.

There are two chordotonal organs at this joint in the Nephropsidae. Clarac and Masson (1969) have described the organization of IM1 in Astacus leptodactylus and the arrangement is the same in Homarus. The total number of sense cells in these receptors is about 60 by comparison with the brachyuran Carcinus where only 20-25 have been counted (Clarac, 1968a).

IM2 which is present in Homarus and Astacus appears to be analagous with MCO2 (myochordotonal organ) in the Palinura and Brachyura as it occupies the same position (Clarac and Masson, 1969).

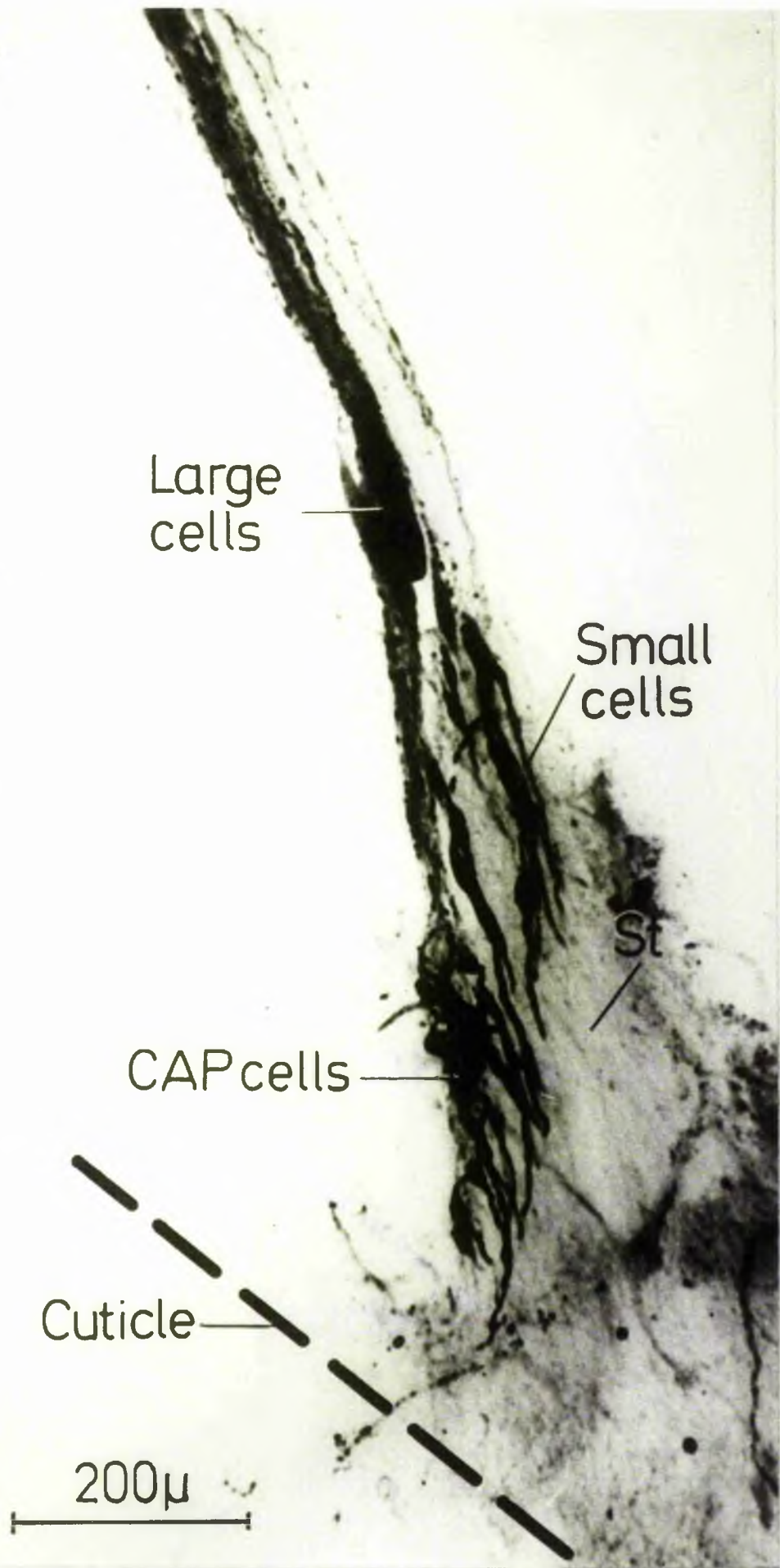
1.3.4. Meropodite-Carpopodite Joint (M-C)

This joint is particularly interesting because of the presence of the accessory flexor muscle and the associated sensory apparatus (MC01, Barth organ). The M-C joint is particularly important in lateral movements and has two large antagonist muscles, the flexor and extensor. The joint is normally held flexed at an angle of approximately 90° and potentially can move through 145° . This is very close to the degree of freedom measured in the pereopod of Carcinus (Bush, 1965c).

This joint also has two chordotonal organs. MC1 is basically similar in disposition to that of Carcinus (Whitear, 1962) and consists of a sheet of connective tissue which is traversed by a strand. The proximal cells, however, are not spread out on the sheet but are confined to the strand and the cells are more evenly dispersed throughout the length of the strand. It also appears that the number of cells stained is slightly less than that of Carcinus.

MC2 (Fig. 5) shows marked differences to that of Carcinus and consists of a very thin strand of connective tissue which crosses the joint to insert into the hypodermis directly above the CAP organs in the carpopodite. The nerve to the proprioceptive organ travels alongside the apodeme of the accessory flexor muscle and is thickened to form a strand which runs from the junction of the apodemes of the accessory flexor and flexor muscles across the joint. Proximally there is very little connective tissue but distally the strand fans out and here its presence is more obvious. All the cells are situated at the most distal end of the strand and they are incompletely divided into

FIG. 5. Photomicrograph of a methylene blue stained preparation of MC2 from the walking leg of Homarus gammarus. This shows the most distal portion of the receptor. The dotted line indicates the approximate position of the internal surface of the cuticle.



two groups, an upper group which is embedded in the strand, and a lower group situated in the hypodermis external to the strand. The lower group is associated with the cuticular articulated peg sensilla (see Experimental 1.3.7).

1.3.5. Carpopodite-Propodite Joint (C-P)

The walking legs (but not the chelae) possess three muscles that control the movement of this joint as described by Wiersma and Ripley (1952) for the Natantia and Stomatopoda. The walking legs of macrurans (Astacus fluviatilis, Palinurus vulgaris, Homarus gammarus and Nephrops norvegicus), anomurans (Eupagurus bernhardus, Galathea strigosa, Dardanus asper) and a single brachyuran (Dromidiopsis dormia) have the facility to rotate the propodite about the longitudinal limb axis but with the exception of Homarus and Nephrops only two muscles, a stretcher and a bender are present. (Dardanus and Dromidiopsis are described by Wiersma and Ripley, 1954).

Articulation of the leg joints is usually accomplished by a pair of symmetrically placed ball and socket joints. At the C-P joint of Homarus the mechanism is more complicated. Primary movement of the limb occurs in the antero-posterior plane (Fig. 3) and the hinge axis lies dorso-ventrally. The dorsal and ventral areas of contact between the coxopodite and the propodite have been enlarged and flattened to form very shallow ball and socket joints which tend to resist rotation of the propodite only when the limb supports the weight of the animal. These hinge pivots project internally towards the longitudinal axis of the limb until there is a gap of only 1 - 1.5mm (in a joint with external diameter of 8-10mm)

between them. The joint permits rotation through a maximum angle of 35° .

The major muscles that affect this joint are the stretcher and bender. The function of the third small muscle, previously undescribed, is not yet clear. The apodeme of this muscle is attached to the internal projection of the ventral portion of the hinge and its position indicates that it is likely to modify the action of the hinge rather than to rotate the distal portions of the leg. I was unable to rotate the limb by pulling the apodeme of the additional muscle either alone or concurrently with either of the other two muscles. I will not here propose a name for this muscle preferring to wait until functional studies make the situation clearer.

As with the *Brachyura* there are two CP receptors, CP1 (Fig. 6) being similar to that described for *Carcinus* (Whitear, 1962) in that the whole organ is located proximal to the joint. In *Homarus*, however, the organ is associated with two nerve trunks. The main leg nerve travels along the inner surface of the bender muscle and joins the connective tissue sheet proximal to the site of the receptor cell somata. A second nerve passes along the ventral hypodermis of the carpopodite between the bender and stretcher muscle heads to innervate some cells which lie 1.5mm or less from the distal attachment of the main strand.

The number of axons in this trunk is small, probably not more than 10 cells being innervated from this source, whilst the total number of cells in CP1 exceeds 80.

CP2 (Fig. 7) occupies a similar position to that of *Carcinus*, but has a different morphology. The two

FIG. 6. Photomicrograph of a methylene blue stained preparation of CP1 from the walking leg of Homarus gammarus. To show the second nerve trunk (Additional Nerve) that consists of the axons of some of the more distally placed sense cells. This nerve runs separately into the main leg nerve.

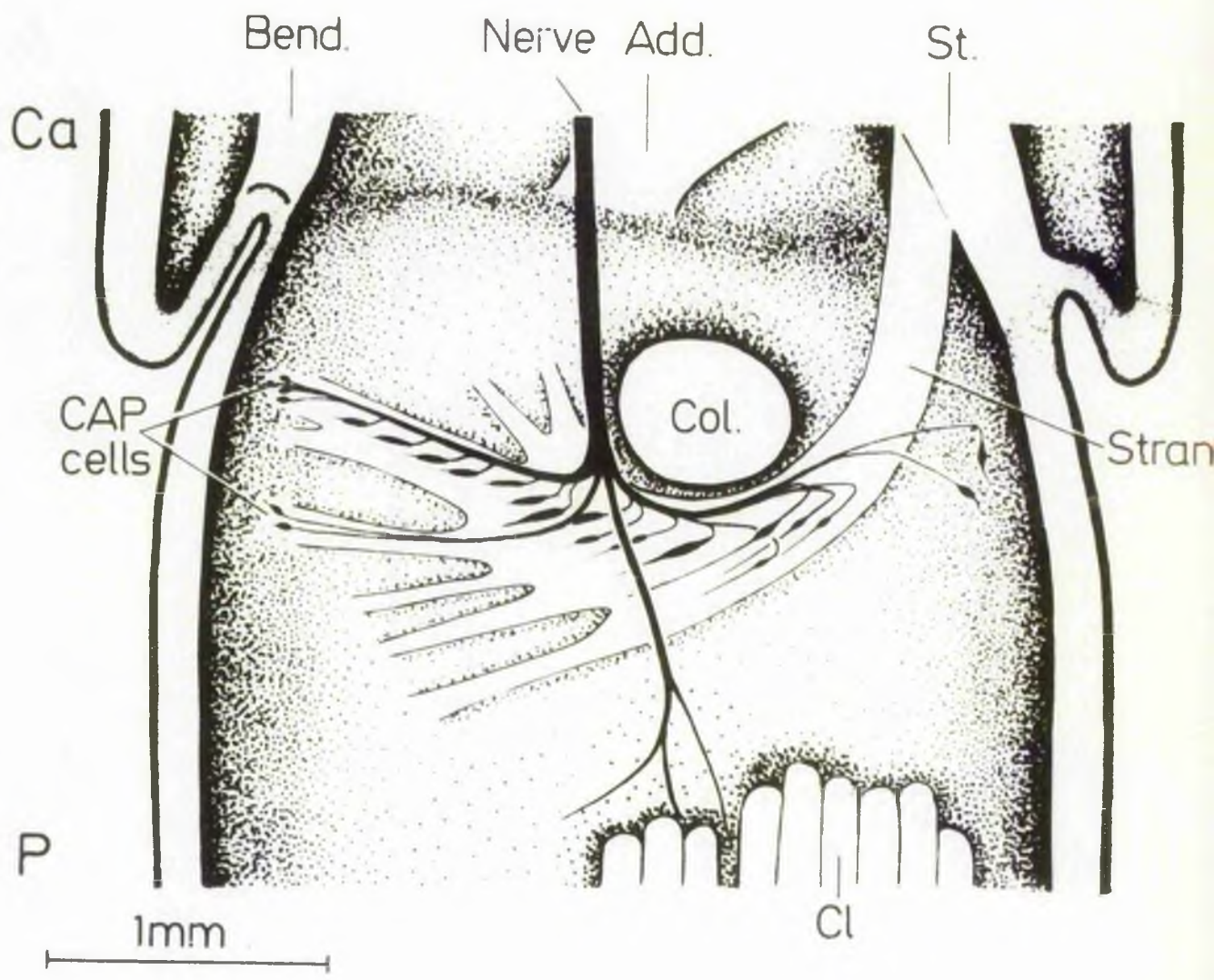
Main nerve group

Additional nerve

500 μ



FIG. 7. A dorsal view of the CP2 receptor in the left 2nd pereopod of Homarus gammarus showing the manner in which it curves round the column of connective tissue to reflect some of the strand back towards the attachment of the additional muscle. Note that some of the axons of the receptor nerve do not innervate the receptor. Carpopodite (Ca), propodite (P), apodeme of bender muscle (Bend.), apodeme of stretcher muscle (St.), additional muscle (Add.), closer muscle (Cl), column of connective tissue (Col.).



internal projections of the hinge are joined by a column of connective tissue (Fig. 7). The receptor strand of CP2 arises from the anterior surface of the stretcher muscle tendon and passes into the propodite posterior to the column. At this point the strand flattens out into a sheet which divides into branches and fans out, some branches being reflected back into the carpopodite. The nerve enters the propodite anterior to the column and curves round to meet the receptor sheet. At this point the nerve divides into several branches some of which pass across the receptor into the hypodermis.

The spindle shaped cell bodies (Fig. 8) of the receptor are situated distal to the joint and the maximum number of cells observed was 27. This number is greater than that quoted for Carcinus.

1.3.6. Pronodite-Dactylopodite Joint (P-D)

As with Carcinus a pair of muscles, an opener and a closer, serve this joint. There are differences in organisation, however, as is evident from the chelate nature of the second and third pereopods compared with the unchelate condition of the corresponding limbs of Carcinus. The fourth and fifth pairs of pereopods of Homarus are non-chelate.

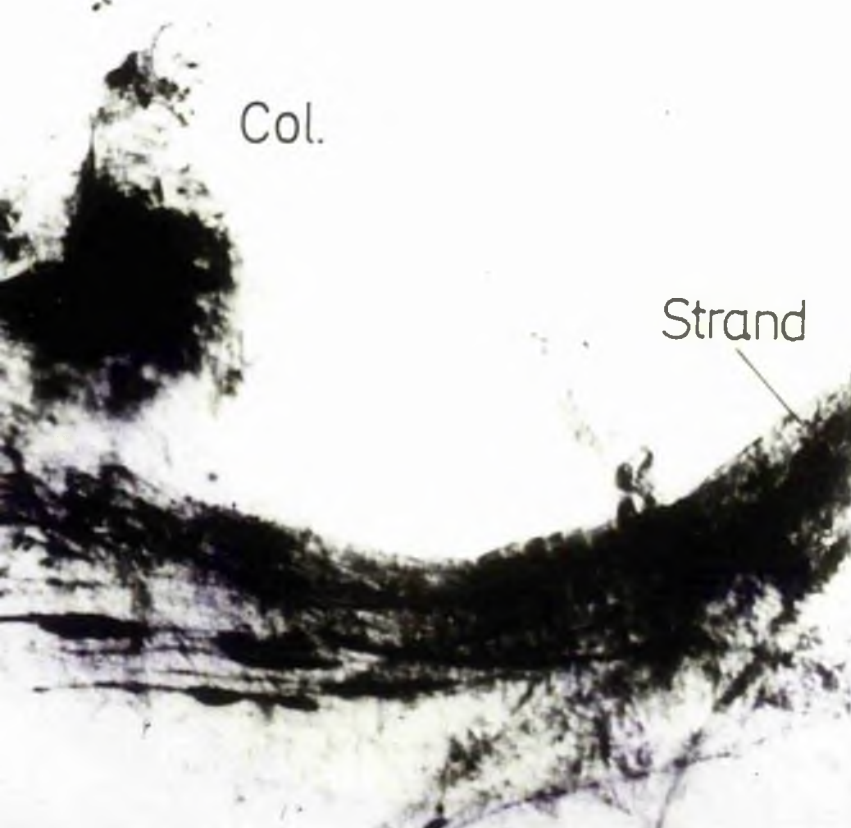
This joint has only one chordotonal organ. The strand arises from the dorsal face of the closer muscle tendon and passes through the joint into the dactylopodite. The connective tissue strand does not attach distally to a "protruberance" as in Carcinus (Burke, 1954), nor does it insert as a single strand but divides into several fibrous strings that fan out and insert into the hypodermis

FIG. 8. Photomicrograph of a methylene blue stained preparation of CP2 from the 2nd pereopod of Homarus gammarus showing the elongated bipolar cells and the curved shape of the receptor strand. Column of connective tissue (Col).



Col.

Strand



of the ventral wall.

The nerve supplying the receptor leaves the main leg nerve ventrally and travels along the medial surface of the closer muscle onto the receptor strand. The cells on the strand are similar in shape, size and distribution to those of Carcinus maenas (Burke, 1954) and in number to Cancer irroratus (Hartman and Boettiger, 1967).

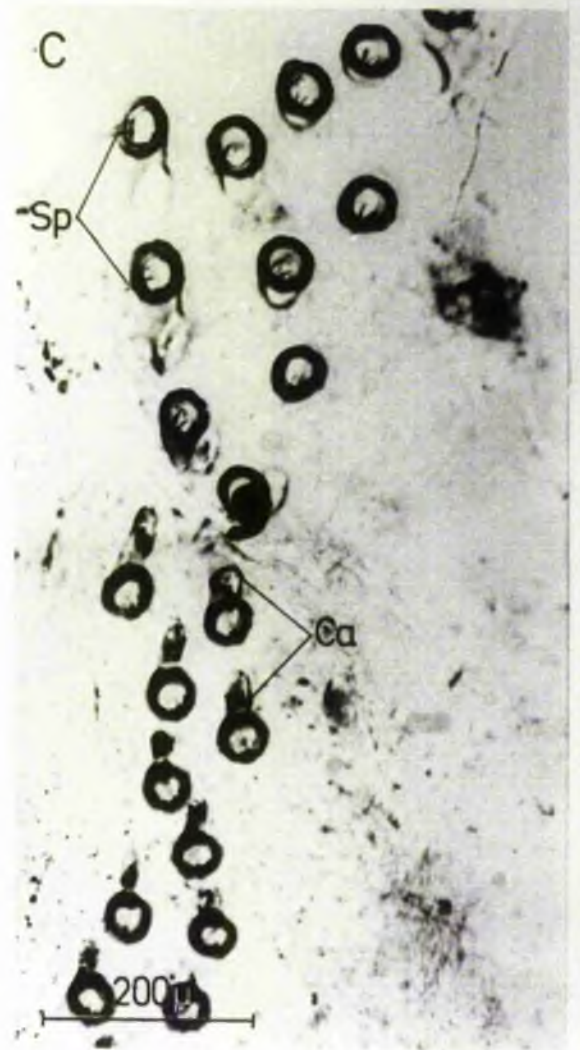
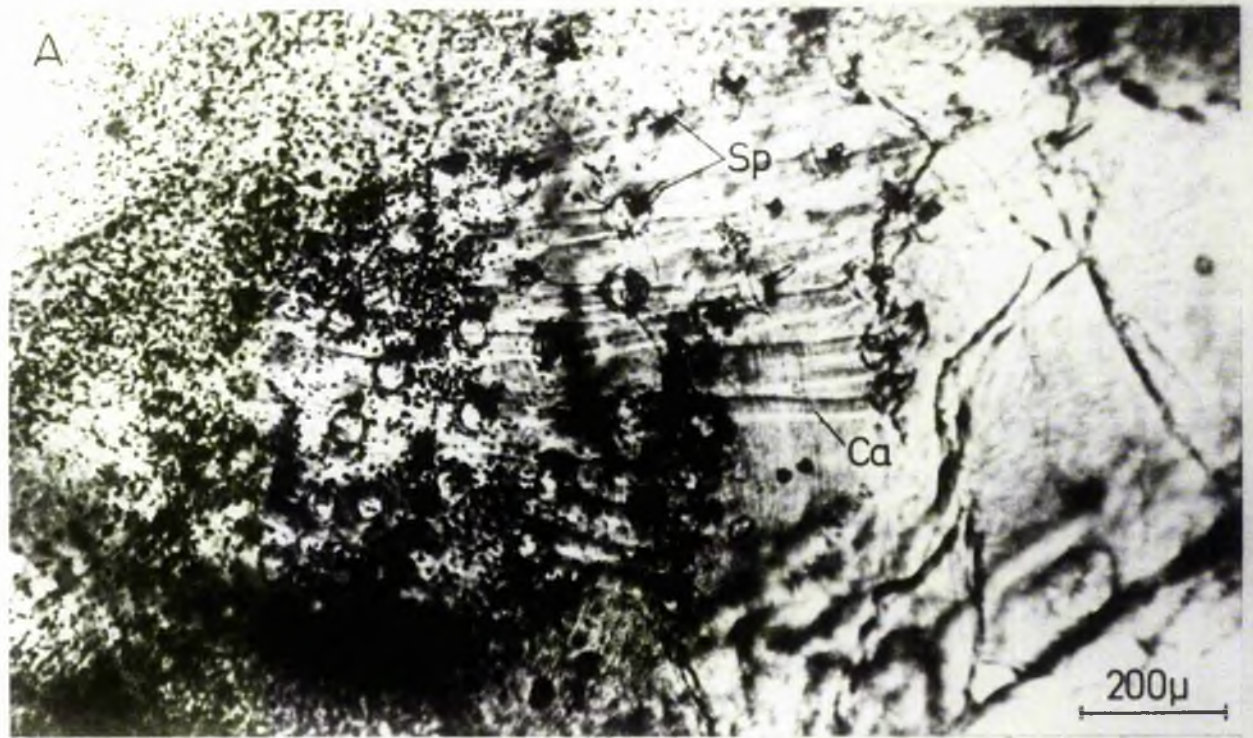
1.3.7. Cuticular Articulated Peg Sensilla (CAP)

Distal to the M-C and C-P joints of the walking legs groups of sensilla are readily observed on the surface of the limb. These sensilla lie close to the endings of internally placed chordotonal organs (MC2 and CP2) and a further group lies at the I-M joint of the walking leg (myochordotonal organ). These sensilla which were previously referred to as "slit sensilla" and described as "pits" (Wiersma, 1959) I have renamed, cuticular articulated pegs (CAPs). My reasons for changing the name are given in the Discussion.

The groups of CAPs are situated distal to the joint and lie in such a position as to be touched by the articular membrane during movement of the joint. At the I-M joint, only half of the group is covered by the membrane even at full reduction. At the M-C joint of the walking leg the articular membrane makes contact with the CAPs when the joint is flexed through 90° and this is the normal position of this joint when the animal is at rest (Fig. 2).

The CAPs are small spines situated in pits at the end of canals through the cuticle (Fig. 9) which "contain the end part of the scolopidia in which terminate the

FIG. 9. Photomicrographs of unstained but cleared CAP sensilla from some representative macruran species. The structure of these sensilla is similar at the different limb joints at which they occur on the same animal. The photographs show the canals (Ca) through the cuticle to the spines (Sp) which are situated on a flexible membrane. A. Nephrops norvegicus. B. Homarus gammarus. C. Panulirus argus. Fig. 9c is reproduced courtesy of Professor M.S. Laverack.



processes of the sensory cells of the respective receptors" (Alexandrowicz, 1969). The spines are of differing lengths in different species, being longer in Nephrops norvegicus (relative to the animal's size), shorter in Homarus and exist only as small knobs in Panulirus argus (Laverack, private communication). The number of sensilla in a group varies between 45 and 85 in Homarus and may vary at the same joint in different animals. The CAPs are closely grouped together and form rows.

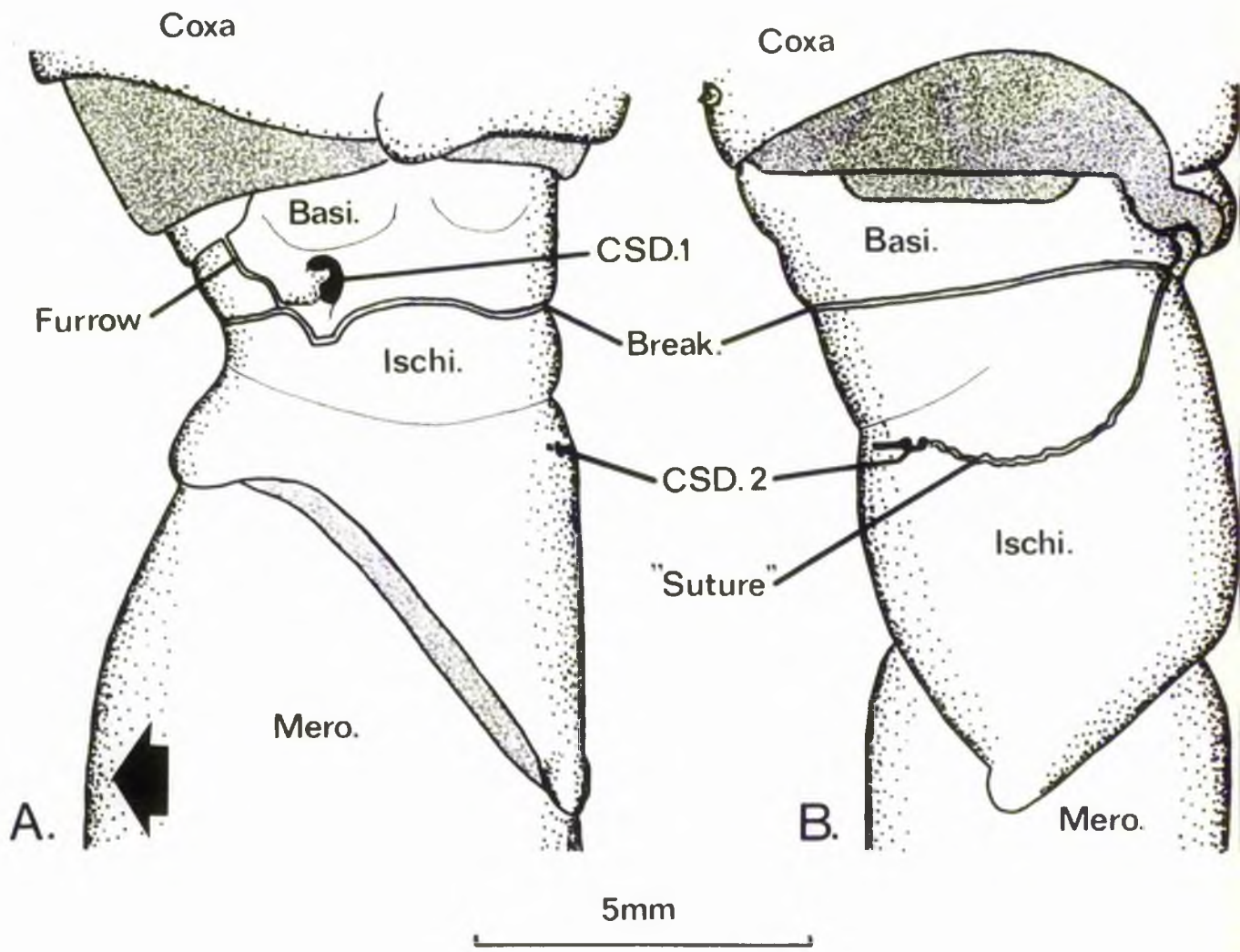
1.4. Receptors of the Basi-ischiopodite Region and Autotomy Plane of Reptantian Decapods

As the muscles of the C-B joint have been shown to be involved in autotomy (Wood and Wood, 1932; McVean, 1970) they are described along with the structure of the preformed breakage plane. The two sensory structures associated with the cuticle in the vicinity of the breakage plane I refer to as Cuticular Stress Detectors (CSD.1 and CSD.2) for reasons to be given later.

1.4.1. Brachyura

In Carcinus the proximal regions of all five pereopods are basically similar, though distally the first and fifth differ from the other three. In all the pereopods the basipodite and ischiopodite have fused to form a single entity, the basi-ischiopodite. As argued later, the position of the preformed breakage plane, which is the only structure circumscribing the fused segment, may be considered to approximate to the division between the "basipodite" and the "ischiopodite" (Fig. 10). The "basipodite" is the smallest segment of the pereopods and it forms a ring of cuticle terminating distally at the breakage plane. The "ischiopodite" is much longer ventrally but shortened dorsally so that the I-M joint is situated at an angle of approximately 50° to the limb axis (see Fig. 10B). Although the preformed breakage plane forms the only complete division of the basi-ischiopodite, there are other externally visible lines. The majority of these are hair-line depressions that mark internally located thickenings of the cuticle but one line situated ventrally in the "ischiopodite" resembles

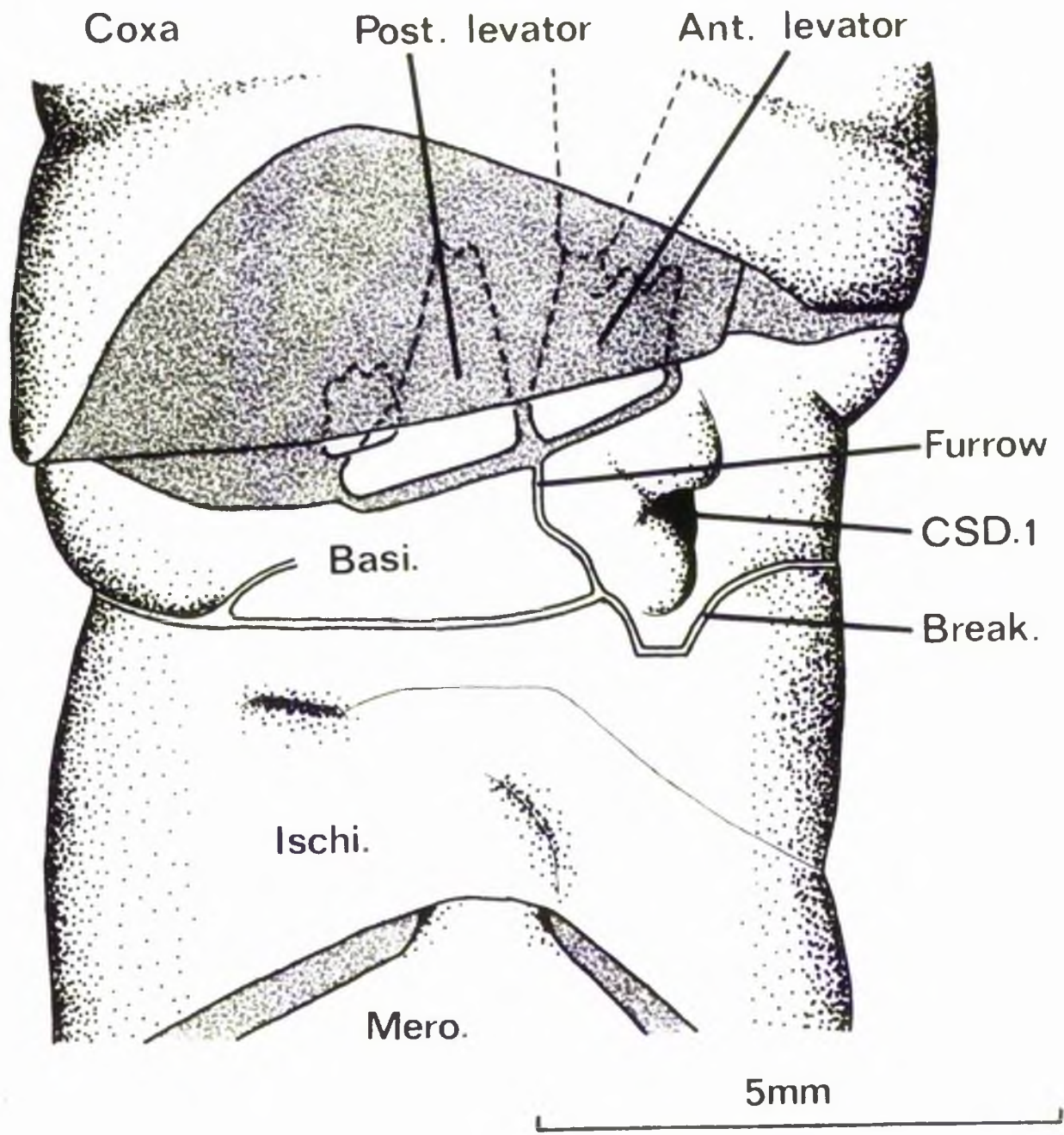
FIG. 10. External anatomy of the basi-ischiopodite region of the 2nd right pereopod of Carcinus maenas. Although the basipodite and ischiopodite have fused to become a single entity the portions of the basi-ischiopodite which approximate to the basipodite and ischiopodite have been indicated separately. View A shows the anterior surface and B the ventral surface of the limb. The arrow indicates the dorsal surface. Coxopodite (Coxa), "basipodite" (Basi.), "ischiopodite" (Ischi.), meropodite (Mero.), preformed breakage plane (Break.), distal "suture" ("Suture"), Paul's furrow (Furrow), soft cuticle associated with CSD.1 (CSD.1), thin cuticle associated with CSD.2 (CSD.2). The articular membrane of the limb joints is indicated by fine hatching.



the breakage plane in its appearance when viewed internally or externally. This line I refer to as the distal "suture" because it is located distal to the breakage plane and is convoluted giving it the appearance of a suture although it is not a junction between two separate segments of the limb exoskeleton (Fig. 10B). The distal "suture" arises posteriorly close to the breakage plane. Near its anterior termination it is deflected distally around the small patch of thin, less heavily calcified cuticle. The "basipodite" likewise bears distinct and consistent external features, the most important of which are situated dorso-anteriorly. At a position distal to the insertion of the anterior levator muscle tendon the breakage plane is deflected distally for a short distance (Fig. 11) and in this region the structure of the "basipodite" is complex. There is a discrete area of easily deformable cuticle which is connected to the breakage plane by a line of less heavily calcified cuticle (CSD.1, Fig. 11). From a point close to the breakage plane just dorsal to the soft cuticle to a position between the insertion of the levator muscle tendons a furrow runs in the cuticle of the basipodite. This furrow appears to be the same as that described by Paul (1915) as a "slanting joint" in the "basal ring of the second limb-segment".

The C-B joint articulates by means of two condyles which lie anteriorly and posteriorly, that is approximately perpendicular to those of the T-C and I-M joints. The musculature of the C-B joint consists of two antagonistic muscle groups, the levators and depressors. There are two separate levator muscles which differ in their locations and modes of attachment. The muscle fibres of the

FIG. 11. A dorsal view of the basi-ischiopodite region of the 2nd pereopod of Carcinus maenas to show the position of the soft cuticle associated with CSD.1 (CSD.1) relative to the insertion of the posterior (Post. levator) and anterior levator muscle tendons (Ant. levator), Paul's furrow (Furrow) and the preformed breakage plane (Break.). Coxopodite (Coxa), "basipodite" (Basi.), "ischiopodite" (Ischi.), meropodite (Mero.).



posterior levator insert posteriorly and dorsally in the coxopodite whilst the posterior levator tendon is attached to the "basipodite" at a point midway between the condyles of the C-B joint (Fig. 11). The muscle is flattened in cross-section and it lies superficially in the coxopodite. The tendon of this muscle is peculiar in that the main blade for muscle attachment does not lie parallel to the muscle fibres but is approximately perpendicular to them. Thus the main blade lies radially in the limb and contraction of the fibres, which attach to its proximal surface only, will tend to rotate the tendon around its attachment to the basipodite until it lies parallel to the muscle fibres. The tendon is prevented from undergoing this rotation because of its close apposition to the tendon of the anterior levator muscle (McVean, 1970). As shown in Fig. 12 the posterior levator tendon is normally in two parts and fibres attached to the posterior portion and to the base of the main blade may be able to produce levation without initiating autotomy (see McVean, 1970).

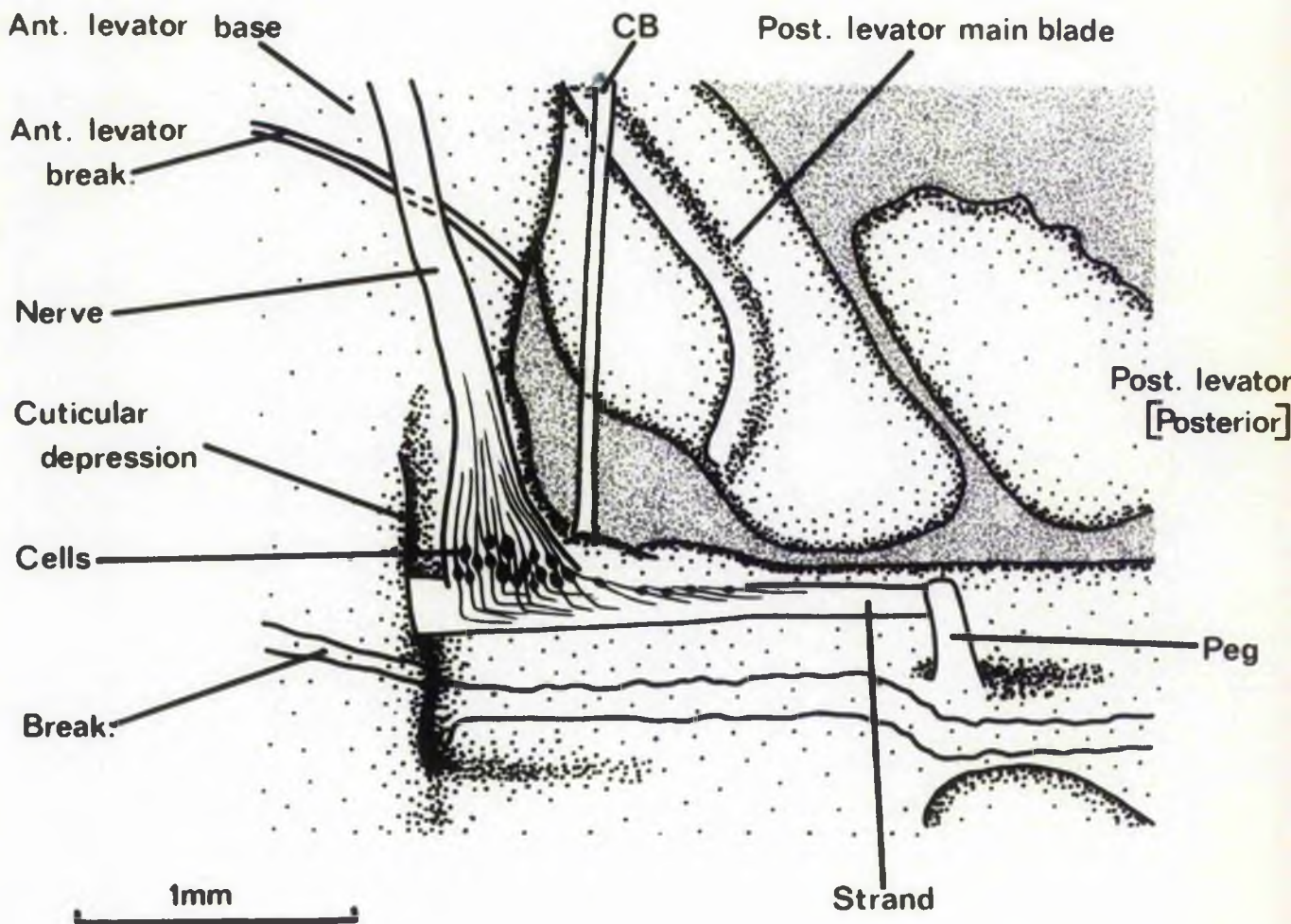
The anterior levator muscle, or autotomiser muscle (Wood and Wood, 1932), is considerably larger than its synergist and it inserts almost completely in the thorax. The muscle traverses both the C-B and T-C joints and on contraction affects the movement and position of both joints. A very small number of muscle fibres insert in the coxopodite but it is not clear what functional significance they may have. The anterior levator is situated deeper in the leg and lies approximately parallel to the limb axis but at 40° to the axis of the posterior levator in the straightened limb. The angle between these

muscles will be greater when the levator muscles of the C-B joint and remotor muscle of the T-C joint are fully contracted. The tendon of the anterior levator inserts onto the "basipodite" anterior to the posterior levator tendon (Fig. 11) but because of the shape of the basi-ischiopodite will gain a similar degree of leverage about the axis of the C-B articulation. The tendon of the anterior levator which is very unlike that of the other limb muscles consists of a block of cuticle which attaches to the "basipodite" and articulates with the large blade to which the fibres attach. As shown in Fig. 12 this block of cuticle in the undisturbed animal is fused to the basipodite at a preformed breakage plane (McVean, 1970).

The depressor muscles are not completely analagous to the levators. There are three depressor muscles the largest of which inserts mainly in the thorax but also to a considerable extent in the coxopodite and is flanked on either side by a very small muscle. Both of the small muscles insert in the coxopodite, but are considerably smaller than the posterior levator muscle. The position of the main tendon on the basipodite like that of the posterior levator is midway between the condyles.

CSD.1 This receptor lies dorsally in the basipodite closely apposed to the hypodermis just proximal of and parallel to the preformed breakage plane. Thus the receptor is orientated perpendicular to the chordotonal organs of the limb joints which generally lie along the limb axis. It consists of a well defined strand innervated by more than 40 bipolar neurones (Fig. 12). The strand inserts anteriorly on a discrete area of soft cuticle (CSD.1, Fig. 11) and posteriorly it attaches to a

FIG. 12. The general disposition of CSD.1 in the right 2nd pereopod of Carcinus maenas as it would appear were all other soft tissue removed from the limb. The top of the Figure corresponds to proximal and the left side to anterior in the walking leg. The receptor strand which lies close to the breakage plane (Break.) is attached posteriorly to a peg and anteriorly to an area of soft cuticle situated in a cuticular depression. The chordotonal organ of the coxopodite-basipodite joint (CB) inserts on a small protrusion close to CSD.1. The block of cuticle at the base of the anterior levator muscle tendon (Ant. levator base) is connected to the "basipodite" at a preformed breakage plane (Ant. levator break). The tendon of the posterior levator muscle is normally in two parts, the main blade, which is orientated perpendicular to the plane of the figure, and a smaller posterior portion (Post. levator (Posterior)).



peg. The nerve to the receptor lies in a small bundle of fibres which arise from the main leg nerve in the coxa. As this nerve travels distally through the coxa it passes anteriorly and then dorsally to join the receptor strand close to its anterior insertion on the soft cuticle. The majority of the sensory cells, which are up to 60 μ diameter, lie in the nerve at its junction with the strand but some smaller cells are distributed along the strand. As shown in Fig. 12, the somata of some of the larger cells lie close to the soft cuticle. The dendrites of the cells are reflected along the strand towards the peg and away from the soft cuticle. Structures associated with dendrites in the strand near its dorsal insertion closely resemble scolopidia. The strand is held taut by the flexible hollow peg to which it is attached and by the elastic properties of the strand. The peg lies perpendicular to the strand and to the breakage plane (Fig. 12), the latter being deflected distally round the base of the peg. The discrete area of soft cuticle onto which the strand inserts is that which lies just anterior to the junction of Paul's furrow with the breakage plane. The soft cuticle which is very consistent in its shape is not flat but forms a gently rounded dome with an irregular surface. The distal border of the soft cuticle is in close association with the breakage plane. Proximally and ventrally the soft cuticle is bounded by heavily calcified cuticle whereas dorsally the change from soft to hard cuticle is not so distinct. This is the area between the soft cuticle and Paul's furrow.

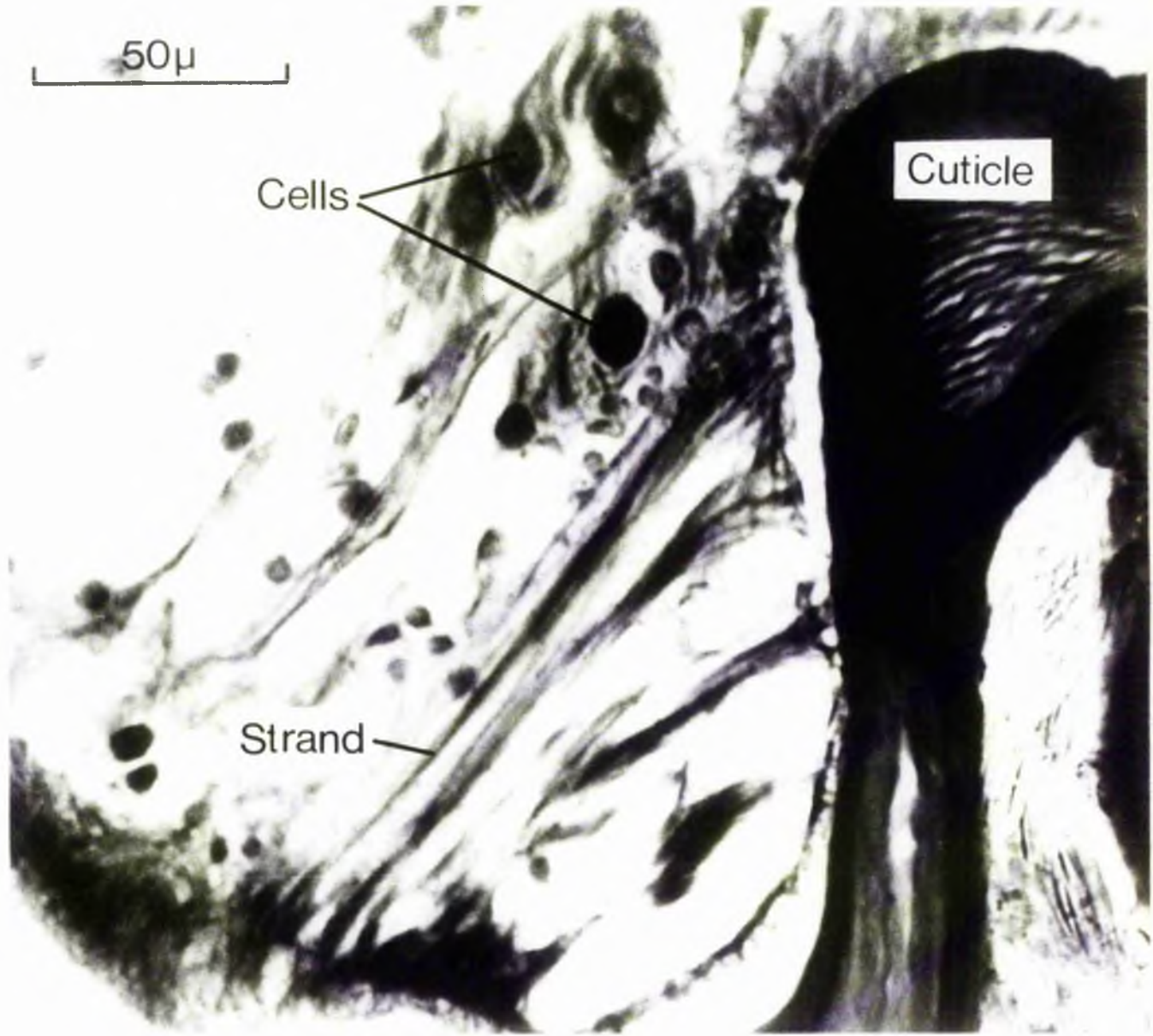
The distal end of the CB chordotonal organ attaches to a small protrusion situated on the "basipodite" between

the insertions of the two levator muscle tendons. CB thus lies close to the strand of CSD.1 but is orientated perpendicular to it and there is no apparent structural connection between the two receptors other than the hypodermis into which they both insert.

CSD.2 This receptor, first observed in Astacus leptodactylus by Clarac and Masson (1969), lies in the proximal ventral "ischiopodite" internal to the kidney shaped area of thin poorly calcified cuticle which is situated close to the anterior termination of the distal "suture" (Fig. 10B). The most proximal head of the inferior reductor lies just distal to the receptor but is not visibly connected to it. CSD.2 in Carcinus is very small and is deeply embedded in dense connective tissue which rendered methylene blue staining techniques ineffective. Thus my knowledge of CSD.2 in Carcinus is derived from conventional histological methods only.

The area of thin cuticle associated with this receptor is very much smaller than that associated with CSD.1 and is circumscribed by heavily calcified cuticle save for the point where the distal suture joins it. This thin cuticle is recessed from the internal and external surfaces of the surrounding cuticle. Internally the site of the thin cuticle is seen as an oval depression which has a small internal projection situated posteriorly. The receptor strand, which is about 150 μ in an animal measuring 50mm across the carapace, inserts on the anterior face of this projection (Fig. 13) and passes into the depression to end on the thin cuticle. As with CSD.1 the main strand of CSD.2 is orientated secantially in the limb. The cells, of which there may be more than 30, are

FIG. 13. Photomicrographs of an Azan stained wax section of CSD.2 in the 2nd pereopod of Carcinus maenas. The sensory cells lie in the nerve bundle close to the anterior insertion of the strand.



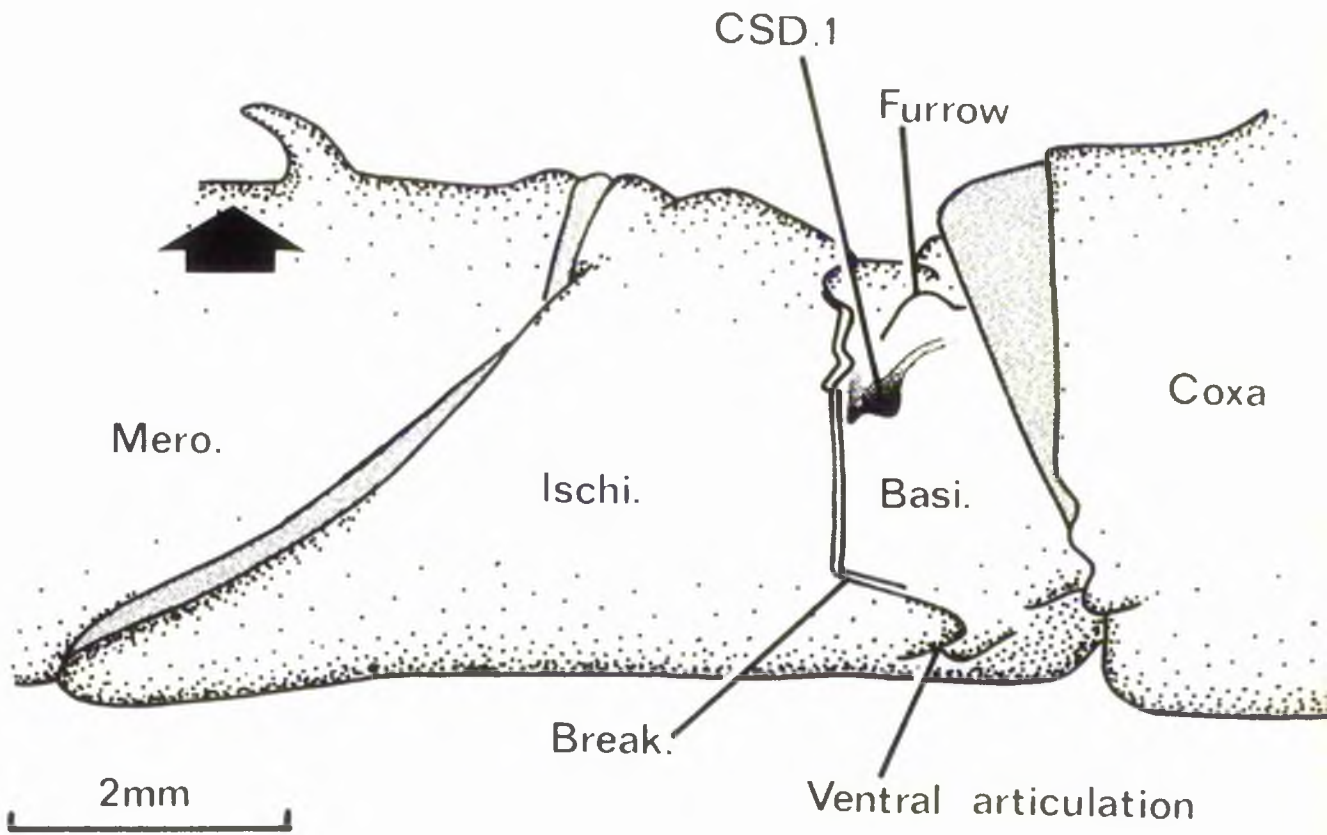
densely grouped in the nerve close to the strand at its insertion onto the cuticular projection. The cells are seldom more than 15 μ in diameter and have dendrites which run from the cuticular projection towards the thin cuticle. The receptor nerve, which is short, passes dorsally from the receptor to join the main leg nerve just proximal to the breakage plane.

The sensory nerve bundles to CSD.1 and 2, like the nerves to other chordotonal organs, also carry fibres which innervate the surrounding hypodermis.

1.4.2. Anomura, Superfamily Galatheidae

The Anomura, like the Brachyura, have lost the B-I joint and possess good ability to autotomise. This is particularly true of the Galatheids. The fifth pereopod of Galathea is much smaller than the four anterior ones and was not included in this study. The soft cuticle associated with CSD.1 is a large structure with a finger like process directed towards the anterior levator tendon (Fig. 14). Paul's furrow is present but does not terminate as close to the breakage plane as it does in Carcinus. Situated ventro-anteriorly on the breakage plane is a structure which appears to be a remnant of the B-I joint ventral articulation because of its shape and position. The distal "suture" is well developed and the soft cuticle associated with CSD.2 is larger than that of Carcinus. The soft cuticle which is virtually kidney shaped, particularly in the more posterior pereopods, is continuous with the "suture". The musculature of the C-B joint is similar to that of Carcinus. The tendon of the anterior levator muscle has a "block" of cuticle interposed between the

FIG. 14. The external anatomy of the basi-ischiopodite region of the 2nd right pereopod of the anomuran, Galathea strigosa showing the rudiments of the ventral articulation of the B-I joint situated on the breakage plane (Break.). The illustration shows the anterior surface of the limb and the arrow indicates the dorsal surface. Coxopodite (Coxa), "basipodite" (Basi.), "ischiopodite" (Ischi.), meropodite (Mero.), Paul's furrow (Furrow), soft cuticle associated with CSD.1 (CSD.1).



main blade for muscle attachment and the "basipodite" but we have not observed this block to be fused to the "basipodite".

1.4.3. Macrura, Superfamily Nephropsidae

Some descriptions of the basic anatomy of the basipodite-ischiopodite region of macrurans exist (Paul, 1915; Wood and Wood, 1932) but as these are either inadequate or inaccurate I have elected to redescribe it. Homarus and Astacus are basically very similar and the description given here for Homarus can with a little adaptation be applied to Astacus. The primary interest of the Nephropsidean pereopods is that, whereas the first pereopod, chela, has lost the B-I joint and has a well developed breakage plane, the walking legs have a moveable joint between the basipodite and ischiopodite and an incomplete breakage plane. This is associated with a poor ability to autotomise.

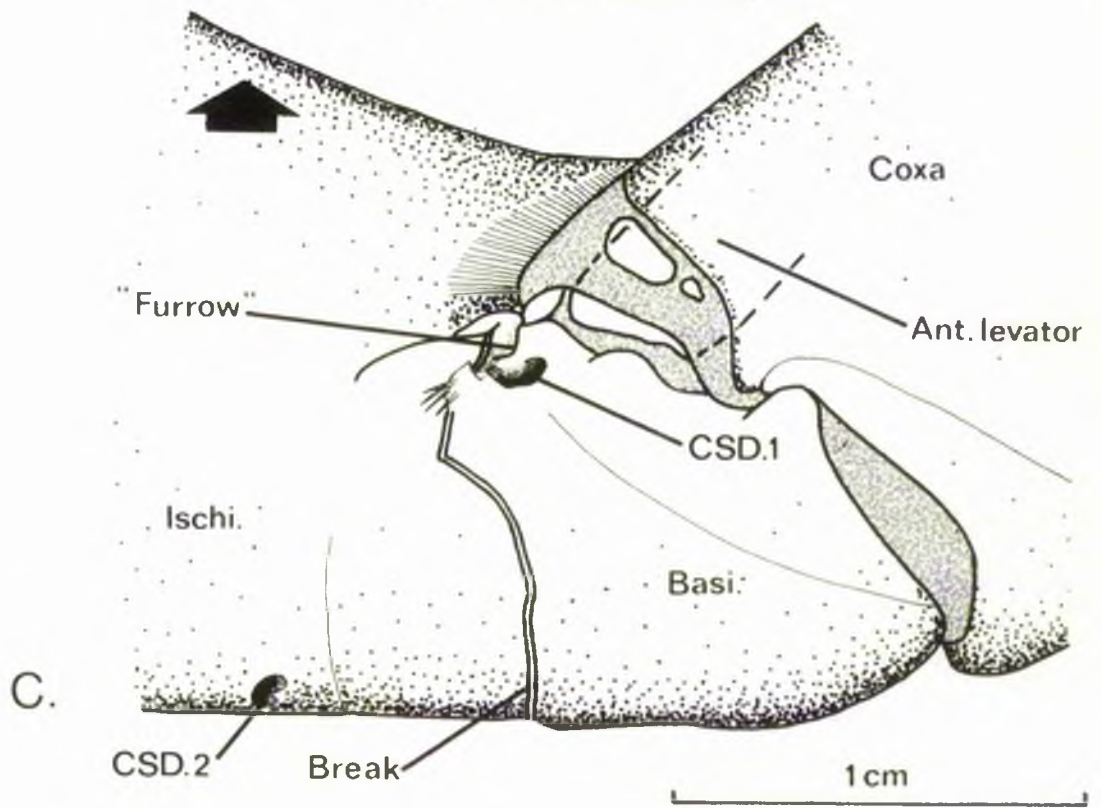
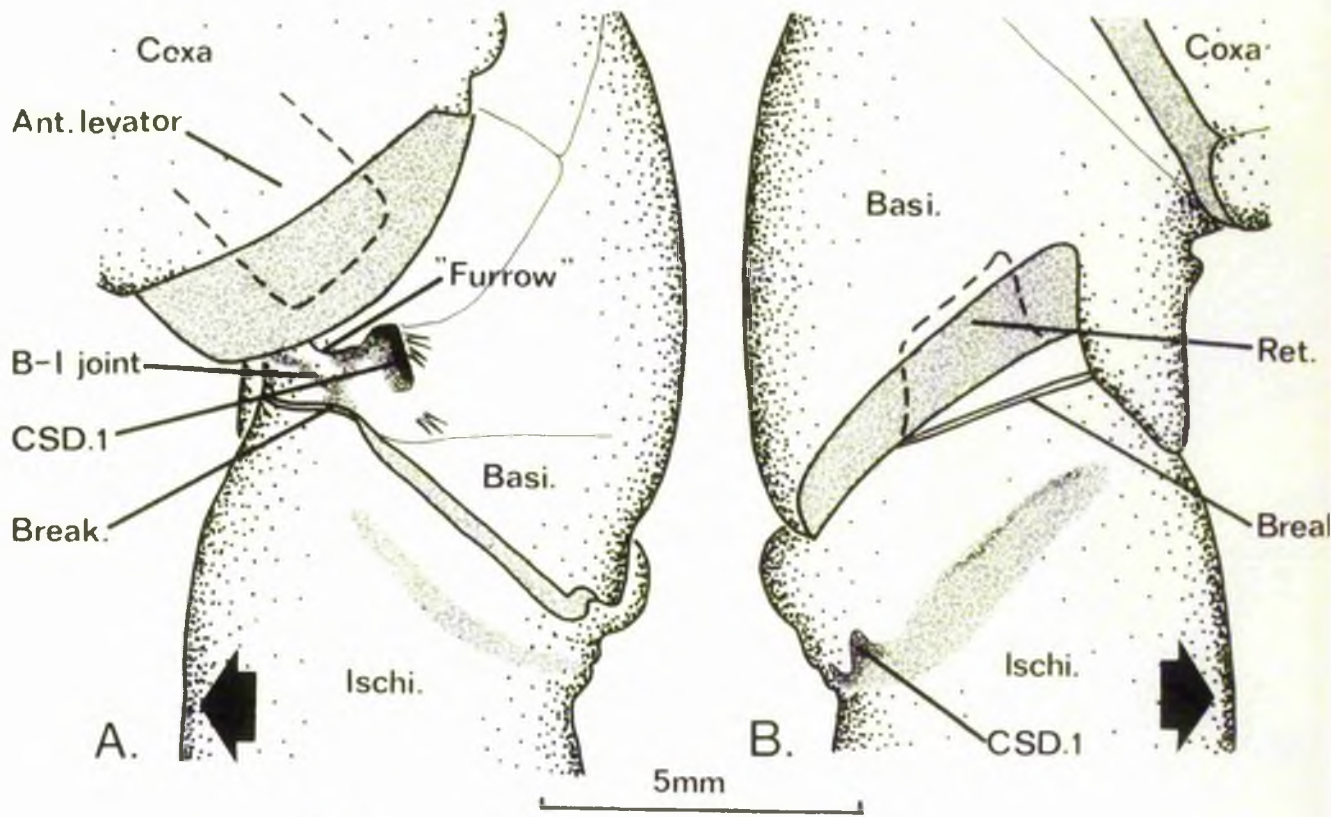
The walking leg of Homarus is not as heavily calcified as Carcinus and some of the cuticular features are less distinct. The B-I joint, which is moved by a single retractor muscle, lies obliquely in the leg at a similar angle to the I-M joint of Carcinus. As described by Paul (1915) the breakage plane in Homarus runs round the dorsal surface of the ischiopodite from a point close to the soft cuticle of CSD.1 to a point just ventral to the insertion of the retractor muscle tendon (Figs. 15A and B). Thus when breakage occurs a small segment of the ischiopodite remains attached to the leg stump and the separation of the limb is achieved by tearing the articular membrane of the B-I joint.

FIG. 15. The external anatomy of the basi-ischiopodite region of the pereopods in Homarus gammarus. In the 1st pereopod the basipodite and ischiopodite are fused as with Carcinus maenas but in the 2nd to 5th pereopods a true joint is present between these two segments.

A. The anterior surface of the 2nd right pereopod.

B. The posterior surface of the 2nd right pereopod.

C. The anterior surface of the 1st right pereopod, the great chela. The arrows indicate the dorsal surface of the limbs. Coxopodite (Coxa), basipodite (Basi.), ischiopodite (Ischi.), preformed breakage plane (Break.), anterior levator muscle tendon (Ant. lev.), retractor muscle tendon (Ret.), soft cuticle corresponding to Paul's furrow ("Furrow"), soft cuticle associated with CSD.1 (CSD.1), soft cuticle associated with CSD.2 (CSD.2).



Homarus americanus is very similar to Homarus gammarus (see Fig. 15) and the position of the breakage plane which Wood and Wood (1932) indicate corresponds to the soft cuticle on which CSD.2 is located. The distal "suture" is totally absent in Homarus where it is replaced by a broad band of uncalcified cuticle.

The basipodite is much larger than the "basipodite" of Carcinus but has many similar features. The soft cuticle associated with CSD.1 is larger but holds a similar position relative to the levator muscle tendons. The soft cuticle and the breakage plane are not as closely associated as they are separated by the relatively inflexible dorsal articulation of the B-I joint. The basipodite also has a structure analagous to Paul's furrow which arises from a point midway between the levator muscle tendons, but it terminates at the soft cuticle of CSD.1 rather than at the breakage plane. These structures are most readily observed in the fifth pereopod. The musculature of the C-B joint is as complex as in the Brachyura.

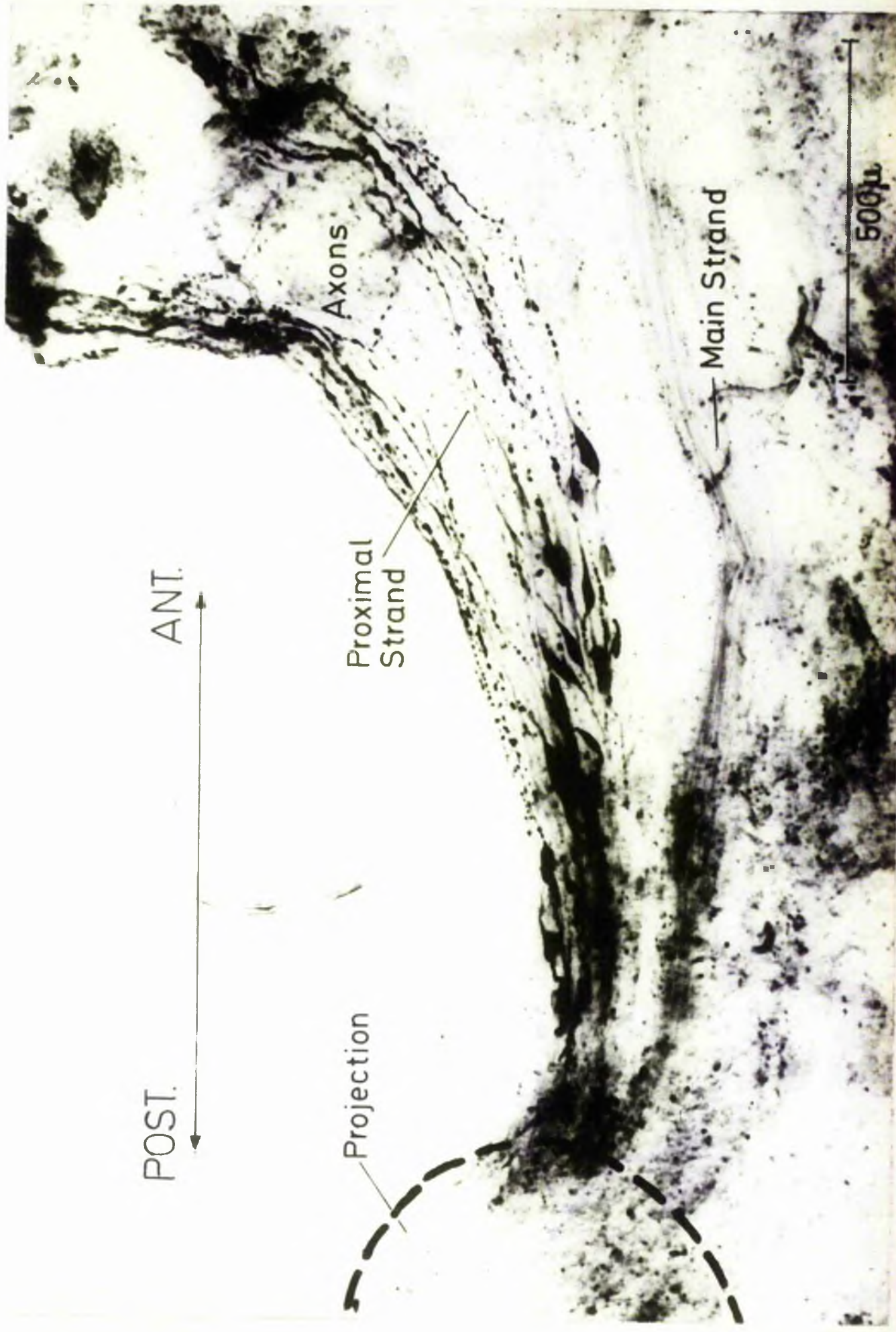
Wood and Wood (1932) state that Homarus has only a single levator muscle but there are in fact two levators which insert in a similar fashion to those of Carcinus (Fig. 11). The tendon of the posterior levator muscle, like that of Carcinus, does not lie parallel to the muscle fibres but in Homarus the angle between the muscle fibres and the main blade of the tendon is not so acute (approximately 45°). The muscle fibres attach to the proximal surface of the tendon as in Carcinus. The anterior levator tendon does not have a block of cuticle interposed between the blade of the tendon and its

attachment to the basipodite.

The chela, 1st pereopod, is much more heavily calcified than the walking legs and as stated above the basipodite and ischiopodite have fused. The soft cuticle of CSD.1 is located on a pronounced cuticular protrusion lying close to the breakage plane (Fig. 15C). The soft cuticle is bounded by heavily calcified cuticle save at its dorsal margin where the change in degree of calcification is more gradual. Paul's furrow is present and although it does not connect with the soft cuticle as in the more posterior pereopods it terminates a short distance from the breakage plane. The musculature of the C-B joint in the chela is very similar to that of the pereopods but the angle between the main blade of the posterior levator and the muscle fibres inserting upon it is greater.

CSD.1. As with Carcinus, the sense organ is situated dorsally in the basipodite and lies in a plane parallel to the diameter of the limb (i.e. secantially). Thus the strand runs across the limb unlike the limb proprioceptors which lie approximately parallel to the longitudinal limb axis. The strand is divided anteriorly into two. The anterior insertion of the main strand is on a small area of soft cuticle whilst the proximal portion of the strand arises from the hypodermis. Both portions of the strand insert posteriorly on an internal cuticular projection. The strand does not cross a joint nor is it attached to a muscle. The nerve to the receptor arises from the main leg nerve close to the sense organ and joins the proximal strand close to its anterior insertion. Scattered through the mid region of the strand

FIG. 16. Photomicrograph of a methylene blue stained preparation of CSD.1 from the 2nd pereopod of Homarus gammarus. Note the division of the receptor strand into the main strand which runs between the patch of soft cuticle and the internal projection and the proximal strand, which contains the cells, inserting onto the same projection. In this preparation the majority of the main strand has been removed. The position of the internal cuticular projection is indicated by the broken line, posterior (POST.), anterior (ANT.).



POST.

ANT.

Axons

Projection

Proximal Strand

Main Strand

500µ

are 20-30 bipolar neurones the dendrites of which are directed towards the cuticular projection. Figure 16 shows the typical distribution of the cells on the strand of Homarus.

CSD.2. This receptor is very difficult to stain with methylene blue methods, probably because of the dense connective tissue which envelops the receptor and prevents penetration of the stain, but it is possible to stain the sensory cells in Astacus. The soft cuticle associated with the receptor in this genus has an area many times greater than that of Carcinus and the receptor organ is a larger and seemingly more important structure. The receptor is located ventrally in the ischiopodite quite close to the ventral articulation of the B-I joint but not visibly connected to the joint by a strand or other structure. CSD.2, which lies distal to the breakage plane, is divided into two distinct parts. The main strand (Figs. 17 and 18) inserts as a broad band, flattened dorso-ventrally, onto the ventro-posterior wall of the ischiopodite. At this insertion, the more centrally placed fibres of the strand are located on relatively soft cuticle but some of the lateral fibres may lie on the adjacent more heavily calcified cuticle. From its posterior attachment the strand runs ventro-anteriorly and in doing so the fibres converge whilst the strand appears to form a half turn of a spiral (Fig. 18). The ventral area of soft cuticle onto which the main strand inserts anteriorly is almost separated from the more posterior portion by a peninsula of more heavily calcified cuticle (Fig. 17). There is a short "suture" in the anterior wall of the ischiopodite which is connected

FIG. 17. A stereodiagram of CSD.2 in the 2nd right pereopod of Astacus leptodactylus as it would appear with all other soft tissue removed. CSD.2 is located ventrally in the proximal ischiopodite close to the ventral articulation of the B-I joint. The receptor is situated on soft cuticle which has narrowed anteriorly to resemble a "suture". The area of soft cuticle is divided by a peninsula of more heavily calcified cuticle. The top of the illustration corresponds to proximal and the left side to posterior in the limb.

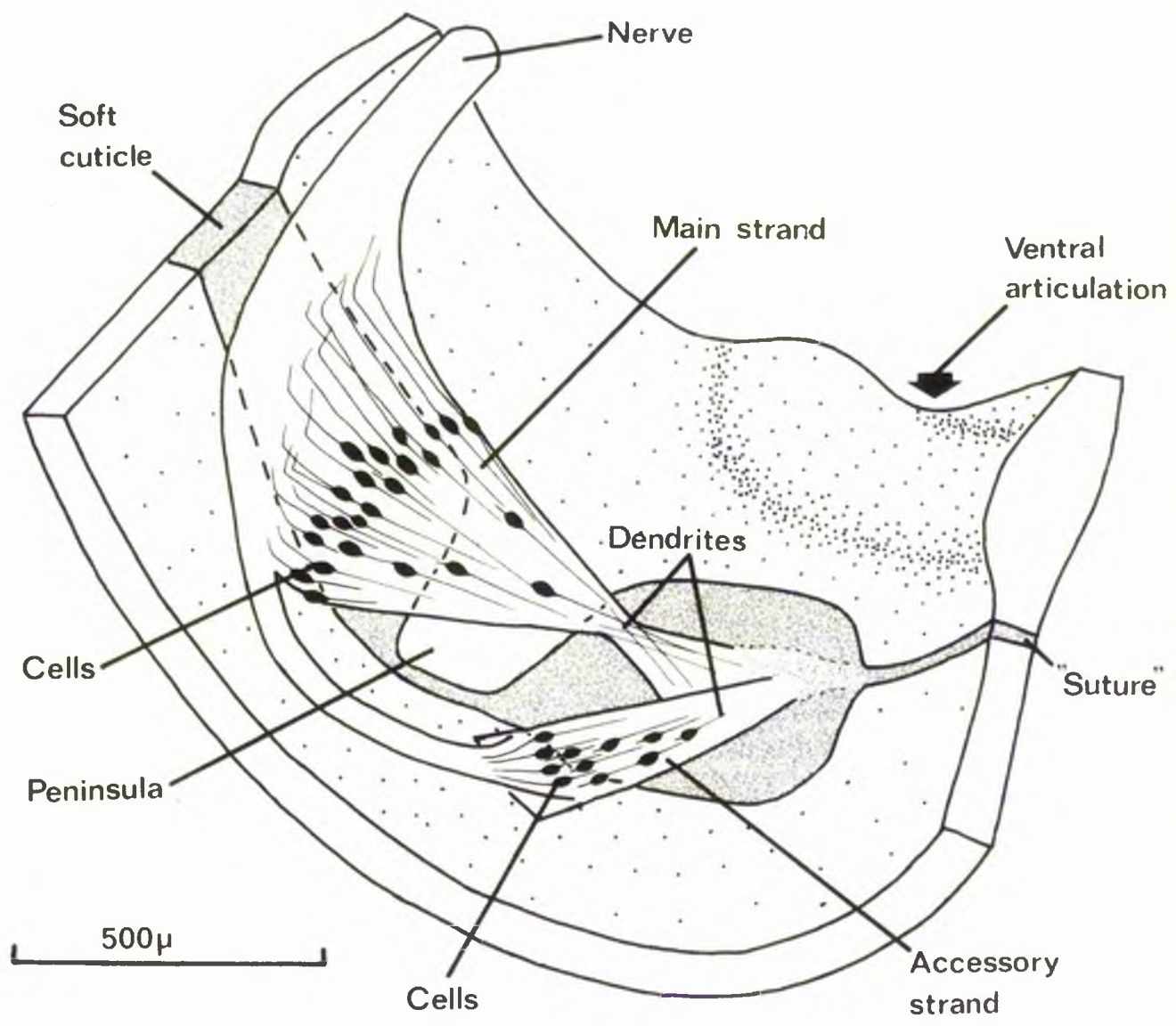
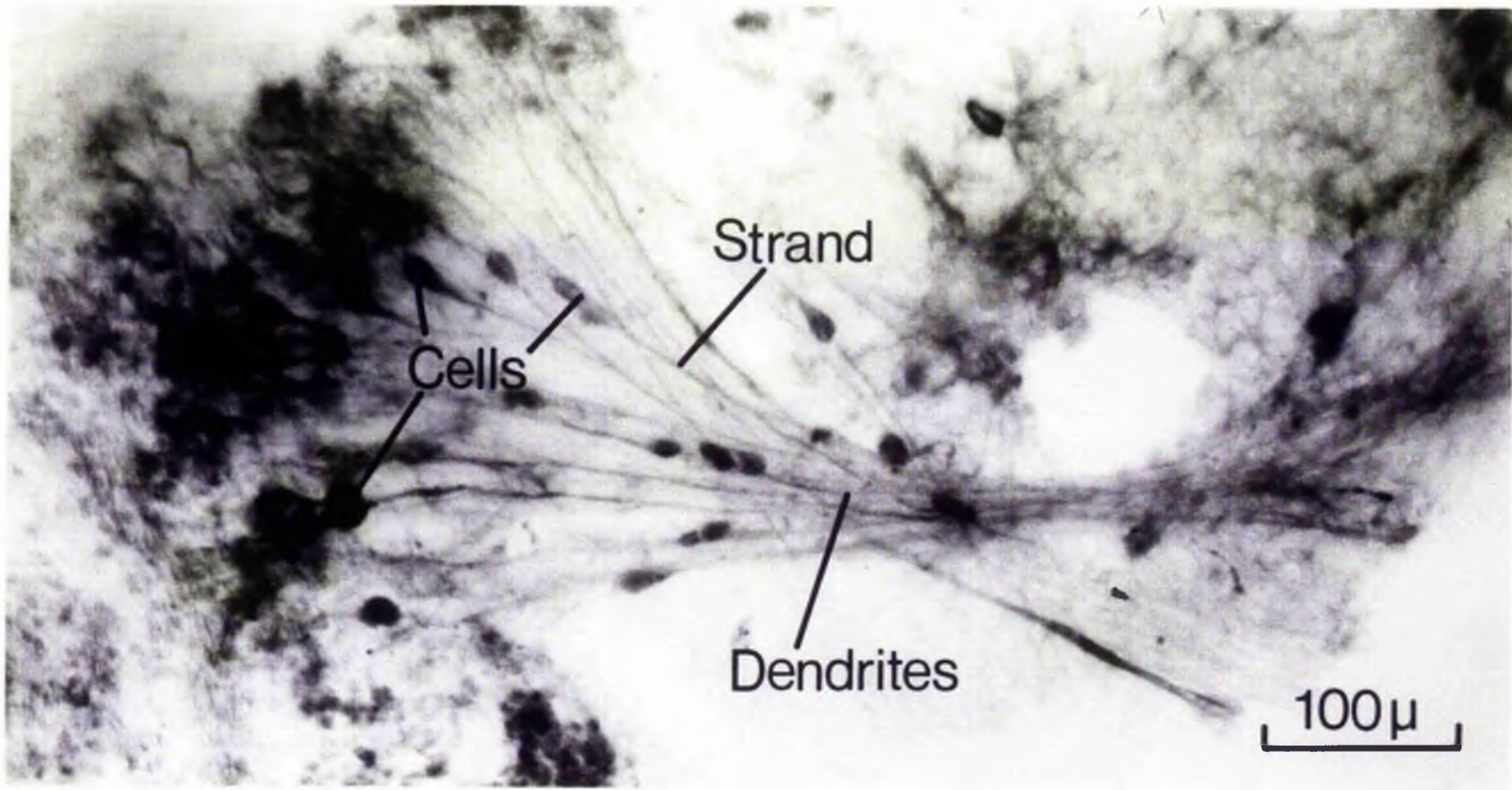


FIG. 18. Photomicrograph of a methylene blue stained preparation of the main strand of CSD.2 in the 2nd pereopod of Astacus leptodactylus. Note how the strand appears to turn through a half turn of a spiral.



to the ventral soft cuticle.

The accessory strand of CSD.2 (Fig. 17) is situated distal to the main strand. The posterior insertion of the accessory strand appears to be entirely onto harder cuticle but the anterior insertion lies close to that of the main strand on the ventral soft cuticle. Externally an island of slightly denser calcification is visible on the ventral soft cuticle and this appears to mark the position of the anterior insertions of both strands.

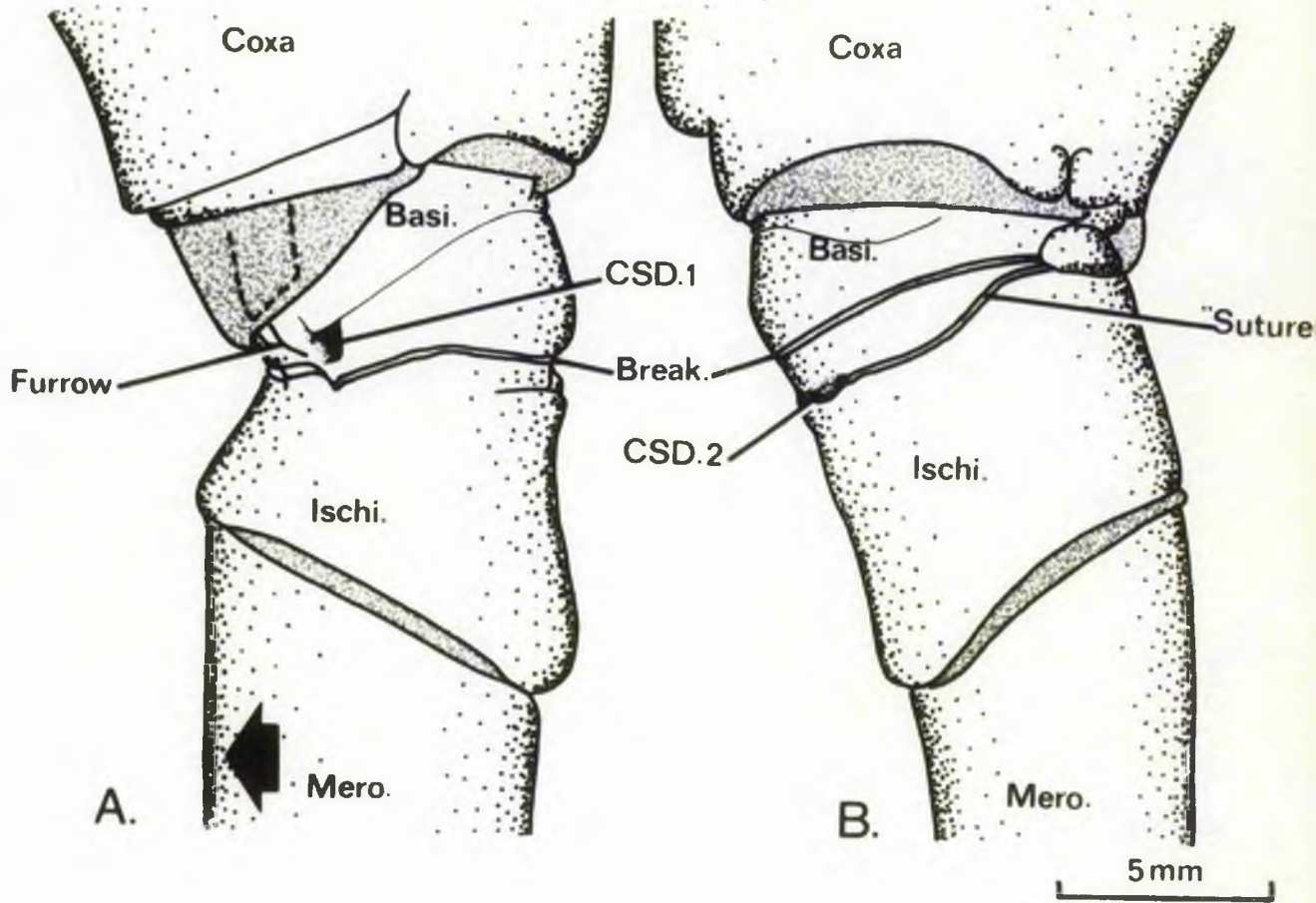
The nerve to CSD.2 leaves the main leg nerve close to the B-I joint and runs onto the hypodermis of the posterior part of the ischiopodite. Close to the receptor the nerve fans out to innervate both strands. The majority of the cells of the main group lie in the connective tissue close to the posterior insertion of the strand, but some cells are seen in the more posterior regions of the strand. The cells of the accessory strand are generally distributed over a greater length of the strand. The sensory cells are typically bipolar and the dendritic processes run towards the anterior insertion as is the case in Carcinus. Moulins and Clarac (Unpublished) have confirmed the presence of scolopidia in the strand of CSD.2.

1.4.4. Macrura, Superfamily Scyllaridae

In Palinurus vulgaris all five pereopods are similar in construction with the basipodite and ischiopodite fused and the breakage plane completely encircling the limb. All of the pereopods are capable of true autotomy.

Palinurus (Fig. 19) is more heavily calcified than

FIG. 19. The external anatomy of the basi-
ischiopodite region of the 2nd right pereopod of
Palinurus vulgaris. View A shows the anterior
surface and B the ventral surface of the limb. The
arrow indicates the dorsal surface. As in the
Anomura and the Brachyura, the basipodite and
ischiopodite have fused in the Scyllaridae to form
a single entity divided only by the preformed
breakage plane (Break.). Coxopodite (Coxa),
"basipodite" (Basi.), "ischiopodite" (Ischi.),
meropodite (Mero.), Paul's furrow (Furrow), distal
"suture" ("Suture"), soft cuticle associated with
CSD.1 (CSD.1), thin cuticle associated with CSD.2
(CSD.2).



Homarus and the areas of soft cuticle are more sharply defined but the cuticle of the limbs is relatively thinner than that in Carcinus. The soft cuticle of CSD.1 is larger in area than that of Carcinus or Homarus and it is a flatter more membrane-like structure which does not protrude beyond the rim of surrounding hard cuticle. The discrete area of soft cuticle bears a similar relationship to the breakage plane, Paul's furrow, and the levator muscle tendons as was described for Carcinus. The distal "suture" is also present but is situated relatively closer to the breakage plane than in Carcinus. As in Homarus the anterior levator muscle does not have a block of cuticle at the base of the tendon. The tendon of the posterior levator is peculiar in that it normally has two blades for muscle attachment and these are orientated perpendicular to one another. One blade lies radially in the limb as described for the other species above and the other lies parallel to the muscle fibres.

CSD.1. The strand of CSD.1 (Fig. 20) is similar in general structure to that of Homarus. It attaches posteriorly to a cuticular projection, which is situated rather closer to the breakage plane than in Homarus and anteriorly to the centre of the large area of thin cuticle. The sensory cells exhibit a wide range of sizes (Fig. 21) and show some variation in shape. The larger cells close to the anterior insertion are spherical whereas some of the smaller ones tend to be spindle shaped.

CSD.2. The thin cuticle associated with CSD.2 forms an externally directed protrusion, unlike that of Carcinus. This protrusion is bounded distally by a deep channel which is continuous with the distal "suture". It was

FIG. 20. A stereodiagram showing the general disposition of CSD.1 and the third group of cells in the 2nd right pereopod of Palinurus vulgaris. The top of the illustration corresponds to proximal and the left side of the illustration to anterior. The dendrites of the third receptor run onto the membrane (Membrane) which occludes the limb after autotomy. Preformed breakage plane (Break.).

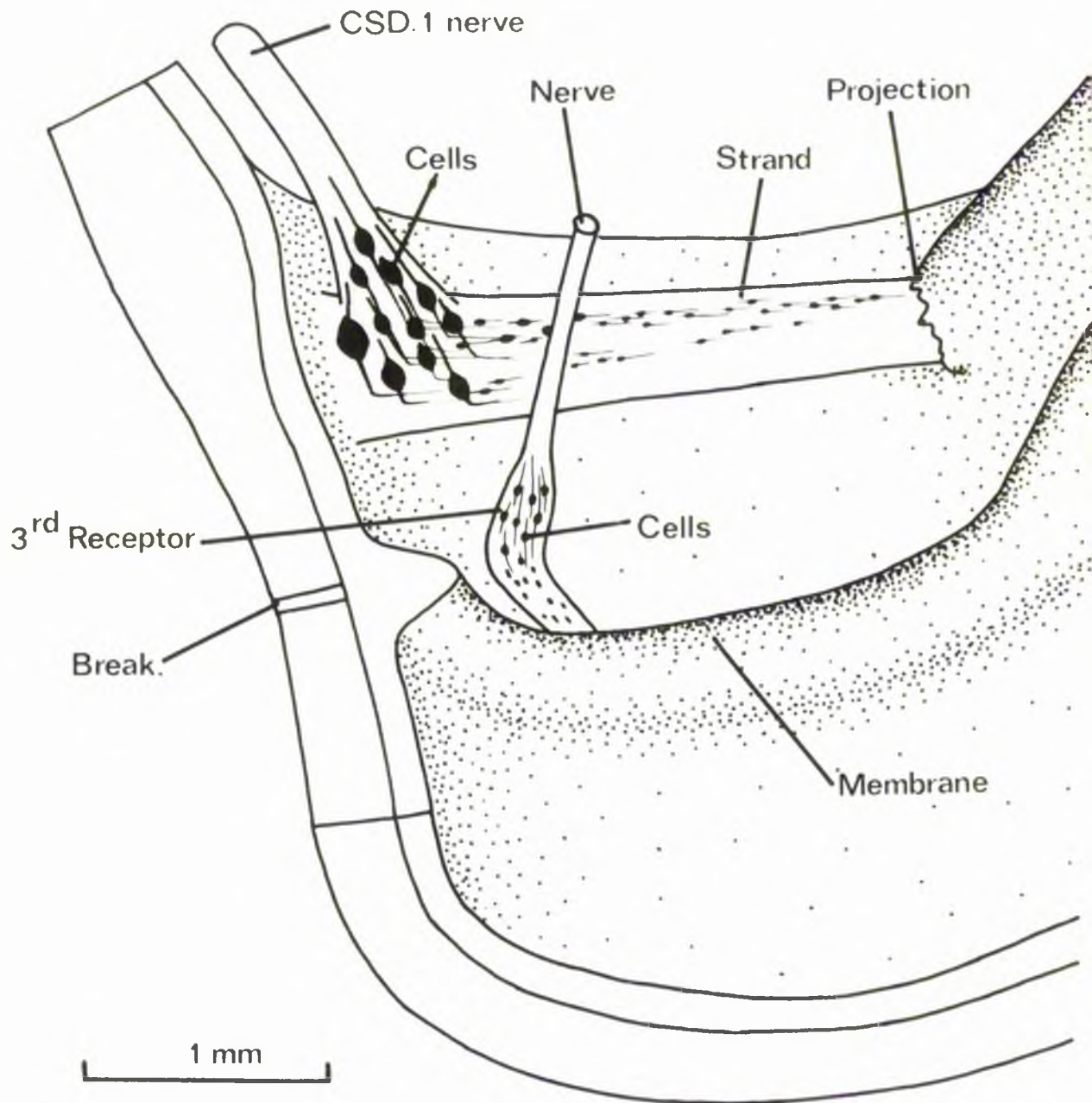
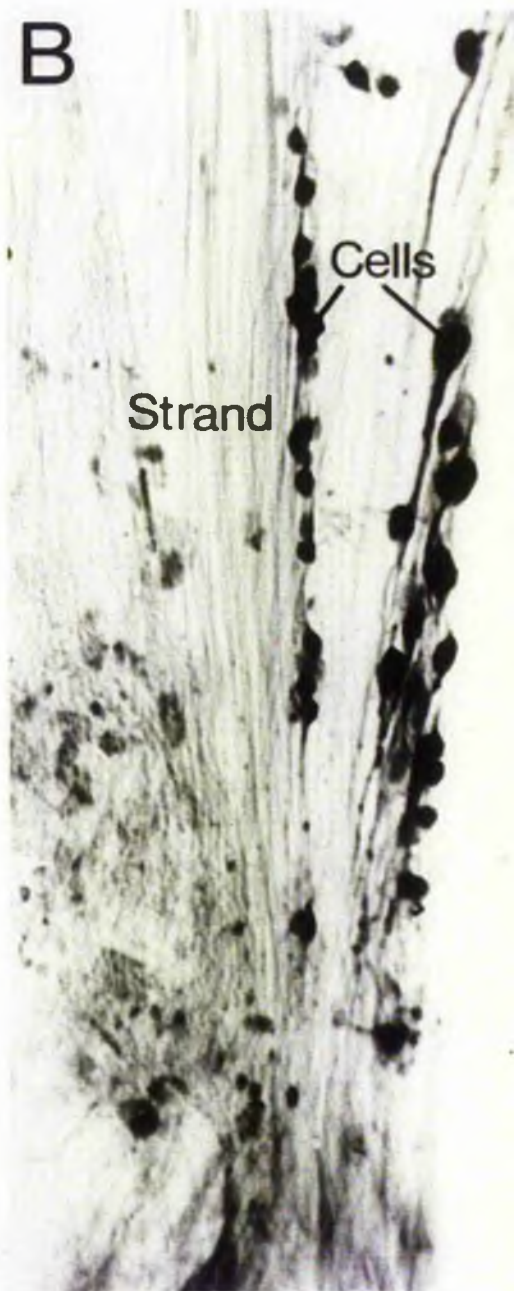


FIG. 21. Photomicrographs of a methylene blue stained preparation of CSD.1 from the 2nd pereopod of Palinurus vulgaris to show the variation in size and the distribution of the sensory cells on the receptor strand. A. shows the more anterior portion of the strand and B. the posterior portion. The top of the illustration corresponds to anterior in both cases.



found difficult to stain CSD.2 in Palinurus with methylene blue but the receptor appears to be intermediate in size and development to those of Astacus and Carcinus.

Close to CSD.1 (Fig. 20) lies a third group of sensory cells, the dendrites of which run onto the membrane that occludes the exposed end of the limb after autotomy. The group of cells of which there may be more than 30, do not appear to be associated with a strand. The cells are much smaller than those of CSD.1, those closest to the membrane being the smallest.

1.5. Responses of the Limb Joint Proprioceptors

The responses of the chordotonal receptors at the limb joints of the decapod walking leg are well documented (see Appendix 1). However, within the scope of this thesis the following two facets required investigation.

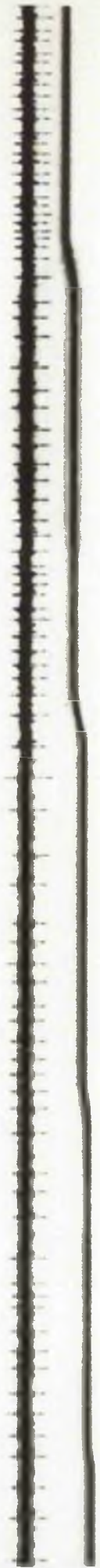
1.5.1. Response of CP2 and Rotation of the C-P Joint

The pereopod C-P joint is capable of rotation about the longitudinal axis of the limb and an additional muscle is present at this joint. As mentioned previously, the position of distal insertion of this muscle suggests that it is unlikely to produce rotation.

When the joint is reduced or produced CP1 and CP2 are active (as demonstrated by Bush, 1965c). If the joint is rotated CP2 shows activity in very few units, frequently only one or two (Fig. 22). These units respond to movement in a clockwise direction (as seen from the proximal end of the limbs). At rest there is no discharge but the units are positionally sensitive with increasing steps of rotation. There is a short dynamic phase that is evident during movement and a tonic discharge at any given displacement. The return movement leads to cessation of firing during movement, a return of a low tonic discharge when maintained at a set position and no discharge when the limb is again straightened. A short movement in the counter clockwise direction from rest invokes a short discharge during the initial stages of movement but no tonic discharge.

To ascertain whether the additional muscle of this joint was capable of producing rotation as does the third muscle of the Natantia and Stomatopoda (Wiersma and Ripley,

FIG. 22. Recording from CP2 of the walking leg of Homarus gammarus to show that some of the units respond to rotation of the propodite about the longitudinal limb axis. The lower recording is a continuation of the upper. The lower trace in both cases monitors rotational movement of the propodite such that the upward deflection of the trace indicates an inward turning of the dactylopodite. The unit shown is a tonic position sensitive unit, more responsive to a final position approached by inward than by outward turning.



1 sec

1952), I stimulated the muscle electrically. The preparation for this experiment was made without damage to the joint by sectioning the leg through the carpopodite and the propodite 1cm on either side of the joint and fixing the preparation by the carpopodite so that the propodite was suspended freely in sea water. The stimulating electrodes were then lowered into the carpopodite and applied to the head of the additional muscle. By this method I found that stimulation of the additional muscle alone produced a weak bending of the limb but no detectable rotation.

1.5.2. Response of CAP Sensilla to Mechanical Stimulation

Attempts were made to record the response of these sensilla to mechanical stimulation at the C-P joint of the walking leg and at other joints. Recordings were made of the activity in the appropriate sensory nerve and on occasions there seemed to be a response among the smaller units when the sensilla were touched with a fine brush. Similar activity could, however, be observed when the brush was moved close to, but not touching, the CAP sensilla. Hence the observed response may have been from other more sensitive sensilla close to the CAP group. No responses that can unequivocally be demonstrated as CAP activity have been recorded.

1.6. Cuticular Stress Detection in the Basi-
ischiopodite of the Reptantian Decapods

The responses of CSD.1 and CSD.2 examined in a number of species were found to be consistent. Thus in the following description the results are not for a single species and may be applied to any of the species listed in the section on materials and methods (Experimental 1.2.) and probably to most reptantian decapods.

1.6.1. Responses of the CSD Receptors to Different Modes
of Stimulation

If the isolated walking leg of Carcinus maenas is sectioned at the ischiopodite-meropodite joint all main proprioceptive organs situated distal to the basi-ischiopodite are either removed or rendered non-functional. It is then not difficult to detect the activity of the CSD receptors by recording from selected small bundles of the main leg nerve in the coxopodite. A number of units are always active in the unstimulated receptors. Application of pressure to the basi-ischiopodite produces a dramatic response as shown for CSD.1 in Fig. 23. The degree of receptor activity is dependent on the magnitude of the force applied and shows little adaptation during the application of constant pressure. On removal of the stimulus the receptor activity rapidly diminishes to the original resting level.

1.6.1.a. Response to Waterborne Vibrations

Although the CSD receptors bear little resemblance to auditory organs, perhaps with the exception of CSD.1

FIG. 23. A-B. The response of CSD.1 in the walking leg of Carcinus maenas to pressure applied to the dorsal surface of the basi-ischiopodite by means of a blunt probe.

Scale mark represents 1 second.

A



B



in Galathea and Palinurus, it is possible that they are vibration sensitive like the connective chordotonal organ of the PD joint (Burke, 1954). It was found, however, that the receptors exhibit no detectable response to manually propagated pressure waves. They may be responsive to higher frequencies.

1.6.1.b. Response to Substrate-borne Vibrations

Responses were observed after strong tapping of the bench on which the experimental equipment was resting, but these were of low magnitude compared with the responses observed to normal stresses imposed on basi-ischiopodite. Under experimental conditions the basi-ischiopodite was applied to the substrate, whereas in the standing animal substratumborne vibrations would have to be conducted past 4 or 5 leg joints to reach the receptors.

1.6.1.c. Stimulation of the Soft Cuticle

It was not possible to rapidly apply and remove a force of sufficient magnitude to deform the entire basi-ischiopodite for analysis of the sensory response. The CSD receptors are, however, associated with discrete areas of soft cuticle which can be easily deformed by the small force produced by the relay mounted probe described above.

When pressure is applied to the soft cuticle of CSD.1 both phasic and tonic units respond (Figs. 24A and 26A). On release a further short burst of phasic activity occurs whilst the tonic activity ceases (Fig. 24A). In many preparations (Fig. 26A) the level of receptor activity immediately after the phasic OFF response remains briefly above the previous resting level which is only attained

after approximately 1 second. The tonic units of the receptor maintain a high level of activity during prolonged stimulation of several minutes. The response characteristics differ with the position of the probe on the soft cuticle and it is necessary to adjust the precise position of the probe to obtain the optimal response.

Recordings were made from small bundles of axons to aid identification of the unit types. The majority of units are ON units, that is they respond to the application of pressure to the external surface of the soft cuticle. Figure 24B shows two tonic ON units, the larger of which is active in the resting condition, whereas the smaller ceases to be active in the absence of stimulus. The phaso-tonic unit in Figs. 24C-D responds to rapidly repeated stimulation largely as an ON unit. After an initial high frequency discharge and rapid adaptation this unit shows a relatively constant discharge during extended periods of stimulation unlike the unit in Fig. 26C which adapts more slowly over a prolonged period. The unit in Figs. 24C-D is active in the absence of stimulus as is the larger unit in Fig. 24B but they differ considerably in their response. On removal of the stimulus the latter undergoes a short period of adaptation with a gradual increase in pulse interval and hence reduction in frequency to reach the resting level, whereas the unit in Figs. 24C-D exhibits a dramatic increase in pulse interval. After a short pause, impulses occur at a very low frequency but the pulse interval reduces slowly to reach the resting level. Figure 25 compares typical examples of the two types of response which have been observed in both CSD.1 (see Figs. 24B-D) and CSD.2 (see Figs. 27B-C). Tonic units which

FIG. 24. The activity from CSD.1 in the walking leg of Carcinus maenas in response to the application of constant pressure. The force was applied to the area of soft cuticle by a blunt probe. Upward movement of the lower trace indicates application of stimulus.

A. Activity in a large bundle of axons. The majority of the units are tonic or phaso-tonic but some units respond phasically to application and removal of stimulation. B. A recording from a small bundle of axons. The small tonic unit is active only during the period of stimulation but the larger tonic unit continues to fire at a reduced frequency on removal of pressure. C-D. This unit responds phaso-tonically to stimulation by a burst and rapidly adapts to a constant frequency with maintained pressure. On removal of the stimulus, the activity ceases then returns at a reduced frequency.

Scale marks represent 1 second.



FIG. 25. A semi-logarithmic scatter diagram to show two distinct unit responses observed in ON units of both CSD.1 and CSD.2 on removal of the probe. \log_{10} of the pulse interval is plotted to a linear base of time for 0.5 secs. preceding and one second following stimulus removal. The arrow indicates the moment of removal of the probe from the soft cuticle. One type of unit (white triangle) shows a gradual increase in pulse interval to attain the lower impulse frequency exhibited in the absence of stimulus. The second unit type (black circle) undergoes a dramatic increase in pulse interval which decreases slowly to reach the normal resting level of activity.

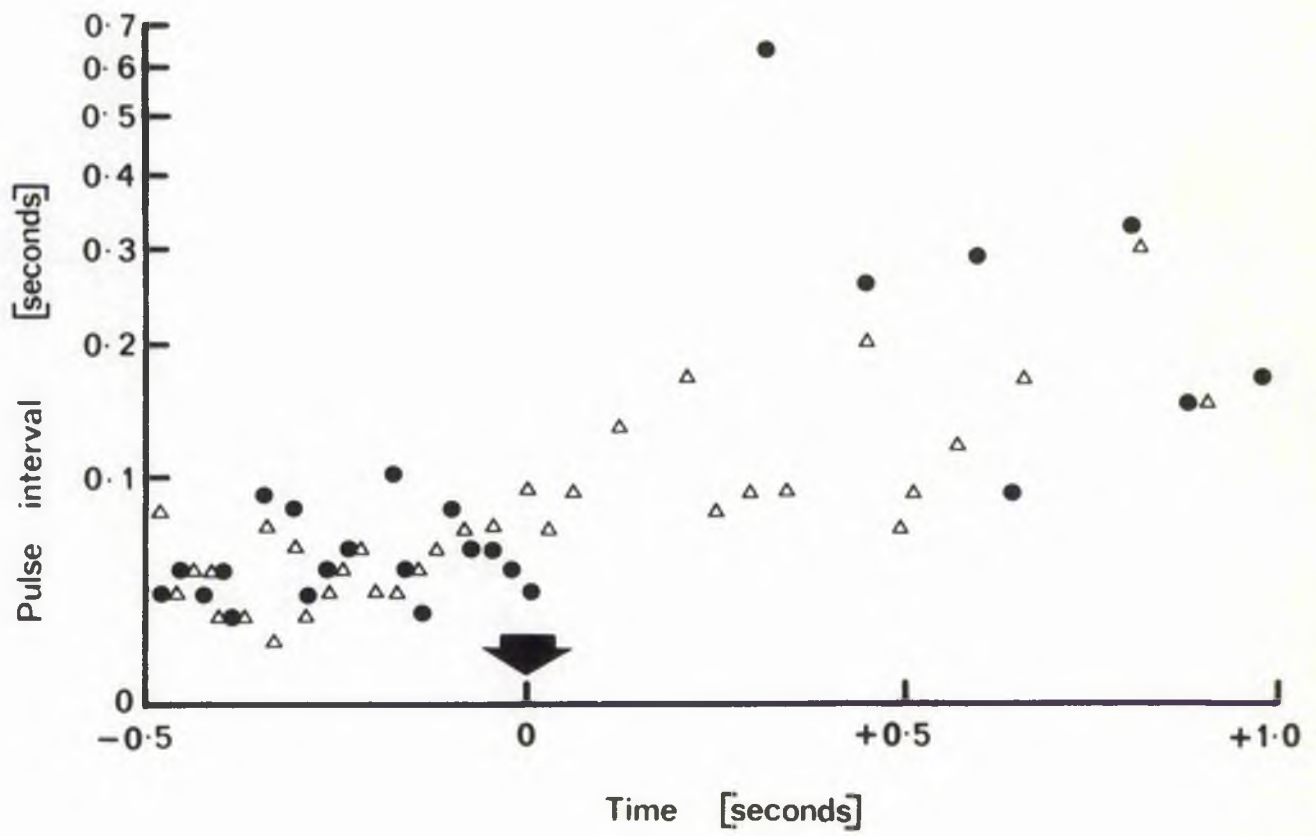


exhibit an increased frequency on removal of the stimulus, OFF units, are less frequently encountered. These units exhibit a normal adaptation phase as shown for CSD.1 in Fig. 26D and for CSD.2 in Fig. 27D. The unit in Fig. 26D is almost exclusively an OFF unit but it does exhibit a small phasic burst to application of the stimulus. The area of soft cuticle is smaller in CSD.2 but it was possible to utilise the same method of stimulation and hence facilitate comparison of the response from the two receptors. CSD.2 is basically similar to CSD.1 in its general response and in the types of units detected but less phasic activity was observed and the OFF response is reduced (Fig. 27A). Figure 27C shows a unit which responds in a very similar fashion to the unit in Fig. 24D. Activity returns slowly after the stimulus has been removed but remains at a frequency considerably below that attained during stimulation. Figure 27D shows a mixture of ON and OFF units. On close examination, the small unit responding to application of pressure appears to be a different unit from that which is active on the removal of the stimulus. The larger tonic OFF unit is irregular in frequency. The results in Fig. 27B are unusual in that some of the units increased in frequency during the period of stimulation. This may have resulted from the probe moving on the external surface of the soft cuticle so that the pressure applied was not constant for the period of stimulation.

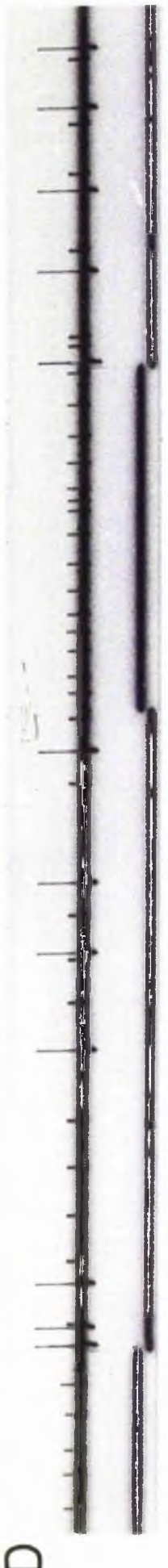
1.6.1.d. Response to Increased Tension in the Tendons of the C-B Joint Muscles

The response of the CSD receptors to tension in the

FIG. 26. The activity from CSD.1 in the walking legs of other decapods in response to constant pressure applied to the discrete area of soft cuticle. Upward movement of the lower trace indicates application of stimulus. A. Hyas araneus. This recording from a large bundle of sensory axons shows the typical OFF response to removal of stimulus. B. Galathea strigosa. A recording from a small bundle of axons which contained a unit responding phasotonically to application, and phasically to removal, of the probe. Some other units present respond phasically to either removal or application of the stimulus. C-D. Homarus gammarus. Records from small bundles of axons showing in C a unit which adapts slowly with constant pressure and in D a unit responding mainly to removal of stimulus. This unit does respond to application of the stimulus but only with a short burst. Scale marks represent 1 second.



FIG. 27. Activity recorded from CSD.2 in the walking leg of Carcinus maenas in response to constant pressure applied to the discrete area of thin cuticle lying external to the receptor by means of a blunt probe. Upward movement of the lower trace indicates application of stimulus. A. A recording from the whole nerve showing that a large number of units are active during maintained pressure but the OFF response is less than in CSD.1. B. The response to application of pressure is normally instantaneous and decreasing with time, but some of the units in this bundle increase in activity with time. The unit adapting on removal of the stimulus is also active during stimulation. C. This unit, which is similar to that in FIG. 24 C-D, responds phasotonically to application of pressure. On removal of the stimulus it ceases firing then slowly increases to a frequency much lower than that attained during stimulation. D. A small bundle of sensory axons with one unit responding to stimulation and two units active only on removal of the stimulus. Scale mark represents 1 second.



muscles at this joint is particularly interesting as the anterior levator is the muscle which has been shown to be of primary importance in the autotomy of the walking legs (Wood and Wood, 1932). The tendons of crustacean pereiopod muscles articulate with the segments on which they insert by means of a strong but flexible membrane. This allows some movement of the tendon to occur without effecting movement of the joint. The CSD receptors show no detectable changes during this initial movement of the tendons (Figs. 28A-D). The CSD receptors respond to tension in both the antagonist muscle groups of the C-B joint (Fig. 28) although the effect of the depressor muscle on CSD.1 was noticeably smaller than that of the anterior levator. When the tension is maintained, the receptors retain a high level of tonic activity with little adaptation but in this case the tension is produced manually and some fluctuations occur that are reflected in the receptor output. As shown in Fig. 28 the receptors generally respond to the initial release of tension by a small burst. The tension developed in the muscle tendons was not measured but in the case of the anterior levator it was insufficient to produce autotomy.

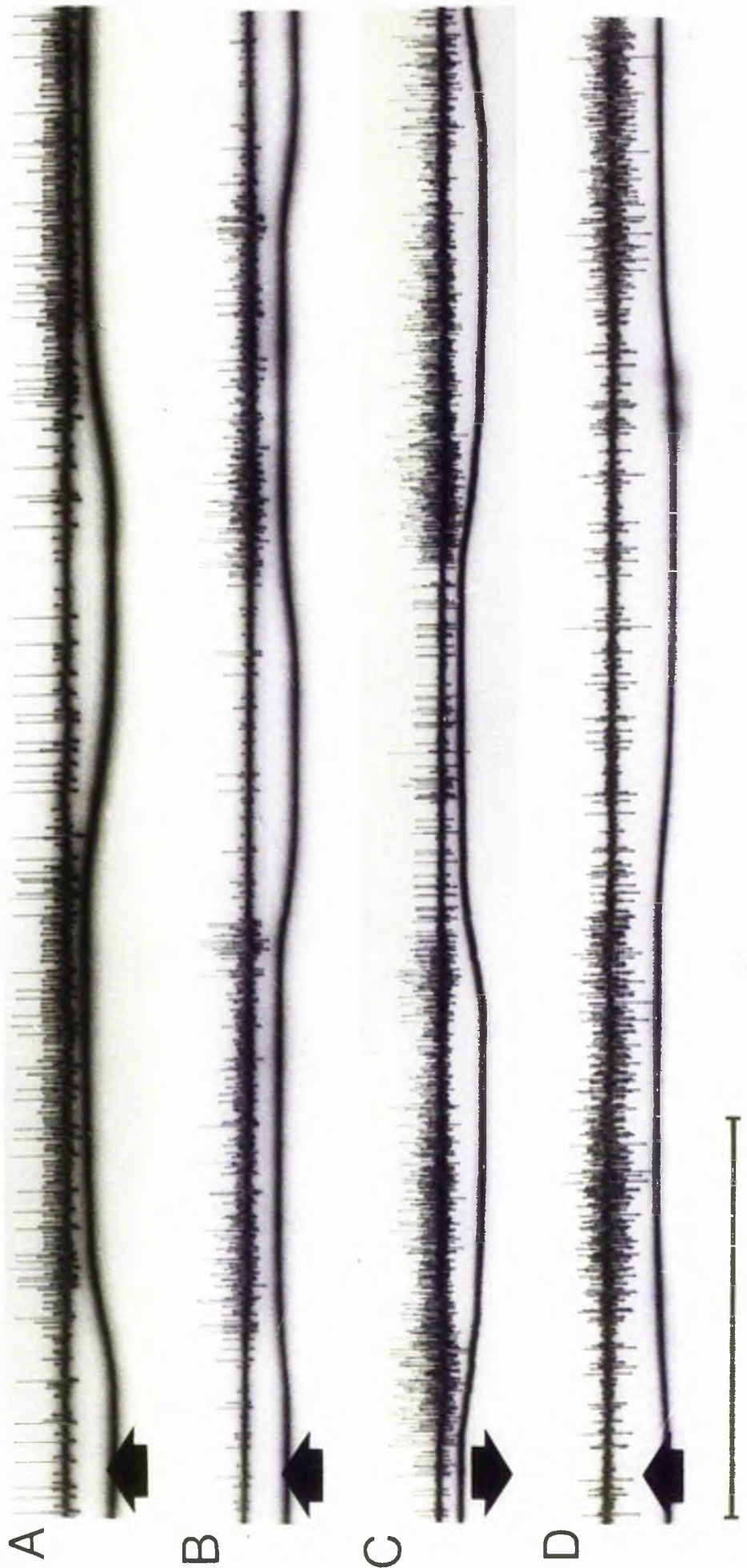
1.6.1.e. Responses of the CSD Receptors to Joint Movement

The above results indicate that the receptors respond to cuticular stress and if this is so they would be expected to respond during movement of the B-I and I-M joints and to tension in the muscles at these joints as they will stress the cuticle on which the receptors lie.

The B-I joint of nephropsideans and the I-M joint of brachyurans are similar in their general disposition and

FIG. 28. Activity recorded from the CSDs in the walking leg of Carcinus maenas in response to manipulation of the muscle tendons at the coxo-basipodite joint. Movement of the lower trace in the direction of the arrow indicates pulling of the tendon. A. The response of a small number of units from CSD.1 to movement of the anterior levator tendon. B. The activity in the whole nerve from CSD.1 on pulling of the depressor tendon. C. The response in the whole nerve of CSD.2 on movement of the anterior levator tendon. D. The response in the whole nerve from CSD.2 on movement of the depressor tendon.

Scale mark represents 1 second.



in the degree of movement which they permit. It is not practicable to record from the CSD receptors whilst stimulating the musculature at these joints and I have restricted my investigations to the effect of passive movement. The relative merit of such an experiment in assessing the response of the "in vivo" receptor is discussed later. The rest position of the joints lies close to the retracted position for the B-I joint and the reduced position for the I-M joint. The movement imposed in the experiments described below is from the rest position to full production (or protraction) and the return to the rest position.

Figure 29A shows the activity of a small group of units in CSD.1 of Homarus. There is a good response when the B-I joint is almost fully protracted and a small burst of activity also occurs when the ischiopodite is returned towards the rest position. To test the specificity of these units I stimulated the soft cuticle of CSD.1 with the relay mounted probe and the same units responded (Fig. 29B). Similar responses were obtained by manipulation of the I-M joint in Carcinus where CSD.1 responds but primarily when close to the extremity of joint movement (Fig. 29C). Units may respond during movement in both directions or to unidirectional movement as illustrated by the small unit of Fig. 29D.

The responses observed in CSD.2 (Fig. 30) are very similar to those of CSD.1 but occur over a wider range of joint position. The response of CSD.2 to movement of the B-I joint in Homarus is small (Fig. 30A) whereas the response in Carcinus to manipulation of the I-M joint is similar in magnitude to CSD.1. Figure 30A shows a small

FIG. 29. A-B. The activity of a small number of units of CSD.1 in the walking leg of Homarus gammarus in response to passive movement of the basi-ischiopodite joint and to pressure applied to the soft cuticle. Upward movement of the middle trace indicates stimulation of the soft cuticle as in FIGS. 26 and 27. Upward movement of the lower trace represents protraction of the joint. C-D. Response of CSD.1 in the walking leg of Carcinus maenas to passive movement of the ischio-meropodite joint. Upward movement of the lower trace indicates production of the joint. C. The response in the whole sensory nerve bundle. D. The response of two units.

Scale mark represents 1 second.



FIG. 30. A. The response in a small number of units of CSD.2 in the walking leg of Homarus gammarus to passive movement of the basi-ischiopodite joint. Downward movement of the lower trace indicates protraction of the joint. B-D. The activity from small bundles of sensory axons from CSD.2 in the walking leg of Carcinus maenas to passive movement of the ischio-meropodite joint. Upward movement of the lower trace indicates production of the joint. A. Generally the units which respond to production and reduction are different. C. A single unit active only during production. D. Two units which respond to both production and reduction of the joint. Scale mark represents 1 second.



A



B



C



D



group of units activated mainly during protraction of the B-I joint in Homarus and here the activity occurs over most of the range of imposed movement. Figures 30B-C, showing the response of CSD.2 to I-M joint manipulation in Carcinus, illustrates some of the unit types. Individual units may respond to unidirectional movement as in Fig. 30B where there are unidirectional units for both directions. Figure 30C shows a single unit which responds to production for most of the range of movement. Figure 30D shows two units which respond to movement in both directions but as with CSD.1 they are only active when the ischiopodite has been moved several degrees away from the rest position.

The responses of CSD.1 and 2 to joint movement in the other direction, that is reduction or retraction, is very similar in nature to that described above.

1.6.2. Responses of the CSD Receptors During Autotomy

As described previously, the CSD, receptors, particularly CSD.1, are anatomically close to the preformed breakage plane and the soft cuticle of CSD.1 appears to be structurally associated with it. I have shown above that the receptors are responsive to changes in tension as produced by activity in the muscles of the C-B joint and it is the anterior levator of this joint which has been demonstrated as functional in the production of autotomy (Fredericq, 1891). It is therefore of value to know the response of the CSD receptor during autotomy.

For the purpose of analysing the receptor response I have considered autotomy to consist of two phases. The initial phase is the fracture of the cuticle at the

breakage plane and the second phase is the rupture of the soft internal structures required to produce separation. It is possible experimentally to produce the first phase without the second. Autotomy was effected in an isolated limb attached to the experimental dish through the meropodite by holding the anterior levator muscle tendon in a pair of artery forceps attached to the micromanipulator-potentiometer system referred to previously. Tension in the anterior levator tendon was produced via the controls of the micromanipulator.

As tension increases in the anterior levator muscle the activity of CSD.1 increases and it continues to increase until the first phase of the breakage occurs at which time the receptor activity decreases dramatically. This is demonstrated in Fig. 31A where there is some movement artefact at the actual moment of breakage but it can be seen that receptor activity rapidly returns to the normal resting level. In Fig. 31C the complete separation of the two parts of the limb has been achieved. After the initial breakage there is little noticeable decrease in frequency due to stretch of the soft tissue in which the receptor lies. When complete separation occurs some units in CSD.1 may be damaged and discharge at a high frequency but the receptor as a whole can be seen to subsequently decrease its activity.

CSD.2 is very different from CSD.1 in that it lies distal to the breakage plane and is therefore lost in the second phase of autotomy. During the first phase CSD.2 activity increases until cuticular breakage occurs, but the receptor nerve is severed in the second phase and a gross discharge is observed (Fig. 31D) as will presumably occur in all fibres of the leg nerve which traverse the

FIG. 31. The activity in the CSD receptors in the walking leg of Carcinus maenas during autotomy produced by pulling the tendon of the anterior levator muscle of the extirpated limb. A. CSD.1 shows increasing activity as the tension of the muscle tendon increases but the activity decreases immediately after the cuticle has fractured. Upward movement of the lower trace indicates increasing tension in the tendon. The arrow indicates the moment of cuticular fracture. B. Stimulation of the soft cuticle of CSD.1 shortly after autotomy shows the receptor to respond normally. C. If tension is maintained in the anterior levator tendon after cuticular fracture (indicated by first arrow) the level of activity is maintained until separation is complete (second arrow). Frequently one or occasionally two units are destroyed. D. The response monitored in the sensory nerve of CSD.2 proximal to the autotomy plane is dramatic as a result of the nerve bundle breaking. Scale mark represents 1 second.



breakage plane.

1.6.3. Post Autotomy Responses in CSD.1

1.6.3.a. Stimulation of the Soft Cuticle

Although minor damage may occur to the receptor as shown above the soft cuticle associated with the receptor is not damaged and remains intact. Immediately after autotomy CSD.1 can be shown to be capable of a normal response to stimulation of the soft cuticle as shown for a small number of units in Fig. 31B.

1.6.3.b. Stimulation of the Breakage Plane Membrane

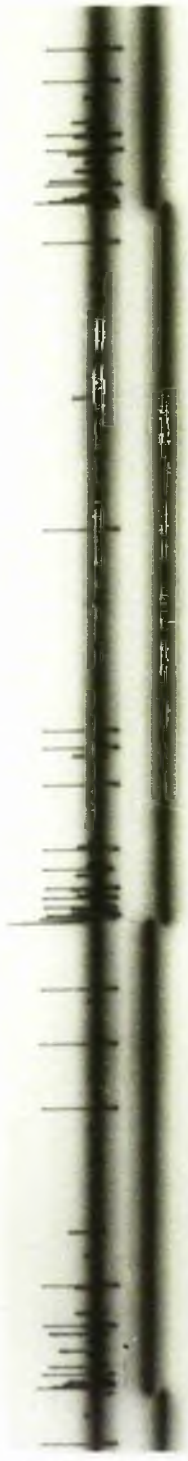
In the autotomised limb all distal receptors are lost, only the T-C complex, the CB chordotonal organ and CSD.1 remaining. CSD.1 is in a position very close to the soft tissue of the closed wound and is situated where it may respond to movement of the occluding membrane. Figures 32A-C show the response of CSD.1 in Carcinus to touch of the breakage plane membranes in the region of the receptor by means of the relay mounted probe. The response of the receptor is not large even though the stimulus is gross and it is dependent on the distance between the receptor and the area stimulated. As illustrated by Figs. 32A and B the nature of the response may vary greatly with the area stimulated. In Fig. 32A the "ON" and "OFF" responses are of approximately equal magnitude whereas in Fig. 32B the "OFF" response is much greater than the "ON". Figure 32C shows the response of a single unit to touch of the breakage plane tissue and it responds mainly to relaxation of the membrane. This is

the same unit as shown in Figs. 24C-D responding to stimulation of the soft cuticle.

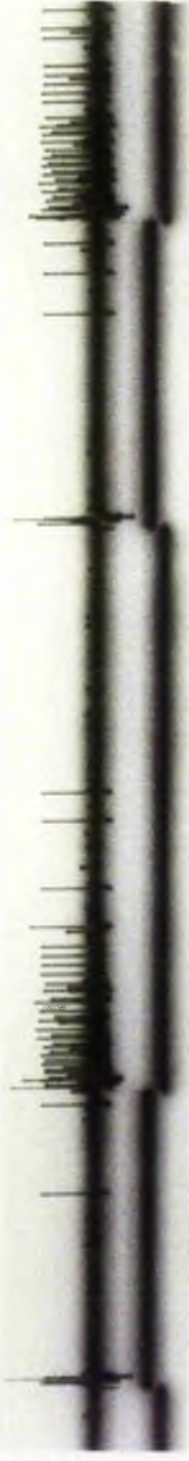
1.6.3.c. Movement of the Regenerating Limb Bud

The crustacean limb shows a high degree of regenerative ability at the breakage plane. During the initial stages of regeneration a bud develops and extends along the limb axis. This bud is a relatively soft structure compared to the rest of the limb and is therefore easily deformed. Figure 32D shows the response of a small number of units from CSD.1 to linear movement of the bud along the limb axis. Such movement of the bud causes movement of the tissue between the base of the bud and the basipodite. The response of the receptor is not large in spite of the gross movement of the limb bud as demonstrated by Fig. 32D, whereas the soft cuticle when stimulated by the relay mounted probe produced a more distinct response (Fig. 32E).

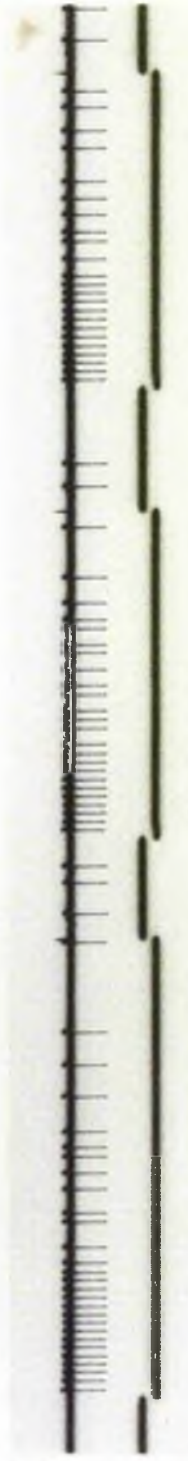
FIG. 32. Post autotomy responses from CSD.1 in the walking legs of Carcinus maenas and Homarus gammarus. A-C. Carcinus. Upward movement of the lower trace indicates mechanical stimulation of the membrane, which occludes the limb after autotomy. A and B show that the response observed in the same nerve bundle differs considerably with the area stimulated. C. A rapidly adapting tonic unit which responds mainly to removal of the probe. This is the same unit as that in Fig. 24 C-D. D-E. Activity of CSD.1 in Homarus to manipulation of the regenerating limb bud and to stimulation of the soft cuticle. Upward movement of the middle trace indicates stimulation of the soft cuticle as in Figs. 26 and 27. Upward movement of the lower trace represents axial movement of the limb bud away from the basipodite. Scale marks represent 1 second.



A



B



C



D



E

EXPERIMENTAL

2. PROPRIOCEPTION IN THE 3RD MAXILLIPED

2.1. Introduction

The 3rd maxilliped is the macruran decapod appendage which most closely resembles the generalised malacostracan limb as typified by the pereopod of Anaspides (Snodgrass, 1952). It may thus be argued that the 3rd maxilliped is morphologically less specialised and more primitive in form than the pereopods. The relatively unspecialised structure of this limb is indicated by the uniform mobility available at all but the basipodite-ischiopodite joint.

The thoracic appendages anterior to the 3rd maxilliped are modified to a greater or lesser extent for feeding whilst those situated caudally are mainly locomotory. In Homarus gammarus the 3rd maxilliped is utilised for holding larger particles of food, the smaller particles being passed directly by the anterior pereopods to more anterior mouth parts. The food is grasped between the toothed edges of the ischiopodite and the more distal segments are reflected to retain the food. They are also utilised in antennal cleaning, the antennae being pulled between the extended maxillipeds and in digging when they act in conjunction with the 2nd and the 3rd pereopods. In the latter action, the 3rd maxillipeds are held apart and extended with the pereopods brought up underneath to add support and form a scoop (see Frontispiece). By this method the lobster can perform considerable excavations in search of food (see Herrick, 1895). The macruran 3rd maxillipeds are thus more versatile than the analagous maxillipeds of Anaspides which are never used in digging (Manton, 1930). The functions of the 3rd maxillipeds do not require the same degree of precision as the 2nd pereopod of Homarus.

Because of their orientation, the 3rd maxillipeds are

not exposed to the same environmental hazards as the walking legs and decapods are extremely reluctant or possibly unable to autotomise this limb. Wood and Wood (1932) were not able to provoke Homarus into autotomising the 3rd maxilliped. On one occasion they did produce autotomy artificially but the break was not clean.

The proprioceptors of the 3rd maxilliped are previously undescribed.

2.2. Materials and Methods

The proprioceptors were examined in the 3rd maxilliped of Homarus gammarus only. The lobsters were caught locally and maintained in tanks of circulating sea water until required.

The methods used to examine the anatomy of the limb and the morphology of its proprioceptive organs were as described in Experimental 1.2.

It would be necessary to write a somewhat bulky section in order to describe the dissection techniques used to allow access to each of the chordotonal organs examined. However, the position of each of the proprioceptive organs is illustrated in Figs. 33B and 34B. Wherever possible access to the nerve trunk from the receptor was gained with little or no damage to the articulation by removing the exoskeleton from the opposing surface of the segment, proximal to the joint. The nerve to the chordotonal organ was easily identified electrophysiologically by the gross activity exhibited to joint movement.

Afferent fibre activity was detected via platinum wire electrodes, amplified differentially and recorded by conventional means. Movements of appropriate joints were made by a micromanipulator-potentiometer system (Shelton and Laverack, 1968).

2.3. Morphology of the Limb Joints and Associated Proprioceptors of Homarus

The disposition of the 3rd maxilliped of Homarus is completely different from that of the walking leg (Fig. 12) since it usually lies along the body axis rather than at a right angle to it. Thus the posterior face of the walking leg is equivalent to the external or lateral wall of the 3rd maxilliped. The terms "anterior" and "posterior" have been used to facilitate comparison with the walking legs though it would be more meaningful to refer to the "lateral" and "medial" surfaces. The 3rd maxilliped does not support any of the body weight and when not in motion it adopts one of two characteristic attitudes. The limb may be extended, the distal portion gently curving downwards and inwards so that the tips of the dactylopodites are closely apposed (Fig. 12B) or the distal three segments may be reflected back under the proximal segments by complete flexion of the M-C joint (Fig. 12A).

The distal segments (carpopodite, propodite and dactylopodite) of the 3rd maxilliped are ovoid and the "ischiopodite" is triangular in cross section. The basipodite and ischiopodite are fused to form the longest segment (35% of total limb length) whereas the meropodite is the largest in the walking leg (30% of the total limb length). There is also a noticeable diminution in relative size of the distal segments of the limb by comparison with the walking leg. The P-D joint of the 3rd maxilliped is not chelate.

There are different capacities for movement at each of the joints with respect to the pereopod (see Figs. 33B and 34B). In particular the C-P joint differs from the

FIG. 33. A and B. Ventral view of the left 3rd maxilliped of Homarus gammarus. As explained in the text, it would be more appropriate to use the terms lateral and medial to describe the orientation of this limb rather than posterior (POST.) and anterior (ANT.), but use of the latter terms facilitates comparison with the pereopods. A. To show the musculature and the position of the externally located articulated peg sensilla (CAPs). B. To show the position of the internal chordotonal organs and the extent of movement possible at each of the joints. Segments: coxopodite (Co), "basipodite" (B), flagellum (F), "ischiopodite" (I), meropodite (M), carpopodite (Ca), propodite (P), dactylopodite (D). Muscles: flagellum extensor (F. Ext.), flagellum flexor (F. Flex.), productor (Prod.), flexor (Flex.), extensor (Ext.), stretcher (St.), ventral bender (V. Bend.), dorsal bender (D. Bend.), closer (Cl.), opener (Open.). Receptors: The receptors are named by the initials of the limb segments which constitute the joint at which they are situated. Autot? indicates the position of CSD.1.

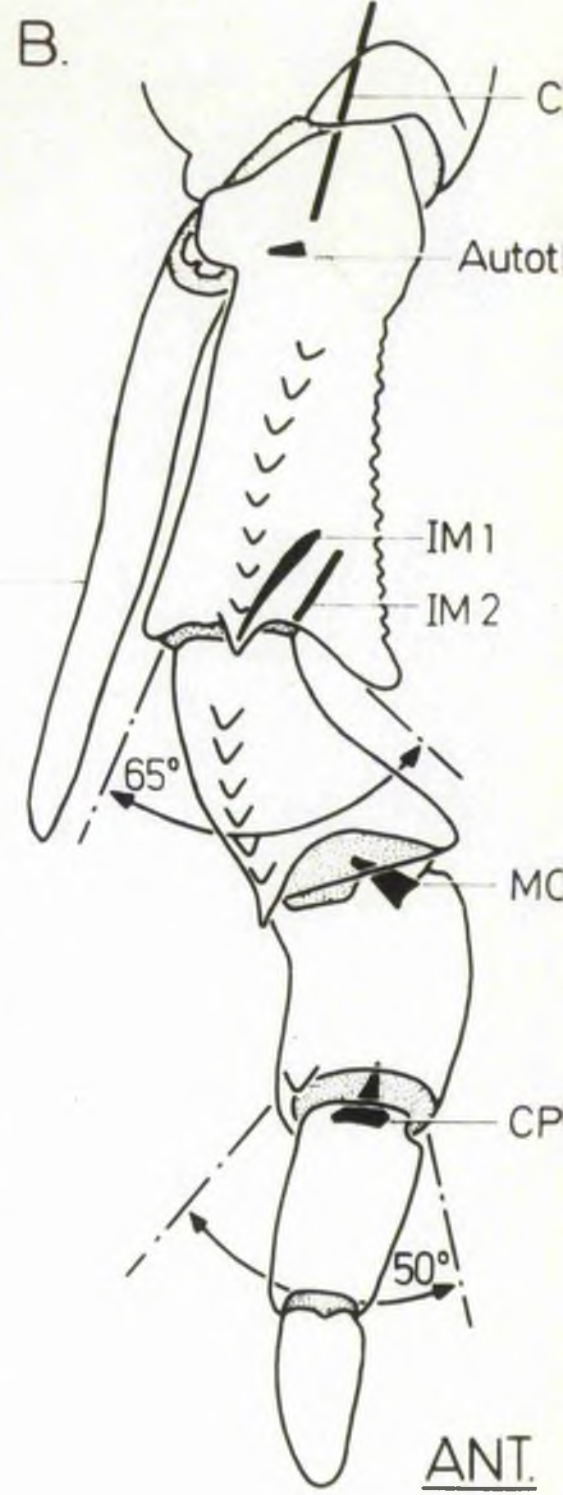
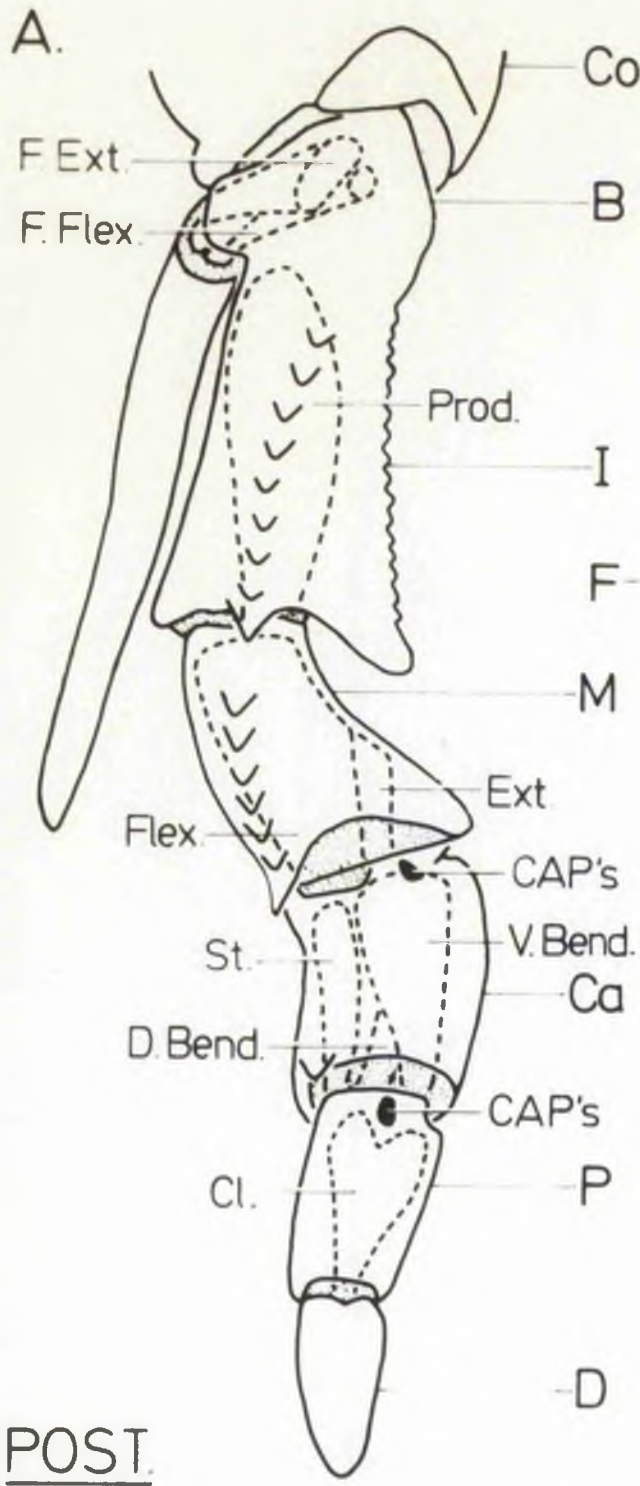
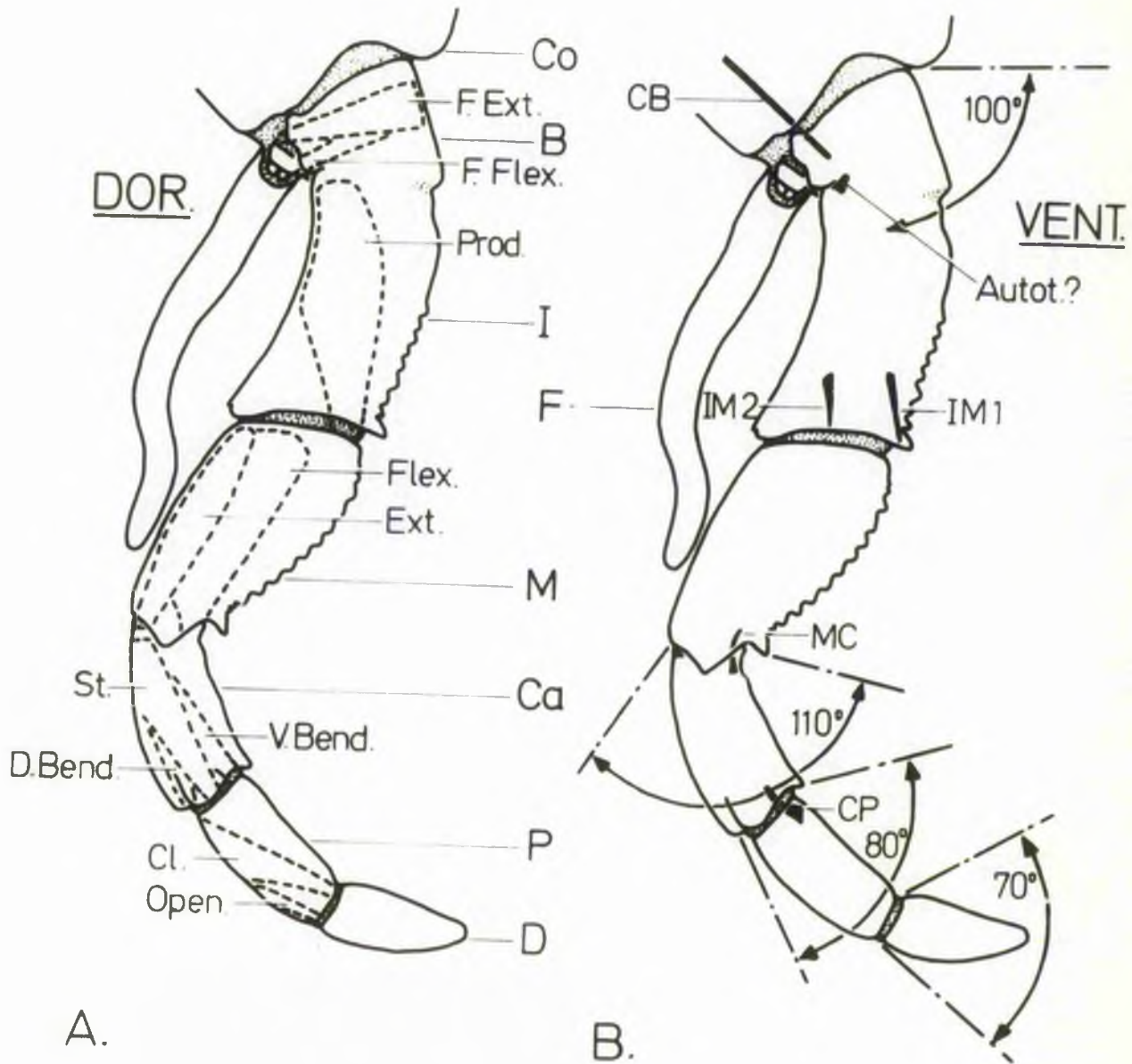


FIG. 34. A and B. Posterior views of the left 3rd maxilliped of Homarus gammarus. A. To show the musculature and the position of the externally located cuticular peg sensilla (CAPs). B. To show the position of the internal chordotonal organs and the extent of movement possible at each of the joints. The lettering is as for Fig. 33.



walking leg in that it does not have the ability to rotate but its movement is not restricted to a single plane. The degrees of freedom at the different joints do not vary as much as in the 2nd pereopod and all joints are capable of being moved through at least 50° . The 3rd maxilliped thus maintains a considerable degree of flexibility throughout its length.

Figures 33 and 34 summarise the anatomy of the 3rd maxilliped in Homarus. The muscles of the 3rd maxilliped were described and named by Schmidt (1915) but, as with the pereopod, I have used the nomenclature of Bush, Whitear and Wiersma in recent papers on the decapod walking leg.

2.3.1. Thorax-Coxopodite and Coxopodite-Basi-ischiopodite Joints (T-C, C-B)

The muscles of the T-C and C-B joints are very important in orientation of the 3rd maxilliped. It is primarily these muscles which raise the appendage so that food may be placed between the mandibles and lower it when aiding the mandibles to disjoin large food particles.

As with the 2nd pereopod the musculature of this region is complex. The T-C and C-B joints may move independently by use of the promotor and remotor or levator and depressor muscles respectively (see Schmidt, 1915). However, a large number of the levator and depressor muscle fibres originate in the thorax and their action must affect the movement of both joints. Neither the T-C nor the C-B joint has a plane of movement parallel to the body axis so when the 3rd maxillipeds are utilised to tear food the muscles of both joints are active to maintain a hold on the

food whilst pulling ventrally. This ventral movement is produced by the depressor muscle which has a very long tendon passing through the coxopodite and into the thorax.

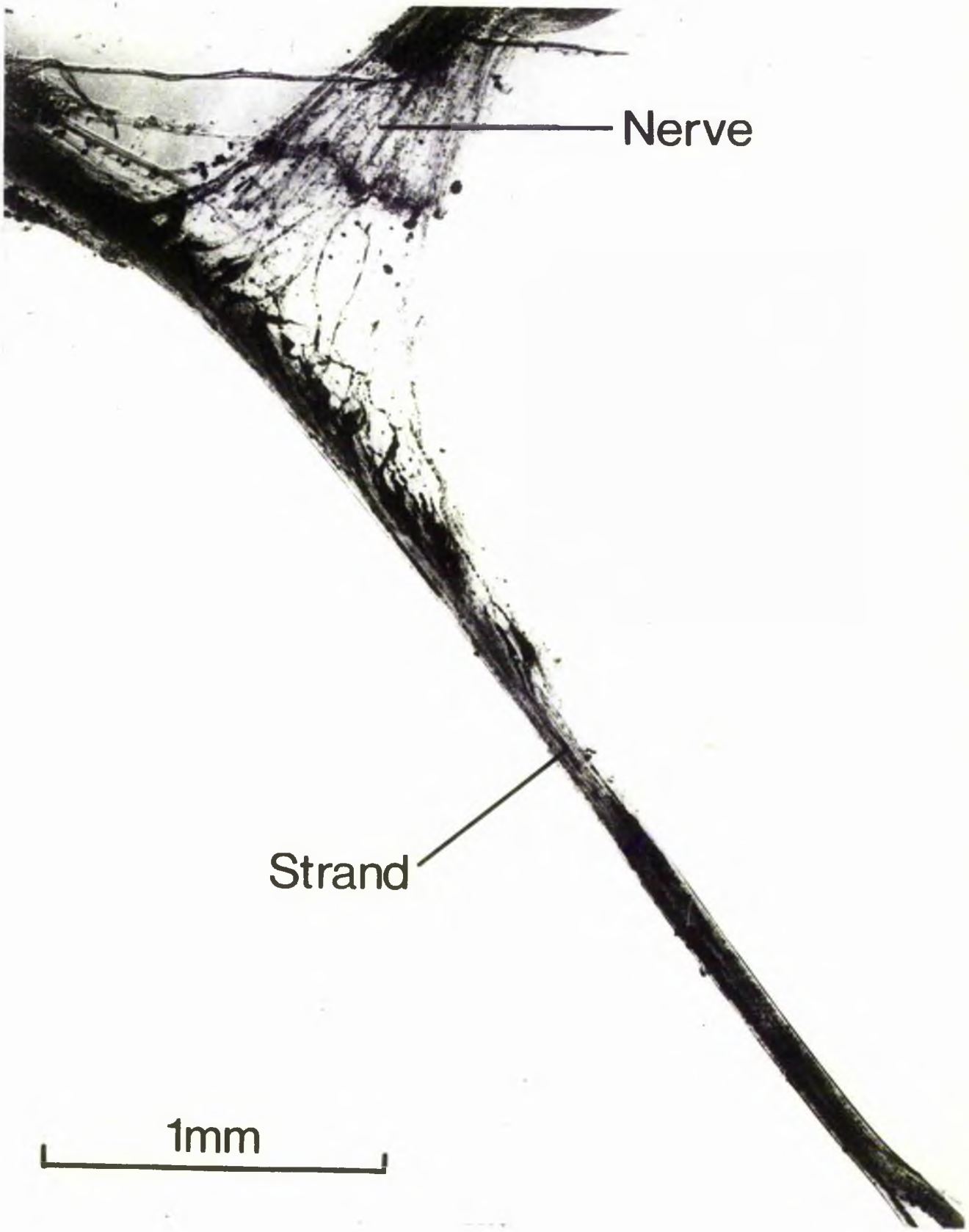
Despite numerous attempts I have been unable to demonstrate the presence of a chordotonal receptor at the T-C joint and must assume that it is not present. The muscle receptor system is similar to that in the walking legs. The levator and depressor elastic strand receptors are present. A chordotonal receptor is present at the C-B joint (Fig. 35) and it is very similar in disposition to that in the walking leg. As the sensory nerve approaches the elastic strand it fans out to greater degree than in the walking leg. The elastic strand inserts proximally in the coxopodite close to the anterior hinge of the T-C joint and distally in the basipodite near to the receptor at the B-F joint. The bipolar cells of the receptor are scattered over most of its length, but the majority lie in that region where the nerve joins the strand.

2.3.2. Basipodite-Flagellum Joint (B-F)

This joint is present only in the 3rd maxilliped as the pereopods in the adult do not carry a flagellum. The movement at this joint is produced by a pair of antagonistic muscles, an extensor and a flexor, which insert onto the ventral wall of the basipodite. This differs from the brachyura which have only one muscle, an extensor, flexion being produced by the elasticity of the joint. The motor control of flagellar movement in the Brachyura and Anomura is described by Burrows and Willows (1969).

No connective chordotonal organ could be found at this joint but CSD.1 (Fig. 40) is situated close to the base of

FIG. 35. Photomicrograph of a methylene blue stained preparation of the CB receptor from the 3rd maxilliped of Homarus gammarus.



Nerve

Strand

1mm

the flagellum and may respond to flagellar movement.

2.3.3. Basipodite-Ischiopodite Joint (B-I)

As with the 1st pereopod, the basipodite and ischiopodite have fused to form a single entity and the B-I joint muscles and chordotonal organ are absent. The structure of the basi-ischiopodite is described in Experimental 2.4.

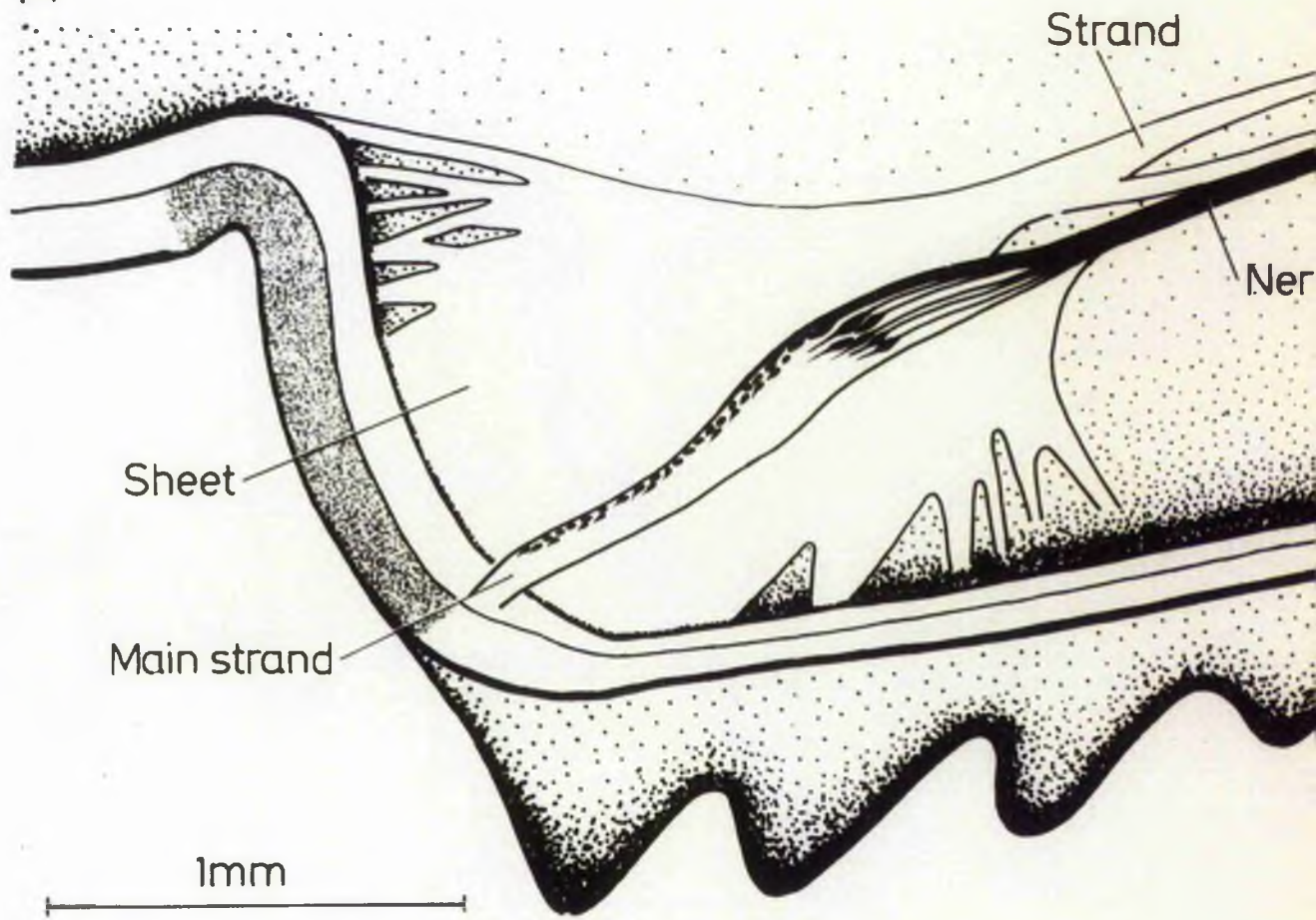
2.3.4. Ischiopodite-Meropodite Joint (I-M)

The degree of movement possible at this joint is similar to the 2nd pereopod but the musculature differs considerably. Whereas the pereopod has two reductor muscles the 3rd maxilliped has a single producer muscle which moves the meropodite ventrally and medially (anterior).

The IM1 receptor (Fig. 36) is located in the ventral corner of the ischiopodite. It consists of a sheet of connective tissue which spans the joint and is connected proximally to the producer muscle by a long thin strand. The anatomy suggests that the organ is capable of responding to either active muscle movement or to passive joint movement. The nerve to IM1 runs parallel to the thin strand and where it reaches the sheet joins a thick connective tissue strand (main strand) which lies across the sheet at an angle approximately normal to the direction in which the sheet is deformed by joint movement. The main strand of the organ is attached proximal to the joint. The cell bodies (30-40) are situated on the main strand proximal to the joint with the smallest cells most distally placed. They form a column of sensory cells running the whole length of the strand. The dendrites project distal

FIG. 36. A posterior view of the IM1 receptor from the left 3rd maxilliped of Homarus gammarus. Note the grouping of the large cell bodies proximally and the linear arrangements of the smaller distal cells. Ischiopodite (I), meropodite (M).

M



to the cell bodies but their terminations are unknown.

IM2 is very difficult to locate and stain by methylene blue techniques in Homarus and my knowledge of this receptor is incomplete. However, it appears to be morphologically similar to the corresponding receptor in Astacus leptodactylus as described by Wales, Clarac, Dando and Laverack, (1970). The receptor (Fig. 37) lies in the anterior corner of the distal ischiopodite (i.e. that with the largest tooth).

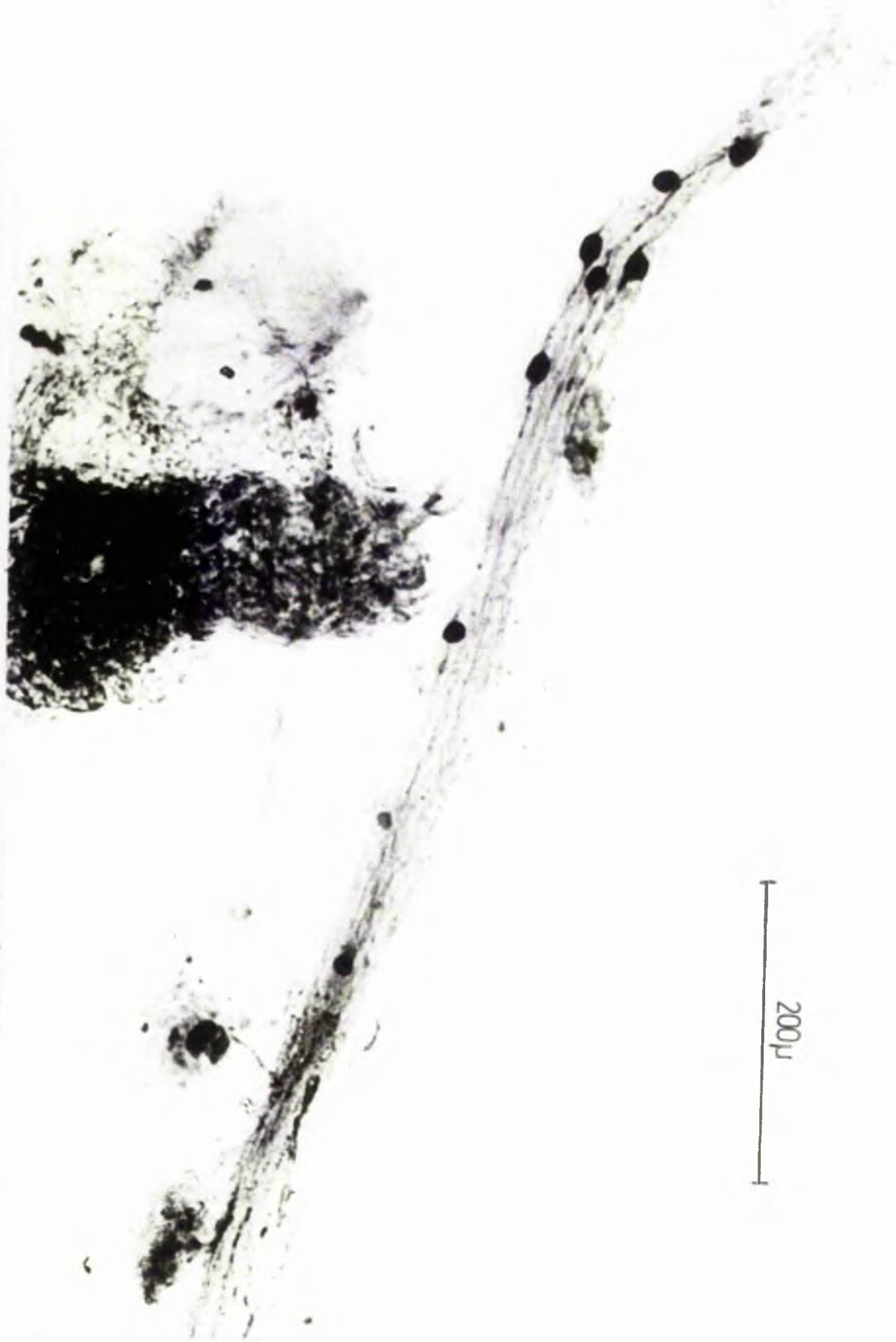
2.3.5. Meropodite-Carpopodite Joint (M-C)

The condyles for articulation of the M-C joint are poorly developed and the degree of freedom is reduced (Fig. 34B). The antagonistic flexor and extensor muscles are present but the accessory flexor muscle, which is associated with the myochordotonal organ of the pereopod, is absent. The M-C receptor (Fig. 38) is attached proximally to the apodeme of the flexor muscle and distally spreads out to form a triangular sheet which covers the region of the carpopodite occupied by the CAPs. The receptor nerve runs alongside the flexor muscle to join the connective tissue close to its attachment on the apodeme. The cell bodies all lie distal to the joint and are divided into two groups. One group lies medial to the sheet and these are the larger cells. The second group situated proximal to the first group lies in the hypodermis external to the sheet. It is possible that the latter group is associated with the CAP organs.

2.3.6. Carpodite-Propodite Joint (C-P)

In the third maxilliped there are no distinct

FIG. 37. Photomicrograph of a methylene blue stained preparation of the IM2 receptor from the left 3rd maxilliped of Astacus leptodactylus (by courtesy of F. Clarac). Note the small number of cells (10-15) and how they are spread along the strand.



200µ

FIG. 38. Photomicrograph of a methylene blue stained preparation of the MC receptor from the 3rd maxilliped of Homarus gammarus. This receptor shows a distinct division into two cellular groups, the larger of which are more distal than the smaller cells. The latter group appears to be associated with the CAP sensilla.



Small
cells

Large
cells

200µ

points of articulation and the joint is a very flexible one, with maximal movement possible in the dorso-ventral plane (Fig. 34B), but some movement is allowed in all other directions. The three muscles that control the joint are so positioned that movement of the propodite in all directions is possible upon contraction of one or combinations of these muscles. Any single muscle opposes the action of the remaining two muscles. By virtue of their position I label two as benders (dorsal and ventral) and one a stretcher.

As is the case with the M-C joint there is only a single receptor present at the C-P joint (Fig. 39) and from its position this is probably equivalent to CP2 of the walking leg. The connective tissue which is attached proximally to the ventral bender muscle, spreads out as it crosses the joint. There are two distinct groups of sensory cells. The anterior group is situated internal to the area occupied by the CAP sensilla and the cells of this group lie in the strand or in the hypodermis external to it. The posterior group of cells is peculiar in the manner in which the axons or in some cases the dendrites reflect back towards the joint. The main limb nerve at the C-P joint is divided into a large number of smaller nerve trunks which lie close to the receptor. The nerve to the receptor joins the posterior part of the strand distal to the joint, as is the case with CP2 of the walking leg.

2.3.7. Propodite-Dactylopodite Joint (P-D)

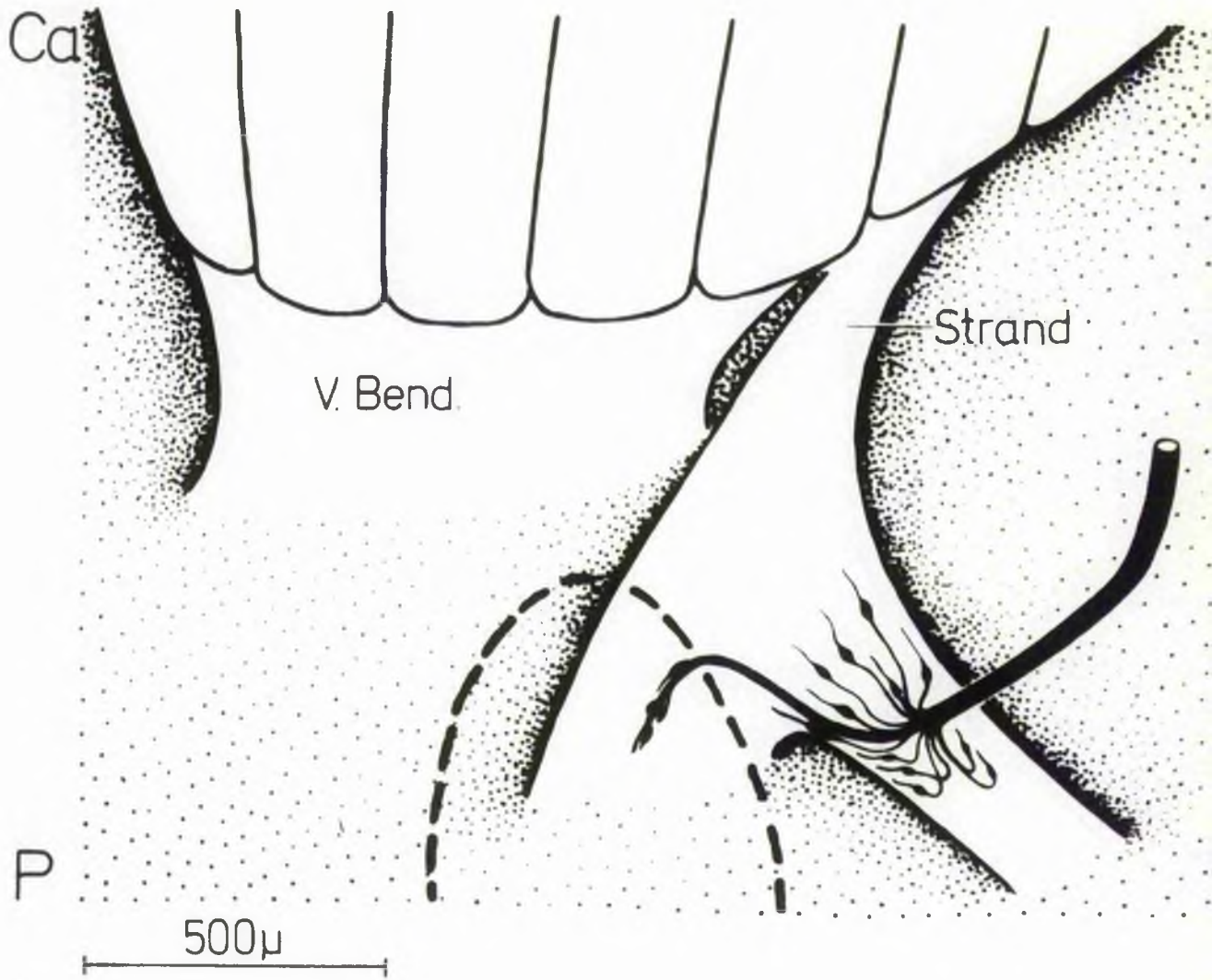
Like the C-P joint there are no distinct points of articulation and the joint is flexible but as movement is

produced by a pair of antagonistic muscles, an opener and a closer, it occurs in a single plane. Despite repeated attempts to locate a receptor at the P-D joint of the maxilliped there is no indication that a receptor exists. Methylene blue and electrophysiological methods have failed to reveal any sign of a receptor and it is concluded that there is no PD in this limb of Homarus.

2.3.8. Cuticular Articulated Peg Sensilla (CAP)

Groups of CAP sensilla are located distal to the M-C and C-P joints of the 3rd maxilliped. The sensilla which are similar to those in the walking leg (Experimental 1.3.7.) lie external to the distal insertion of the MC and CP chordotonal organ strands.

FIG. 39. Dorsal view of the CP receptor of the left 3rd maxilliped of Homarus gammarus. The cells are divided into two groups, one of which is situated internal to the CAP sensilla the position of which is shown by the broken line. The second is peculiar in the way the cells reflect back towards the carpopodite. Ventral bender muscle (V. Bend.), carpopodite (Ca), propodite (P).



2.4. Receptors of the Basi-ischiopodite Region and Autotomy Plane of Homarus

The form of the 3rd maxilliped basi-ischiopodite is considerably different from that of the macruran chela or brachyuran pereopod. The "ischiopodite", which has become greatly lengthened and has a serrated ridge dorso-anteriorly, is valuable to the feeding process (Experimental 2.3.1.). The preformed breakage plane is present but is much less distinct, particularly on the ventral surface. This may indicate that retrogression of the breakage plane has occurred.

The "basipodite" of the 3rd maxilliped differs from that of the pereopods in that it is relatively longer and it articulates with the flagellum. Nevertheless the "basipodite" exhibits most of the features described in the pereopods. The soft cuticle associated with CSD.1 is present and it holds a similar position relative to Paul's "furrow", the breakage plane and to the levator muscle tendons. The thin cuticle associated with CSD.2 is a prominent feature of the ventral ischiopodite. As in the chela it is a discrete area surrounded by more heavily calcified cuticle and the distal suture is absent.

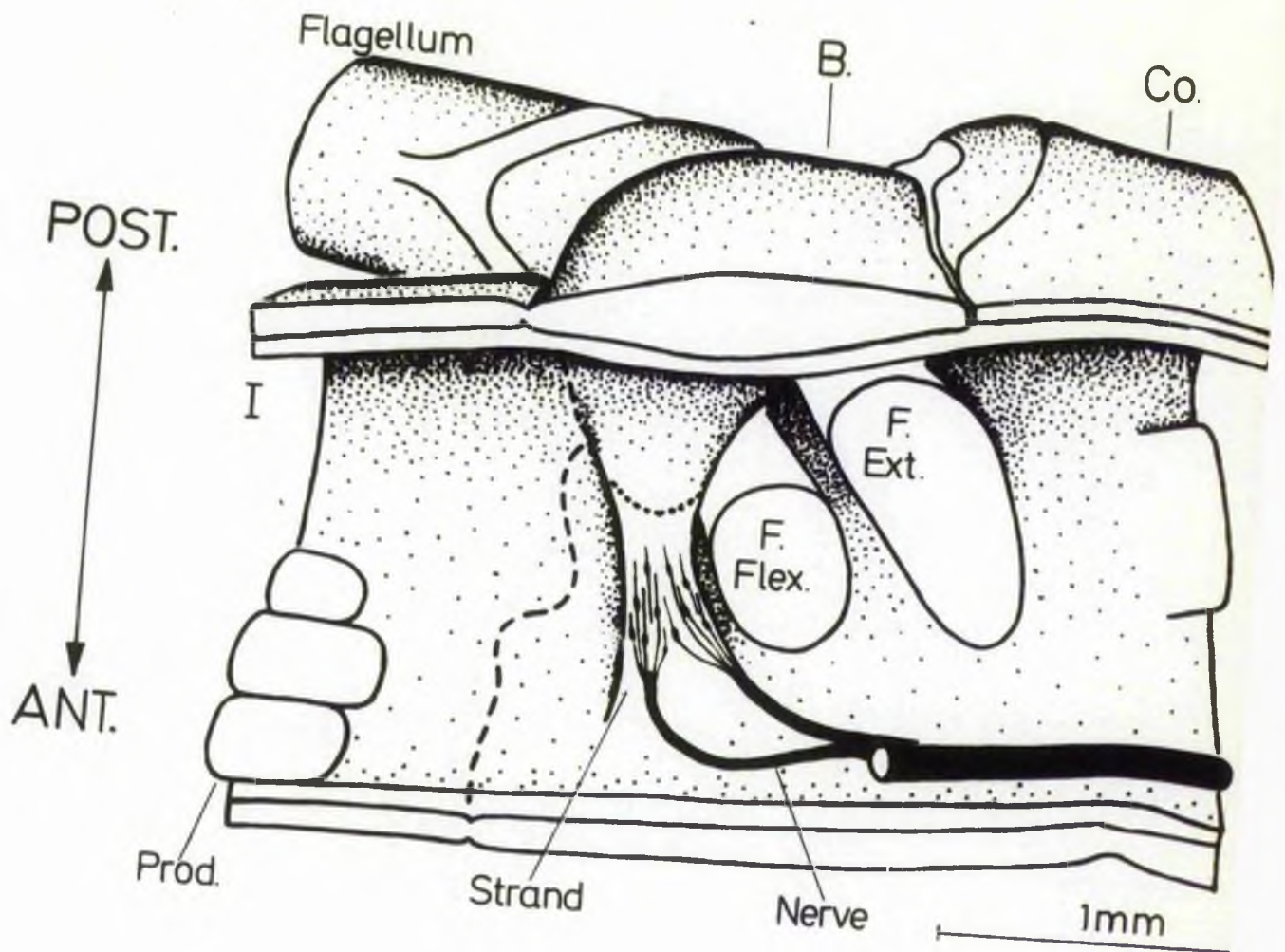
The muscles of the C-B joint show some interesting differences to those described in the pereopod (Experimental 1.4.). As with the pereopods there are two separate levator muscles, the posterior levator originating in the coxopodite and the anterior levator originating in the thorax. The anterior levator muscle is much smaller relative to the other muscles of the C-B joint, and the difference in size of the two levators is thus much reduced. The depressor muscle, which is much

larger than the levators, is incompletely divided into three heads. The two lateral heads originate in the coxa and the large central head, which has a very long tendon (Experimental 2.3.1), originates largely in the thorax.

CSD.1. is situated posteriorly between the flagellar insertion and the line of fusion between the basipodite and the ischiopodite (Fig. 40) and is similar to that described in the walking leg. The strand is not divided into two portions, but consists of a column of tissue with a core of stronger fibres. As with the walking leg, the strand is inserted posteriorly on an internal cuticular projection and anteriorly on a small distinct area of soft cuticle. The nerve trunk to the receptor does not arise directly from the main leg nerve but from a smaller branch which passes close by the anterior insertion of the strand. The receptor nerve invariably splits into two branches both of which innervate the strand. The neurones in the strand are smaller than those of the walking leg receptor and they are situated within the mid region of the strand.

CSD.2. As with the pereopod of many species this receptor is very difficult to stain in the 3rd maxilliped by methylene blue techniques. Thus, no details were obtained of this receptor's morphology.

FIG. 40. CSD.1 is present near to the articulation of the flagellum with the "basipodite" of the 3rd maxilliped. The figure shows a ventral view of a portion of the left 3rd maxilliped of Homarus gammarus. The main leg nerve runs close by the receptor and has been removed in this diagram. This receptor is attached posteriorly to an internal cuticular projection (dotted line) and anteriorly to an area of soft cuticle. The broken line indicates the line of fusion which corresponds to the breakage plane of the pereopods. Basipodite (B), coxopodite (Co), ischiopodite (I), produtor muscle (Prod.), flagellum flexor muscle (F. Flex.), flagellum extensor muscle (F. Ext.), posterior (POST.), anterior (ANT.).



2.5. Responses of the Limb Joint Proprioceptors

2.5.1. C-B Joint Receptor

The CB receptor of the 3rd maxilliped, like the corresponding organ of the walking leg, is stretched by depression of the limb. Figure 41 shows the response of the receptor to passive movement of the basi-ischiopodite. The majority of the position sensitive units are more active when the limb is depressed whereas the populations of units responding to the two counter movements are more equal in number.

The distal insertion of the CB receptor strand lies close to the basipodite-flagellum (B-F) articulation. Small passive movements of the flagellum produce no detectable change in the activity of CB. Larger movements tend to produce small but inconsistent changes of activity, particularly at the extremes of movement. It is probable that the response was due to very small movements of the C-B joint as it was found very difficult to hold this joint rigid without imposing restrictions on movement at the B-F joint.

2.5.2. I-M Joint Receptor

IM1 contains units unidirectionally sensitive to production of the joint (Figs. 42A and B). These sensory cells discharge when the strand is released after stretching. During the experiments recorded in Fig. 42 the I-M joint was moved by application of a micromanipulator mounted probe to the meropodite. When the joint is reduced the sense cells do not fire but they do upon recoil, thus the strand of IM1 is stretched by reduction

FIG. 41. Recording of the response of the CB receptor of the 3rd maxilliped. The lower recording is a continuation of the upper. The lower trace in both cases monitors joint movement, downward movement denoting depression. The population of positional units responding to depression is larger than that active in elevated positions.



1 sec

FIG. 42. A-D. Recording of the response of the IM receptors of the 3rd maxilliped of Homarus gammarus to passive movement of the meropodite. The lower trace in A and B and upper trace in C and D monitor joint movement. Downward movement denotes reduction.

A. IM1 shows an increasing activity on passive production of the joint. B. The units of IM1 are unidirectionally sensitive to production. C. IM2 has position sensitive units which increase their frequency on reduction. D. The units of IM2 are unidirectionally sensitive to reduction.

A



B



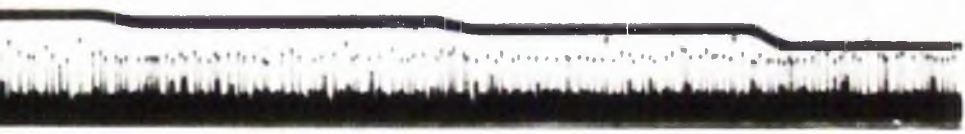
C



D



1 sec



and released during production so that the receptor will fire when the muscle contracts. Some of the units are movement and others slow adapting position receptors.

IM2 responds to movement in the opposite direction, that is to reduction of the I-M joint (Figs. 42C and D). If the joint has undergone reduction and is allowed to straighten under elastic recoil the receptor frequency falls dramatically. When movement of the limb stops, a low tonic frequency appears. This frequency rises again on reduction of the joint. The tonic units are position sensitive (Fig. 42C), but have a dynamic component also since they fire at a higher frequency during reduction than they do when at rest in a given position.

The IM receptors are attached to the productor muscle and not to its tendon. Hence, as my results were obtained by passive movement and not by muscle stimulation, it is possible that the receptor output in vivo may differ slightly from that which we have recorded.

2.5.3. M-C Joint Receptor

The MC receptor, which responds to both stretch and release, is attached to the apodeme of the flexor muscle and is stretched by contraction of the muscle. In my recordings (Fig. 43) the joint was moved by micro-manipulator-mounted forceps attached to the flexor apodeme, and the results will be comparable with those obtained by muscle stimulation. The chordotonal organ discharges during movement of the joint in either direction but with more activity evident during extension. Unidirectional units are found which respond to opposing directions of movement and are not active when the limb

FIG. 43. Recording of the activity of the MC receptor of the 3rd maxilliped of Homarus gammarus to movement of the joint produced by manipulation of the flexor muscle apodeme. The lower trace monitors movement of the joint, upward movement denotes flexion. This receptor responds to flexion and to extension of the joint by discharge of unidirectional units.



1 sec

1 sec

is stationary. Some units have a tonic phase which does not seem to indicate specific position but merely that the joint is at rest.

2.5.4. C-P Joint Receptor

It is difficult to define the movements of the C-P joint in terms of the muscles producing the movement as the musculature is more complex and the joint is capable of a wider range of movements. Unlike the pereopod the greatest movement at the C-P joint of the 3rd maxilliped occurs in approximately the same plane as the M-C joint and during the experiments shown in Fig. 44 the propodite was moved in this plane only. I therefore use the terms flexion and extension to indicate movement in the same direction as produced by the flexor and extensor of the M-C joint.

The strand of the CP receptor is attached to the ventral bender muscle and is stretched by contraction of the muscle. The sensory cells of the receptor respond to stretching of the strand which will be produced by contraction of the muscle or by passive extension of the joint. There is slight residual activity in the sensory nerve supplying the CP receptor when the joint is maintained in the flexed condition. When the limb is released it moves by elastic recoil back towards a straightened position and during this time the receptor becomes more active, recruiting further units (Fig. 44A). Further extension of the joint, equivalent to dorsal bender contraction brings more units into action. Some of these are position sensitive and usually relate to the spikes of greatest amplitude (Fig. 44B). The smaller units are

movement sensors with a tonic phase at rest. When the joint is moved rapidly (Fig. 44C) responses are observed only during extension and not at all during flexion but tonic activity returns during any prolonged stationary period.

As with the receptors of the I-M joint differences in the above results would be expected with movement of the joint produced by muscle stimulation. In vivo the receptor will respond primarily to contraction of the ventral bender and hence activity will be observed during flexion rather than extension.

FIG. 44. A-C. Recording from the CP receptor of the 3rd maxilliped of Homarus gammarus. The lower trace in each case monitors movement of the joint, a downward movement of the trace indicates flexion produced by movement of the propodite (see text). A. Extension of the flexed limb by elastic recoil. The activity of the receptor is greatly reduced by flexion but activity increases on extension by increased frequency of individual units and recruitment of other units. B. Further extension of the joint in a step fashion (dots indicate onset of movement) demonstrates the presence of position sensitive units. C. The smaller units are movement sensitive responding to extension of the joint and have a tonic phase at rest.

A



B



C



EXPERIMENTAL

3. PROPRIOCEPTION IN THE MANDIBLE

3.1. Introduction

The mandible, which is the most anterior of the crustacean mouthparts, is a feature common to most arthropods and has been the subject of some comprehensive comparative studies (Manton, 1964; Snodgrass, 1952).

The mandible of Homarus may be considered to consist of two parts, the heavily calcified body of the mandible and a small flexible palp. The mandibles are biting or crushing jaws which are capable of severing quite substantial thicknesses of calcified cuticle. The efficiency of the mandibles is probably limited by their gape rather than by their strength. The small palp, which has a large number of stiff hairs, obviously has some sensory function but is probably also used to remove any matter adhering to the gnathal surface and to raise food particles to within reach of the labrum.

The skeletal structure and musculature has been described in varying detail for a number of decapods. The major muscles have been described in Homarus americanus (Snodgrass, 1952) where there appear to be minor differences from Homarus gammarus described here.

The proprioceptive systems of the mandible and its palp are previously undescribed. The receptors which have been termed "mouthpart receptors" (Dando and Laverack, 1968; Laverack and Dando, 1968; Moulins, Dando and Laverack, 1970) are not part of the series of limb joint receptors.

3.2. Materials and Methods

The skeletal anatomy of the mandible of Homarus gammarus was examined in fresh specimens and in preparations from which all the soft tissues had been eroded with concentrated NaOH. The latter method facilitated examination of the internal surfaces and the mandible articulation. The muscles and the pattern of main nerve trunks were observed in Bouins fixed material (Pantin, 1948). The sensory cell groups and finer nerve bundles were examined using methylene blue staining techniques (see Appendix 2).

The morphology of the mandibular muscle receptor organ (Mand. MRO) was further determined by observation of serial wax sections stained in Heidenhains Azan (Pantin, 1948) and of ip sections of araldite embedded material stained with toluidine blue and mounted for light microscopy in cedar wood oil. The material for araldite embedding was fixed in situ for 2-4 hours in a 1M solution of 3% glutaraldehyde buffered at pH 7.5 and, after further dissection, post fixed in 2% osmium tetroxide for 1 hour (after Cloney & Florey, 1968). Sections were cut from this material with a glass knife on a Porter-Blum microtome.

The sarcomere length of the receptor muscle and muscles M1-2 was measured in living tissue on a Zeiss microscope using Nomarski interference-contrast illumination.

Preparations for electrophysiology were obtained by bisecting the animal through the sagittal plane. Sharp pointed scissors were inserted through the carapace at the base of the antenna to section the circum-oesophageal

commissures. This cut was continued round the cephalothorax to remove the antennae, eyes and rostral region. The abdomen, pereopods, and then the dorsal carapace were removed, the latter being cut at the level of the endophragmal skeleton. In order to free the carapace it is necessary to section the oesophagus and the apodemes of the posterior adductor muscles, M9. The preparation was then placed ventral side down in a dish of sea water and the oesophagus removed at the mouth after sectioning the oesophageal and gastric muscles at their insertions onto the endophragmal skeleton and epistoma. The remaining lower portion of the cephalothorax was then bisected on the sagittal plane and mounted with the sectioned suboesophageal ganglion uppermost. Removal of the remainder of the circum-oesophageal connective allowed access to the Mand. MRO nerve (imn 4).

The receptor muscle was detached at its dorsal insertion and held by micromanipulator mounted forceps to allow change of muscle tension via muscle stretch. Mandibular movements were produced and monitored by forceps mounted on a micromanipulator-potentiometer system (Shelton and Laverack, 1968) which were attached to the apodeme of muscle M9.

A similar preparation was used to record from the PSN (omn 4) but the preparation was then mounted ventral side downwards.

Stimulation of the receptor muscle was produced by DC squarewave pulses applied directly to the muscle via two platinum electrodes. Electrical activity in afferent fibres was detected via platinum wire electrodes amplified differentially and recorded by conventional means.

3.3. Morphology of the Mandible and its Musculature

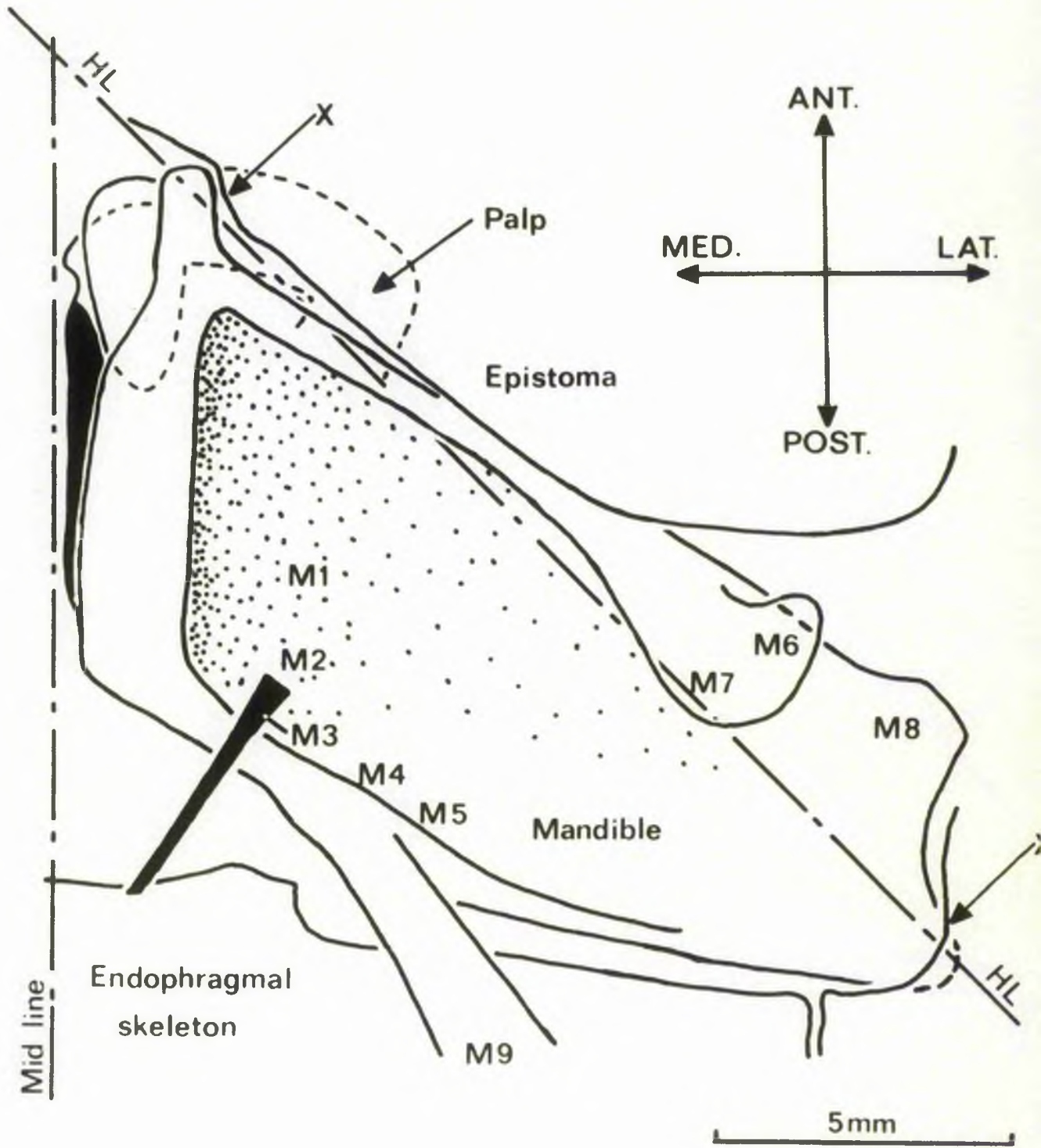
3.3.1. Skeletal Anatomy

The mandible of Homarus gammarus (L) is similar to those of the other Nephropsideans. Homarus americanus (Snodgrass, 1950), Cambarus longulus (Snodgrass, 1952) and Astacus fluviatilis (Netz, 1917). The mandible articulates laterally with the carapace and anteriorly with the epistoma (x,x Fig. 45). Additionally the articular membrane joining the mandible to the epistoma makes an effective hinge. Movement of the mandible is thus restricted to a single plane which lies perpendicular to the hinge line (HL, Fig. 45). The planes of movement of the mandibles are orientated at approximately 45° to the saggital plane and hence do not directly oppose one another. When opening, the mandibles swing ventro-laterally and in closing they move dorso-medially. The gnathal lobe of the mandible has two processes, a dorsal molar process of calcified cuticle and a ventral incisor process with a chitin like cutting edge. The more anterior portions of the gnathal surfaces gain greater mechanical advantage for biting but, because of the orientation of the planes of mandibular movement, this portion opens to a lesser degree and will accept smaller particles of food. Movement of the mandible about the hinge axis is limited, having a maximum of approximately 15° from the closed position.

Figure 45 shows the general outline of the mandible with the points of origin or insertion indicated. As can be seen in this figure processes for muscle attachment have developed to give a greater moment about the hinge line.

A palp is located on the medial anterior face of the

FIG. 45. A dorsal view of the right mandible of Homarus gammarus to show the skeletal morphology of this appendage and the approximate points of insertion of the mandibular muscles (M1-9). The location of the receptor muscle, M3, is illustrated in black. The hinge line (HL) is orientated at approximately 45° to the midline and the mandible articulates with the cephalothorax at two points (X,X).



mandible (Fig. 45). The palp consists of only three podomeres, the more proximal of which is considered to represent the basipodite (Snodgrass, 1950) as evidenced by the biramous nature of the palp of Calamus but the homology of the more distal segments with those of the walking leg is not known. In this thesis the segments of the mandible will be referred to according to their location - proximal, medial and distal (Fig. 49).

3.3.2. Musculature

I have elected to number rather than name the muscles, for two reasons. First, names appointed on anatomical evidence alone can lead to misunderstanding when utilised for other species. This is illustrated by the abductor muscles which Schmidt (1915) named "minor" and "major" in his description of Astacus. In Homarus gammarus and Homarus americanus (Snodgrass, 1950) the "abductor minor mandibulae" (M8) is as large as the "abductor major mandibulae" (M7). Secondly, careful examination has shown that a number of small but distinctly separate muscles (Fig. 48) underly the "adductor anterior mandibulae" (M1) and with the exception of muscle M3 the function of these muscles is unknown. In this thesis I use Schmidt's terms "adductor" and "abductor" only to indicate whether the insertion of the muscle is such that it will produce a moment which will tend to open or close the mandibles respectively. The terms are not intended to imply that this is necessarily their function. The numbering system used here does not imply homology with the muscles numbered by Manton (1964).

Table 1 compares the musculature of Astacus

fluviatilis (Schmidt, 1915) with that of Homarus gammarus and correlates the nomenclature of Schmidt with the numerical system used here.

a. The Ventral Muscle Group

This group contains the largest number of muscles though many of them are very small.

M1 (adductor). This muscle arises from the medial ventral floor of the mandible and inserts via a small number of cuticular fibres onto the anteriormost lip of the endophragmal skeleton dorsal to the sternal canal (Fig. 47). At its origin this muscle is consistently divided into three heads (a, b and c), whereas in Astacus (Schmidt, 1915) only two heads are described.

M2 (adductor). This ribbon-like muscle (Figs. 48 and 60) lies posterior to muscle M1b and is closely apposed to it and to muscle M3 throughout its length. Muscle M2 is slightly tapered, being broader at its ventral origin. The function of this muscle is unknown.

M3 (adductor). This muscle which lies posterior to muscle M2 (Figs. 45 and 48) is the muscle of the mandibular muscle receptor organ which is described in detail in Experimental 3.4.

M4 and M5 (adductors). These muscles have their ventral origin on the posterior rim of the mandible just lateral to the insertion of the apodeme of muscle M9 (Fig. 48). The muscles pass anterior of the apodeme and have their

Table 1. A comparison of the nomenclature used in this thesis for the mandibular muscles of Homarus gammarus and that used by Schmiät (1915) for Astacus fluviatilis.

Table 1

Mandible muscles		Homarus		Astacus	
M1a	Musculus Adductor Anterior Mandibulae (Schmidt 1915)	Yes	Yes	Yes 1	Yes 1
1b	"	"	"	"	"
1c	"	"	"	"	"
M2	Previously undescribed	Yes	Yes	No	No
M3	"	Yes	Yes	Yes	Yes
M4	"	Yes	Yes	No	No
M5	"	Yes	Yes	Yes	Yes
M6a	Musculus Adductor Lateralis Mandibulae (Schmidt 1915)	Yes	Yes	Yes 1	Yes 1
6b	"	Yes	Yes	"	"
6c	"	Yes	Yes	"	"
M7	Musculus Abductor Major Mandibulae (Schmidt 1915)	Yes	Yes	Yes	Yes
M8	Musculus Abductor Minor Mandibulae (Schmidt 1915)	Yes	Yes	Yes	Yes
M9	Musculus Adductor Posterior Mandibulae (Schmidt 1915)	Yes	Yes	Yes	Yes
<u>Mandibular palp muscles</u>					
P1	Musculus Flexor a Palpi Mandibulae (Schmidt 1915)	Yes	Yes	Yes	Yes
P2	Previously undescribed	Yes	Yes	No	No
P3	Musculus Flexor b Palpi Mandibulae (Schmidt 1915)	Yes	Yes	Yes	Yes
1.	Differs in number of heads.				

FIG. 46. A dorsal view of the right anterior-ventral cephalothorax of Homarus gammarus dissected to show the muscles and main nerve trunks.

Mandibular muscles: M1-9 see table 1 and text for details. Other muscles: musculus abductor coxopoditis 1 maxillae (abd. c), musculus lateralis coxopoditis 1 maxillae (add. 1c), musculus dorsoventralis anterior (dva), muscles dilatateurs lateraux de l'estomac (gl), musculus levator II antenna (lev), muscle dilatateur lateraux de l'oesophage (oel), muscle dilatateur de l'oesophage (oep), musculus remotor II antenna (rem), Ligamentum ventralis capitis (v.c.).

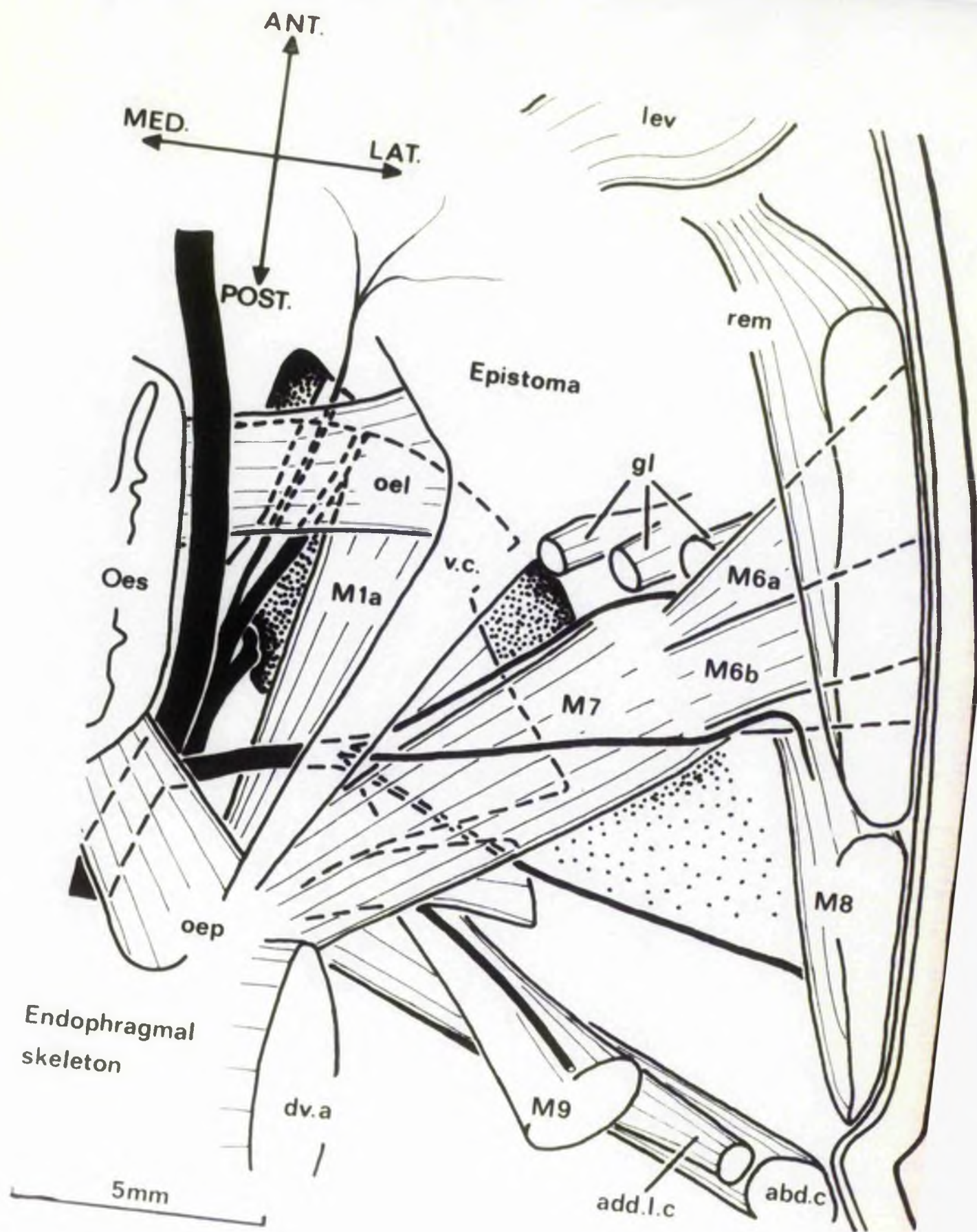


FIG. 47. A dorsal view of the right anterior-ventral cephalothorax of Homarus gammarus further dissected to show the insertions of more ventrally located muscles. Muscles: paragnathal retractor (ret. para), other abbreviations as for Fig. 46.

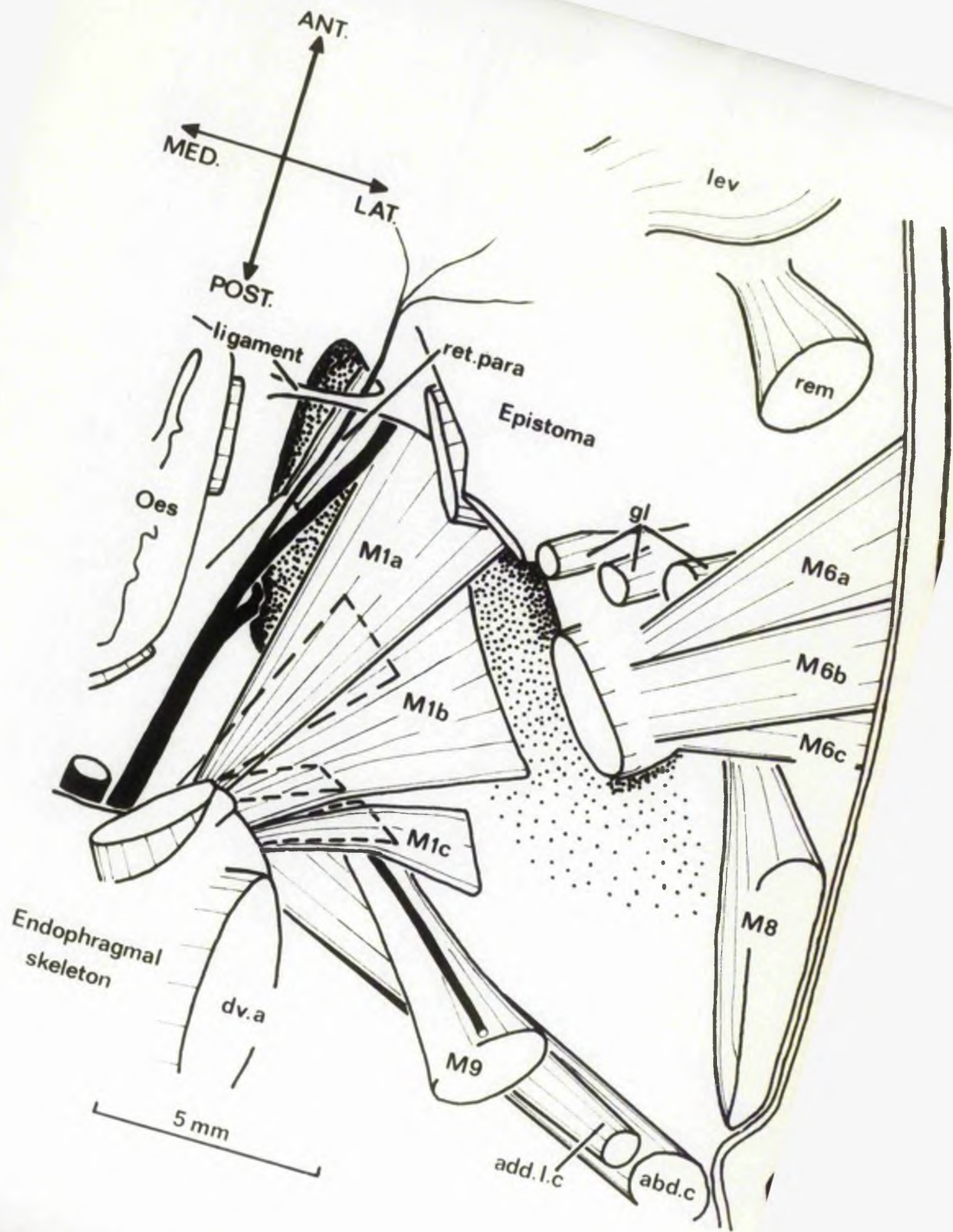
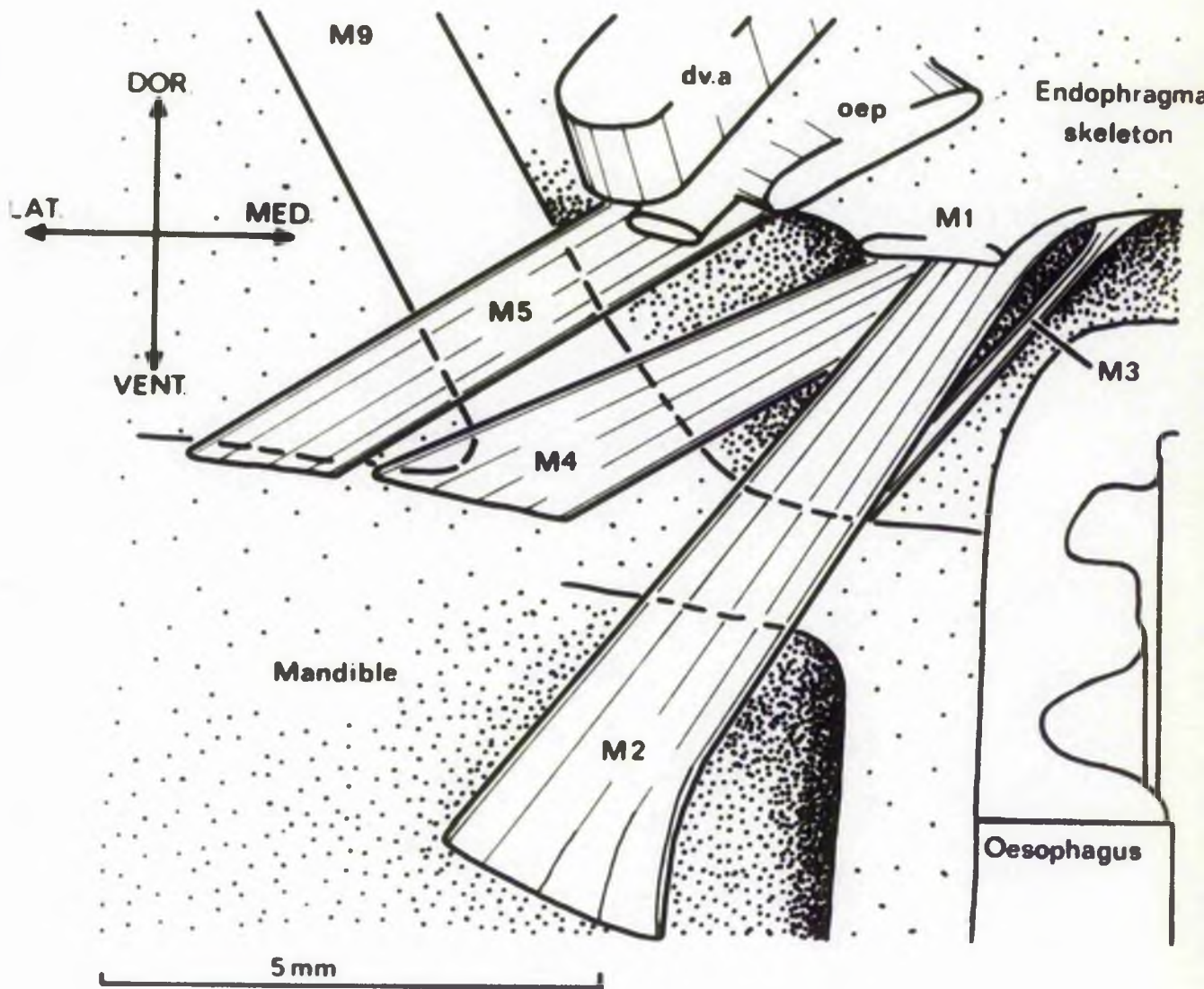


FIG. 48. An anterior view of the group of small muscles located in the medial-posterior corner of the mandible of Homarus gammarus. The illustration shows the right mandible with the larger muscles M1 and M7 and all nerve trunks removed.



dorsal origin on the endophragmal skeleton. Muscles M4 and M5 arise ventral to the insertions of muscles M1 and M7 respectively. The function of these muscles is not known.

M7 (abductor). This muscle which originates on a dorsally directed projection of the anterior rim of the mandible (Fig. 46) inserts close to muscle M1 on the anterior lip of the endophragmal skeleton.

b. The Anterior Muscle Group

There are only two muscles in this group and they are functionally antagonistic.

M6 (adductor). This muscle, which has three distinct heads at its origin on the lateral carapace (Fig. 47), inserts onto the same cuticular projection as muscle M7. Thus M6 and M7 are linearly opposed.

M8 (abductor). Like muscle M6, this muscle (Fig. 47) arises from the lateral wall of the carapace but it inserts onto a separate projection of the mandible. This projection lies close to the lateral mandibular articulation (Fig. 45).

c. The Posterior Muscle Group

In this group there is a single muscle but it is by far the largest of the mandibular muscles.

M9 (adductor). This muscle, which has its origin on the

dorsal carapace, has two heads located several millimetres apart, being separated by the origin of the "Musculus gastricus posterior" (Keim, 1915). Both heads attach to the same long apodeme which articulates with posterior rim of the mandible (Fig. 45).

d. Muscles of the Mandibular Palp

The general structure of the mandibular palp is shown in Fig. 49. It is the distal segment of the palp which is functionally important in manipulation of food particles and the function of the palp muscles is therefore described according to their effect upon the distal segment.

P1. This, the largest of the palp muscles, arises from the posterior gnathal wall of the mandible and inserts on the proximal segment (Fig. 49). Contraction of this muscle will move the tip of the palp in a posterior direction and push the food towards the oesophageal opening.

P2. This muscle arises from the dorsal surface of the proximal segment (Fig. 49), and inserts onto the ventral rim of the medial segment. Contraction of this muscle will move the tip of the palp dorsally and thus lift food particles up to the labrum.

P3. This muscle, which inserts onto the distal segment (Fig. 49) moves the tip of the palp laterally to make contact with the gnathal surface to the mandible.

e. Other Muscles

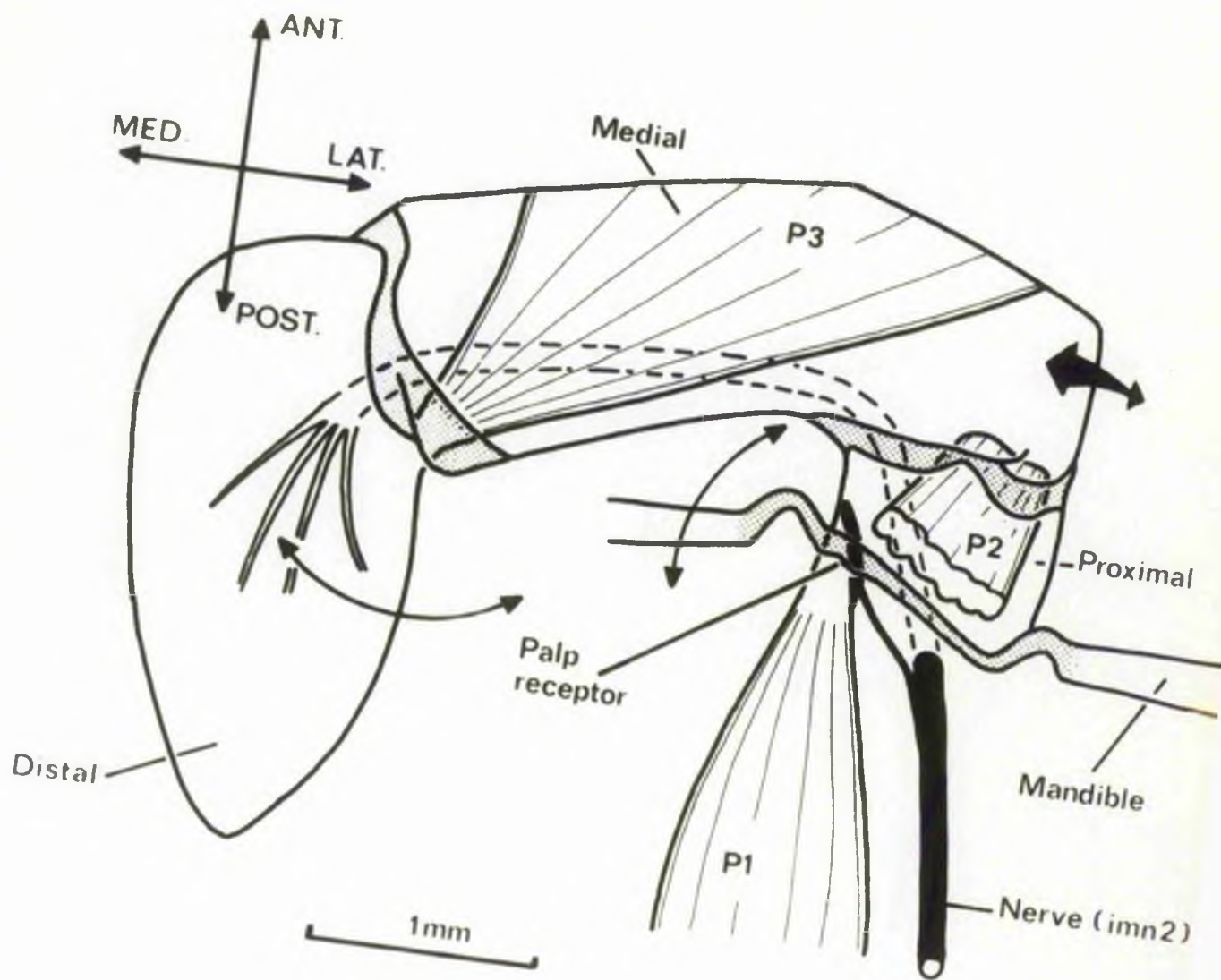
Table 2 shows the source from which the names of all other muscles shown in Figs. 46 and 47 were obtained, with the exception of the paragnathal retractor which is previously undescribed.

Table 2. The source of names for all muscles other than the mandibular muscles illustrated in Figs. 46 and 47.

Table 2

abd. c	Musculus Abductor Coxopoditis I Maxillae	(Schmidt, 1915)
add. lc	Musculus Lateralis Coxopoditis I Maxillae	(Schmidt, 1915)
dva	Musculus Dorsoventralis Anterior	(Schmidt, 1915)
gl	Muscles dilatateurs lateraux de l'estomac	(Nocquard, 1885)
lev	Musculus Levator II Antenna	(Schmidt, 1915)
oel	Muscles dilatateur lateraux de l'oesophage	(Nocquard, 1885)
oep	Muscle dilatateur posterieur de l'oesophage	(Nocquard, 1885)
rem	Musculus Remotor II Antenna	(Schmidt, 1915)
ret. para	Paragnathal retractor	(undescribed)
v.c.	Ligamentum Ventralis Capitis	(Bals, 1941)

FIG. 49. A dorsal view of the right mandibular palp of Homarus gammarus with the musculature and innervation seen in transparency. The arrows indicate the plane of movement at each of the joints. The only proprioceptive organ found is situated at the articulation of the palp with the mandible. Muscles: P1-3 see text and table 2 for details.



3.4. The Mandibular Innervation

As described for Astacus fluviatilis (Keim, 1915) and Cambarus affinis (Chaudonnoret, 1956), the mandible of Homarus gammarus is innervated by two nerve trunks. These are the inner mandibular nerve (imn. Fig. 50) from the suboesophageal ganglion and the outer mandibular nerve (omn. Fig. 50) which arises from the peri-oesophageal connectives at the site of the commissural ganglion. In Homarus, however, there are differences in the numbers of branches, which these nerve trunks produce, and in the number of muscles which they innervate. Table 3 compares the innervation of the mandibular muscles of Homarus with Astacus fluviatilis and Cambarus affinis.

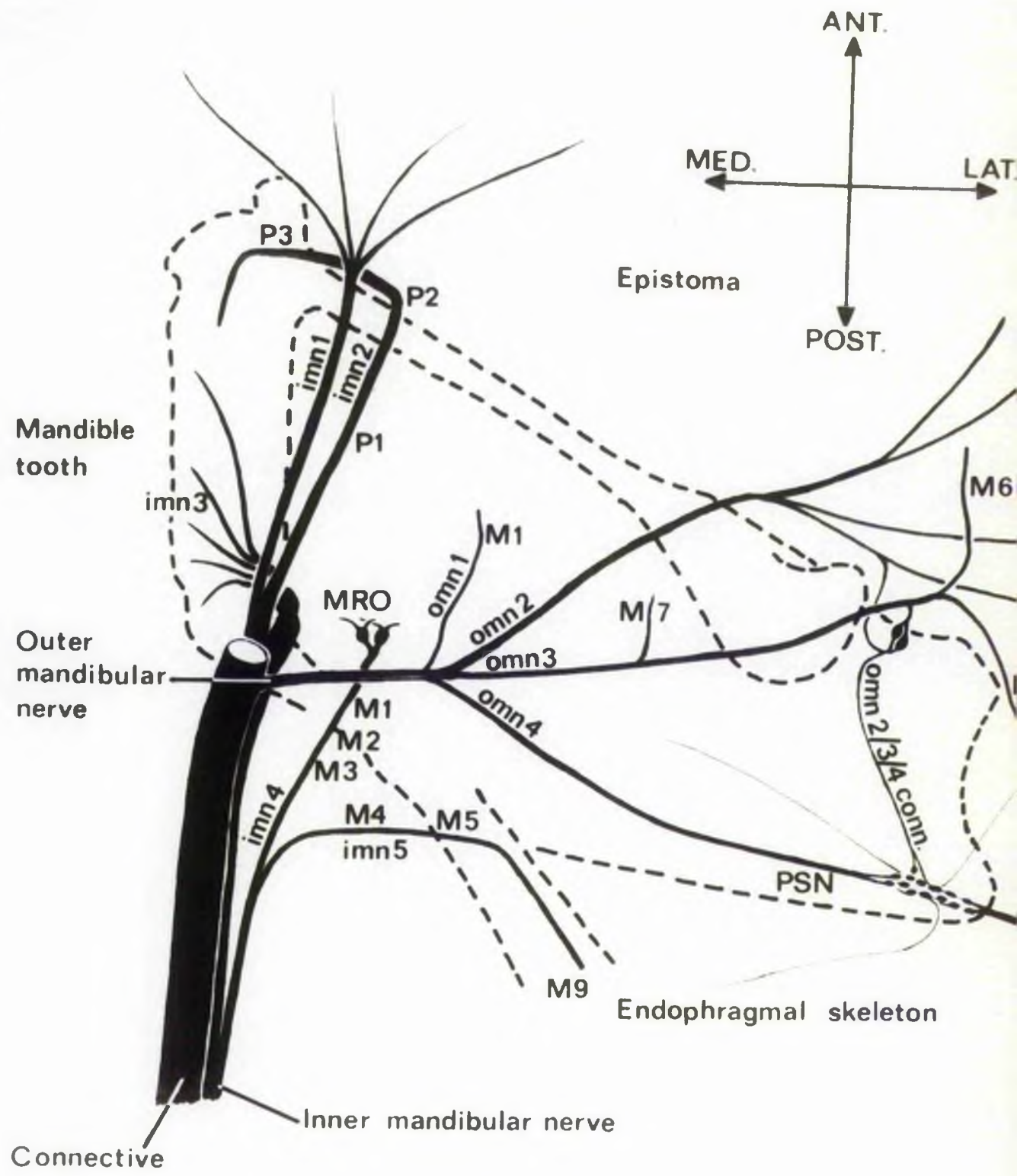
Figure 50 shows the general pattern of innervation in Homarus displayed against the outline of the right mandible. The muscle numbers are placed alongside the nerve which innervates them. For ease of reference the nerve branches have been numbered in a clockwise fashion as seen from the dorsal aspect in the right mandible. Thus the most medial branch of the inner mandibular nerve is imn 1.

3.4.1. Inner Mandibular Nerve (imn)

This nerve trunk arises from the sub-oesophageal ganglion ventro-lateral to the peri-oesophageal connective. The trunk divides into five main branches which innervate the mandibular cavity and muscle M9.

imn 1. This branch does not innervate the mandible but is a tegumentary nerve which radiates over the epistomal hypodermis. Methylene blue staining frequently reveals bipolar cells in this region but they are evenly dispersed

FIG. 50. The innervation of the right mandible of Homarus gammarus as seen from a dorsal aspect. The mandible is innervated by two main trunks, the inner mandibular nerve (imn) and the outer mandibular nerve (omn). The branches of these nerves have been numbered in a clockwise fashion and where a branch innervates a muscle the muscle number is printed alongside. Mandibular muscle receptor organ (MRO), posterior stomach nerve (PSN).



and not concentrated into discrete sense organs.

imn 2. This branch innervates the muscles and sense organs of the mandibular palp.

imn 3. This large group of nerves ramify in the connective tissue which pervades the gnathal lobe of the mandible. The function of this rich innervation is unknown. There are no sensilla on the gnathal surface and cuticular pores have not been observed. However, it is possible that the mandible has sensory structures similar to the intradental sensory endings of the mammalian teeth (Anderson, Hannam and Matthews, 1970) located in the hypodermis of the gnathal lobe.

imn 4. This branch travels in close association with imn 5 to where they emerge from the sternal canal then it passes ventrally into the mandible closely apposed to muscles M2 and M3. As it passes ventrally it gives off motor nerve bundles to muscles M1, M2 and M3. The nerve terminates in the mandibular muscle receptor organ (Figs. 53 and 54).

imn 5. This branch separates from imn 4 as they leave the sternal canal and passes posterior to M3. It travels laterally to the apodeme of the large adductor muscle, M9, which it ascends. This nerve supplies motor innervation to muscles M4, M5 and M9.

3.4.2. Outer Mandibular Nerve

This nerve is particularly interesting in Homarus as

it innervates a greater number of muscles than does the corresponding nerve in either Astacus fluviatilis or Cambarus affinis (Keim, 1915; Chaudonneret, 1956) and is associated with two interesting groups of cells.

omn 1. Very close to where the outer mandibular nerve passes under the Ligamentum Ventralis Capitis (Fig. 46), it splits into a number of branches. The three major branches continue laterally (omn 2-4, Fig. 50) but one (or more) small branches pass ventrally onto muscle M1.

omn 2. This, the more anterior of the three major branches, is a tegumentary nerve to the lateral carapace and does not innervate the mandible.

omn 3. This branch runs laterally over the dorsal surface of muscle N7 which it innervates, then passes ventrally onto the posterior surface of muscle M6. Here the nerve divides to give branches which carry the motor innervation to the heads of muscles M6 and N8.

omn 4. This branch, previously referred to as the Posterior Stomach Nerve (Heath, 1941), has been described in Homarus by Dando and Laverack (1969) (see Experimental 3.6.).

omn 2/3/4 Connective. As omn 3 reaches muscle M6, a small nerve bundle separates and runs ventrally down the posterior surface of the muscle heads M6b and M6c onto the hypodermis close to the mandible articular membrane. At this point the nerve divides with one branch running posteriorly across

the mandibular surface to join omn 4, PSN, and the other passing anteriorly, ventral to M6 to join omn 2 (Fig. 50). Between omn 3 and the point where this nerve divides, methylene blue staining has revealed a group of up to 8 neurones located in the nerve. As shown in Fig. 51, where these cells are located at the nerve division, they are frequently tripolar and send a process into each of the three nerve branches. Where the cells are located some distance from the junction, they are usually bipolar but their ventral process is frequently observed to divide at the junction. However, some cells stained (Fig. 52) appear to be bipolar and have only two processes one of which goes either towards omn 2 or omn 4. There are also nerve fibres, not associated with these cells, which pass from each of these branches into the others.

It is not possible to say with certainty which process is axonic and which dendritic as the processes from these cells are directed centrally where they enter omn 2, omn 3 and possibly in some cases omn 4.

Table 3. A comparison of the pattern of mandibular muscle innervation in Homarus gammarus with that described by Keim (1915) for Astacus fluviatilis and Chaudonneret (1956) for Cambarus affinis. The main differences occur in the innervation of muscles M1 and M7.

Homarus gammarusAstacus fluviatilis

(Keim, 1915)

M1	imn 4 and omn 1	Innerer Mandiblenerv b&c
M2	imn 4	not described
M3	imn 4	"
M4	imn 5	"
M5	imn 5	"
M6	omn 3	Ausserer Mandiblenerv a1
M7	omn 3	Innerer Mandiblenerv a
M8	omn 3	Ausserer Mandiblenerv b1
M9	imn 5	Innerer Mandiblenerv a
P1	imn 2	Innerer Mandiblenerv d
P2	imn 2	no muscle
P3	imn 2	Innerer Mandiblenerv d

Cambarus affinis
(Chaudonneret, 1956)

Nerf mandibulaire interne f

not known

"

"

"

Nerf mandibulaire externe b&c

Nerf mandibulaire interne c

Nerf mandibulaire externe d

Nerf mandibulaire interne d

Nerf mandibulaire interne hp

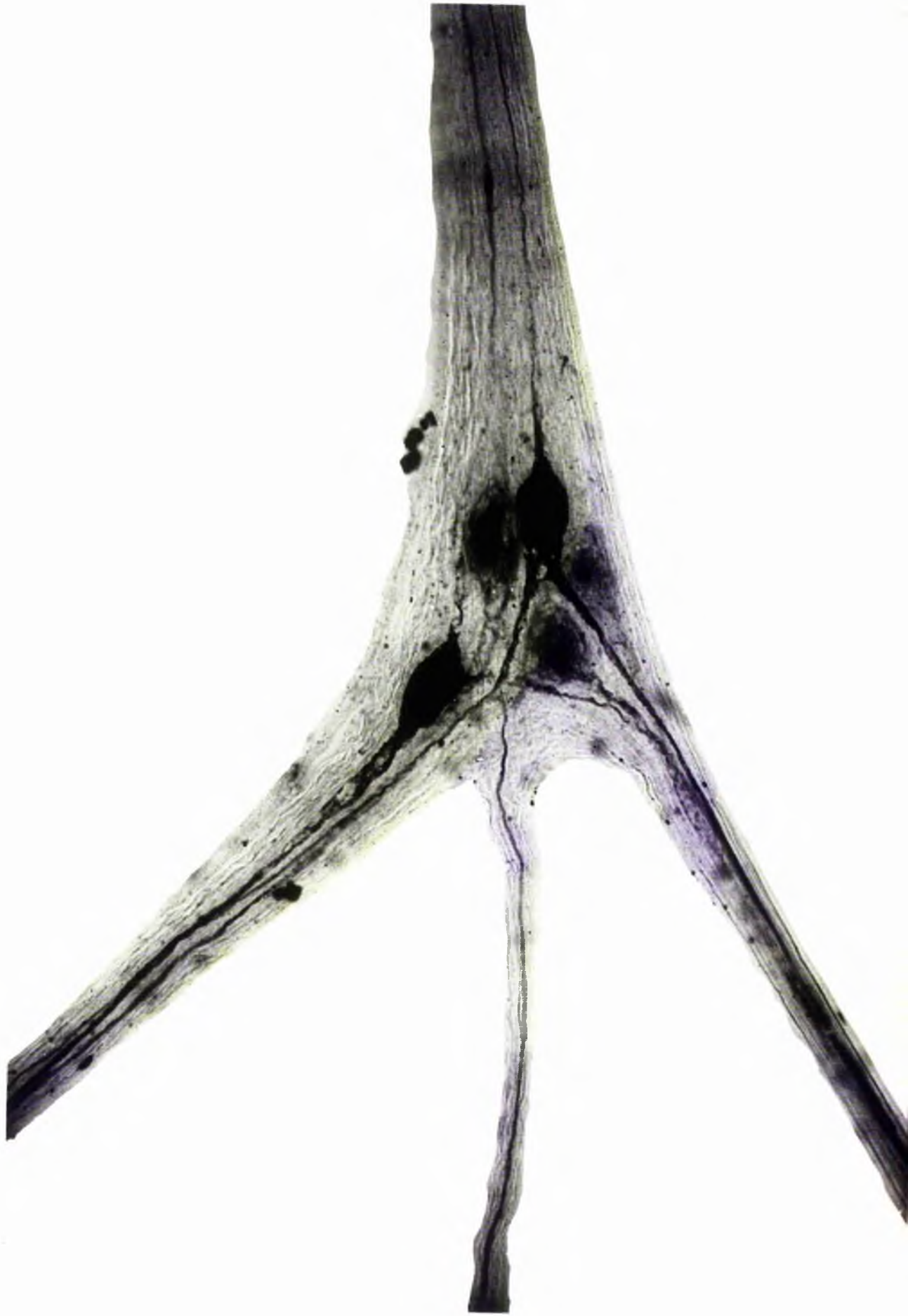
not known

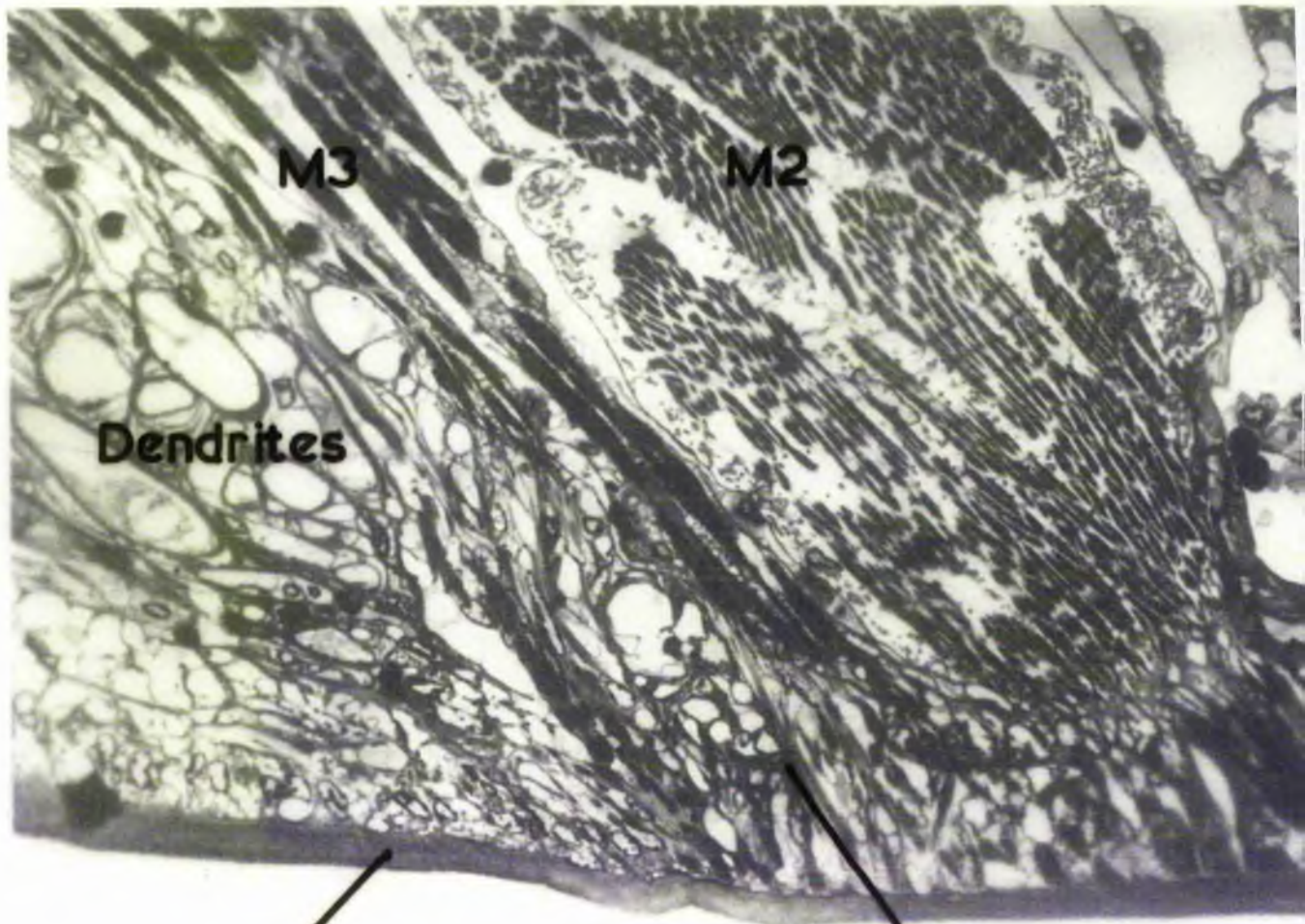
Nerf mandibulaire interne

Table 3

FIG. 51. Photomicrograph of a methylene blue stained preparation of the cells at the junction of the connective between the outer mandibular nerve branches omn 2, 3 and 4 (omn 2/3/4 conn. fig. 50). Note that the two most densely stained cells have processes in each of the three main branches.







Uncalcified cuticle

Tonofibrils

100 μ



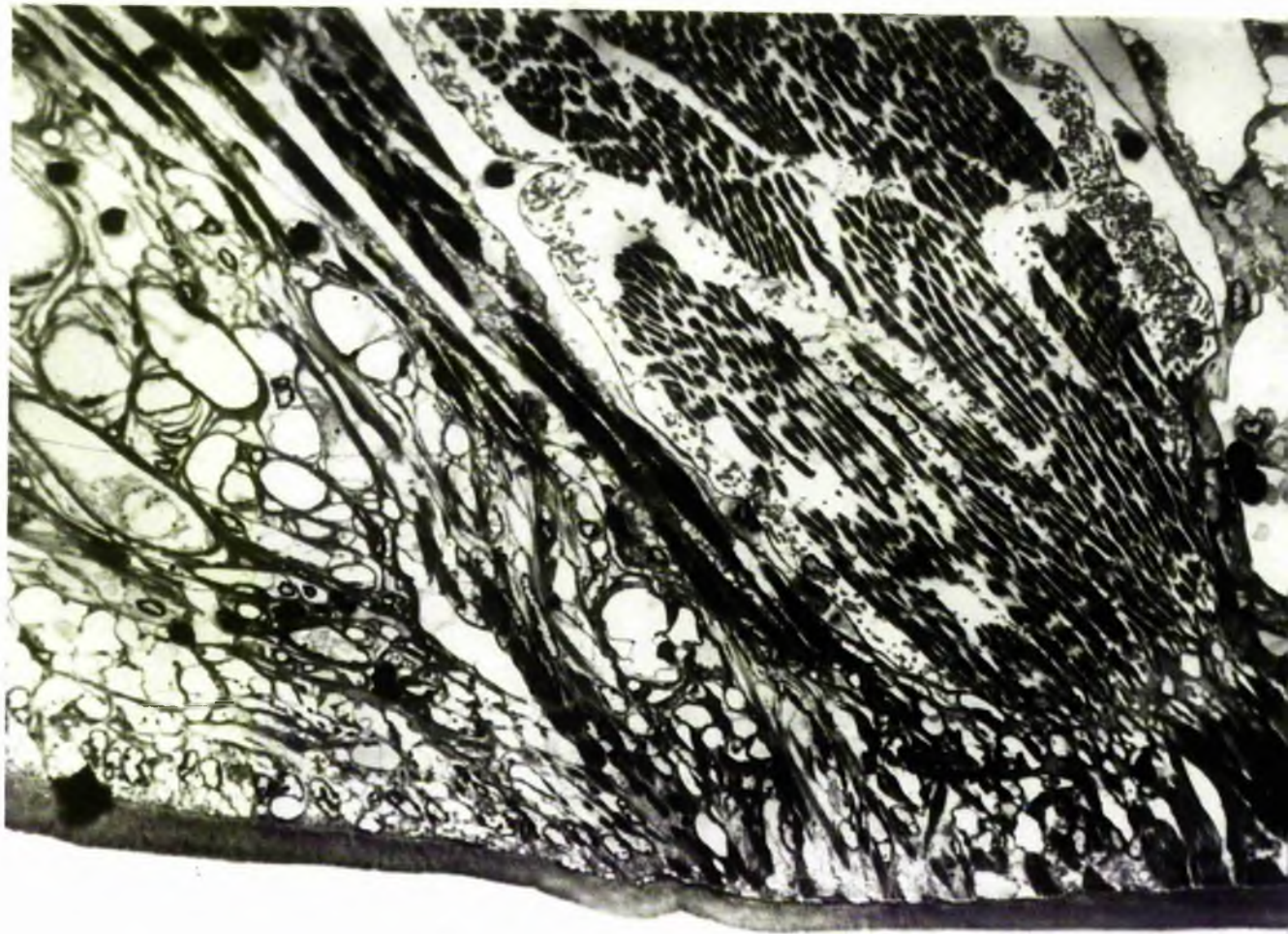


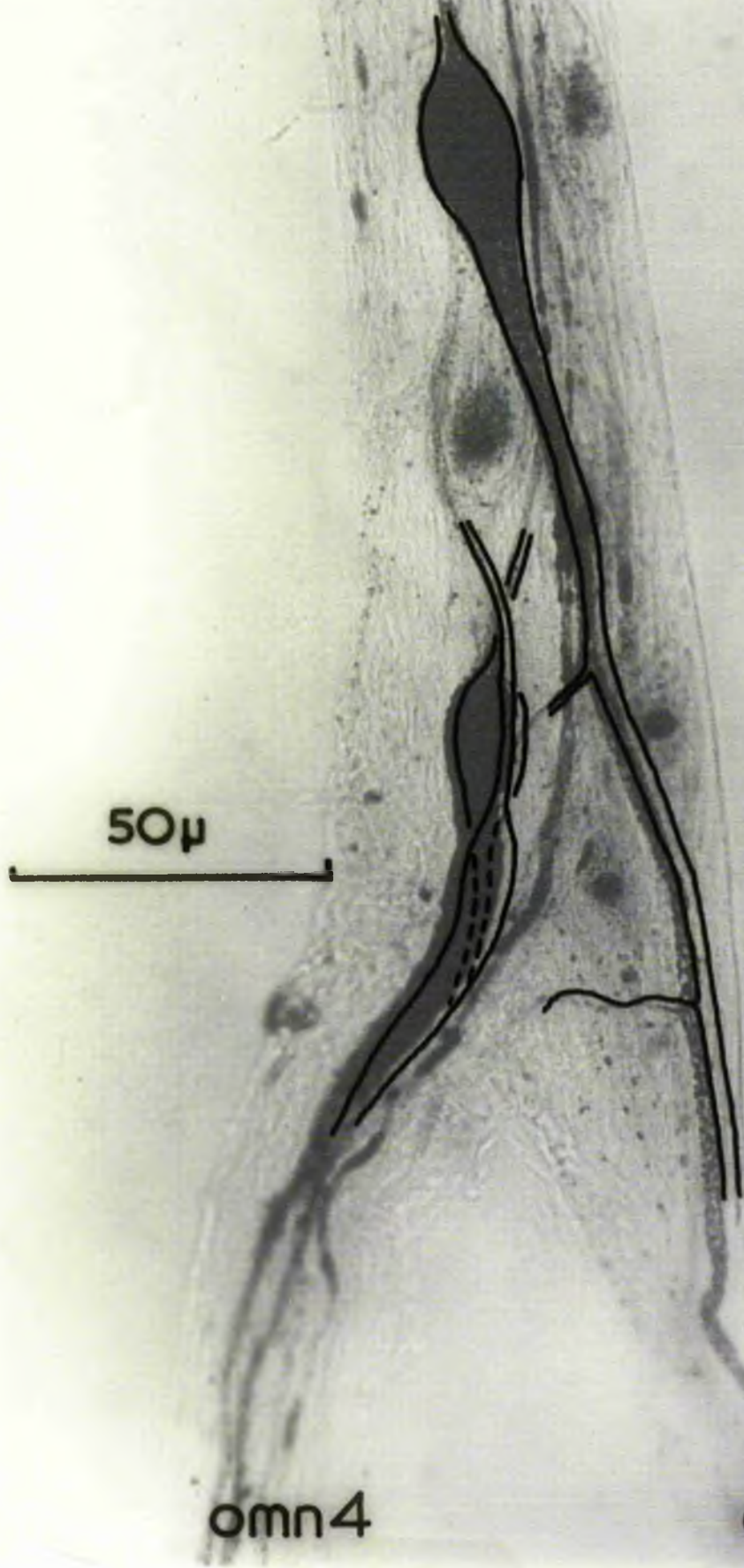
FIG. 52. Photomicrograph of a methylene blue stained preparation of the cells of the omn 2/3/4 connective in which some of the cells are apparently bipolar. Note that one cell sends two branches into nerve omn 4. See fig. 50 for identification of the nerve branches.

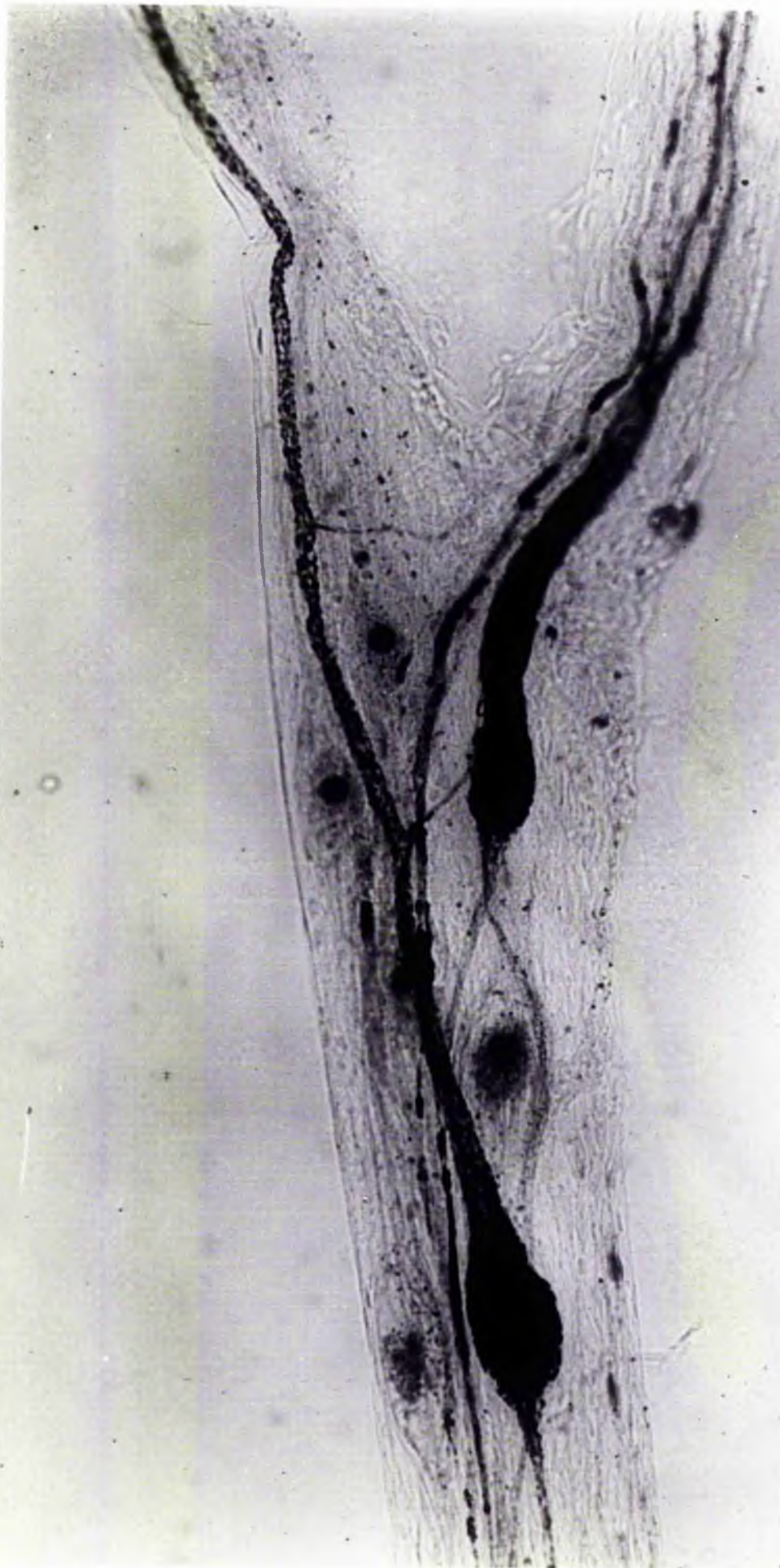
omn 3

50μ

omn 4

omn 2





3.5. The Mandibular Muscle Receptor Organ

A muscle receptor organ (Mand. MRO) is present in the mandible of macruran decapods. The Mand. MRO has been observed in the nephropsideans Homarus gammarus, Nephrops norvegicus, Astacus astacus, Astacus leptodactylus and the scyllarideans, Palinurus vulgaris and Fanulirus argus. The description given in this thesis is for the Mand. MRO of Homarus gammarus.

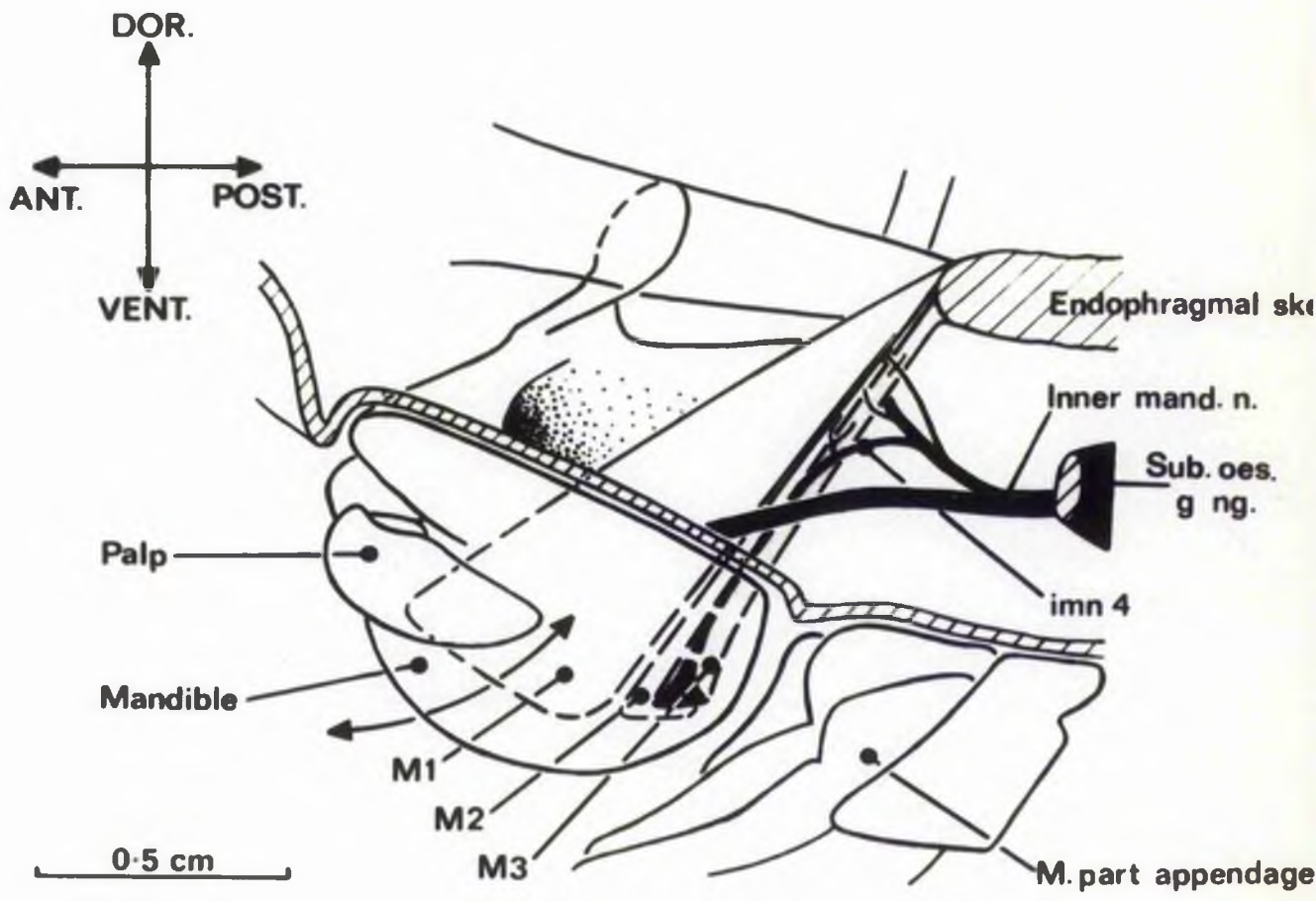
3.5.1. Mandibular MRO Morphology

The Mand. MRO consists of a strip of muscle which is innervated by a group of sensory cells at its insertion onto the mandible. The receptor is situated posterior to the anterior adductor muscle, M1, and muscle M2. It is one of the muscles in the ventral group situated furthest from the hinge line (Fig. 45) and hence will undergo a greater change in length during mandibular movement. The receptor muscle (M3, Fig. 53) arises dorsally from the endophragmal skeleton over the sternal canal. At this point the muscle lies medial to the insertion of muscle M1 and in an animal of 20cm long (rostrum to telson) it lies about 1mm from the sagittal plane. The receptor muscle passes antero-ventrally into the medial posterior corner of the mandibular cavity (Figs. 48 and 53). Throughout much of its length muscle M3 is closely apposed to muscle M2.

3.5.1.a. The Receptor Muscle

Muscle M3 is 1.0 to 1.2cm long in an animal of 20cm body length. It is circular in cross section (Ca.

FIG. 53. A sagittal section through the anterior cephalothorax of Homarus gammarus (L). The diagram is of the right side viewed from the cut surface. The ventral portion of the anterior adductor muscle (m1), muscle M2 and the receptor muscle (M3) are seen in transparency through the mandible. Muscle M3 is stippled to differentiate it from muscle M2 and the larger M1 which overlie it. The mandibular muscle receptor organ is innervated by a branch of the inner mandibular nerve (Inner mand. n.) which arises close to the suboesophageal ganglion (Sub. oes. gang.). This nerve divides giving rise to two main branches one of which passes beneath M3 to innervate the posterior adductor muscle, M9, and the other is the mandibular MRO nerve (imn 4). The mandibular MRO nerve contains the efferent fibres to muscles M3, M2 and, to a small extent, M1 as well as the afferent fibres of the sensory cells. Endophragmal skeleton (Endophragmal skel.), the other mouthparts (M. part appendages), anterior (ANT.), dorsal (DOR.), posterior (POST.), ventral (VENT.). The arrows indicate the direction of mandibular movement.



150 μ diam.) at its dorsal insertion and it flattens to a ribbon (Ca. 1mm wide at its base) as it passes ventrally into the cavity of the mandible. If the muscle is sectioned close to its extremities and in the mid region, it can be seen to vary not only in shape but also in cross-sectional area throughout its length (Fig. 54). The sections from which these drawings were made are from a muscle which was fixed in situ and thus the differences in cross-sectional area will be similar to those of the intact living muscle. The cross-sectional area at the extremities, particularly at the ventral insertion, is greater than that of the mid region. Examination of toluidine blue stained araldite embedded sections suggests that these differences are largely due to the amount of cytoplasm in the muscle fibres at these different levels. The myofibrils are evenly and densely packed in the dorsal regions of the muscle but become dispersed in small bundles throughout the cytoplasm of the muscle fibres as they approach the ventral insertion. This dispersion gives the receptor muscle a mottled appearance when viewed in T.S. as shown in Fig. 55 where it is compared with muscle M2. There may also be some differences in the amount of connective tissue present. Thus, in spite of the observed differences in cross-sectional area, there seems no a priori reason to assume that any of the muscle fibres do not travel the length of the receptor muscle.

When viewed with a dissecting microscope the receptor muscle is readily distinguished by virtue of its fineness of structure as the muscle fibres are not grouped into large bundles like the other muscles of the ventral group. This difference in structure can be readily seen in Fig. 55. All the muscle fibres of M3 are of similar

FIG. 54. T.S. of the receptor muscle at three different levels to show the shape of the muscle and its cross-sectional area in arbitrary units. The outline drawings were made from sections of a receptor muscle fixed in situ with glutaraldehyde. A. A section close to the dorsal insertion, B. through the mid region, C. near the ventral insertion.

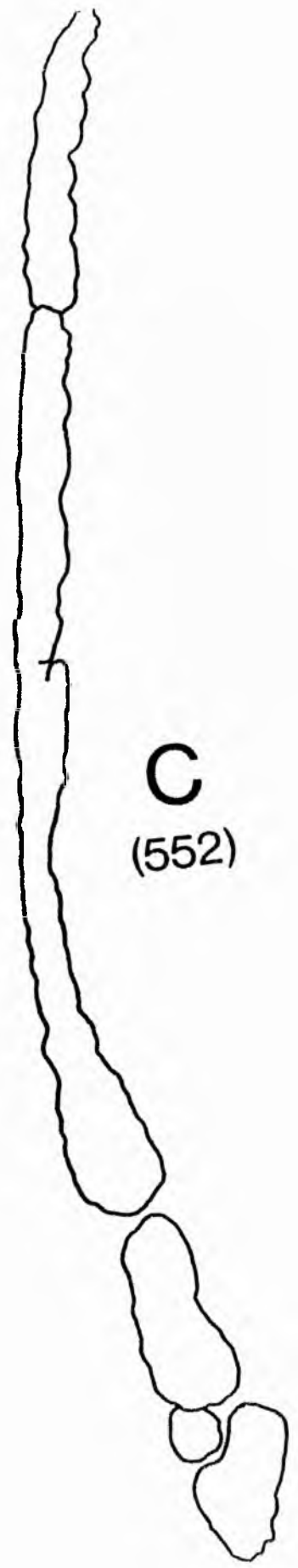
A (380)



B
(287)



C
(552)

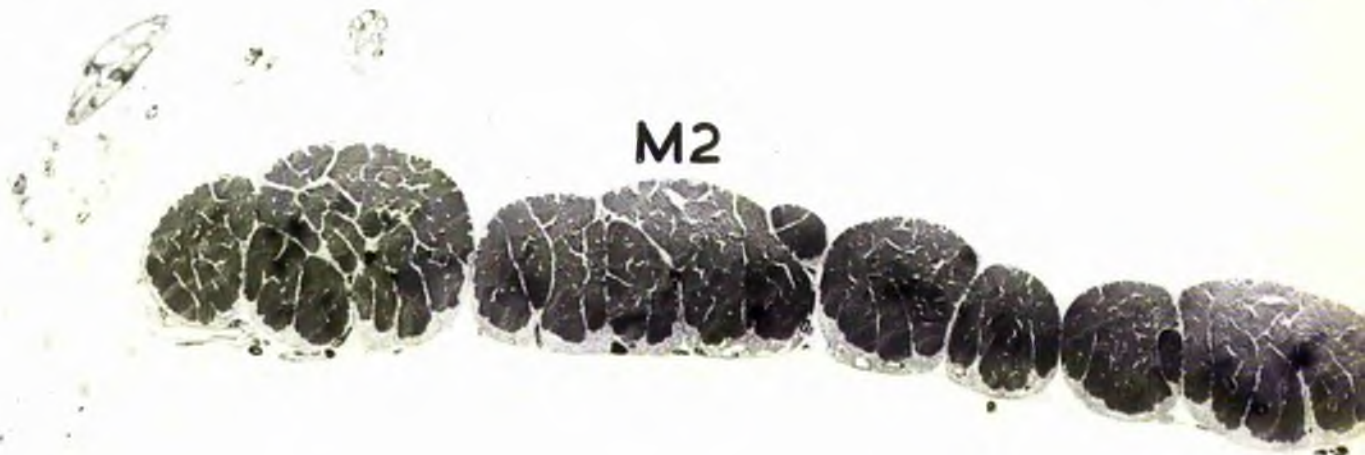


250μ

FIG. 55. Photomicrograph of muscles M2 and M3 in T.S. from glutaraldehyde/osmium tetroxide fixed, araldite embedded material stained with toluidine blue. This illustration shows the remarkable difference in structure between these two muscles. The sections are cut within 1mm of the ventral insertions of these muscles.



M3



M2

250μ

type and a histogram of sarcomere length, measured in the living muscle by interference-contrast microscopy, gives a normal distribution with a peak between 6 and 7 μ (Fig. 56). The muscle is bounded by a fine connective tissue sheath.

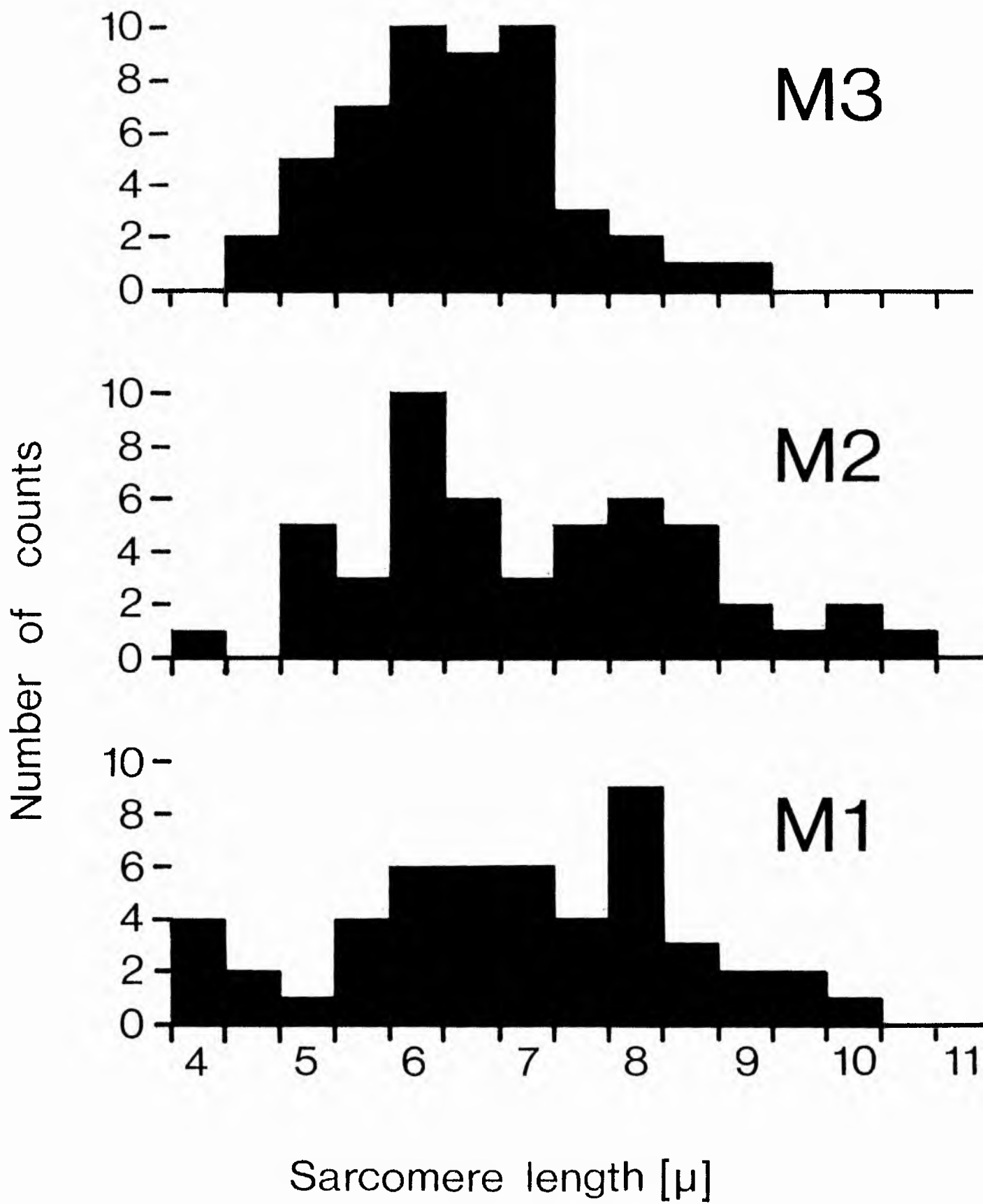
The receptor muscle, which is a broad thin ribbon at its ventral insertion, inserts onto the mandibular endocuticle via tonofibrils. The tonofibrils associated with this muscle are of greater length than those at the insertion of muscle M2 and may exceed 100 μ in some cases. The muscle is not associated with tendons or apodemes at either of its insertions. Muscle M3 is occasionally observed to be split at its ventral insertion but in most cases it attaches as a single entity. The ventral attachment of muscle M3 normally lies posterior to that of muscle M2 but where the latter muscle is split some degree of interdigitation may occur.

3.5.1.b. Afferent and Efferent Innervation

Both the afferent and efferent fibres of the Mand. NRO run in nerve inn 4 (Fig. 53). This nerve meets muscle M3 approximately one third of its length from the dorsal origin and it remains closely apposed to muscles M2 or M3 throughout the remainder of its travel. As it passes ventrally, nerve inn 4 supplies motor innervation to muscles M2, M3 and to the posterior face of M1.

The receptor muscle appears to receive a denser innervation than the other muscles of the ventral group when this region is stained with methylene blue. However, this may be a result of the peculiar ribbon-like structure of the muscle which has resulted in a higher

FIG. 56. Histogram of the sarcomere lengths in unfixed preparations of the mandibular muscles M1, M2 and the receptor muscle, M3, measured by interference-contrast microscopy. As the number of counts per muscle was low (50) the individual peaks may not be significant but it is evident that the receptor muscle has a much narrower spectrum of sarcomere length than either of the other two muscles.



proportion of the motor axon branches and terminals being superficial where they will be more readily stained. Figure 57 shows a portion of the receptor muscle with its motor innervation stained by methylene blue. The muscle is innervated by at least two and probably three motor axons. The endings of the motor axon on the muscle fibre are seen as expansions, 6-9 μ diameter, which are frequently grouped in clusters. These structures which are presumably the motor end plates are in many cases terminal on the axonal branch but preterminal expansions are often observed.

1 - 1.5mm from the receptor muscle base the nerve gives off no more motor branches and may be considered to be purely afferent. Sections of the nerve cut in this region (Fig. 58) reveal many large fibres which may exceed 25 μ diameter and are enclosed in a substantial sheath. The nerve also contains many small fibres, most of which pass into the hypodermis in bundles (Fig. 59). Methylene blue staining shows the presence of some of these smaller fibres in the region of the sensory cells and their dendrites. The somata of these small fibres have not been observed and it is possible that they are efferent rather than afferent. They do not appear to make contact with the sensory cell somata or dendrites but several of these fibres have been observed to pass into the muscle insertion where in the terminal dendritic processes of the sensory cells are located. Approximately 500 μ from the receptor muscle insertion the nerve fans out to innervate the base of the muscle (Fig. 59) and the afferent axons reduce in diameter by a factor of 4 or 5 (Fig. 60).

FIG. 57. A montage of photomicrographs of a methylene blue stained preparation of the receptor muscle to show the motor innervation. This muscle received at least two, probably three, motor axons. The motor endplates are distinct swellings occurring at the terminal region of axonal branches and are frequently grouped in clusters.



200μ



FIG. 58. Photomicrograph of the afferent innervation to the mandibular muscle receptor organ of Homarus gammarus from glutaraldehyde/osmium tetroxide fixed, araldite embedded material stained with toluidine blue. This section of the "sensory" nerve was obtained by sectioning the nerve close to where it fans out to innervate the multipolar cells. The largest axons in this bundle exceed 25 μ diameter.



100μ

FIG. 59. A three dimensional illustration of the ventral portion of the mandibular muscle receptor organ of Homarus gammarus. This is a posterior view of the muscle receptor in the right mandible. The receptor muscle, M3, is closely apposed to muscle M2 throughout most of its length.

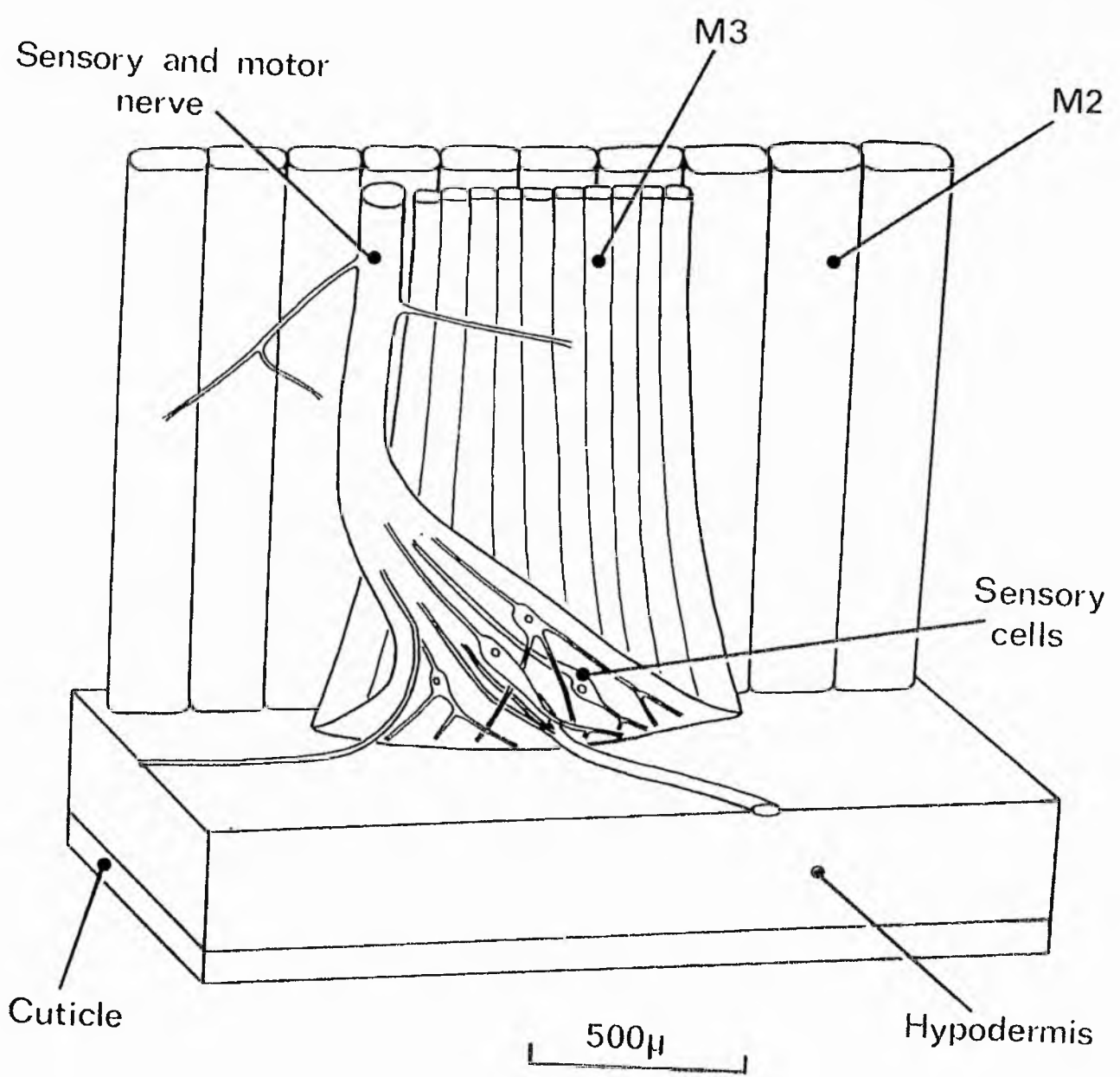
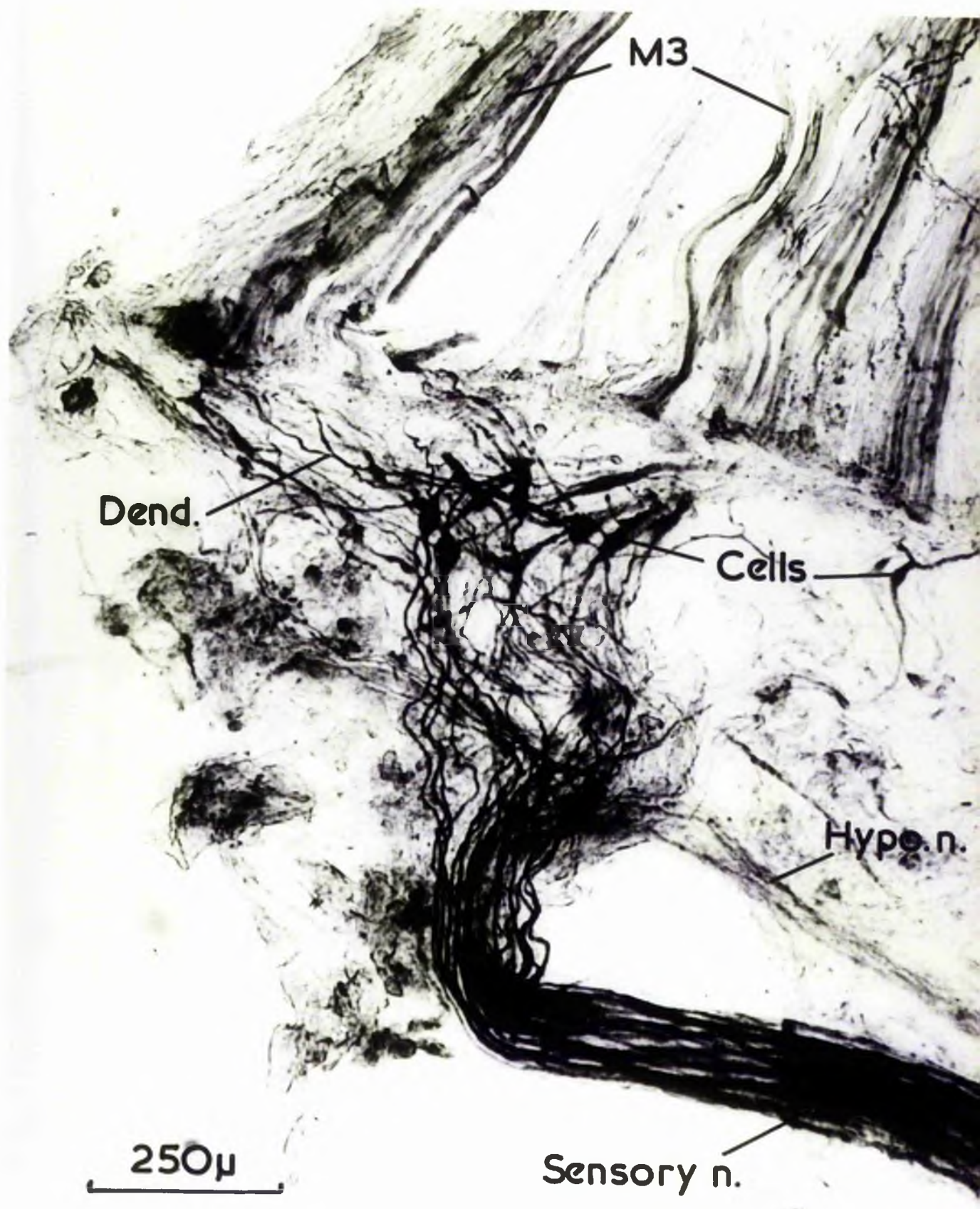


FIG. 60. Photomicrograph of a methylene blue stained preparation of the mandibular muscle receptor organ from Homarus gammarus (L.). The sensory nerve trunk (Sensory n.) and cells are normally closely applied to the receptor muscle (M3) at its base and have been pulled apart in the preparation to allow the stain to penetrate to the cells and their dendritic processes (Dend.). Some bundles of small axons pass into the hypodermis (Hypo. n.).



3.5.1.c. The Sensory Cells

The somata of the sensory neurones are located between the receptor muscle and the hypodermis close to the ventral insertion of the receptor muscle. The cells are frequently bipolar but tripolar and multipolar cells are also observed. All of the cells are multiterminal and dichotomous branching of the dendritic process may occur some distance from the soma. It is not possible to follow the dendrites to their termination in the muscle insertion using methylene blue techniques and it is not known if further dendritic branching occurs within the insertion. In the lack of this information it seems probable that the number of dendritic processes produced by each of the sensory cells is small, probably 2 to 6 in most instances. The number of sensory neurones counted in both methylene blue stained whole mounts and azan trichrome stained serial wax sections is between 10 and 20. The cells are generally between 10 and 40 μ diameter and the dendrites may exceed 500 μ in length.

As shown in Fig. 61, the dendritic processes of the sensory neurones penetrate the muscle insertion. The cell in this figure has three dendrites, the axon being absent from this section. The dendrites form bundles which run along the posterior surface of the muscle base towards both the medial and lateral extremities of the muscle insertion. Methylene blue stained preparations (see Fig. 60) demonstrate that the dendrites meet the muscle base at many points throughout its width. Yet, toluidine blue stained araldite sections of the muscle insertion (Fig. 62) indicate that the number of dendrites tends to decrease rather than increase towards the

FIG. 61. Photomicrograph of an Azan stained longitudinal section through the ventral insertion of the receptor muscle. The preparation has been stripped from the mandible and no cuticle is present. The sensory cell (Cell) dendritic processes (Dend.), which lie at the level of the hypodermis (Hypo.), are situated between the muscle fibres (M. fibres) and tonofibrils of the receptor muscle.



M.fibres

Dend.

Tonofibrils

Hypo.

Cel.

100μ

FIG. 62. Photomicrograph to show the association of the sensory cell dendritic processes with the insertion of the receptor muscle, M3. This is a vertical T.S. of the muscle insertion cut from glutaraldehyde/osmium tetroxide fixed, araldite embedded material stained in toluidine blue. The epicuticle and calcified portions of the endocuticle were removed prior to embedding, leaving only the thin layer of relatively uncalcified cuticle.

extremities of the receptor muscle insertion. This suggests that the dendritic terminations are not restricted to a specific area but occur over most of the muscle base.

It is not possible to determine by standard histological methods whether the dendrites terminate at the level of the tonofibrils in the hypodermis or between the muscle fibres.

3.5.2. Responses of the Mand. MRO to Mechanical Stimuli

Like other muscle receptor organs, the afferent input from the Mand. MRO is dependent upon the tension generated by the receptor muscle. This tension will be varied actively by contraction of the receptor muscle and by changes in mandible position produced passively or by the action of the mandibular muscles. Due to the inclusion of the afferent and efferent nerve fibres of the Mand. MRO in the same nerve branch, it is not possible to record afferent activity in response to motor nerve stimulation. In the experiments described below, the receptor muscle was detached from its dorsal insertion and held with a pair of micromanipulator mounted forceps. This facilitated the production of passive tension in the receptor muscle by allowing it to be stretched and so permitted the range of tension developed during the normal range of mandibular movement to be varied. In the following text the term "receptor muscle stretch" will be used to refer only to the stretch controlled by the micromanipulator mounted forceps.

3.5.2.a. Afferent Activity on Direct Stimulation of the Receptor Muscle

As described above, the dorsal insertion of the

muscle was severed and the muscle held stretched with the micromanipulator mounted forceps. The muscle was then released to a point where all units were quiescent. Direct stimulation of muscle M3 invokes activity of the MRO sensory neurones (Fig. 63). The muscle contraction produced by this method of stimulation is very slow and the tension developed is dependent upon the period of stimulation. Increased periods of stimulation produce increases in unit frequency and the recruitment of other units.

3.5.2.b. Afferent Responses to Mandibular Movements

The input from the Mand. MRO during mandibular movement varies greatly with the degree of receptor muscle stretch. In the experiment shown in Fig. 64 the mandible was moved in step fashion through its normal range of opening. As the tension produced in the receptor muscle increases, the first response observed is a small phasic burst during change in mandible position. When the maintained tension produced at any position is above threshold, some units fire tonically. The frequency of the units and the number of units active increases with the total tension developed. Thus the activity of the receptor increases as the mandible is opened (from 0 to 15° , Fig. 64) and as the degree of muscle stretch is further increased (from A to C, Fig. 64).

During movement of the mandible in a cyclical fashion the activity varies with the rate of opening and closing. As the rate increases (Fig. 65) the frequency of the units increases and recruitment of further units occurs. It is thus evident that the receptor is sensitive not only to

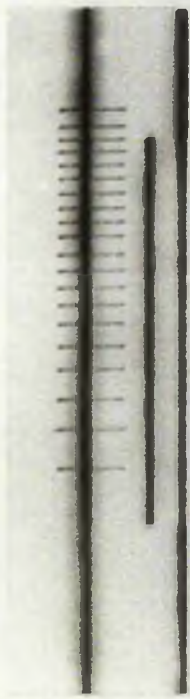
FIG. 63. A-C. The response of some units of the Mand. MRO to contraction of the receptor muscle.

A, B and C show the effect of increasing the period of stimulation, the duration of stimulation being monitored by the lower traces in each case.

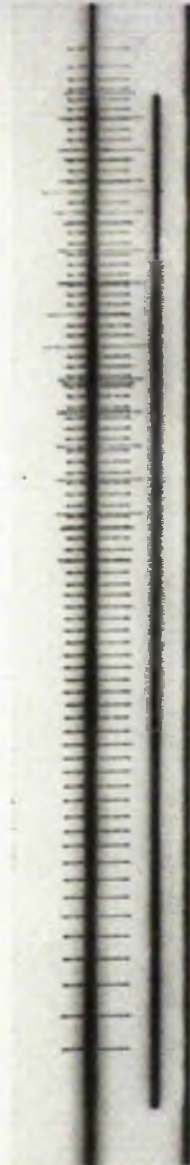
The muscle fibres were directly stimulated at a frequency of 100 Hz.

Scale mark represents 1 second.

A



B



C

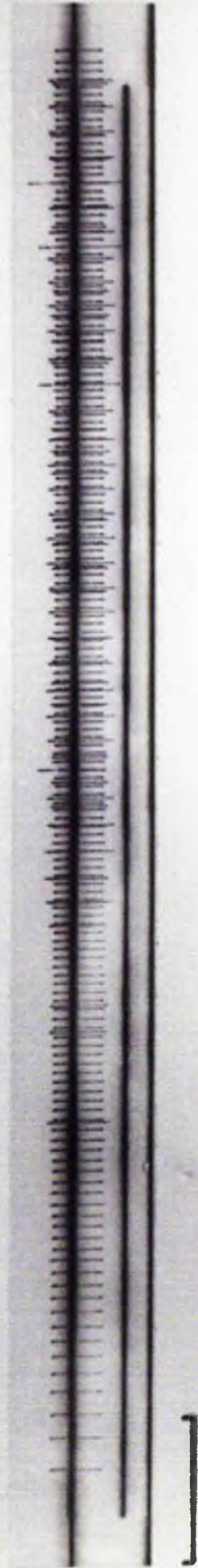


FIG. 64. The response of the Mand. MRO to mandibular movement and different degrees of tension in the receptor muscle. "Muscle tension" was produced passively by holding the muscle in a stretched condition by means of micromanipulator mounted forceps. The degree of stretch increases from A to C. The lower trace in each recording monitors the mandibular movement, the angle given being relative to the closed position. The dots indicate the moment at which movement occurs. Scale mark represents 1 second.

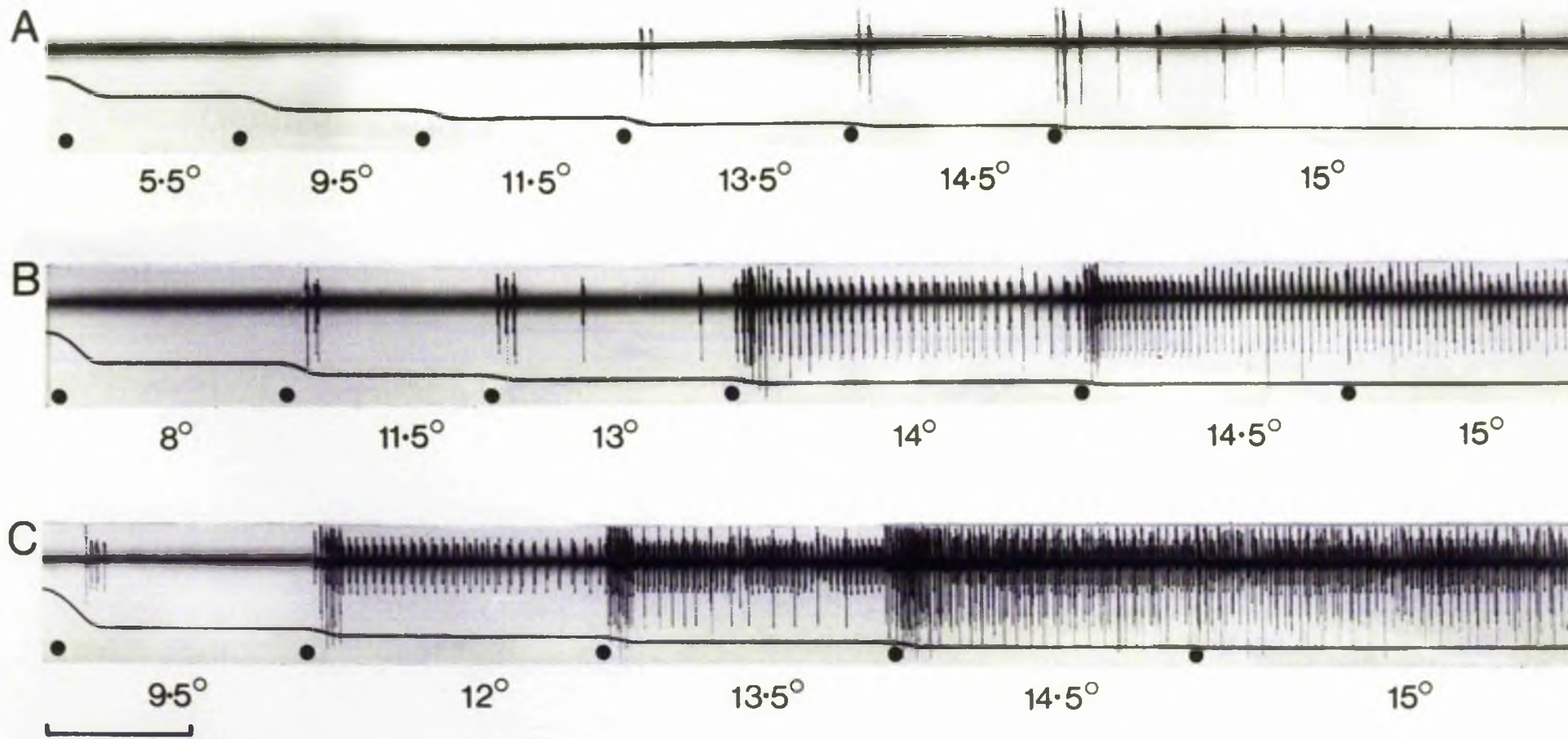
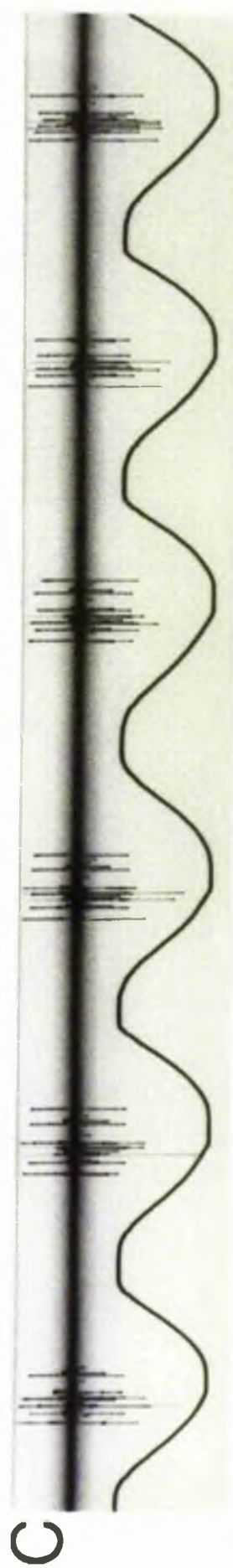


FIG. 65. The response of a small number of units of the Mand. MRO to different rates of mandibular movement. Downward movement of the lower trace indicates mandible opening. Scale mark represents 1 second.



maintained tension in the receptor muscle but also to the velocity of changes in tension.

3.5.2.c. Sensory Unit Types

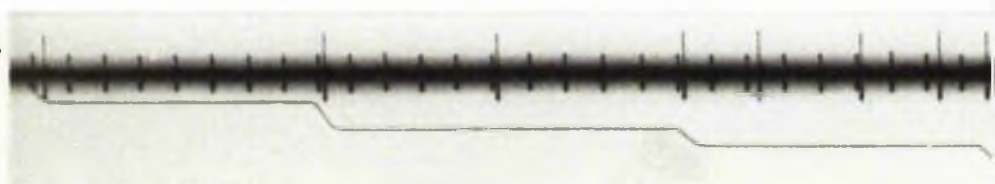
The vast majority of units must be considered to be of similar type in that they respond tonically during maintained tension. However, they vary considerably in their thresholds to tension and in the frequency range which they exhibit. As a general rule, the units with a higher frequency range have a higher threshold. This is well illustrated in Fig. 66 where two tonic units are active. The smaller of the two has a lower threshold but varies very little in frequency throughout the range of tension imposed whereas the larger unit, which becomes active as the tension is increased, exhibits a much larger frequency range.

When the mandible is opened in small steps, a unit will tend to be active during mandible movement as its threshold tension for tonic activity is approached (Figs. 64A and 66A). Figure 67 shows the tonic activity of a unit at a series of mandible positions for two different ranges of receptor muscle tension. When the muscle is further stretched, the unit becomes active at a smaller angle of mandible opening but the frequency attained at maximum opening only increases slightly. As a result the frequency response curve becomes less steep as the overall range of tension is increased.

In many preparations, units are observed to fire at frequencies which closely follow each other throughout the range of tension imposed (Figs. 64 and 68). Figure 69 shows the tonic frequency of two such units for a

FIG. 66. Response of a small number of sensory cells of the Mand. NRO to mandibular opening in steps. A and B show a unit which responds typically as in Fig. 65. B. Shows the unit response during increased passively produced receptor muscle tension. The smaller unit in A and B is extremely tonic and changes very little over the range of tensions applied. C. A tonic unit from a different preparation which reaches maximum frequency between 11.5° and 13.5° during opening. At the fully open position the frequency decreases slightly. Note that the small unit in this record is active only at the position of maximum opening. The lower trace in each case monitors opening of the mandible. Scale mark represents 1 second.

A



5°

9.5°

11°

B

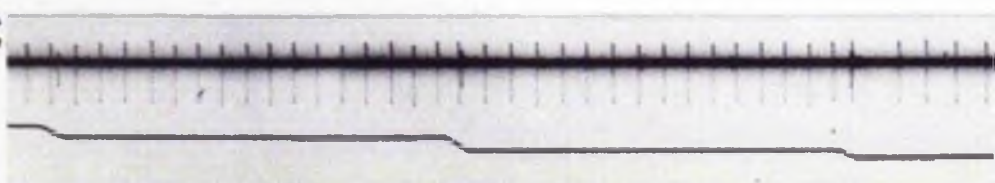


10.5°

12°

13°

C



11.5°

13.5°

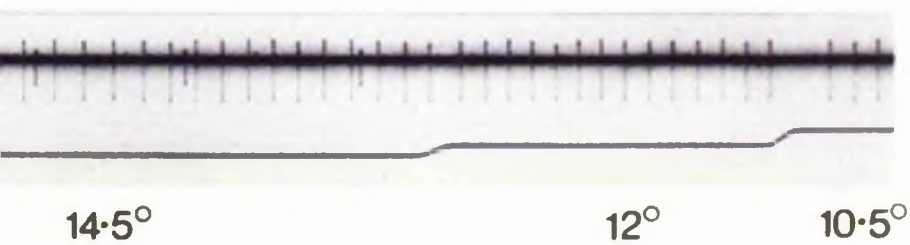
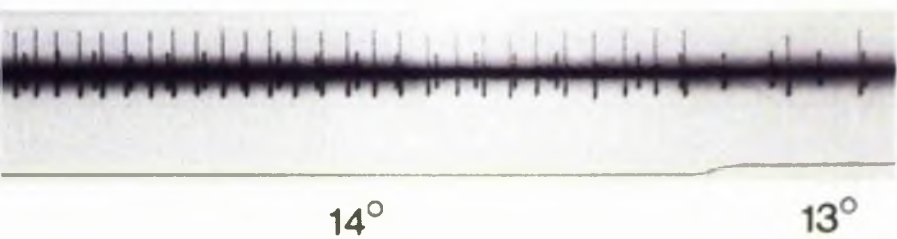
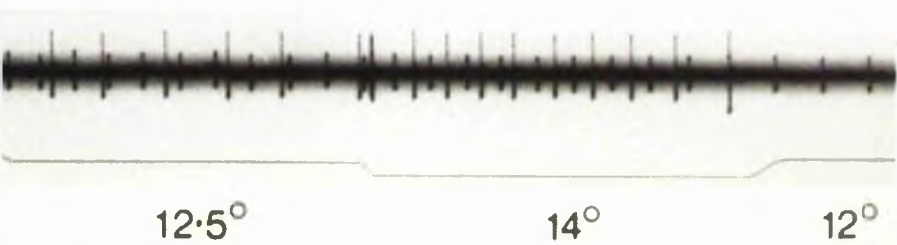


FIG. 67. A graph of the change in activity of a single tonic unit of the Mand. MRO to mandibular opening in steps (see Fig. 66) at two levels of passively produced receptor muscle tension. Abscissa = angle of opening in degrees, measured from the closed position; ordinate = mean frequency in Hz measured over a period of approximately one second following the mandibular movement.

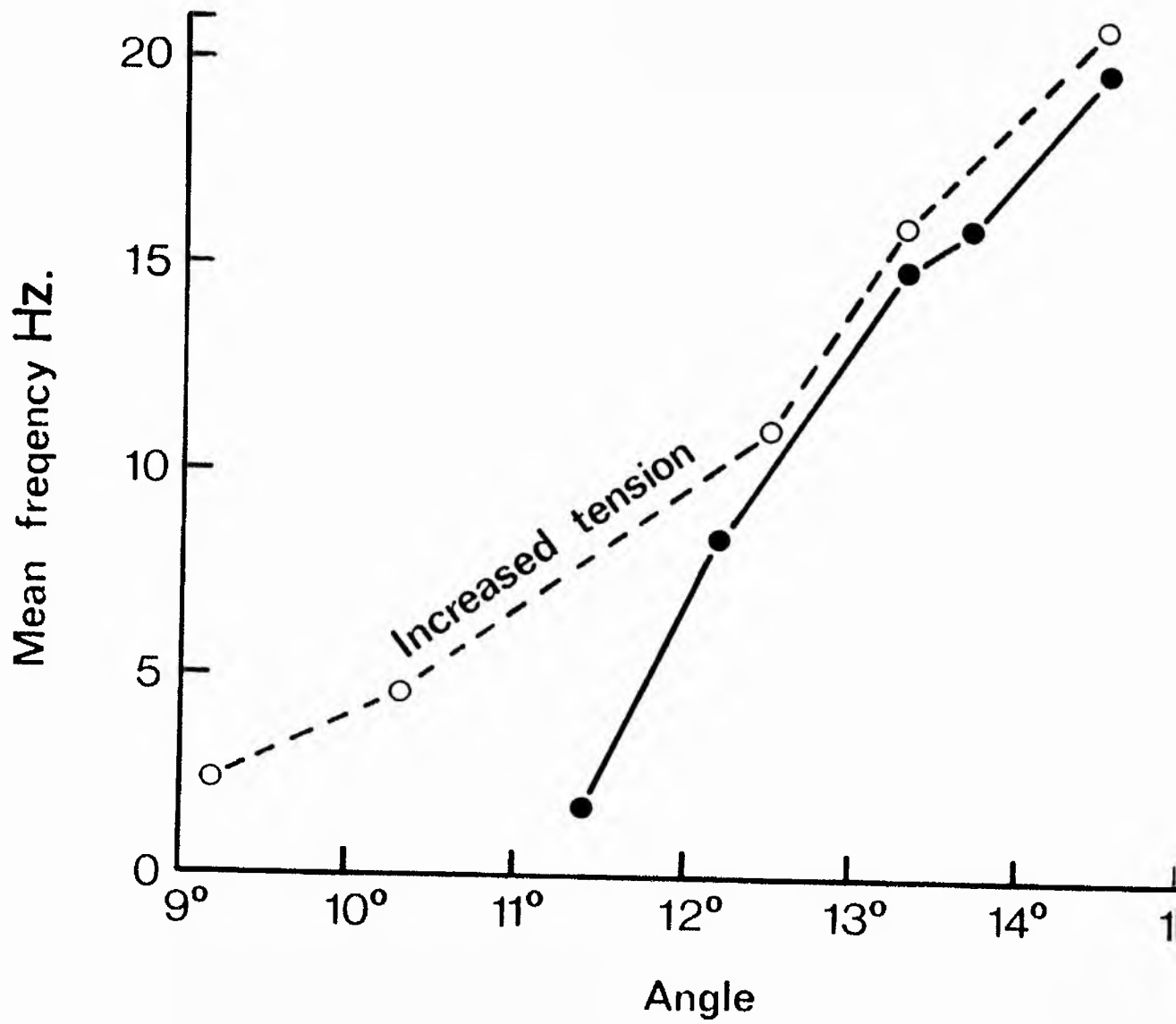
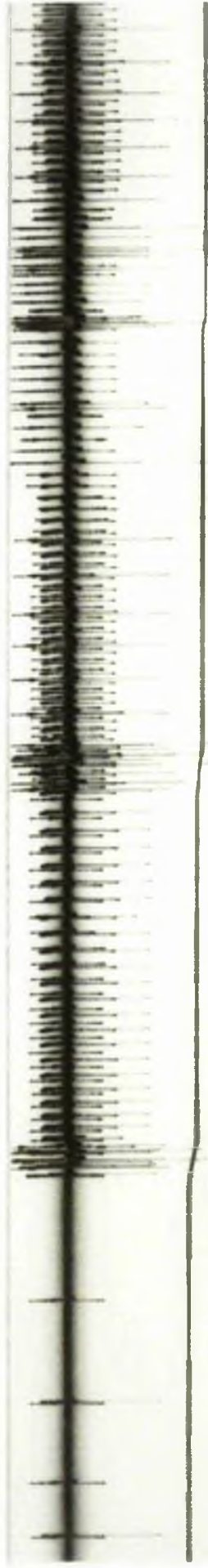


FIG. 68. Response of a large number of units of the Mand. NRO to different degrees of mandibular opening. As in Fig. 64B, several units can be seen to fire at closely similar frequencies (see Fig. 70). The large tonic unit active at 13° of opening is not active at other positions. The lower trace monitors the degree of mandibular opening. Scale mark represents 1 second.



12°

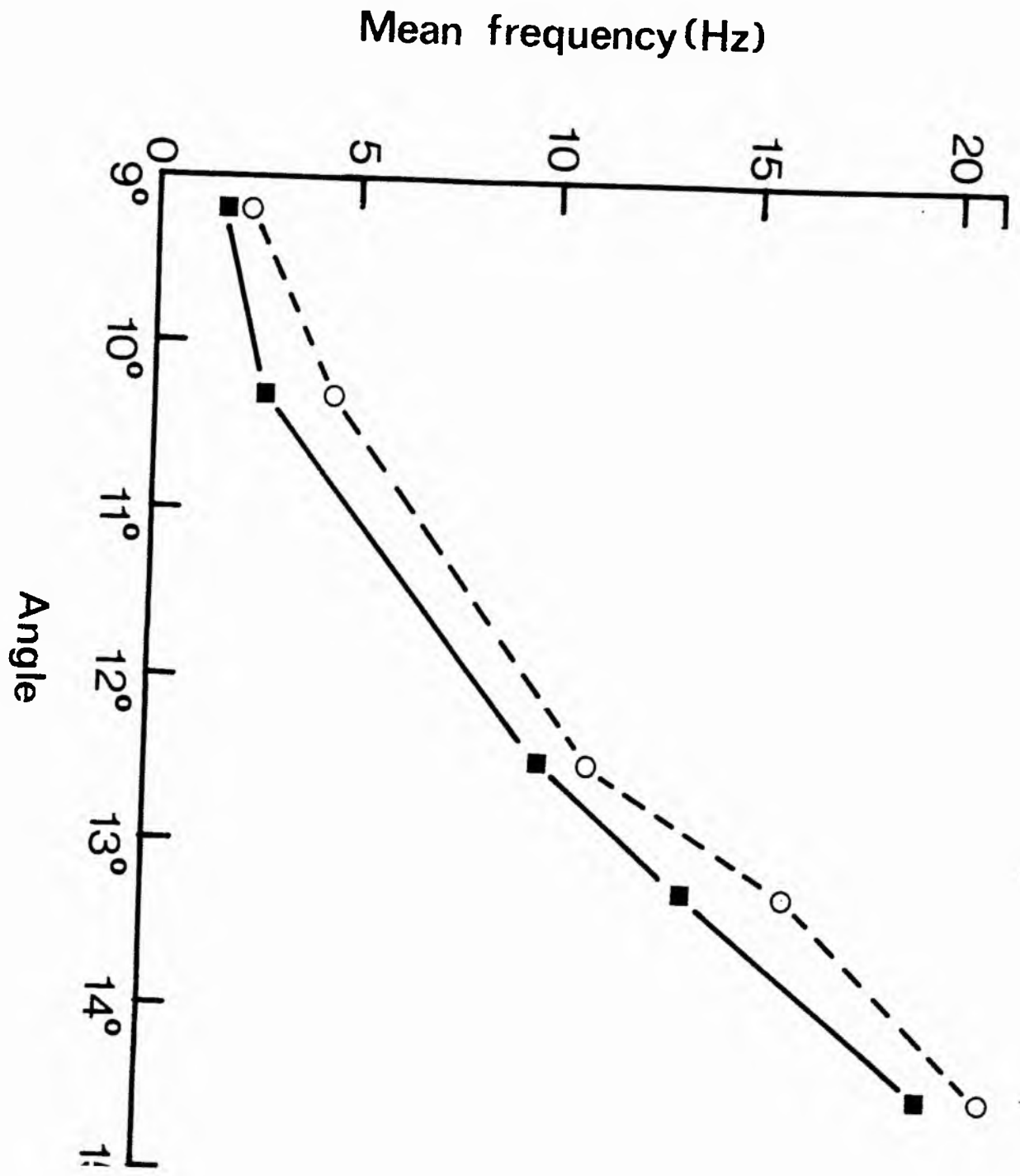
13°

14°

15°



FIG. 69. A graph of the positional frequency response of two tonic units from the same Mand. PRO preparation during mandibular opening in steps.



range of mandible positions. These units have very similar frequency response curves which vary only slightly in their frequency amplitude.

The response of units to constant angular velocity movements and to acceleration are shown in Figs. 70 and 71. Acceleration occurs at the commencement of mandible movement and when the velocity of movement is changed (Fig. 70) but no response to acceleration can be detected in these or other records from this receptor. The responses of any unit during constant velocity movements is dependent upon the angular velocity employed. When the angular velocity is low ($1.6^{\circ}/\text{sec}$, Fig. 70) the unit exhibits a linear frequency response curve and the frequency at any stage of the movement is equivalent to the tonic level of activity which the unit would exhibit were the mandible maintained in that position. Therefore for very low velocities the unit responds as a purely positional receptor and the frequency has no velocity component. At higher velocities (Figs. 70 and 71) the frequency at any stage of the movement tends to be above that which would result were the position maintained and the unit may be considered to be velocity sensitive. It is not clear from the results which I have obtained whether or not a definite relationship exists between unit activity and angular velocity (or more significantly, rate of change of receptor muscle tension).

On cessation of movement a rapid drop in frequency normally occurs (Fig. 70 and unit 2, Fig. 71). This drop in frequency is greater with higher angular velocities and is absent with low rates of movement where no "velocity response" is observed. Unit 1 (Fig. 71) is

FIG. 70. A graph to show the response of a single "tonic" unit of the Mand. MRO to mandible opening at different angular velocities. The instantaneous frequency (Hz) of a single impulse is the reciprocal of the interval between that impulse and the preceding one. The unit response was plotted for three different angular velocities, $1.6^{\circ}/\text{sec}$. (open circles), $4.1^{\circ}/\text{sec}$. (closed circles), $10^{\circ}/\text{sec}$. (stars). The stated angle of mandibular opening is measured from the normal closed position.

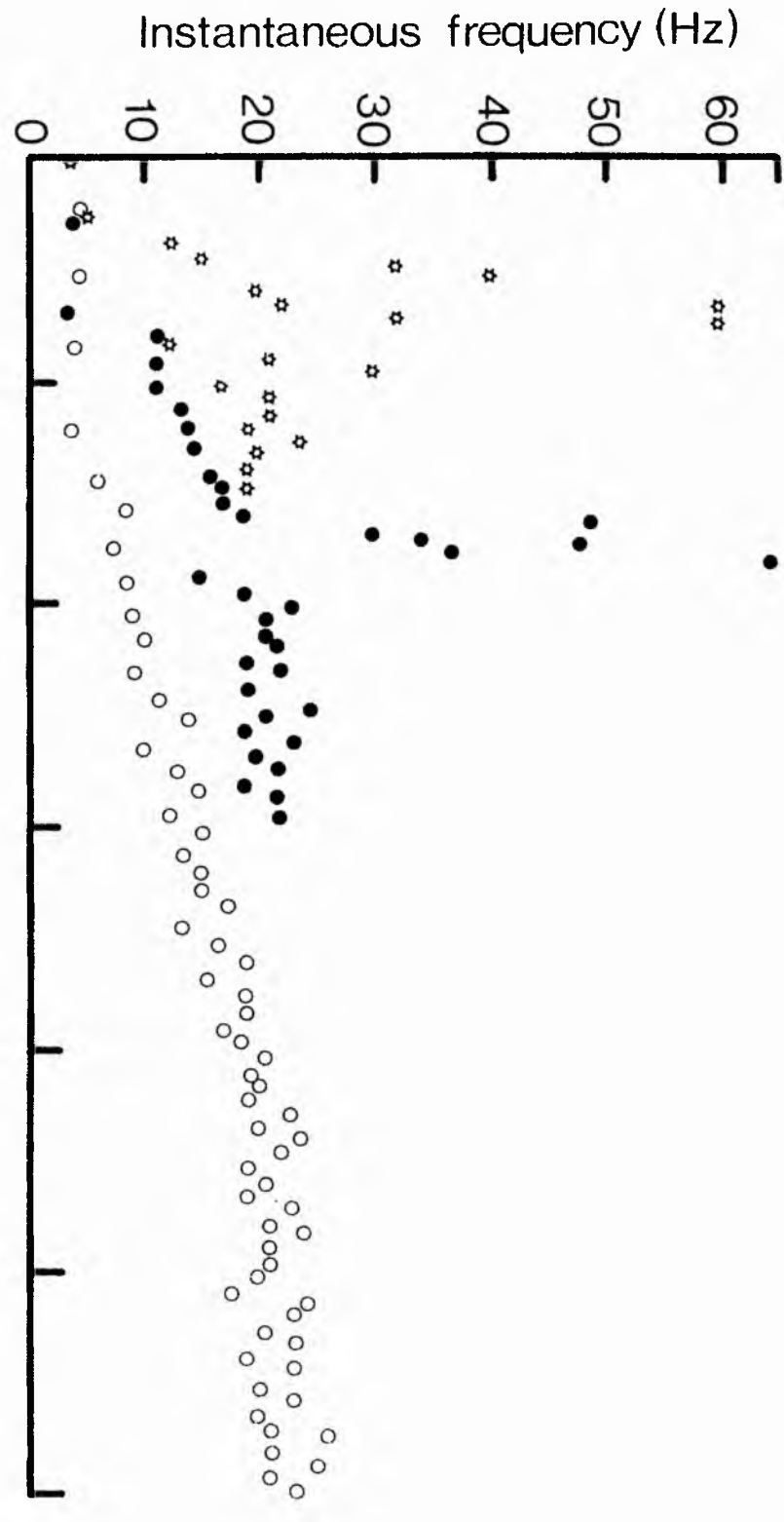
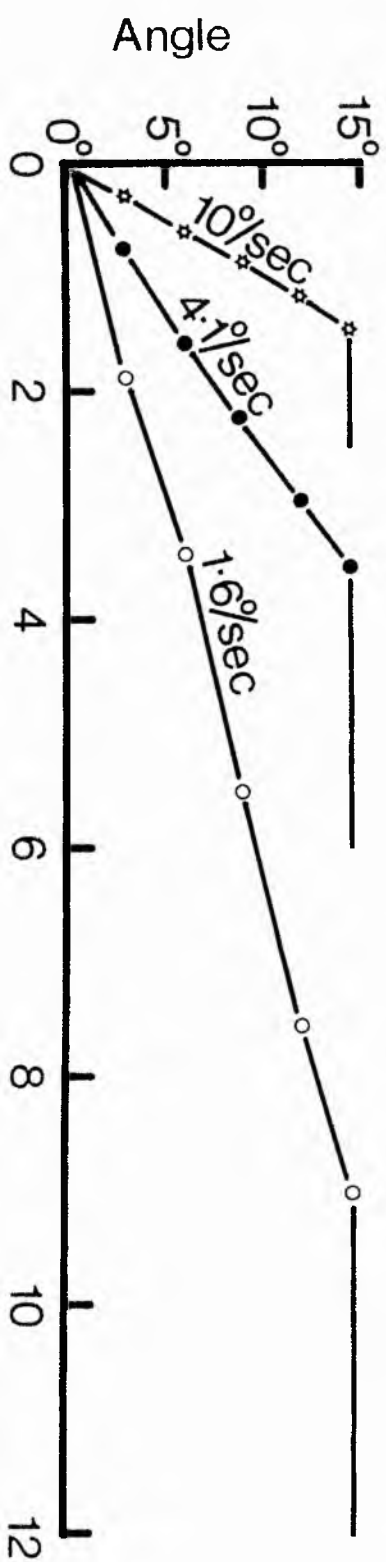
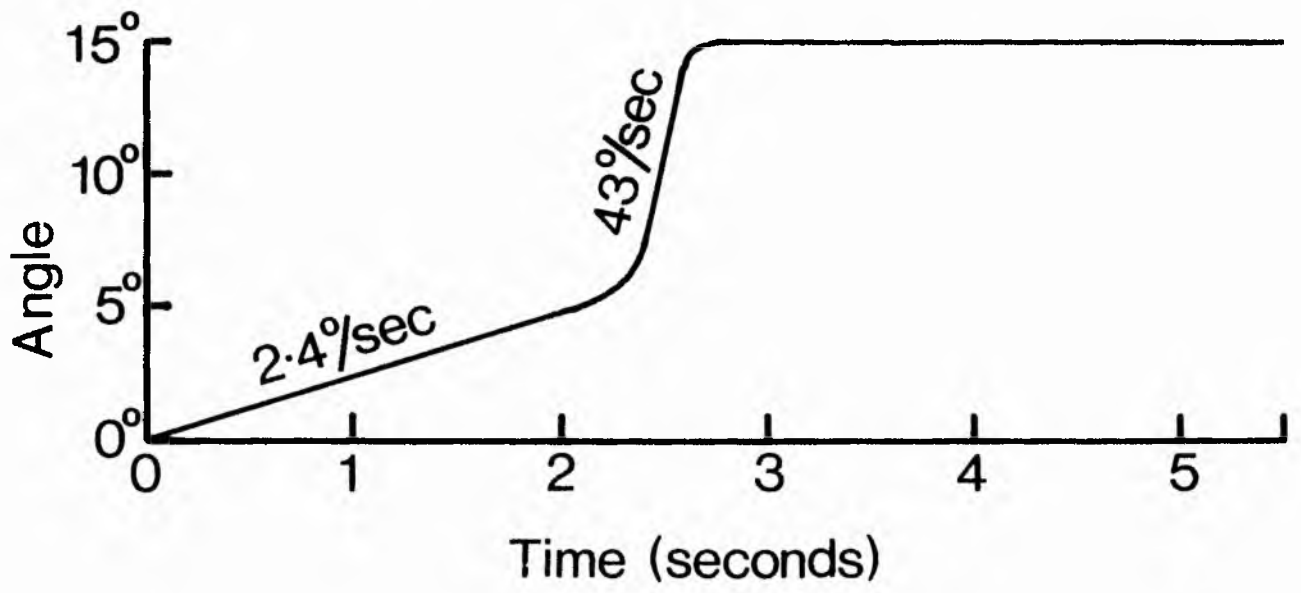
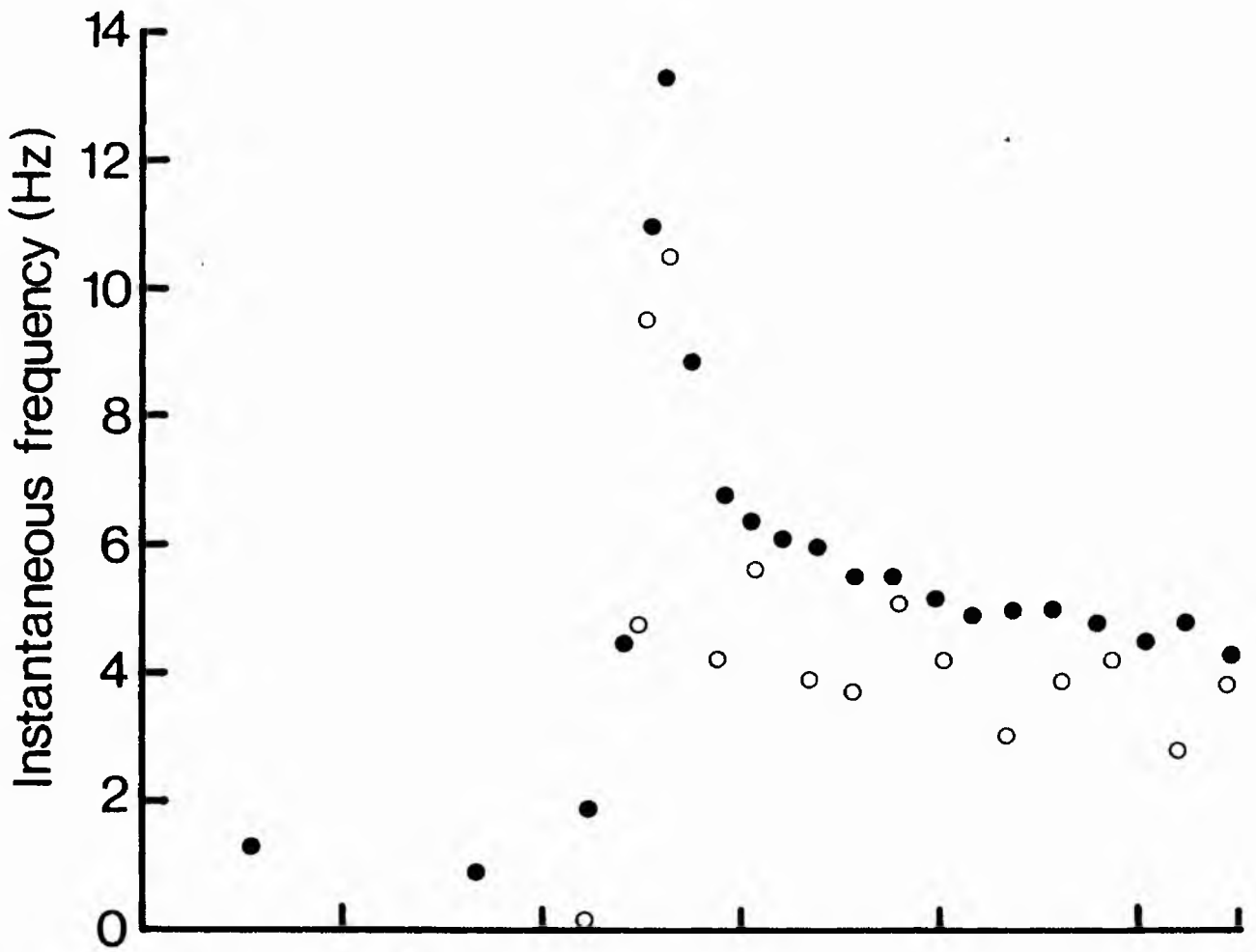


FIG. 71. The response of two tonic units from the same preparation of the Mand. NRO to a change in angular velocity of mandibular opening. Unit 1 (e), Unit 2 (o). See text for explanation. Abscissa and ordinates as for Fig. 70.



unusual in that it exhibits an initial rapid adaptation and not a sudden reduction in frequency as seen with unit 2.

The response to constant velocity movements will obviously vary between units and be dependent upon both the rate of change of tension and the range of tension encompassed by the movement.

Some units are found which have unusual characteristics but they are very much in the minority. The most common aberration is for the unit to exhibit a maximum frequency at an intermediate position (Figs. 66c and 72). Such units decrease in frequency if the tension is increased after the maximum activity has been attained and in some cases may cease to be active. In one instance (Fig. 68) a unit was observed to be active during a very narrow range of tension. This tonic unit can be seen to be active when the mandible is opened by 13° but is not active at positions 1° either side of this. Unfortunately this unit was not observed during closing of the mandible and it is not known if it is direction sensitive.

Figure 73 shows a direction sensitive unit which is active only during closing of the mandible. This unit exhibits normal tension sensitivity and shows maximum frequency at higher receptor muscle tension. A similar unit is seen in Fig. 74. This unit is active during opening of the mandible but exhibits maximum frequency during closing. An increase in the overall level of tension (Fig. 74B) produces an increase in both the opening and closing responses. Such a unit is primarily monitoring the rate of decrease in tension.

FIG. 72. A graph of the positional frequency response of a tonic unit from the Mand. NRO which does not exhibit its maximum frequency at maximum mandibular opening (see Fig. 66C).
Abscissa = angle of opening and closing, measured from the closed position; ordinate = mean frequency in Hz measured over a period of approximately one second following the mandibular movement.

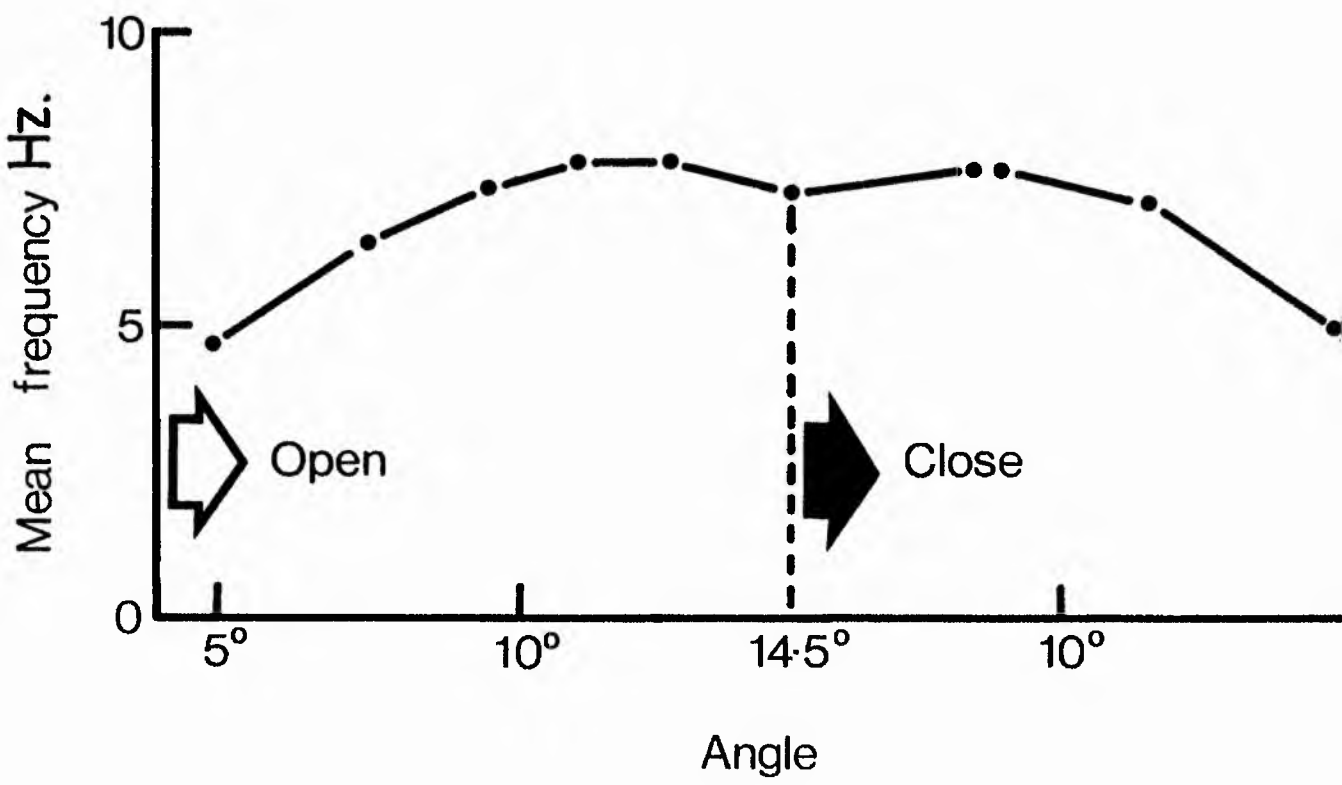


FIG. 73. A group of units of the Mand. MRO, one of which responds during mandible closing only. The onset of activity in this tonic unit is indicated by arrows. A. The response to mandible opening. B. The response to closing. C. Activity during one cycle of mandible movement. Downward movement of the lower trace denotes opening of the mandible. Scale mark represents 1 second.



FIG. 74. Response of a small number of units of the Mand. MRO to the normal range of mandibular movement at two different degrees of muscle stretch.

The passively produced receptor muscle tension is greater in B than in A. The large unit responds primarily during mandibular closing and shows greater activity in B. This unusual unit appears

to be monitoring the decrease in muscle tension.

The small unit marked by a horizontal bar in B exhibits a normal response to tension change.

Downward movement of the lower trace indicates mandibular opening.

Scale mark represents 1 second.



A



B



3.6. The Posterior Stomach Nerve (omn 4)

The posterior stomach nerves (PSN), "which in Homarus are branches of the outer mandibular nerves, are symmetrically arranged on each side of the animal. Each PSN proceeds ventrolaterally along the mandible and then turns dorsally to run up the side wall of the thorax just anterior to the cervical groove. The nerve then enters the ventral surface of the posterior adductor muscle "M9", of the mandible and after passing through this muscle runs onto the gut by way of the posterior external gastric muscle". (From Dando and Laverack, 1969).

Between the lateral edge of the mandible and where the nerve enters muscle M9 are a large number of neurones. These cells are variable in their position, distribution and number as seen after methylene blue staining. In some preparations the cells are restricted largely to two groups, one lying on the lateral edge of the mandible and the other larger group in the nerve close to muscle M9. It is not unusual, however, for the cells to be evenly scattered along the nerve between these two points. The work of Dando and Laverack was restricted to the cells monitoring movement of the gastric mill. These cells are mainly located in the more dorsal group. Dando and Laverack also noted the presence of cells innervating the hypodermis in the region of lateral edge of the mandible. These are the cells which are presumably responding to mandibular movement (see Experimental 3.6.1.).

Figure 75 shows the PSN as it traverses the lateral edge of the mandible. This preparation is perhaps atypical in the number of cells observed lying outside the PSN but it illustrates the point that some cells in

FIG. 75. A montage of photographs from a methylene blue stained preparation of the posterior stomach nerve, omn 4, where it overlies the lateral articulation of the mandible. A large number of neurone somata are located in this region, mostly within or apposite to the nerve but some lie a short distance from it (black arrows). The white arrows indicate the main nerve bundles. The peripheral PSN (Peripheral), the central PSN (Central), endophragmal skeleton (Endo. skeleton).



the PSN do innervate the hypodermis in this area. Some of the fibres leaving the PSN do so individually but the majority are organised into bundles some of which pass into the mandible cavity and others onto the epistoma close to the lateral articulation. In this preparation it can be seen that there are a number of cells lying outside the main tract of the PSN but in most preparations fewer outlying cells are observed. The cell lying at the junction of the omn 2/3/4 connective is bipolar and, as its process in the PSN passes peripherally, afferent information from the cell must pass into the connective.

The cells in this region are bipolar or tripolar (Fig. 76) but as many of the nerve processes in this region are seen to branch it is probable that most of the cells are multiterminal. The processes of such cells seldom pass into the hypodermis in the same bundle and commonly one process passes peripherally in the PSN. It thus seems likely that single cells may have widely separate non-overlapping sensory fields.

3.6.1. Afferent Activity in the PSN

If the PSN is sectioned peripheral to the lateral articulation of the mandible and the afferent activity recorded from the nerve central to the cells described above it can be seen that a number of mechanoreceptive units are present. Figure 77 shows the change in activity of the nerve bundle produced by gently touching the hypodermis of the epistoma and endophragmal skeleton some 4-5mm from the PSN.

The activity of the PSN is modulated by mandibular movement (Fig. 78). Units respond during opening and

closing of the mandible with the activity increasing towards the extremes of movements. Opening and closing of the mandible in steps (Fig. 79) indicates the units to be largely phasic but in most instances it seems that the activity occurs after movement not during it. Thus the majority of units are phasic or phaso-tonic position sensitive units. The only recognisable tonic unit in these results fires on closing (Fig. 79D) and it adapts within one second.

It was not possible to obtain recordings from single units of the PSN by nerve splitting techniques and thus the types of unit present in the PSN are incompletely known.

FIG. 76. Photomicrographs of methylene blue stained preparations of some of the Posterior Stomach Nerve cells which innervate the hypodermis. A. A tripolar (Tri.) and a bipolar (Bi.) multidendritic cell. B. A tripolar cell.

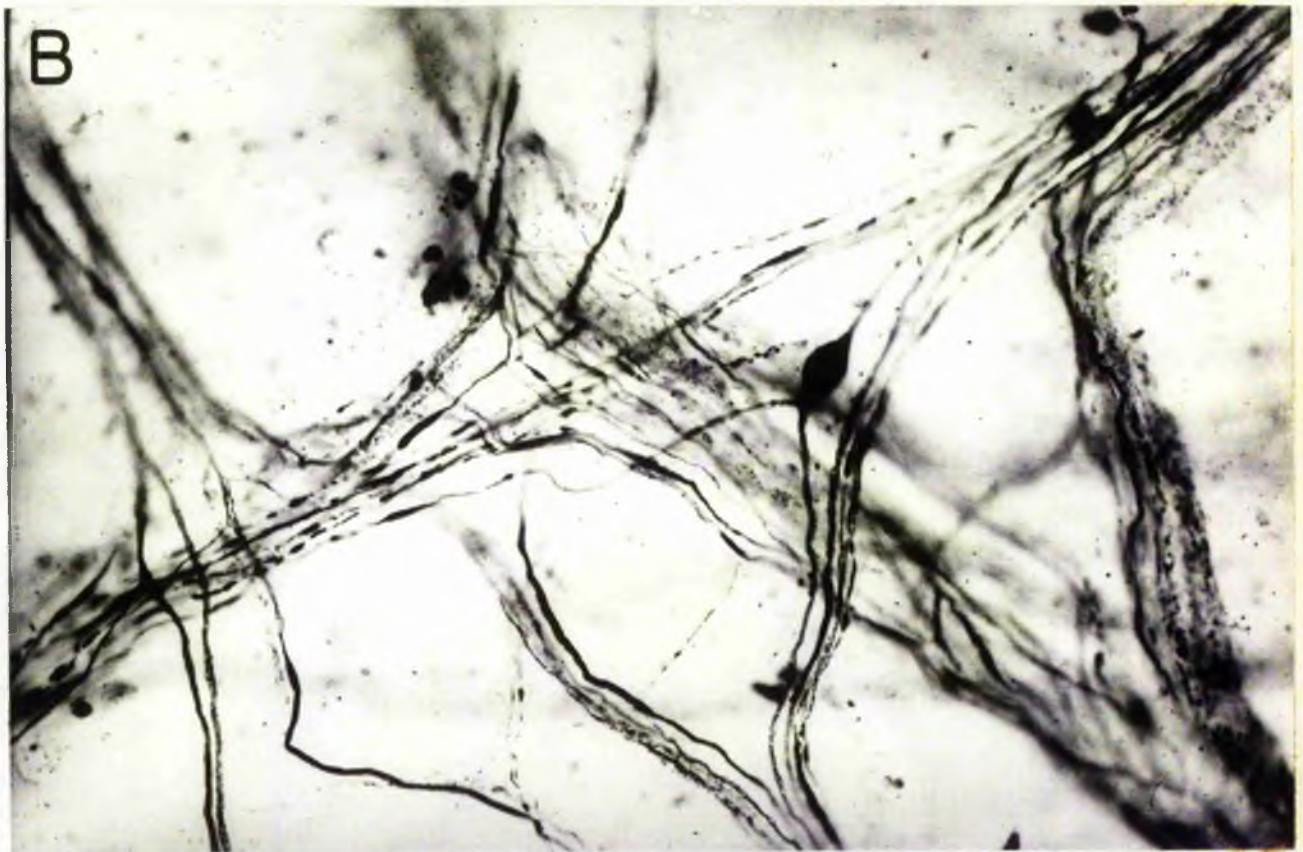
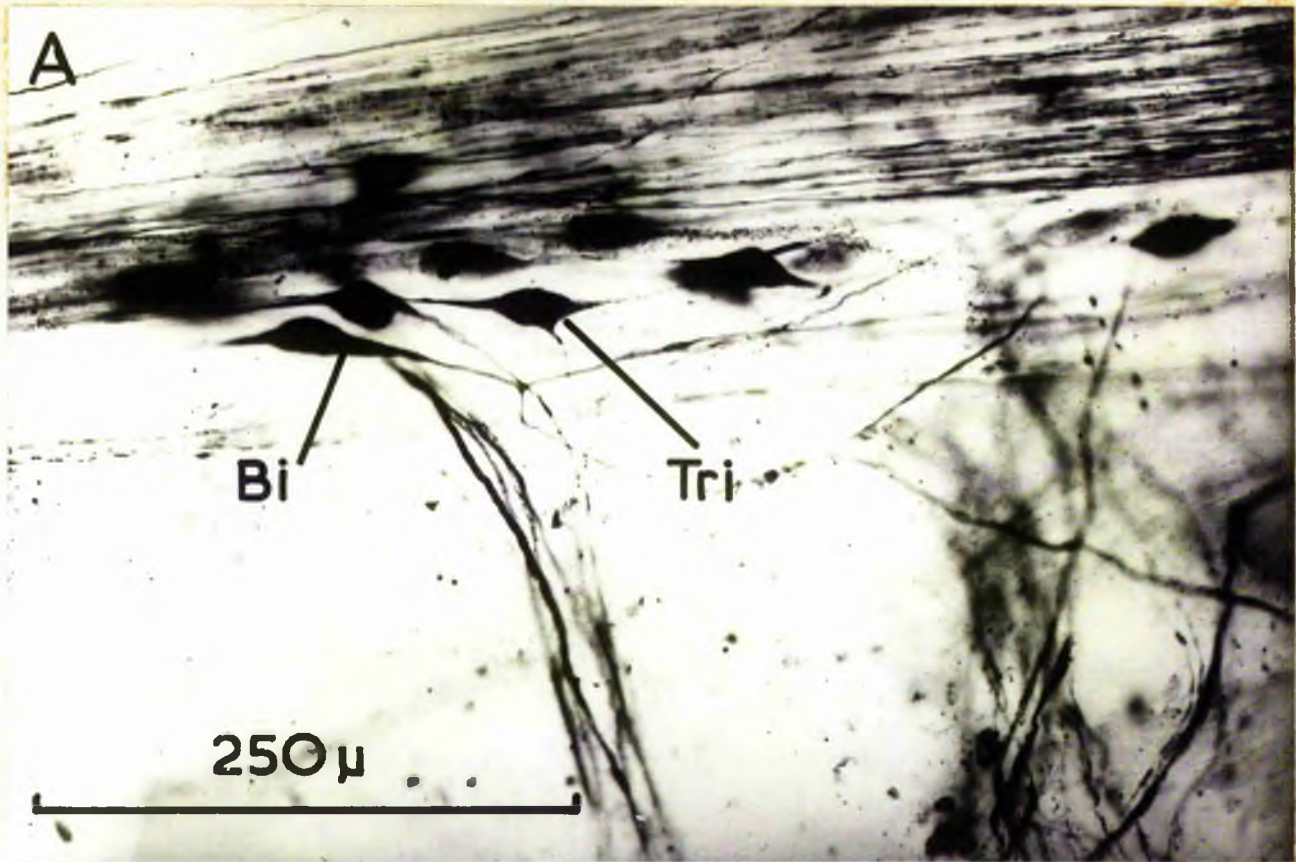


FIG. 77. The afferent response recorded from the PSN to touch of the hypodermis in the vicinity of the lateral articulation of the mandible. Arrows indicate the time of touching. Scale mark represents 1 second.



FIG. 78. Afferent response from the PSN recorded during cyclical movements of the mandible. Downward movement of the lower trace denotes opening of the mandible. Scale mark represents 1 second.

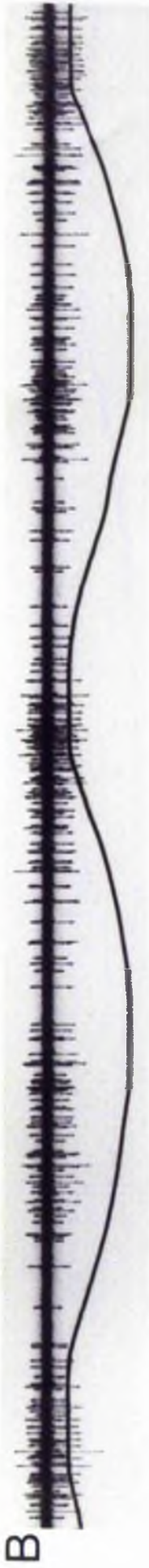
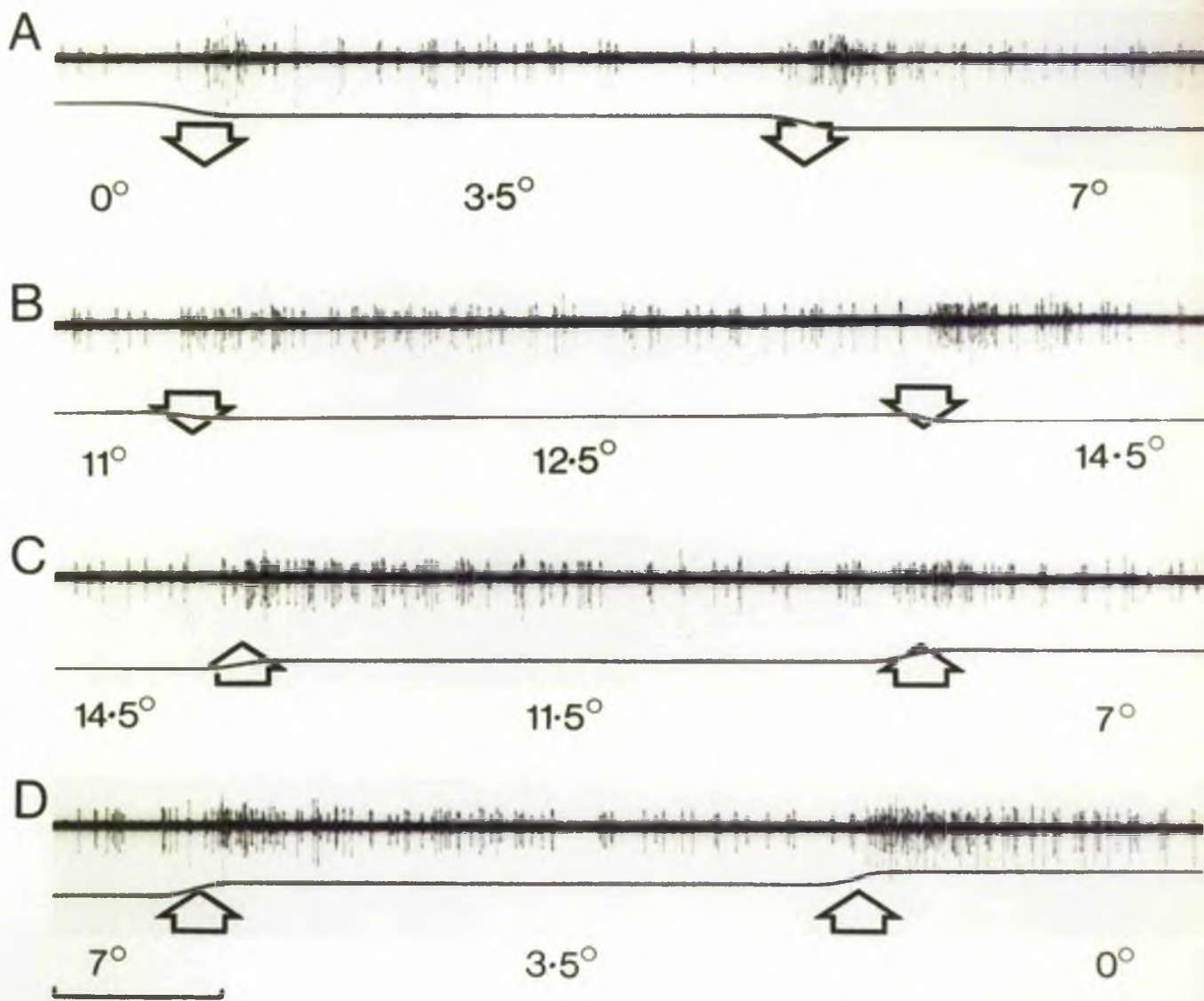


FIG. 79. Afferent responses recorded from the FSN during movement of the mandible in step fashion. Downward movement of the lower trace indicates mandible opening, the occurrence and direction of each movement is indicated by an arrow.



DISCUSSION

DISCUSSION

1. The Definition of a Proprioceptor

Since its conception by Sherrington (1906), the term "proprioceptor" has been redefined a number of times by different authors. The proposed definitions have varied in their complexity from the simple:

"A mechanoreceptor which normally signals movement or position of the parts of the body (Bullock and Horridge, 1965)

to the more precise:

"An internal mechanoreceptor involved in short term reflexes of movement or position (which is not a statolith organ)", where an internal mechanoreceptor is "a receptor monitoring position or movement of parts of the main body" and "internal refers to function not location" (Dando, 1969).

Although by precedence the correct definition must be that proposed by Sherrington (1906), this definition, like that of Dando (1969) is not in accordance with popular usage as this term "proprioceptor" is freely used for receptors whose reflex function is not proven (Dando and Laverack, 1968; Finlayson, 1968; Horridge, 1962; Sandeman, 1963; Sutterlin and Saunders, 1969). However, the definition proposed by Bullock and Horridge (1965) is inadequate as its imprecision may lead to confusion and the term as used in this thesis will refer to:

'Sense organs capable of registering continuously deformation (changes in length) and stresses (tensions, compressions) in the body, which can arise from the animal's own movements or may be

due to its weight or to other external mechanical forces' (Lissman, 1950).

2. The Connective Chordotonal Organs of the Limb Joints

Table 4 compares the proprioceptors present at the joints of the walking leg of the brachyuran Carcinus with the walking leg and 3rd maxilliped of Homarus. The pereopod of Carcinus is the limb of which most is known, due to the work of Bush, Clarac, Whitear and Wiersma (see Appendix 1).

The macruran walking leg possesses a connective chordotonal receptor at the T-C joint, whereas it is absent in the brachyuran walking leg (Alexandrowicz and Whitear, 1957). As the chordotonal receptor is the typical decapod limb joint receptor, its presence at the macruran T-C joint is more likely to be the basic pattern rather than a specialisation. The retention of this receptor in the macrurans may well be associated with their ability to walk with equal ease forwards and backwards, as well as laterally, as this joint is important in anterior-posterior movement of the limb. The loss of the BI receptor in brachyurans is to be expected in view of the fusion of the joint. The IN2 receptor is not lost in the Brachyura, but becomes involved in the MCC complex as MC02 (Clarac, 1968a). The total number of chordotonal organs, therefore, remains the same but involvement of this IN receptor in monitoring movement of the M-C joint reflects the increased importance of this joint in lateral movements.

The strand organs of the crab walking legs adopt different forms in the macruran limbs. MC2 is a strand,

TABLE 4

Receptor	<u>Carcinus</u> walking leg	<u>Homarus</u> walking leg	<u>Homarus</u> 3rd maxilliped
TC MRO	Yes	Yes	Yes
TC ES	Yes	Yes	Yes
MCO 1*	Yes	Yes	No
2	Yes	No	No
Connective Chordotonal Type			
TC	No	Yes	No
CB	Yes	Yes	Yes
BI	No joint	Yes	No joint
IM1	Yes	Yes	Yes
IM2	No	Yes	Yes
MC1	Yes	Yes	No
MC2	Yes	Yes	Yes
CP1	Yes	Yes	No
CP2	Yes	Yes	Yes
PD	Yes	Yes	No

Table 4. Presence or absence of receptors at the various joints of the pereopod and 3rd maxilliped of Homarus and the walking leg of Carcinus. The information for Carcinus is extracted from Alexandrowicz and Whitear (1957), Clarac (1968a) and Whitear (1962). Muscle receptor organ (MRO), elastic strand (ES), Myochordotonal organ (MCO).

*This is the nomenclature used by Clarac (1968a).

but the disposition of the cells differs markedly from that of the brachyuran limb. CP2 is in the form of a sheet and PD, the cells of which are similar to that of brachyurans in disposition, has a broader and more diffuse strand. The sheetlike receptors CP1 and MC1, however, are similar to those in Carcinus (Whitear, 1962).

The macruran 3rd maxilliped and 2nd pereopod show several differences. Like the brachyuran walking leg, the macruran 3rd maxilliped lacks a chordotonal receptor at the T-C joint. Movement of this joint may be of reduced importance as it is restricted by its close apposition to the chelae. The loss of the BI receptor may again be correlated with the fusion of this joint.

A major difference is the absence of a myochordotonal organ (MCO) in the 3rd maxilliped. Evoy and Cohen (1969) have shown that the input from the myochordotonal organ excites its own receptor muscle on joint movements away from the set rest position. They suggest that interactions of this input with the MC chordotonal inputs (which affect the receptor muscle in the same sense as the main flexor) provide the system with a dynamically determined reference point for the basic postural position. Barnes, Evoy and Spirito (unpublished) have shown that the chordotonal proprioceptors of the brachyuran walking leg are functional during walking by imposing passive movements upon the centrally determined pattern of P-D joint movement. Electromyograms from the muscles moving this joint clearly show that resistance reflexes occur during walking to bring the joint position back into phase with the motor output. It is, therefore, reasonable to assume that the MCO is also functional during walking.

It is largely the muscles of the M-C joint which produce the propulsive force during lateral walking and the part played by any one limb in producing this motion will depend on the force developed by the other legs. The MCO may thus ensure that optimum use is made of all the walking legs by maintaining the velocity of M-C joint movement in phase with the central command. The third maxilliped, however, is not subject to such changing loads and in life tends to be held in set positions.

In the 3rd maxilliped the M-C and C-P joints have but single receptors and these, in their structure, position relative to the joint and association with the CAP sensilla, correspond to CP2 and MC2 of the walking leg. Thus, the more complex CP1 and MC1 are absent. It is interesting that CP1 and MC1 are associated with the bender and flexor muscles respectively, and do not cross the joint, hence not one but three receptors associated with muscles are absent in the 3rd maxilliped. This difference, by analogy with the MCO, may indicate the value of CP1 and MC1 in the locomotory processes. It would be interesting to compare the effect on walking of the ablation of MCO, MC1 and CP1 with the ablation of MC2 and CP2.

Norch (1971) has recently demonstrated that the MCO in the walking legs of Ocypode is extremely sensitive to substratumborne vibration and contends that it is an organ for hearing and vibration sense. Although it has been known for some time that the connective chordotonal organs of decapods were vibration sensitive (Burke, 1954), it has yet to be demonstrated that this sensitivity is of functional significance.

The PD receptor is apparently absent in some

macrurans e.g. Homarus gammarus and Nephrops norvegicus but is present in Panulirus argus (Wales, Clarac, Dando and Laverack, 1970). This difference may well reflect the difference in use of this limb by Panulirus which uses its 3rd maxilliped vigorously to clasp its prey in a scissor-like action (D.M. Maynard, unpublished). Homarus gammarus is apparently capable of catching active prey such as fish, presumably by means of its chelae (Herrick, 1895) whereas Panulirus lacks the large chelae.

From a general survey it appears that the receptors form flat sheets where the articulation of the joint is of a looser nature, or where the musculature can produce movement in more than one plane (CP2 of the walking leg, MC, CP and PD of the 3rd maxilliped). The sheets may represent an early stage in strand development having been formed by a condensation of a more diffuse system of cells and connective tissue fibres. Comparatively simple receptor structures that consist of cells with lengthy strands of connective tissue inserting via scolopidia at the cuticle have been described in the isopod Ligia by Alexander (1969). Not all of these receptors need be primitive in form, however, as flexibility may be due to specialised requirements rather than regression. This is most probably true of the C-P joint, where flexibility is accompanied by differences in the musculature by means of which the joint can be moved in more than one plane.

The physiological results obtained confirm that the units in the chordotonal organs examined resemble those described in the Brachyura and the comparable receptors in the brachyuran and macruran walking legs contain elements responding to the same gross stimulations of

stretch and release. For the maxilliped, however, differences in the form and function of the appendages have clearly been reflected in functional changes in the receptors. For example, CP, which is analagous to CP2 of the walking legs, responds in a directly opposite way to that receptor. More significantly, MC, which is analagous to MC2 of the walking legs, responds to both stretch and release instead of release only. This probably indicates the importance of the MC joint in the function of the maxilliped. This fact also follows from Wiersma's (1958) investigation of sensory collecting neurones where he found that the marker unit number 1 had an important input from the maxilliped M-C joint. The only other interneurones with important inputs from the maxilliped joints were either specifically activated by the basal joints or activated by many joints.

No connective chordotonal organ was found at the thorax - mandible articulation and this is in accord with the T-C joint of the 3rd maxilliped and the 2nd maxilla (Pasztor, 1969). A receptor is present at the insertion of muscle P1 onto the proximal segment of the palp but the sensory cells are not associated with a distinct strand. Neither methylene blue staining nor electrophysiological recording revealed the presence of chordotonal organs at the more distal articulations of the palp.

3. The C-P Joint and its Additional Muscle

The presence of the additional muscle, previously undescribed in this group of decapods, is reminiscent of the Stomatopoda and Natantia which also possess a supernumerary muscle at the C-P joint. The muscle

present in these groups produces rotation of the propodite (Wiersma and Ripley, 1952) whereas the additional muscle of Homarus gammarus apparently does not. This is demonstrated by consideration of the structure of the joint and the insertion of the muscle and the results of stimulation experiments. Stimulation of the additional muscle alone produces weak bending at the joint in the straightened limb of Homarus gammarus, but it seems probable that this muscle acts in conjunction with the stretcher since it shares at least one motor axon. The stretcher, however, is its apparent antagonist. Sherman and Atwood, (1971) have since examined this muscle in Homarus americanus and found the shared axon to be inhibitory. The additional muscle has a single excitatory axon which is apparently not shared with either the stretcher or bender muscle. They found that excitation of the muscle causes the proximal and distal points of the articulation to be drawn together. This is followed by slight rotation of the propodite followed by slight bending at higher stimulation frequencies. They conclude from these observations that the additional muscle like that of the *Natantia* is a rotator. It should be noted, however, that though the possible degree of rotation is large (35° , Fig. 4B), Sherman and Atwood only observed slight posterior rotation of the propodite.

The C-P joint is capable of rotation in many reptantian decapods which possess only two muscles at this joint. Rotation has been shown to be achieved by activity of the bender muscle in the anomuran Dardanus asper and the brachyuran

Dromidiopsis dormia (Wiersma and Ripley, 1954).

It is probable that this is the mechanism for rotation employed in other reptantian decapods including those with an additional muscle and that this muscle has a different function from the third muscle of the Natantia. What this may be is at present only a matter for speculation. It is noticeable that the C-P joint of the pereopod is very flexible (Figs. 3B and 4B) but in the walking animal the joint is moved very little, regardless of the animal's direction of movement. Sherman and Atwood (1971) observed that the muscle pulled the points of articulation together and it is possible that this will stiffen the joint allowing it to be held more rigidly when bearing weight. This function is presumably achieved by maintained tension in the bender and stretcher where only two muscles are present.

The 3rd maxilliped does not bear weight and hence does not require to be stiffened at the C-P joint. Here the three muscles are more uniform in size and all are involved in movement of the propodite.

4. The CAP Sensilla

The groups of sensilla found distal to the C-P and M-C joints of both the 3rd maxilliped and the pereopod and the I-M joint of the pereopod have been renamed; cuticular articulated peg (CAP) sensilla. These sensilla originally described by Wiersma, (1959) as being pits in the cuticle were referred to by him as "slit sensilla". This choice of name was unfortunate because of its possible association with the lyriform organs of

arachnids. The lyriform organs are elongated cuticular slits a few micra wide and may be more than 100 μ long. They have no articulated peg or like structure (see Barth and Libera, 1970). The articular membrane of the CAP sensilla is approximately circular and bears a peg the length of which is variable. Alexandrowicz, (1969) states that the sensilla are innervated by the cells of the respective receptors (MCO, NC2 and CP2 in the pereopod, MC and CP in the 3rd maxilliped). Evidence from methylene blue stained preparations in Homarus gammarus suggests that, although the CAP sensilla are innervated by the same nerve trunk as the chordotonal receptor, the two groups of cells are separate. This observation is supported by Clarac and Masson, (1969) who have shown that the MCO of Astacus leptodactylus is innervated by a separate group of cells from those of the CAP sensilla of the IM joint. Alexandrowicz, (1969), however, considers that the cells of the respective chordotonal organs terminate in the CAP sensilla and he has shown that the dendrites which terminate in the CAP canals have scolopidia.

From their structure, one would suspect the normal stimulus of the CAP sensilla to be movement of the peg and their location is such that the articular membrane of the joint will make contact when the joint is flexed except in the case of the I-M joint where only about half of the sensilla make contact with the membrane even at full reduction. Attempts to record the response of the sensilla to peg movement were inconclusive. The main difficulty is that the sensory nerve to the CAP sensilla and chordotonal organ innervates other sensilla

in the area (see Fig. 7). As it has been shown that some types of sensilla are very sensitive to water currents and other surface disturbances (Laverack, 1962) it is difficult to be certain that any activity observed had not arisen from sensilla other than the CAP sensilla.

5. The Cuticular Stress Detector (CSD) Organs

CSD.1 and CSD.2 are interesting for several reasons - they have a novel structure, they are located in a structurally complex region and they are in the proximity of the preformed breakage plane. They are both orientated perpendicularly to the chordotonal organs of the limb joints. They do not cross a limb joint nor are they attached to muscle or tendon and they are unique amongst crustacean connective chordotonal organs in their consistent association with discrete areas of thin cuticle (also see Horch, 1971). These receptors are clearly not part of the series of limb joint proprioceptors though the strand and cells of CSD.1 are similar to those of the other connective chordotonal organs in the limb. Although CSD.1 and 2 have common features they are essentially different and must be considered separately.

An important difference between CSD.1 and 2 is that CSD.2 lies distal to the fracture plane and will be lost in autotomy. Even in the more primitive Nephropsidae CSD.2 differs considerably from CSD.1 and the other chordotonal organs in the limb. CSD.2 in Astacus is divided into two distinct groups of cells, the dendrites of which run towards the receptor's attachment onto the thin cuticle whereas in CSD.1 the dendrites are directed away from the soft cuticle. The posterior insertion of

the two strands of CSD.2 in Astacus is divided into two distinct groups of cells, the dendrites of which run towards the receptor's attachment onto the thin cuticle whereas in CSD.1 the dendrites are directed away from the soft cuticle. The posterior insertion of the two strands of CSD.2 in Astacus is not to a distinct projection, but is spread over a wide area relative to the length of the strand. CSD.2 is not visibly connected to the breakage plane in the Nephropsidae although the receptor does lie close to the B-I joint through which the break occurs. In the other decapods examined CSD.2 lies some distance from the breakage plane and its only connection is via the distal "suture" which runs between the receptor and the breakage plane. CSD.2 is largest in the Nephropsidae and considerably smaller in the Brachyura.

The third group of cells described in Palinurus is quite separate from CSD.1. They innervate the membrane which occludes the limb after autotomy and are not associated with cuticle. This group of cells has not been observed so far in any of the other species examined but I cannot yet say conclusively whether or not they exist in other decapods. The presence of scolopidial structures was indicated close to the breakage plane in the cricket, Acheta domestica by Brousse-Gaury, (1958) but in this case the cells are located proximal to the breakage plane and are thus not homologous to the cells in Palinurus.

CSD.1 and 2 show a degree of specialisation not observed in the other decapod connective chordotonal organs in their association with areas of thin and soft

cuticle, which must be indicative of their function. The chordotonal organs of insects have been specialised in a variety of ways (Howse, 1968) but no organ similar to the CSDs has been described, the closest parallel being the insect tympanal organ which is developed to detect airborne sound waves.

5a. Determination of the Normal Stimulus

Previously undescribed sensory systems and receptors, such as the CSD organs, demand some indication as to the 'normal' form of stimulation. Chordotonal organs are mechanoreceptors (Bullock and Horridge, 1965) and the Cuticular Stress Detectors are connective chordotonal organs. They are not, however, in any way linked to joints in the leg and hence must differ in their properties from all previously described crustacean appendage proprioceptors. Most of the types of stimulation that have been utilised in this investigation were designed to mimic in some way the stresses and strains that would be encountered in the free walking animal.

Stimulation of the soft cuticle was chosen because it allowed a constant force of measurable duration to be applied. The receptors respond to pressure applied externally at the cuticular region where the strand inserts. Since these areas are situated on the anterior or ventral surface they are unlikely to make contact with hard surfaces in the environment and pressure applied directly to the soft cuticle is not to be considered to be a 'normal' stimulus.

The integrity and position of the limb in the

standing animal are maintained by the joint muscles and articulations. These will generate complex forces resulting in equally complex stresses in the cuticle of the basi-ischiopodite region. A study of the isolated preparation was necessary to allow the effects of the different forces to be observed, but this necessitated the development of some form of device to hold the portion of limb. Embedding the limb in modelling clay avoided the use of clamps or pins and produced no observable differences in the resting level of receptor activity but undoubtedly resulted in 'abnormal' stress during the application of some of the 'normal' forces. During passive movement of the B-I and I-M joints, for example, the method of attachment most probably contributed to the receptor response. The stresses generated by passive joint movements in vivo will be very different as there will normally be some tension in the muscles of these joints. I was unable to demonstrate the effect of tension in the musculature of the B-I and I-M joints upon the CSDs.

On examining the receptor response to tension in the tendons of the C-B muscles, I was only able to pull one muscle at a time. In the normal walking animal the position of the C-B joint is maintained by the moments produced by the depressor and levator muscles about the joint articulation. The combined pull of the antagonistic muscles tends to withdraw the basipodite into the coxopodite. As this is prevented by the two points of articulation the muscles will tend to bend the 'basipodite' about the hinge axis. It is thus likely that the receptors will respond even more readily in this situation

than I have demonstrated in my preparation where the resistance to movement is offered by friction between the basi-ischiopodite-meropodite and the modelling clay.

Although the modes of stimulation which I have applied are not identical to the forces experienced by the receptors in the walking animal they adequately demonstrate that the CSD organs respond to a number of parameters which are capable of stressing the cuticle. The receptors do also respond to joint movement but the response is much less than that observed in connective chordotonal joint receptors in the same animal. The response to joint movement is dependent on the degree of cuticular stress generated and not the position of the joint, although there is a degree of correlation between these two factors. Tension in the tendons of the C-B joint muscles produced a much stronger response. This is not surprising as the anterior levator muscle is capable of generating sufficient cuticular stress to initiate the fracture at the breakage plane. CSD.1 will respond after autotomy to touch of the wound membranes and to movement of the limb bud but a gross stimulus is required to produce a modest response. Thus there is no a priori reason to suppose that CSD.1 will serve a different function after autotomy and CSD.2 is lost during autotomy.

The soft or thin cuticle associated with the receptors most probably serves as a transducer by being buckled under the stresses present and producing a change in length of the strand. The degree of strand distortion will depend on the change of shape at the soft cuticle and this will depend on the nature of the stresses. The

CSDs are thus complex organs responding to cuticular stress like the simpler campaniform organs of insects (Pringle, 1938) or crustacea (Shelton and Laverack, 1968) and the lyriform organs of arachnids (Pringle, 1955).

5b. Classification of Unit Types

Wiersma, (1959) described the type of units in the connective chordotonal organs of the P-D, C-P and M-C joints. These he divided into four main categories, two populations of unidirectional movement fibres and two populations of position sensitive fibres. This general classification is useful but more recent investigations have shown the presence of intermediate unit types (Clarac, 1968b; Wiersma and Boettiger, 1959; Wyse and Maynard, 1965).

It is difficult to see exactly how the mechano-receptor units of the CSD organs fit into these categories, since there are problems in considering the effect any given mode of stimulation will have on the connective tissue strands. Application of a force to the external surface of CSD.1 soft cuticle will cause an inward deflection of the cuticle and thus should shorten the strand whilst a force perpendicular to the membrane in an autotomised limb will be perpendicular to the strand and stretch it. The latter statement was confirmed visually and the truth of the former is evidenced by the results shown in Figs. 24C-D and 32C. Figure 32C shows a unit which responds primarily to removal of the probe from the membrane showing the unit to be responsive during relaxation of the strand. Figure 24C-D shows the response of the same unit to distortion of the soft cuticle and the

unit clearly responds to application of the stimulus confirming that this causes relaxation of the strand.

As the application and removal of the probe is a rapid event the response of movement sensitive units will likewise be of short duration, providing that the cuticle is flexible enough to follow rapidly. The phasic bursts observed on application and removal of the stimulus in Figs. 24A, 26A, 27A, 32A, B and E are most probably from units responsive to changing stress (movement). I have also observed that the degree of activity in a unit depends on the force applied as is shown by Fig. 32A-B where a change in the point of stimulus application and hence an alteration in the degree of stretch produces a different level of activity in units (position sensitive). Thus CSD.1 appears to have the same range of unit types as have been described for the other connective chordotonal organs and this is probably also true of CSD.2.

The units are not specifically sensitive to a single mode of stimulus. This is illustrated by Fig. 29A-B where the same group of units can be seen to respond to joint movement and to soft cuticle stimulation and again in Fig. 32D-E where the same units respond to both limb bud movement and soft cuticle stimulation. Frequently the same units respond to different directions of joint movement (Fig. 30D) showing that the degree of stress and not the direction of movement is the important factor. The dynamic stress generated during joint movement will be greater than that generated in the static limb for any position within the normal range of movement. This is indicated by Figs. 29D and 32D where the unit

activity can be seen to decrease when the joint is maintained for a short period in the position of maximum flexion.

5c. The Autotomy Mechanism and the Association of the CSD Organs with the Breakage Plane

Wood and Wood, (1932) and Busson, (1935) describe the autotomy plane as being situated in the ischiopodite. The reasons for Busson's statement are not clear but the conclusion of Wood and Wood is based on erroneous observation. Wood and Wood, (1932) wrongly describe the breakage plane of Homarus americanus as being a complete ring located in the proximal ischiopodite and conclude that by homology the breakage plane in crabs must also be located in the ischiopodite. In this thesis I have shown that, as for Homarus gammarus (Paul, 1915), in Homarus americanus the break occurs in the ischiopodite dorsally but on the ventral side it occurs through the articular membrane of the B-I joint (Fig. 15). I have also shown that rudiments of the ventral articulation of the B-I joint are visible on the breakage plane in the two anomurans examined. Where fusion has occurred it is difficult to detect the remnants of the dorsal articulation which is less distinct than the ventral articulation in the walking legs of Homarus. Thus from a study of the adults it would seem more logical to conclude that the preformed breakage plane approximates to the position of the B-I joint. Perhaps a study of the developing larvae would show whether the portion of ischiopodite located between the B-I joint and the breakage plane in Homarus is lost or becomes incorporated into the "basipodite" in

those limbs where the B-I joint is absent.

The basi-ischiopodite shows a consistency of structure in the species which we have examined. The musculature of the C-B joint is particularly consistent even in the walking legs of Homarus and Carcinus which differ greatly in their ability to undergo autotomy. The walking legs of Homarus are considered to undergo autospasy rather than autotomy (see Wood and Wood, 1932 for definition). The musculature consists basically of a posterior levator which arises in the coxa, an anterior levator arising in the thorax and the antagonistic depressors, the main head of which arises from both the coxa and the thorax. The papers of Fredericq, (1883, 1891) and Wood and Wood, (1932) are concerned with identifying which one of those muscles is instrumental in the production of the cuticular break but it is apparent from the work of Demoor, (1891) and more recently Clarac and Wales, (1970) and McVean, (1970) that more than one muscle is involved. Breakage of the limb can only be produced if resistance is offered to the limb movement produced by contraction of the anterior levator muscle, yet Demoor, (1891) observed autotomy occurring in the crabs Pachygrapsus and Portunus which were lying on their backs with their walking legs extended. Wood and Wood explain this phenomenon as being due to the basi-ischiopodite making contact with the coxopodite but if this is true, as the anterior levator muscle traverses both the C-B and T-C joints the promotor muscle of the T-C joint must prevent movement of the coxa. It is therefore evident that in some cases at least a description of the mechanism

of autotomy must involve more than one muscle. It is possible that the depressor muscle may be capable of resisting movement about the C-B joint during the production of autotomy in some species.

Fredericq, (1883, 1891) demonstrated that the muscle responsible for the production of the cuticular break along the preformed breakage plane is the anterior levator. This fact was confirmed by Wood and Wood, (1932) who further demonstrated that, if the levator muscles of Carcinus maenas are functionally removed by sectioning the tendons at their insertion on the basi-ischiopodite, the loss of the anterior levator "was not noticed in the gait until the animal was fatigued". "Loss of the posterior levator muscleinterfered seriously with walking" but providing that the anterior levator tendon is intact, the animal retains normal powers of autotomy. Bush, (1965b) described the resistance reflexes mediated by the CB receptor in Carcinus and demonstrated that the depressor and the anterior levator muscles are involved in the control of posture. He did not demonstrate whether the posterior levator is also involved. Clarac and Wales, (1970) observed that the posterior levator muscle of Carcinus is active in free walking crabs. They further demonstrated that the posterior levator is reflexly activated by CSD.1 and thus may be implicated in autotomy. McVean, (1970) described the function of the levator muscles of Carcinus and confirmed that the anterior levator is functional both in control of posture and autotomy. The dual function of the anterior levator muscle is achieved by means of a preformed fracture plane at the insertion of the anterior levator tendon onto the basi-

ischiopodite (Break 1, Fig. 80). Whilst the plane remains unfractured the muscle can be utilised for posture and walking but once fracture has occurred autotomy is readily produced by contraction of the anterior levator muscle. McVean has further shown that it is the posterior levator muscle which initiates autotomy by fracturing the anterior levator tendon. The above evidence, as summarised in Table 5, clearly indicates that both levator muscles serve a dual function. McVean, (1970) demonstrated how this duality of function is attained in the anterior levator muscle of Carcinus but it remains to be described how it is achieved in the posterior levator muscle and in the anterior levator muscle of those species where the tendon does not have a preformed fracture plane.

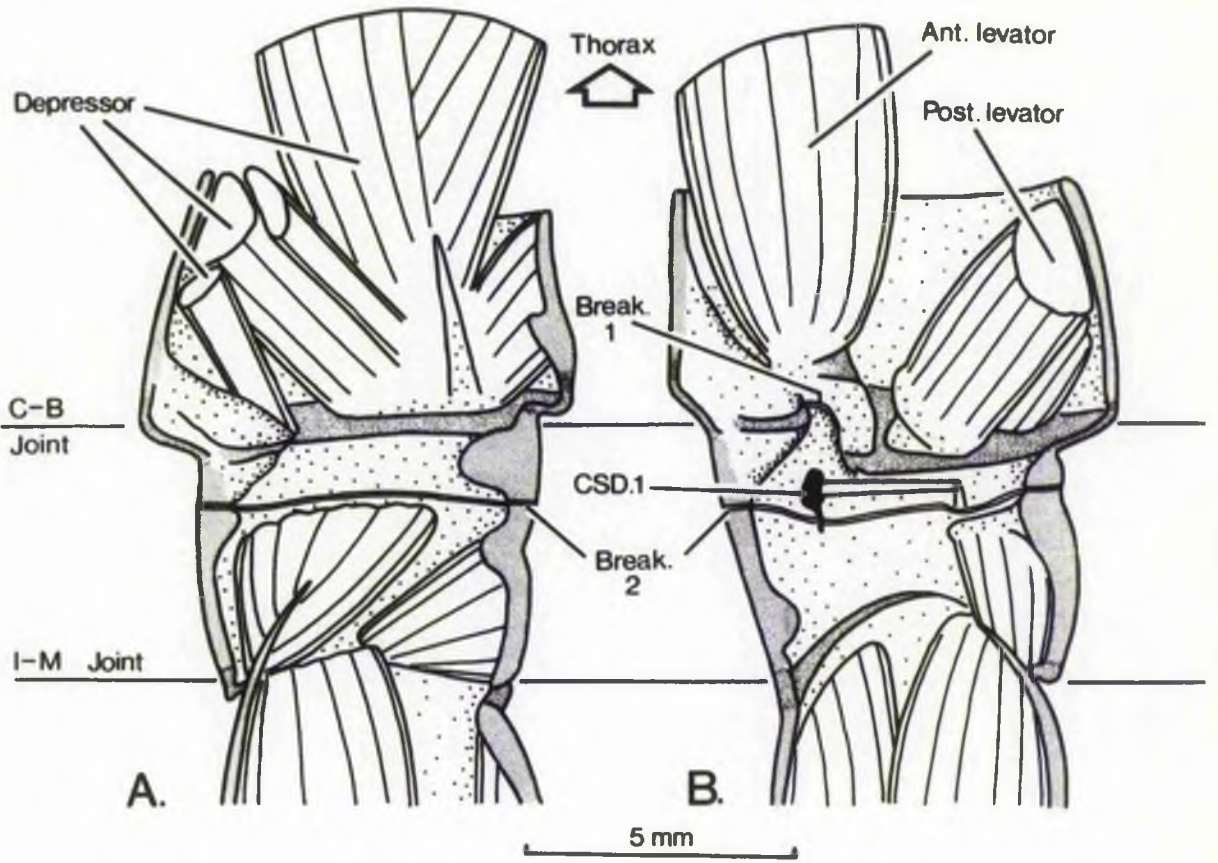
Throughout the species examined the basi-ischiopodite region has exhibited consistent features such as the asymmetrical insertion of the levator tendons, the occurrence of Paul's furrow and the position of the discrete area of soft cuticle associated with CSD.1 relative to the other structures. The mechanism of autotomy involving the furrow as proposed by Paul, (1915) for Carcinus is wrong for reasons set out by Wood and Wood, (1932) but the furrow is present in all the species I examined and it may have some function in the autotomy process. Some differences exist between the three sections of the reptantian decapods and it is very difficult to separate possible evolutionary trends from those differences due to the degree of calcification and thickness of the cuticle. The soft cuticle associated with CSD.1, for instance, is largest in area in the Scyllaridae, Galatheidae and

TABLE 5

MUSCLE	AUTOTOMY	POSTURE AND WALKING
Anterior levator	= Autotomiser muscle (Fredericq (1883, 1891) confirmed above + ablation experiments Wood and Wood (1932) confirmation of muscle involved in both functions (McVean, 1970)	resistance reflexes (Bush (1965b)
Posterior levator	initiates autotomy (McVean 1970) reflex control by CSD.1 (Clarac and Wales, 1970)	ablation experiment (Wood and Wood 1932) muscle activity recorded in the walking animal (Clarac and Wales, 1970)
Depressor	Not known, but may counteract turning moment produced by anterior levator.	resistance reflexes (Bush, 1965b)

Table 5. Summary of the evidence for dual function in the C-B joint musculature of Carcinus maenas.

FIG. 80. The pereopod of Carcinus maenas sectioned longitudinally in the anterior-posterior plane to show the position of the muscles, and other internally located structures, relative to the preformed breakage plane. A. shows the ventral and B. the dorsal portion of the limb. Anterior levator (Ant. levator), posterior levator (Post. levator), the proximal cuticular stress detector organ (CSD.1), breakage plane at the base of the anterior levator muscle tendon (Break. 1), preformed breakage plane (Break. 2).



Paguridae and smallest in the more heavily calcified Brachyura. The thin cuticle associated with the CSD.2 shows a much clearer trend, being largest in the Nephropsidae and decreasing in size through the Scyllaridae and Anomura to the Brachyura whereas the development of the distal "suture" is more dependent on the degree of calcification and is equally well developed in Palinurus, Galathea and Carcinus.

CSD.1 is apparently more important in autotomy as it is associated intimately with the preformed breakage plane and with the autotomiser muscle. Apart from any movement of the hypodermis or connective tissue which may occur, any changes in the strand can only result from cuticular movement in the intact limb. The posterior position of attachment of the strand which varies from a large rounded inflexible projection in Homarus to a distinct flexible peg in Carcinus is unlikely to affect the length of the strand. The anterior insertion, however, is to the discrete area of flexible cuticle which can be easily deformed. Wood and Wood, (1932) consider that this "membrane"-like area of cuticle allows deformation of the cuticle to occur at the breakage plane and hence initiates the break. It is now apparent that this cuticle is essentially part of an internally located receptor system but this does not necessarily invalidate their hypothesis. The soft cuticle, which lies between the breakage plane and the anterior levator muscle, will undoubtedly be subjected to stress during contraction of this muscle.

5d. Receptor Function

Mendelson, (1969) has shown that the remotor muscle

in the second antenna of Homarus americanus can follow frequencies of over 100/sec. and it is probable that many decapods use soundwave for communication. However, the cuticle associated with CSD.1 in some species and CSD.2 in all species examined does not appear flexible enough to respond to low amplitude propagated pressure waves. The areas of cuticle associated with CSD.1 in Palinurus and Galathea are possible exceptions.

Horch and Salmon, (1969) have shown that Ocypode responds to sound stimuli and contend that the organ for sound detection is located in the walking legs. Electrodes in the meropodite and the thorax were used to record whole leg nerve activity and in both cases the response to sound was similar suggesting that no specific hearing organ exists in the proximal pereopod. Horch, (1971) has demonstrated that the MCO of Ocypode is extremely sensitive to substrateborne vibrations and proposes that this is the organ of hearing, not only in Ocypode where the AFM proximal head inserts onto thin cuticle but also in the other decapods. However, although it has been known for some time that chordotonal organs are vibration sensitive (Burke, 1954) it has yet to be demonstrated that this vibrational sensitivity is of functional significance.

It is unlikely that CSD.1 and 2 monitor changes in hydrostatic pressure as the large areas of articular membrane present at all movable joints will allow the internal and external pressure to equalise at all but extreme changes in depth.

The C-B joint is unusual in having a complex musculature associated with dual function. The muscle

innervation of this joint is not well described but Bush, (1965b) has shown activity in 3 motor axons to the anterior levator and in 4, possibly 5, motor axons to the depressor muscle. He was not able to show the presence of an inhibitor in the motor nerve to either muscle. Bush assumes that the posterior and anterior levator are similarly innervated but Clarac and Wales, (1970) were not able to demonstrate the presence of more than 2 motor axons in acute preparations of Homarus gammarus or with chronically implanted electrodes in the crab Carcinus.

The situation is complicated by the presence of two separate proprioceptive systems which respond to different modes of stimuli. A proprioceptive reflex is initiated by the C-B joint chordotonal receptor (Bush, 1965b). The CB receptor responds only to movement of the C-B joint and has units responding to both movement and joint position (Bush, 1965a). This receptor initiates a resistance reflex, that is it activates one of the two antagonistic groups of muscles to counteract the movement stimulating the receptor and so restore the status quo. A second reflex involves CSD.1 (Clarac and Wales, 1970) but its function is not clearly understood. Stimulation of the soft cuticle of CSD.1 in many species produces a contraction of the posterior levator muscle which is visible through the articular membrane. In both Homarus and Carcinus recording from the posterior levator muscle or its motor nerve shows that a phasic burst occurs in the larger of the 2 motor axons and it continues for the duration of the stimulus. In the stationary crab the smaller and more tonic of the two units is normally active and if

CSD.1 is stimulated this activity is abolished but returns some time after the phasic unit stops firing. As shown in this thesis one of the most potent natural stimuli to CSD.1 is increased tension in the tendon of the anterior levator muscle. Thus strong contractions of the anterior levator will activate the synergistic posterior levator. Due to technical difficulties Clarac and Wales, (1970) were unable to demonstrate reflex control of the anterior levator or depressor muscles by either of the CSD organs. Work is in progress to determine the full extent of CSD control of the C-B joint muscles and preliminary results indicate that CSD.1 activity does excite some of the anterior levator motor neurones (Clarac, unpublished).

Figures 81 and 82 show the possible interactions between the two proprioceptive reflexes in the absence of central control. During levation (Fig. 81) contraction of the anterior levator muscle will increase the stress developed in the basi-ischiopodite and providing this is of sufficient magnitude the activity in CSD.1 will reflexly excite the larger phasic motor unit and inhibit the smaller tonic unit of the synergistic posterior levator muscle. The levation of the C-B joint produced by those two muscles will relax the strand of CB and thus produce reflex activity in all 4 or 5 motor axons (Bush, 1965b) to the antagonistic depressor muscle which will tend to return the limb to its rest position. This will result in an increase in tension at the insertion of the anterior levator tendon and thus reinforce the CSD.1-posterior levator muscle reflex. Thus the paradoxical situation may arise where the two proprioceptors are

FIG. 81. A diagram to illustrate the possible interactions between the reflexes initiated by the CB joint receptor and CSD.1 during active elevation of the limb. Excitatory pathways are shown by solid line, the thicker line indicating higher threshold, and inhibitory pathways are shown by broken line. Dotted lines indicate other probable connections. Posterior levator (Post. lev.), anterior levator (Ant. levator). See text for explanation.

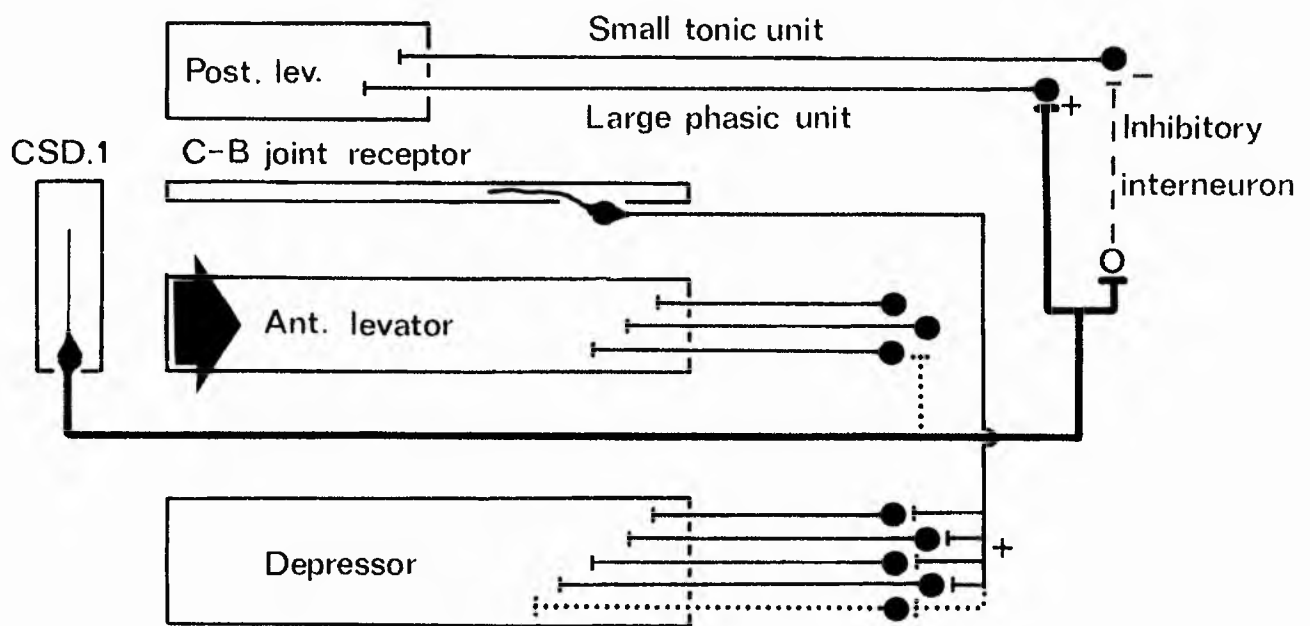
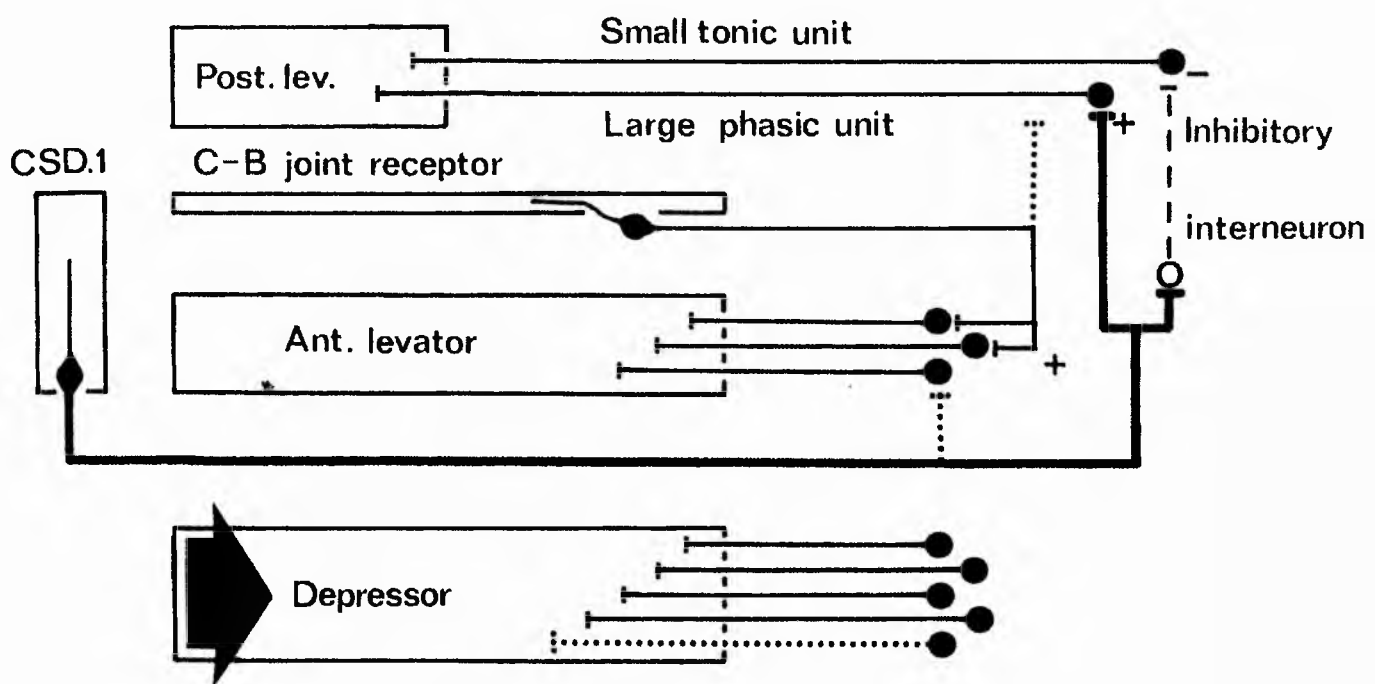


FIG. 82. A diagram to illustrate the possible interactions between the reflexes initiated by the CB joint receptor and CSD.1 during active depression of the limb.
Details as for Fig. 81.



promoting antagonistic reflexes.

During depression of the limb (Fig. 82) the CB receptor will be stretched and this will reflexly excite two of the motor axons to the anterior levator muscle (McVean, 1970) and possibly the posterior levator. Contraction of the anterior levator may then stimulate CSD.1 which, providing the activity reaches the threshold for the reflex, will excite the posterior levator muscle and possibly the anterior levator muscle to reinforce the resistance reflex.

The extent to which interaction between the two reflexes can occur is undetermined but depression of the CSD.1 soft cuticle is a relatively gross stimulus and the CSD.1-levator muscle reflex probably has a high threshold. Whitear, (1962) proposed that CB may be important in autotomy by monitoring the degree of elevation of the joint and thus preventing the levator muscles from contracting beyond the safe point and Wiersma and Bush, (1963) have confirmed the importance of the CB receptor by demonstrating the presence in the ventral nerve cord of interneurons which respond to passive levation and depression of the C-B joint. However, as stated by Bush, (1965a) "CB is not concerned solely with elevation of the limb, still less with elevated position only" but has movement and position fibres for both elevation and depression of the limb.

As shown above there is now considerable evidence of dual function in the posterior and anterior levator muscles but our knowledge of the innervation of these muscles is incomplete. McVean, (1970) confirms that the posterior levator muscle has only two motor axons

whereas the anterior levator has three and he postulates that the largest of the three axons is of primary importance in autotomy. It is not known if any of the motor axons is common to both levator muscles. McVean, (1970) has further shown that the posterior levator muscle initiates autotomy in the brachyuran, Carcinus maenas, by fracturing the tendon of the anterior levator muscle at its insertion onto the basi-ischiopodite, thus redirecting the force exerted by the muscle.

Therefore if Carcinus is held fast by a limb and attempts to elevate the limb, as it does when walking, then the contraction of the anterior levator will activate CSD.1 which in turn will excite the posterior levator. In the presence of an appropriate stimulus this could result in the initiation of autotomy and the release of the crab from its captor. However, the fracture plane on the anterior levator muscle tendon is not common to all reptantian decapods and it is not known how the levator muscles can serve their dual function in those sections other than the Brachyura. Nor is it understood how the posterior levator muscle serves its dual function in any of the reptantian decapods.

The CSD organs possibly control the occurrence of autotomy by monitoring the stress developed in the basi-ischiopodite and CSD.1 appears to be involved in the initiation of autotomy but autotomy is not a simple reflex. This is well demonstrated by certain sem-terrestrial crabs (e.g. Gecarcinus) which attach their chela to a predator and autotomise the limb to make good their escape (Robinson, Abele and Robinson, 1970) yet the chelae may be used for other functions without the limb

being autotomised. Thus autotomy is controlled centrally to a degree which may vary considerably between species and between individuals as the threshold of autotomy increases with age (Carlisle, 1957) and with the number of limbs which have been lost (Gomez, 1964).

CSD.2 is not anatomically connected with the breakage plane and hence may not be involved in the control of autotomy. The connective chordotonal organs at the limb joints of decapods supply information about joint movement and position but no receptors are known to monitor the tension generated by the muscles at these joints. There is, perhaps, little requirement for "force-measuring proprioceptors" (Pringle, 1961) except to monitor the load (i.e. that portion of the body weight) borne by each of the walking legs. Decapods walk on the distal extremities of their limbs (dactylopodite or propodite) but it is mainly the action of the proximally situated depressor muscles upon the basi-ischiopodite which raises the animal's body above the substratum. Thus the stress developed in the basi-ischiopodite during walking will bear some relation to the load borne by that limb. The input from CSD.2, and possibly CSD.1, may enable the animal to distribute the total load evenly between those limbs in contact with the surface.

The crustacean campaniform organs of the epicuticular caps (Shelton and Laverack, 1968) will also give some measurement of limb loading but their response will depend upon the nature of the substratum whereas the response of the more proximally located CSDs will not.

The function of the CSDs in the 3rd maxilliped is more difficult to postulate as these appendages cannot

autotomise and do not share a common load with a number of other appendages. However, they may monitor the tension developed during contraction of the powerful depressor muscles.

6. The Evolution of the Crustacean Connective
Chordotonal Organs

It has been shown that the primary sense cells of the insect chordotonal organ (Schon, 1911) and the insect campaniform sensilla (Wigglesworth, 1953) are derived from the hypodermal layer. This and other similarities between these two types of proprioceptor led Pringle, (1961) to propose that they may have a common origin. He further suggests that "the ultimate stimulus to any mechanical sense organ is the straining of its terminal process or processes, and the specialisation of the proprioceptors in arthropods can be thought to have occurred by the progressive restrictions of the conditions producing this strain". This implies that the ancestral sensilla from which the connective chordotonal organs have been derived were sensitive to cuticular stress.

The CAP sensilla receive the terminal processes of the scolopidia associated with the dendritic processes of some of the chordotonal organ neurons (Alexandrowicz, 1969). Alexandrowicz has also shown that the CAPs are lost at the I-M joint of the anomuran pereiopod and at all joints of the brachyuran pereiopod. He contends that this loss of the CAP sensilla must be correlated with the withdrawal of the chordotonal sensilla from the cuticle. Thus it would appear that the CAP may represent the ancestral sensilla or their rudiments. The existence of a peg,

or short hair indicates that the CAP are, or have been, mechanoreceptive hairs rather than simple strain sensitive sensilla.

A second point of interest is that the CSDs have retained the "ancestral" function by responding to general cuticular stress and yet they are connective chordotonal organs. This seems to indicate that evolutionary pressures, other than restriction of the conditions producing strain, have influenced the development of crustacean chordotonal organs. However, the dendritic processes of CSD.1 are directed towards the peg, not the soft cuticle and this may indicate that this receptor is monitoring stress at a location other than the site of the ancestral sensilla. If we accept Pringle's hypothesis then we must assume the association of the CSDs with discrete areas of soft cuticle to be a secondary development resulting in a change of function of the sense organ.

7. Proprioception in the Nephropsidean Mandible

The mandible is considered to have evolved from the same type of ancestral appendage as the pereopod and 3rd maxilliped, and the main body of the mandible may represent an enlarged coxopodite which has become specialised for biting and crushing (see Experimental 3.1.). If the T-C joint of the pereopod corresponds to the mandibular articulation as this evidence suggests, one would hope to find similarities in the musculature and proprioceptors of both joints. According to Snodgrass, (1952) the T-C joint of the primitive crustacean limb probably had four functional groups of muscles. In

Experimental 3.3.2. the mandibular muscles have been grouped according to Snodgrass, the ventral group having been derived by fusion of two functionally antagonistic groups during the evolution of this limb. It is of interest that the ventral group includes the block of anterior adductor muscles, M 1-5 and the antagonistic abductor muscle M7. It is not known whether the presence of antagonistic muscles in this group is a primitive feature or a more recent development. Certainly, if Snodgrass is justified in including muscles M6 and M8 in the same group then the antagonism of these muscles cannot be considered primitive. As shown in Table 3 (Experimental 3.4.) the ventral group of muscles is innervated by the same nerve trunk, inner mandibular nerve in Astacus fluviatilis and Cambarus affinis whereas muscle M7 and part of muscle M1 in Homarus gammarus are innervated by a branch of the outer mandibular nerve. In all three species muscles M6 and M8 are innervated by branches of the outer mandibular nerve though the pattern of innervation varies considerably. The evidence for the Snodgrass theory of mandibular muscle evolution remains inconclusive but a study of mandibular ontogeny may help to verify or repudiate it.

The known proprioceptive systems of the mandible are not based on the connective chordotonal organ but on multiterminal sense organs of central origin (Pringle, 1961). The pereopod T-C joint has a chordotonal organ in the nephropsidae only and in all decapods examined so far a muscle receptor organ and a system of innervated elastic strands have been found (Alexandrowicz and Whitear, 1957; Alexandrowicz, 1958).

The topography and morphology of the muscle receptor organs (MRO) described at the pereopod T-C joint (Alexandrowicz and Whitear, 1957) and the Mand. MRO suggests that they are not analogous. The T-C MRO receptor muscle (RM) lies anterior to the T-C joint articulation, is innervated by three dendrites at its proximal attachment onto the thorax and the receptor is stretched by posteriorward movement of the coxa. The Mand. MRO RM lies posterior to the hinge line, is innervated by 10-20 sensory cells at its distal attachment to the mandible and is stretched by anteriorward movement of the mandible. The T-C MRO is novel in that it decrementally conducts the receptor potential direct to the CNS. The adoption of this mode of conduction has no doubt been accompanied by morphological specialisation and one may not exclude the possibility that the differences observed are specialisations which mask the common ancestry of the two MROs. Further comparison of MROs is made below (Discussion 7b).

The elastic strand organs designated mouth-part receptors (MPR) by Dando and Laverack, (1968) are not specifically concerned with mandibular proprioception but respond to movement of those structures associated with the mouth, the labrum, paragnatha, mandibles and oesophagus. Moulins, Dando and Laverack, (1970) conclude that this proprioceptive system monitors the movements associated with the act of ingestion of food. Although all three MPRs clearly respond to mandibular movements (Laverack and Dando, 1968) ingestion necessarily requires co-ordinated movements of mandibles, labrum, paragnatha and oesophagus and it has yet to be demonstrated that the CNS can

discriminate between the movement of one part or another from the MPR input alone. However, the responses of the three cell groups do alter with the movement imposed (Moulins, Dando and Laverack, 1971). The MPRs are clearly not specifically associated with the mandibular articulation and thus are not homologous with the innervated elastic strands of the pereopod T-C joint.

The proprioceptive cells associated with the PSN are not organised into a distinct organ but their input to the CNS is clearly modulated by mandibular movement. This is obviously an important sensory input in determining the angle of opening of the mandible whereas the Mand. MRO, as discussed below, is most probably part of an error detecting servo-mechanism. The cells of the PSN in some cases are tripolar or bipolar with dichotomously branching dendrites and it is not known how widespread the endings of a single cell are. In some cases one process passes into the hypodermis near the lateral articulation of the mandible whilst a second process passes peripherally in the PSN and may innervate areas more than 1cm apart. The cells of the PSN are similar to those described in the first and second roots of the abdominal ganglia (Pabst and Kennedy, 1967). It is probable that other similar cells observed on the epistomal hypodermis will also respond to mandibular movement to some degree.

The curious group of cells in the omn 2/3/4 connective was included in this review of mandibular proprioceptors as they may well prove to be sensory. However, very little is known of these recently discovered cells and it is not even certain which of their processes

are axonal and which dendritic. These cells will be examined further at a later date.

The most interesting aspect of mandibular proprioception is undoubtedly the structure and function of the Mand. MRO.

7a. Muscle Receptor Organs of the Decapod Crustacea

Muscle receptor organs (MRO) are defined by Bullock and Horridge, (1965) as being:-

"Special receptors in arthropods, cephalopods and vertebrates, having a multipolar peripheral sensory cell with dendrites closely applied to a special muscle fibre".

This definition is inadequate for a number of reasons.

1. It excludes the functionally analagous myochordotonal organs of the pereopods which are innervated by unidendritic bipolar cells (Clarac, 1968a).
2. It excludes the T-C MRO where the somata of the sensory cells are located in the thoracic ganglia. (Alexandrowicz and Whitear, 1957).
3. It takes no account of the thoracic and abdominal MROs of Homarus where the dendrites of the sensory cells are associated with an intercalating tendon and not with the muscle fibres (Alexandrowicz, 1951, 1952, 1967b).
4. The receptor muscles of decapods are generally composed of a number of muscle fibres (Alexandrowicz, 1967b; Whitear, 1965; Fahrenbach, 1967 and this thesis). This is also true of the vertebrate muscle spindle (Matthews, 1964).

Because of the high degree of morphological variation in the decapod MROs it is advantageous to use a functional

classification and for the purposes of this thesis a muscle receptor organ is defined as:-

"A proprioceptive organ consisting of a special muscle which is ineffective in producing positional changes of the body segments that it spans but upon contraction is capable of producing changes in the level of activity of the sensory neurones associated with it".

This definition necessarily excludes those chordotonal organs associated with walking leg muscles (IM1, MC1 and CP1) as the functional significance of their association is not known.

The MROs of the decapod crustaceans can be divided into two groups, those innervated by unidendritic bipolar cells and those innervated by multiterminal neurones. In the former class there is only one known example, the myochordotonal organ (MCO) (Clarac, 1968a). The thoracic and abdominal MROs (Abd. MRO) (Alexandrowicz, 1951, 1952), the thoracic-coxal MRO (T-C MRO) (Alexandrowicz and Whitear, 1957) and the Mand. MRO (this thesis) all fall into the second category. These two categories correspond to Pringle's (1961) type I and type II proprioceptors respectively.

It is of interest to compare the three multiterminal MROs as they are functionally analogous but morphologically diverse.

7b. A Comparison of the Multiterminal Muscle Receptor Organs of Decapods

Of the MROs described to date, the Mand. MRO is innervated by the largest number of sensory neurones.

The Abd. MROs generally have but a single cell associated with each of the receptor muscles. Where the articulation between thoracic segments has been lost some regression of the receptors may occur leading to the association of more than one sensory cell with the receptor muscle. This is evidenced by the median thoracic MRO of Leander serratus which is innervated by 4 cells. These neurones are believed to be derived from the 5th to 8th segments (Alexandrowicz, 1956). The number of sensory cells innervating the T-C MRO appears to be two as only the S and T fibres have been demonstrated to respond to muscle stretch, (Ripley, Bush and Roberts, 1968). It is possible, however, that some of the smaller fibres may also be afferent (Alexandrowicz, 1967a).

The sensory neurones of the Abd. MROs are generally multipolar and the dendritic branches undergo a high degree of branching. The somata are closely applied to the receptor muscles and the dendrites are short. With the Mand. MRO the somata generally lie more than 100 μ from the muscle base. The neurones are frequently bipolar and produce a small number of dendritic branches which are several times longer than those of the Abd. MRO. The somata of the T-C MRO sensory neurones are unknown as dye injections of the afferent S and T fibres have so far failed to reveal the cell somata (Bush, unpublished). The dendrites of the S and T neurones are several millimetres long and branching is restricted to their distal extremities.

The receptor muscles (RM) of each of the three types of multiterminal MRO contain homogenous populations of muscle fibres. Alexandrowicz, (1951) does not give

finite measurements of sarcomere length but states that "for every 10 sarcomeres of the dorsal muscles there are approximately 14 of the muscle RM1 and 23 of RM2". The dorsal muscles referred to are the superficial extensor muscles and if we assume they have an average sarcomere length of 10μ like the superficial flexor muscles (Kennedy and Takeda, 1965) this gives a measurement of 7μ for RM1 and 4.5μ for RM2. The RM of the T-C MRO has a sarcomere length similar to RM1 (Alexandrowicz and Whitear, 1957) as has the Mand. MRO (Fig. 56). This would suggest that these muscles may have similar physiological properties to RM1 but, whereas the myofibril bundles of the T-C MRO RM and Abd. MRO RM1 are closely packed, sections of the Mand. MRO through the ventral regions exhibit the distinctly punctate distribution of myofibril bundles associated with fast muscles (Fahrenbach, 1967). The sarcomere length is not always a reliable guide to muscle properties as those of the Mand. MRO measure 6.5μ approximately and this is intermediate in the range of $2-3\mu$ for fast muscles and $10-12\mu$ for slow muscles measured in the crustacean MCO (Cohen, 1963a). Jahromi and Atwood, (1969) found that the "tonic" superficial extensor muscles of the lobster abdomen have fibres with sarcomeres as short as 6μ but some of the fibres in this muscle showed electrically excitable membrane responses.

The muscle fibres of the Abd. MROs do not always travel the length of the muscle. In Homarus (Alexandrowicz, 1951) the RM is virtually divided by an intercalated tendon. Some muscle fibres terminate on the muscle sheath short of the muscle extremities. In Astacus (Florey and Florey, 1955) and Cambarus (Bodian

and Bergman, 1962) the tendon is not intercalating and the majority of muscle fibres are continuous throughout this connective tissue region. The latter situation is more akin to that observed in the Mand. MRO of Homarus where the myofibrils are connected to the tonofibrils and no interposing block of connective tissue is present. These differences observed in the Abd. MRO may bear some functional significance as the muscle fibres interrupted by the intercalating tendons will obviously stretch the tendon when they contract whereas those fibres which span the tendon will tend to oppose this. Although the adequate stimulus for the Abd. MROs in both Homarus (Eyzaguirre and Kuffler, 1955) and Astacus (Krnjevic and van Gelder, 1961) is muscle stretch, the deformations undergone by the dendritic endings in these two situations may well be of a different nature.

Studies of the fine structure of the Abd. MRO (Bodian and Bergman, 1962; Nadol and Darin de Lorenzo, 1969) show that in Homarus and Procambarus the dendritic terminations are largely onto connective tissue but also to some degree onto the sarcolemma of the muscle fibres. The dendritic endings of the T-C MRO are not directly associated with the muscle fibres (Whitewar, 1965). The fine dendritic branches of the T fibre pervade the connective tissue strands of the RM proximal attachment and the S fibre branches permeate the flanking strands of connective tissue which run parallel to the T-C MRO RM. The fine structure of the Mand. MRO has not yet been studied.

Both the T-C MRO (Alexandrowicz, 1958; Whitewar, 1965) and the Abd. MRO (Alexandrowicz, 1967b) are

innervated by accessory fibres. One of these fibres in the Abd. MRO is inhibitory (Kuffler, 1954) but the function of the T-C MRO accessory innervation is completely unknown. The Mand. MRO likewise appears to be innervated by a number of small fibres of unknown function some of which may prove to be inhibitory.

7c. Afferent Unit Activity in Muscle Receptor Organs

Comparisons between the afferent activity of different muscle receptor organs must be made with some reservation as the unit response will depend not only upon the characteristics of that neurone but also upon the physical properties of the tissues through which the deforming force is presented to its dendrites. With the Mand. MRO it was not possible to record the receptor response whilst stimulating the motor nerve to the receptor muscle as both afferent and efferent fibres lie in the same bundle. Attempts to split nerve inn 4 and so permit simultaneous stimulation and recording were without success and tension was produced in most experiments by muscle stretch, either directly or by means of micromanipulator forceps or indirectly by mandible movement. Muscle stretch as a stimulus allows observation of the receptor response to passive movements but in the active muscle increased tension will more normally occur during attempted muscle shortening or isometric contractions.

The effect of stretch upon muscle is not purely mechanical. As summarised by Florey, (1966) externally applied muscle tension affects "(1) the muscle fibre membrane, (2) the elastic components of the muscle, (3)

the contractile elements and (4) the nerve endings." Muscle stretch decreases the membrane potential and in some cases produces an active response.

The mechanical properties of muscle are complex (see Roberts, 1967). Muscle and connective tissue have elastic and viscous elements. They are compliant over their natural range of stretch but because of viscous damping both connective tissue and inert muscle tend to regain their resting state slowly when released. Muscle will of course more readily take up slack on receipt of efferent activity. The stiffness of an inert muscle increases with stretch (Hill, 1953) and thus tension change will not be proportional to change in length but will depend upon the range of stretch administered. It is extremely difficult with different preparations to ensure that the tension range and rate of change are comparable.

The relationship between tension and stretch is shown for the Abd. MRO of Astacus by Krnjevic and van Gelder, (1961) and for the isolated frog muscle spindle by Husmark and Ottoson, (1970, 1971). Krnjevic and van Gelder (1961) found the stretch - tension relationship at a series of muscle lengths to be non linear and that the tension developed for a given stretch in different preparations varied by a factor of up to 30. The latter fact is no doubt related to the difficulty of determining the resting length of the muscles. They did not examine the tension change during constant velocity stretch but from the results of Husmark and Ottoson, (1970) it is apparent that the stretch - tension relationship would be similar, that the increase in curve slope would occur

more rapidly and that the tension developed at any point will be greater than if the muscle were maintained at that degree of stretch. During constant velocity stretch, tension rises to a peak which decays rapidly on cessation of movement to reach a level appropriate to the final degree of stretch. The height of this dynamic phase increases with the amplitude of stretch (Krnjevic and van Gelder, 1961; Husmark and Ottoson, 1970) and with the rate of stretch Husmark and Ottoson, 1970. The rate of tension decay following the dynamic phase increases with stretch amplitude and the magnitude of tension change is dependent upon the difference in amplitude between the dynamic and static tensions (Husmark and Ottoson, 1971).

Stretch of an MRO alters two parameters, length and tension, and the relative importance of these to the crustacean MROs is incompletely known. The myochordotonal organ of the brachyuran walking leg has two groups of sensory cells, MCO1 and MCO2 (Clarac, 1968a). The neurones of MCO1 terminate in connective tissue at the insertion of the accessory flexor muscle proximal head. This group of cells apparently responds to receptor muscle tension (Clarac, 1968b; 1970; Hwang, 1961). The neurones of MCO2 are inserted in a connective tissue strip like the connective chordotonal organs and are attached to the connective tissue sheath of the accessory flexor muscle by an elastic strand (Cohen, 1965). The strand of MCO2 is stretched when the accessory flexor muscle lengthens (Clarac, 1968b; Cohen, 1963b) and thus the adequate stimulus is change in receptor muscle length. The brachyuran MCO is therefore potentially capable of

monitoring isometric and isotonic contractions of the accessory flexor muscle.

The sophistication of being able to monitor both muscle length and tension apparently also occurs in the T-C MRO. This receptor has only two known sensory fibres but like the vertebrate muscle spindle (Matthews, 1964) the endings of these fibres show different specialisation. As indicated by Alexandrowicz, (1958) the S fibre innervates strands which flank the muscle whereas the T fibre innervates the connective tissue of the receptor muscle insertion. Thus the former may monitor muscle length and the latter muscle tension. This is supported to some degree by Ripley, Bush and Roberts, (1968) who suggest that the T fibre may have a higher threshold to muscle stretch.

The sensitivity of the Abd. MRO and Mand. MRO to the two facets of muscle stretch is more difficult to ascertain from morphological features. As stated above (Discussion, 7a) the Abd. MRO in Homarus has an intercalated tendon whereas in Astacus and Cambarus a much larger number of muscle fibres is present in the region of sensory endings. The situation is further confused by the dendrites ending on both connective tissue and muscle fibre sarcolemma. It has been demonstrated electrophysiologically that the Abd. MRO increases its activity with both muscle stretch (Wiersma, Furshpan and Florey, 1953) and receptor muscle contraction (Kuffler, 1954) indicating that it effectively responds to muscle tension. Furthermore it has been shown there is little apparent difference in the receptor responses from Homarus and Procambarus (Kuffler, 1954) which suggests that the observed morphological differences have no gross functional significance. It is probable

that the Mand. MRO will also prove to be sensitive to tension rather than muscle length.

A comparative study of unit activity is thus rendered difficult by lack of knowledge as to the precise mechanical properties of each type of MRO. The T-C MRO further hinders comparison as the graded receptor potential is decrementally conducted to the CNS in large diameter dendrites of high length constant and not encoded into propagated action potentials (Ripley, Bush and Roberts, 1968). Because of these difficulties one may not categorise the units of multiterminal MROs as has been attempted with the connective chordotonal organ (Wiersma, 1959) and the myochordotonal organ (Cohen, 1963b) but it is profitable to examine the response of MRO units to the component parts of the mechanical stimulus.

The MRO of the larval lepidopteran Antheraea pernyi responds to the onset of receptor muscle stretch with a burst of spikes which adapts rapidly to a level appropriate to the rate of stretch. Weevers, (1966) has shown that this is in fact an "acceleration response" which is produced on rapid increase of stretch velocity. A similar but much less marked response has been observed from the muscle spindle (Jansen and Matthews, 1962) but it occurs only at the onset of movement. No "acceleration" response has been described for the T-C or Abd. MRO and, as shown in Figs. 70 and 71 the Mand. MRO is no exception to this rule.

All MROs exhibit a "velocity" response, that is the impulse frequency generated during constant velocity stretch is greater than that in the static muscle for any degree of stretch. Husmark and Ottoson, (1970) have

shown that the receptor potential of the isolated muscle spindle is similar in form to the dynamic peak of tension which occurs during constant velocity stretch. This peak of tension may be accounted for by relative differences in the visco-elastic properties of the intrafusal fibre contractile region and region of sensory innervation (Matthews, 1964). Thus it may be concluded that the "velocity" response is largely of mechanical origin. Ripley, Bush and Roberts, (1968) give few data as to the qualitative differences between S and T fibre responses in the T-C MRO but comparison of Figs. 2B and 2D of their publication suggests that the T fibre has a much greater velocity sensitivity than the S fibre. This is in accord with the mechanism proposed by Matthews, (1964) as the T fibre innervates the elastic tendon of the relatively viscous receptor muscle whereas the S fibre lies parallel to the muscle bundle and is continuous with the connective tissue muscle sheath. The sensory neurones of the Mand. MRO generally show a distinct response to rapid stretch but vary considerably in their sensitivity.

On cessation of movement MRO units adapt to a level of activity appropriate to the degree of stretch attained. This early adaptation is also largely a mechanical phenomenon in the muscle spindle (Husmark and Ottoson, 1971). Krnjevic and van Gelder, (1961) came to the same conclusion for the Abd. MRO. However, Wendler and Burkardt, (1961) contend that a portion of the adaptation must be attributed to the receptor neurone. The sudden drop in frequency observed on cessation of high velocity stretch in many MROs (Shepherd and Ottoson, 1965; Weevers, 1966, and Fig. 70 this thesis) may be a neuronal phenomenon for as shown by Weevers, (1966) a similar

"silent period" occurs following high frequency antidromic invasion of the lepidopteran MRO sensory neurone. However, Shepherd and Ottoson, (1965) have shown that for the muscle spindle the silent period occurs over a restricted range of stretch intensity.

The activity of the Mand. MRO, like other muscle receptor organs, increases with the degree of maintained stretch (Finlayson and Lowenstein, 1958; Ripley, Bush and Roberts, 1968; Wiersma, Furshpan and Florey, 1953). As mentioned above the most striking difference between the Mand. MRO and the other MROs is the large number of sensory units. These units vary widely in their sensitivity to stretch, their frequency range and rate of adaptation. The units of MROs are generally tonic, though some such as the Fast Abd. MRO2 have a high threshold to stretch. The Abd. MRO2 is the most rapidly adapting unit so far described as it seldom fires for more than one minute even when the abdomen is fully flexed (Wiersma, Furshpan and Florey, 1953). The S & T fibres of the T-C MRO show very little adaptation to maintained stretch but their response to long duration stretch is undescribed. The Mand. MRO is more difficult to analyse because of the large number of units but none of the units isolated so far have been rapidly adapting though many fibres fire only at extreme degrees of stretch.

Weevers, (1966) found the adapted activity of the Lepidopteran MRO to be very nearly linearly related to receptor muscle (RM) length. However, as the receptor frequency clearly increases on RM contraction this can not be considered to indicate that the MRO is monitoring RM length rather than tension. Krnjevic and van Gelder,

(1961) have shown that the impulse frequency of both the slow and the fast Abd. MROs bear a linear relationship to maintained tension but not to RM length. The relationship of the Mand. MRO units to RM tension is undetermined, but consideration of the receptor's structure indicates that it may be similar to the Abd. MRO.

Analysis of the Mand. MRO has revealed the presence of unusual units which generally fall into two categories, 1) unidirectional units and 2) units exhibiting a decline in frequency at higher intensity stretch. The latter units may well have been caused by "overstretch" as neither the tension generated during stretch nor the normal range of tension produced by the RM are known. The phenomenon of "overstretch" has been described for the muscle spindle (Shepherd and Ottoson, 1965) the lepidopteran MRO (Finlayson and Lowenstein, 1958) and the Abd. MRO (Kuffler, 1954). However, "overstretch" can only be conclusively identified by intracellular recording from the neurone where, as shown by Kuffler, (1954), the receptor potential increases though propagated impulses are absent. The other types of units are not explained by any previously described phenomenon and may indicate true specificity of an MRO neurone.

7d. Muscle Receptor Organ Function

Both the crustacean MROs and the vertebrate muscle spindles have been the subject of extensive investigation. Although the amount of work published on the muscle spindles far outweighs that on crustacean MROs, it is the latter which have lent themselves more favourably to

functional analysis.

A MRO, by definition (see Discussion, 7a), is a proprioceptor which possesses a muscle capable of producing changes in the activity of the sensory neurones. These mechanoreceptive cells therefore supply information regarding the state of the receptor muscle (RM) and an understanding of RM function is an essential basis to any hypothesis of MRO function. Two possible functions have been proposed for the RM; 1) to maintain afferent flow in spite of peripheral changes (Hunt and Perl, 1960; Cohen, 1965) and 2) to form the basis of a follow up length servo-mechanism by which any centrally set muscle length or tension may be reflexly maintained (Fields, 1966; Matthews, 1964).

The primary afferents of the muscle spindle are active in a closed loop follow up length servo system, monosynaptically exciting synergistic muscle fibres and inhibiting antagonist muscle fibres when stretched. The relative merits of current theories on muscle spindle function are discussed by Matthews, (1964) in his review of the muscle spindle and it is clear that the complexities of this MRO and its central control in mammals renders its function open to some conjecture. The function of the secondary afferents is even more difficult to understand as they paradoxically excite flexor motoneurones even when located in extensor muscles (see Matthews, 1964).

The Abd. MRO has proven to be much more suited to electrophysiological investigation and the function of the tonic MRO1 has been well described. The Abd. MRO1 acts as an error detector which responds to differences between

a centrally determined set point and the abdominal position (Fields, 1966). Such a system will allow the animal to produce an amount of muscle shortening which is relatively independent of external loading and only slightly affected by loss of muscle power (Barlow, 1961). The afferent input from Abd. MRO1 activates a single motoneurone which extensively innervates the synergistic slow extensor muscles but not the RM (Fields, 1966). It also activates the accessory fibre, which pervades the dendritic processes of the sensory neurone, and produces self-inhibition of afferent activity (Eckert, 1961). The pattern of efferent innervation of the slow extensors and Abd. MRO1 was investigated by Fields, Evoy and Kennedy, (1967) who describe some of the central pathways activating these efferent fibres. They have demonstrated the presence of command interneurons which may separately drive (1) the common motoneurone to the RM and slow extensors and (2) motoneurons to the extensors unshared by the RM (3) the accessory inhibitory nerve to the MRO soma and dendrites. The CNS may thus control the animal's posture via (1), make temporary changes without adjusting the postural reference point via (2) or temporarily remove the length servo control via (3). As the RM shares motoneurone innervation with the extensors it can not be considered to lead activity of the functional muscles as has been proposed for the muscle spindle (Matthews, 1964).

Cohen, (1964) forwarded the hypothesis that the MCO was redundant as a peripheral sense organ and served only to maintain the level of central excitability via the reflex loop. However, Evoy and Cohen, (1969) have since shown that the MCO, like the Abd. MRO1, is involved

in the control of posture but with the important difference that it reflexly activates its own RM.

The T-C MRO initiates resistance reflexes (Ripley, Bush and Roberts, 1968) but the function of the RM is not known.

The Mand. MRO differs from the other crustacean MROs in that it is not involved in posture control as movement of the mandible affects mandible position only. The mandible is moved by a large number of muscles, probably activated by a variety of command interneurons which activate the motoneurons to different degrees as has been shown for other crustacean neuromuscular systems (Evoy and Kennedy, 1967; Fields, Evoy and Kennedy, 1967; Kennedy, Evoy, Dane and Hanawalt, 1967). The tension developed by the mandibular muscles will vary with the degree of efferent activity in the motoneurons innervating the mandibular muscles and with the resistance to mandibular movement offered by the food particles. The mandibles are powerful appendages and the momentum developed in biting may be high even though the angular velocity is low. The Mand. MRO is most probably involved in maintaining the level of tension constant and controlling the rate of change of muscle tension.

CONCLUSIONS

This comparative study has shown major differences in the number and form of proprioceptive organs in the three appendages studied.

The proprioceptive systems of the 3rd maxilliped and pereopod are largely based on the connective chordotonal organ. In their location relative to the

joint muscles, articulations, and where appropriate, CAP sensilla, the CB, CSD, MC and CP organs of the 3rd maxilliped correspond to the CB, CSD, MC2 and CP2 organs of the pereopod. This suggests that at least some of the chordotonal organs in these two limbs are homologous. The number of connective chordotonal organs in the pereopod is greater than in the 3rd maxilliped and it may be significant that the majority of these additional proprioceptors are associated with muscles.

The form of the connective chordotonal organ strand is dependent to some degree on the nature of the joint at which the receptor is located. Those proprioceptors traversing a limb joint which has a less rigid articulation (CP and MC of the 3rd maxilliped) or can move in more than one plane (CP 3rd maxilliped and CP2 of the pereopod) have a more diffuse strand.

The response of CP and MC of the 3rd maxilliped does not lend weight to the hypothesis that they are homologous to CP2 and MC2 of the walking leg as they exhibit marked differences in their sensitivity to the different directions of movement. Pringle's (1961) hypothesis that the evolutionary pressure causing the development of internally located proprioceptors was the need to restrict the strain applied to stress sensitive sensilla appears to be an over-simplification. Alexandrowicz, (1969) has indicated that the CAP sensilla most probably represent the sensilla or the rudiments of the sensilla from which the connective chordotonal organs have been derived. One must thus consider the possibility that the connective chordotonal organs evolved concurrently in the two limbs, which had already become specialised in function, from corresponding

groups of externally stimulated proprioceptors as well as the possibility that the two appendage types were derived from a common type of limb with a fixed pattern of connective chordotonal organs. In the lack of sufficient evidence to support either of these hypotheses one must be cautious when making comparison of the receptors at corresponding joints in the 3rd maxilliped and pereopod.

The proprioceptors so far described in the mandible are apparently not homologous with those described at the T-C joint of the pereopod. The mandibular proprioceptors are not based on the bipolar sensory neurone of the chordotonal but on the multiterminal neurone of possible central origin (Pringle, 1961). It is a reasonable assumption that Mand. MRO is not primarily involved in the control of "mandibular posture" and as such is not functionally analagous to the other crustacean MROs. It is postulated that it is involved in the maintenance of constant tension and the regulation of changes in tension to allow these powerful appendages to be manipulated with minimal risk of fracturing the animal's endoskeleton.

The CSDs, though basically similar to the connective chordotonal organs in most features, are essentially a new class of receptor. The anatomical association of CSD1 with the breakage plane and the reflex excitation of the levator muscles which it produces appear to implicate this receptor in the production of autotomy. However, it is unlikely that these two connective chordotonal organs (CSD.1 and 2), which are relatively more specialised by their association with secondary transducer mechanisms, are redundant save in the production of autotomy which in most decapods is a rare requirement. It is more

probable that these receptors serve some constant function and it is proposed that their primary function is the proprioceptive control of load distribution between limbs.

SUGGESTIONS FOR FURTHER WORK

From the work done for this thesis two interesting lines of research have evolved, both equally worthy of pursuit.

a. CSD organ function

The function of the CSD organs is of particular interest as they are the first examples of crustacean chordotonal organs which are not primarily involved in proprioception at a limb joint with the possible exception of the FCO (Taylor, 1967b). An understanding of CSD function can only be gained, however, when the motor innervation of the T-C and C-B joint muscles is known in some detail. Analysis of the reflexes mediated by CSD organs will provide the key to their function. If they are uniquely involved in the control of autotomy then their reflex effect should be almost exclusively on the muscles of the leg in which they are situated. It is important that the effect of CSD stimulation on the motor output to all muscles of the T-C and C-B joints should be analysed. If, however, they are involved in load distribution as postulated one may expect reflex activation or inhibition to motoneurons of the other walking legs, particularly the ipsilateral limbs but also the contralateral legs under some circumstances.

Location of the levator motoneurons would also be profitable as one may then examine the degree of synaptic input from the CSD organs, particularly to the largest of the three anterior levator motoneurons which McVean, (1970) contends is functional in the production of autotomy.

b. Proprioceptive Control of Mandibular Movement

The presence of a muscle receptor organ (MRO) in the mandible is interesting as the evidence provided for crustacean MRO function implicates these organs in posture control (see Discussion, 7d). It is most improbable that the "rest" position of this appendage is of sufficient importance to warrant a proprioceptor of such complexity and it is reasonable to assume that the Mand. MRO is functional in the biting and crushing processes. An understanding of Mand. MRO function requires that the innervation of the receptor muscle and other mandibular muscles be known in detail. Analysis of Abd. MRO1 function was only achieved by Fields, Evoy and Kennedy, (1967) after sufficient knowledge had been acquired of the pattern of efferent innervation of the extensor muscles and of the central routes of command. The primary obstacle to analysis of Mand. MRO function is that the afferent and efferent fibres share a common trunk and that afferent response from the large number of sensory neurones would mask the efferent activity. However, it appears that the sensory innervation of the Mand. MRO in some species of crayfish lies in a separate trunk from the afferent fibres and it may be possible to find an animal more suited for analysis of Mand. MRO function.

Alexandrowicz, (1967b) argues strongly that the

dendritic processes of the sensory neurones of crustacean MROs are associated with connective tissue and not directly with muscle fibre sarcolemma. Evidence, however, now suggests that the dendrites are associated with sarcolemma (Bodian and Bergman, 1962; Nadol and Darin de Lorenzo, 1969) and it would be worthwhile to study the dendritic terminals in the Mand. MRO to see whether they are associated with muscle fibres, tonofibrils, or connective tissue.

APPENDIX 1

A Summary of the Literature Published on Proprioceptors
in the Appendages of Decapod Crustaceans

This appendix which is basically a catalogue of the literature published to the end of 1970 has been included for two reasons. First it allowed me to dispense with extensive lists of references which I should have been obliged to insert at several places in the text and secondly it amply stresses the lack of comparative information available for appendages other than the pereopods. This section is not intended to be read as part of the thesis but is a reference list to aid the reader in his understanding of the bulk of knowledge which I have endeavoured to supplement.

Part of the material from this thesis has been previously published (Wales, Clarac, Dando and Laverack, 1970) but as the material is included in the text this reference has not been included below.

ANTENNULE

- 1965: WYSE AND MAYNARD - Anatomy and response to joint movement of the connective chordotonal organs at the three peripheral joints.

ANTENNA

- 1967a: TAYLOR - Anatomy and response to joint movement of the flagellar chordotonal organ (FCO).
1967b: TAYLOR - Response of FCO to water displacement and waterborne vibrations.

MANDIBLE

This thesis only.

1st MAXILLA

Nil.

2nd MAXILLA

1969: PASZTOR - Observed no connective chordotonal organs, but describes a novel stress sensitive proprioceptor, the "oval organ", innervated by branching dendritic processes.

1st MAXILLIPED

7
Nil.

2nd MAXILLIPED

Nil, but chordotonal organs present in Scyllaridae (Laverack, unpublished).

3rd MAXILLIPED

This thesis only.

PEREIOPODS

1) The T-C Joint.

1957: ALEXANDROWICZ AND WHITEAR - Anatomy of the TC receptor complex in the nephropsideans Homarus vulgaris (M.Ed) and Astacus astacus and in the brachyurans Carcinus maenas, Cancer pagrurus and Maia squinado. Three receptor types are described.

1) TC MRO. This receptor is present in all species examined.

2) TC connective chordotonal organ. This was only observed in the Nephropsidae.

3) Two innervated elastic strands which attach to the connective tissue sheaths of the levator and depressor muscles close to their termination

on to the basipodite and thus cross both the T-C and C-B joints. These were observed in all the species examined except Maia.

- 1958: ALEXANDROWICZ - Morphology of the receptors in the anomuran Eupagurus bernhardus. The muscle receptor organ and elastic strands are present but no chordotonal organ was observed.
- 1965: WHITEAR - Fine structure of the receptors in Carcinus maenas, Pagurus bernhardus and Astacus pallipes.
- 1967a: ALEXANDROWICZ - Morphology of the receptors in the scyllaridean Palinurus vulgaris. No chordotonal organ was found.
- 1968: RIPLEY, BUSH AND ROBERTS - Recorded from S & T fibres of the TC MRO. They examined Carcinus maenas, Potamon sydeneyi and P. depressus and demonstrated that these fibres conduct graded receptor potentials not propagated action potentials.
- 1968: BUSH AND ROBERTS - Demonstrated that the TC MRO evokes a resistance reflex in the promotor muscle.

2) The C-B Joint

- 1957: ALEXANDROWICZ AND WHITEAR - Morphology of CB in Homarus vulgaris (N. Ed.), Cancer pagurus, Carcinus maenas and Maia squinado.
- 1958: ALEXANDROWICZ - Disposition of CB in Eupagurus bernhardus.
- 1962: WHITEAR - Morphology and fine structure of CB in Carcinus maenas.
- 1965a: BUSH - Response of CB to movement of the C-B joint in Carcinus maenas.
- 1965b: BUSH - Resistance reflexes mediated at the C-B joint by CB in Carcinus maenas.
- 1967a: ALEXANDROWICZ - Disposition of CB in Palinurus vulgaris.

3) The B-I Joint (Nephropsidae only)

- 1969: CLARAC AND MASSON - Disposition and morphology of BI in Astacus leptodactylus. They indicate that this receptor is also present in Homarus gammarus and Nephrops norvegicus.
- 1970: CLARAC - Response of BI to movement of the B-I joint in Astacus leptodactylus.

4) The I-M Joint

- 1962: WHITEAR - Indicated an IM receptor is present in Carcinus maenas.
- 1968a: CLARAC - Morphology of IM in Carcinus mediterraneus. This is not the same receptor as described by Whitear (1962) which apparently corresponds to Clarac's MCO2 (see M-C joint).
- 1968b: CLARAC - Response of IM to joint movement in Carcinus mediterraneus.
- 1969: CLARAC AND MASSON - Two IM receptors shown to be present in Astacus leptodactylus. IM1 occupies the same location as IM of Carcinus and IM2 is homologous with the brachyuran MCO2 (see M-C joint).
- 1970: CLARAC - Characterisation of the response of IM1 and IM2 in Astacus leptodactylus.

5) The M-C Joint

a) The Connective Chordotonal Organs

- 1959: WIERSMA - Analysis of the response of MC1 and MC2 in Carcinus maenas and Homarus vulgaris (M.Ed).
- 1962: WHITEAR - Morphology and fine structure of MC1 and MC2 in Carcinus maenas.
- 1965b: BUSH - Role played by MC1 and MC2 in mediating resistance reflexes at the M-C joint in Carcinus. MC2 active only on release.

- 1965c: BUSH - Further analysis of the response of MC1 and MC2 to joint movement and position in Carcinus maenas.
- 1969: EVOY AND COHEN - Analysis of the role of MC1 and MC2 in posture control.

b) The Myochordotonal Organ

- 1934: BARTH - First description of the myochordotonal organ (MCO) in Dotilla myctiroides and Ocypodide ceratophthalma. Two groups of cells are described, the "Hauptorgane" and the "Proximalorgane".
- 1960: COHEN - Description of group of cells connected by an elastic strand to the proximal head of the accessory flexor muscle (AFM) in Cancer magister which he considered corresponded to the "Hauptorgane". He also demonstrated the response of these cells to M-C joint movement.
- 1961: HWANG - Description of a second group of cells innervating the insertion of the AFM in Cancer magister (Proximalorgane?). These cells are also shown to be sensitive to M-C joint movement.
- 1962: DORAI RAJ AND COHEN - Stimulation of the motor fibres to the AFM of C. magister.
- 1963a: COHEN - Anatomy of MCO "Hauptorgane" (Cohen, 1960) in C. magister and a detailed analysis of unit types. The receptor is shown to respond to M-C joint movement and to manipulation of the AFM or the connective tissue strand.
- 1963b: COHEN - Morphology and histology of the AFM and its innervation in C. magister.
- 1964: COHEN - As for Cohen, 1963a.
- 1964: DORAI RAJ - Electrophysiological investigation of AFM fibre types and innervation in C. magister.
- 1964: DORAI RAJ AND COHEN - Structural and functional correlations for the AFM of C. magister.

- 1965: COHEN - Anatomy of the complete MCO (Hauptorgane and Proximalorgane) in C. magister. He proposes that the myochordotonal organ's primary function is the maintenance of muscle tone to the main leg musculature and thus is setting the central level of excitation.
- 1967: CLARAC - A short description of the MCO in Carcinus maenas.
- 1967: COHEN AND HESS - Fine structure of the AFM in Cancer magister.
- 1968a: CLARAC - Morphology of the two sensory cell groups associated with the AFM in Carcinus mediterraneus. He designates the two cell groups MCO1 (= Hwang, 1961) and MCO2 (= Cohen, 1960). MCO1 is subdivided into two cellular groups which correspond to the "Hauptorgane" and "Proximalorgane" of Barth (1934). The cells described by Cohen (1960 and 1963a) are MCO2 and therefore not part of the myochordotonal organ of Barth.
- 1968b: CLARAC - Comparison of the sensory responses of MCO1 and MCO2 in Carcinus.
- 1968: EVOY AND COHEN - Output of MCO primarily effects the accessory flexor muscle and this feedback loop maintains the M-C joint at a centrally determined rest position.
- 1969: CLARAC AND MASSON - The Nephropsidae have MCO1 only whereas the Scyllaridae and Anomura like the Brachyura have MCO1 and MCO2.
- 1970: CLARAC - Response of MCO1 in Astacus leptodactylus.

6) The C-P Joint

- 1959: WIERSMA - Gross anatomy of CP1 and CP2 in Carcinus. Response and characterisation of the units from both receptors in Carcinus maenas, Homarus vulgaris (M.Ed.), Maia squinado and Eupagurus bernhardus.
- 1962: WHITEAR - Morphology and fine structure of CP1 and CP2 in Carcinus maenas.

- 1962: BUSH - Analysis of motor activity during resistance reflexes at the C-P joint in Carcinus maenas. CP chordotonal organs implicated by ablation experiments.
- 1963: BUSH - Resistance reflexes at the C-P joint in Maia squinado, Portunus puber, Eupagurus bernhardus, Homarus vulgaris (M.Ed.), and Astacus pallipes.
- 1965b: BUSH - Comparison of the control of resistance reflexes by CP1 and CP2 in Carcinus maenas. CP2 active only on release of strand.
- 1965c: BUSH - Analysis of unit activity for CP1 and CP2 in Carcinus maenas.

7) The P-D Joint

- 1954: BURKE - First description of a connective chordotonal organ in the Decapoda. He demonstrated that PD is sensitive to joint movement and position, and to vibrations.
- 1959: WIERSMA - Analysis of unit types in Carcinus maenas, Maia squinado, Homarus vulgaris and Palinurus vulgaris.
- 1959: WIERSMA AND BOETTIGER - A more detailed review of unit type in which they suggest that units of similar type may be located on specific regions of the strand.
- 1962: WHITEAR - Morphology and fine structure of PD in Carcinus maenas.
- 1962: BUSH - An analysis of motor output during resistance reflexes at the P-D joint in Carcinus.
- 1963: MENDELSON - Intracellular and extracellular recording from the isolated PD organ of Pachygrapsus crassipes to determine the adequate stimulus and site of spike initiation.
- 1965b: BUSH - Analysis of the role played by PD in the

the control of resistance reflexes in Carcinus maenas.

- 1967: HARTMAN AND BOETTIGER - Location on the strand of the different unit types in Cancer irroratus. Units of like sensitivity insert in same scolopidia.
- 1967: BOETTIGER AND HARTMAN - As for Hartman and Boettiger, (1967).
- 1970: WIERSMA, VAN DER MARK AND FIORE - Computer analysis of spike interval pattern from movement sensitive units of the PD organ of Carcinus maenas.

PLEOPODS

- 1969: DAVIS - Description of reflex activity produced by undescribed proprioceptors.

UROPODS

Nil.

APPENDIX II

Methylene Blue Staining of Invertebrate Tissue

This is a very valuable, though somewhat capricious, technique of which little information is available and that is scattered throughout a number of papers (see Alexandrowicz, 1932, 1951; Cole, 1934; van Harreveld, 1939). During the course of this comparative study methylene blue was used extensively and a few empirical rules have evolved which will aid others in the use of this stain.

- 1) Methylene blue is a vital stain and it is frequently advantageous to prolong the life of invertebrate tissue by maintaining it at a low temperature (5-8°C). I have successfully stained neurones in Homarus gammarus over periods of 24-48 hours where rapid techniques have failed.
- 2) Do not use very strong or very weak solutions of methylene blue. The former has a tendency to stain non-specifically and to kill the tissue whereas the latter will frequently stain only faintly.
- 3) Keep the portion of tissue to be stained close to the surface of the staining solution as the rate of staining decreases with depth. The uptake of methylene blue most probably is an active process by the nervous tissue and the tissue closest to the surface will be higher up the oxygen diffusion gradient.
- 4) Keep the ratio of the volume of staining solution: volume of tissue reasonably high. If a small volume of solution is used with a large piece of tissue then the concentration of methylene blue in the solution may decrease rapidly.

5) Do not reduce the concentration of the staining solution markedly during the staining process as this frequently stops the uptake of stain and some of the neurones in the preparation may lose colour.

Methods

Methylene blue should be dissolved in distilled water to give a 1% solution. This stock solution should then be diluted with sea water or saline to the required concentration. Methylene blue has a much lower solubility in sea water than in distilled water.

⁷ The most successful method with crustacean proprioceptors is to stain the tissue in a mid blue solution (10-15 drops of stock soln/100ml) at 5-8°C. This method takes 4 or more hours to stain but produces dense staining without killing the tissue.

There are several more rapid methods which are often successful with nerve fibres but not as good for neurone somata. The speed of the process can be increased by raising the temperature of the solution which will shorten the life of the tissue, or by increasing the strength of the solution which will tend to stain the tissue less specifically. More rapid staining is advantageous where progressive dissection of the preparation must be performed to follow the course of the structure being stained.

The Clarac Two Bath Method

Dr. Francois Clarac of the C.N.R.S. Laboratory, Marseille, France, has evolved a useful rapid staining method. The tissue is stained at room temperature in a

dark blue solution (40-50 drops of stock solution/100ml). After 20-30 minutes the tissue is transferred to a bath of seawater or saline (or the solution in the bath may be changed) for further dissection then returned to the staining solution. The periods between observation should be decreased as staining progresses. This method stains nervous tissue more specifically than continuous immersion in a dense blue solution presumably due to surface deposited stain being bleached more rapidly from the non-nervous tissue when placed in sea water.

Methylene blue frequently precipitates, particularly when the experimental dish is metal or where corroded insect pins have been used. The precipitated crystals are very difficult to redissolve and the preparation will not make a suitable permanent mount.

For details of fixation see Alexandrowicz, (1951). It has recently been discovered that a short (30 mins. - 1 hour) initial fixation period in 3-5% Glutaraldehyde buffered at pH 7.5 results in little loss of stain and greatly facilitates dissection of the stained tissue for mounting (Alexandrowicz, unpublished).

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