SOME ASPECTS OF THE ECOLOGY AND BIOLOGY OF TWO ESTUARINE GRAPSOID CRABS.

by

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CONTENTS.

PART I.

I. INTRODUCTION.

The habitat of every animal can be conveniently regarded as having three components: the physical factors, the vegetation and the animal community. Ecology, which includes the study of habitats, thus covers an extremely wide field, and Elton (1953) describes how large specialised branches of research covering different aspects of the science have been built up. One of these sections is devoted to studies of the effects of physical factors upon animals. According to Elton, this phase of ecology can be approached from various angles, including examination of the physical habitat itself, the coordination of such observations with ecological surveys and the influence of these factors upon the fauna.

Although Day and his co-workers (1951, 1952, 1954, 1956, 1958, 1959), and Macnae (1957a & b) have examined the ecology of the major South African estuaries, and Day (1959) has studied the Langebaan Lagoon in the western Cape Province, the main objects of their work were to ascertain the faunistic and floristic components of estuaries and to discover how far truly intertidal (marine) and river faunas invade the estuarine habitat. It was therefore not possible for these authors to investigate more than cursorily the distribution of any particular species.

The present thesis, by way of contrast, describes the distribution in an estuary of two species of animals only. Part I represents the results of an attempt to explain this distribution in terms of the vegetation and certain major physical factors together forming the greater part of the environment. Part II deals with the interrelationships of the animal community.

The two dominant grapsoid crabs inhabiting the banks of the little studied estuary of the Kowie River in the Eastern Cape Province of South Africa are *Cyclograpsus punctatus* M.Edw. and *Sesarma catenata* Ort. Barnard (1950), who describes their anatomy in his "Descriptive Catalogue of South African Decapod Crustacea", notes further that both species are wide-spread round the South African coastline. *C.punctatus* is found on rocky sea shores as well as in estuaries, while *S.catenata* occurs only in the mudbanks of estuaries, salt-marshes and mangroves, and is commonly known as the "marsh crab".

In Part I the distribution of the two species has been related to the vegetation, type of terrain, degree of exposure at low tide and the semi-diurnal salinity fluctuations accompanying tidal ebb and flow. In addition, surveys of burrow density and experimental tests of the resistance of the animals to desiccation and changes in salinity have been made. In this way it was hoped to define the habitat with respect to these selected environmental factors and to determine as far as possible why the crabs are restricted to certain vertical levels and certain areas of the estuarine system. This involves an assessment of the degree of physiological fitness possessed by the animals for coping with the problems imposed by their environment.

Fig.1. Aerial Photograph of the Kowie River Estuary from the Tidal Limit (Z) to the Sea. The up-river stations, R, S & T are as shown. (Photograph, Trigonometrical Survey, Pretoria).

IIA. THE KOWIE RIVER ESTUARY.

1. General Description.

The estuary is similar to others in the south eastern region of South Africa. It is long, with the tidal limit thirteen miles from the mouth. The aerial photograph (Fig.1.) shows that it pursues a winding course to a permenently open mouth. The substantial tidal range, shallowness in relation to width and gently sloping sides, classify it as a drowned **river** valley (Ketchum, 1953), rather like the estuaries of the Delaware and Hudson rivers. During the last century, a project, eventually abandoned, to use the mouth as a harbour, caused the construction of a pier and the straightening of the mouth region for a distance of about a mile by means of building steep, stony dykes. The original path of the river can still be recognised as two series of lagoons. Those on the west bank (Little Beach and Lagoon 4) are tidal. The east lagoons (1, 2 and 3) are more or less isolated, but water enters and leaves them at very high tides via seepage points in the dykes.

The small town of Port Alfred lies along the sea shore, river banks and surrounding hills, and the Town Bridge marks the end of the built up banks. The approximate breadth of the river at the bridge is 75 feet. Beyond this point it widens to about 100 feet and turns westwards forming a shallow bay, known locally as the "Bay of Biscay". Here the northerly bank is flattened and marshy, and traversed by minor tidal tributaries which bring fresh water from the nearby hills during rainy periods.

From the tidal limit to the "Bay of Biscay" the river flows through a deep valley joined at intervals by small tributaries. At the tidal limit the banks and bed are covered with mounds of pebbles. Over most of the

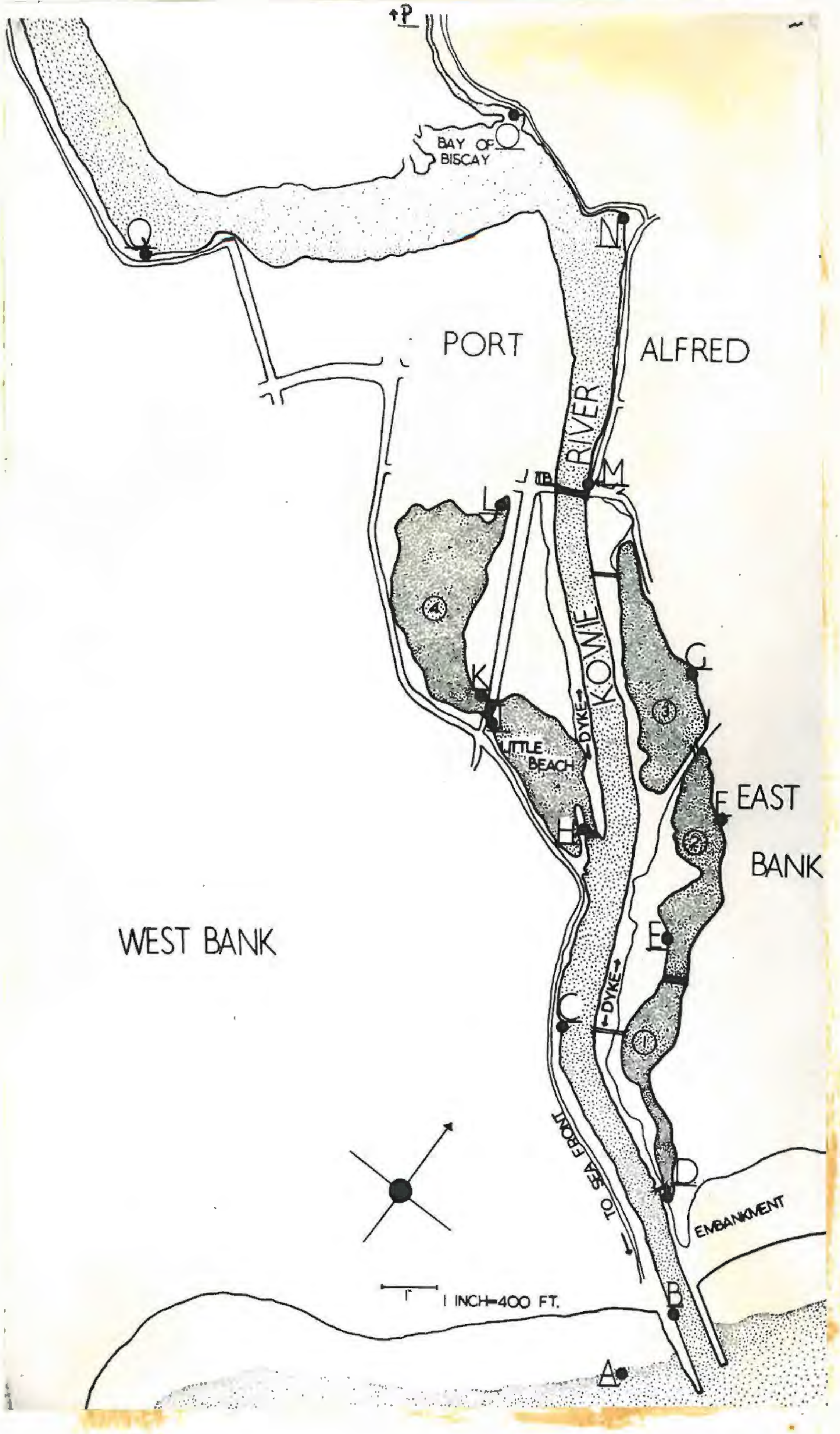


Fig.2. Map of the first two miles of the Kowie Estuary (after H.R. Kuys, 1907), showing the positions of sampling stations A-Q. Black bands = Bridges; T.B. = Town Bridge; Lagoons 1,2 & 3 = Eastern Lagoons; Lagoon 4 & Little Beach = Western Lagoons; Bars across lagoon banks = seepage points.

Table 1.

Station	Position in Estuary
Station A	On the sea shore.
Station B	In the river mouth.
Station C	Half a mile from the mouth.
Station D	At the seaward end of Lagoon 1.
Station E	On the west bank of Lagoon 2.
Station F	On the east bank of Lagoon 2.
Station G	On the east bank of Lagoon 3.
Station H	At the seaward end of Little Beach.
Station J	At the top of Little Beach.
Station K	At the seaward end of Lagoon 4.
Station L	At the top of Lagoon 4.
Station M	At the Town Bridge.
Station N	In the "Bay of Biscay".
Station O	At the mouth of the most easterly tributary entering the "Bay of Biscay".
Station P	At the tidal limit of the tributary.
Station Q	Half a mile from the "Bay of Biscay" on townward bank of the river.
Station R	A mile up river from Station Q.
Station S	Eight miles from the sea.
Station T	A mile up river from Station S.

length of the estuary, extensive, gently-sloping mudbanks, soft and "slurry" in nature, are left exposed at low tides. Normal high tide level is often marked by the presence of short salting cliffs or ridges, surmounted by vegetation. Here and there the mudbanks are interrupted by cliffs and rocky outcrops.

In the lower reaches, below the "Bay of Biscay", the mud contains a large proportion of sand. The east Lagoons and Lagoon 4 all lie upon soft, sandy mud, while the bed and banks of Little Beach are very sandy. On the river side the bank of Little Beach is steep, and covered with boulders.

The map (Fig.2.) shows the lower estuary and lagoons in detail.

2. Sampling and Observation Stations.

Twenty stations were selected where water sampling, collection of animals and observations were carried out. It was not possible to reach the banks along much of the estuary as the water in many places was too shallow to permit the passage of a boat and the mud too soft to effect a landing. Dense bush, steep cliffs and the absence of roads restricted access from the land. Fig. 2. shows the positions of the stations in the lower estuary. Three stations do not appear on the map, but their positions are shown in the aerial photograph (Fig.1.). All sampling stations are recorded in Table 1.

3. The Vegetation.

The types of plants present in any estuary are influenced by salinity and tidal movements of the water. Thus typical salt marsh plants inhabit the banks as far as they become inundated and the whole succession of plant species is governed by their respective affinities for water. The vertical plant distribution was studied by conventional survey methods. In the open river, two zones have been found below high water of springs level (H.W.S.). No inter-or infratidal *Zostera* fields are present in the Kowie river estuary, possibly for the reasons suggested by Tutin (1938), Day (1951) and Macnae (1957a), including the turbidity of the water, the action of waves and the fluidity of the substratum.

Spartina zone: The tall, coarse grass, *Spartina capensis* Nees (*S.stricta* Roth.) first appears on the banks at the "Bay of Biscay". This plant often colonizes large areas in the intertidal zone, and usually disappears above normal high tide level, although it may be scattered amid the higher vegetation for a short distance.

Arthrocnemum zone: The xerophytic lagoon bank bush commences at or above mean normal high tide level. The chief genus in this zone is *Arthrocnemum* which grows nearest the water, and is the pioneer plant in the absence of *Spartina*. The *Arthrocnemum* belt usually extends to H.W.S., and may be a single species community, or be intermingled with *Spartina*, *Triglochin bulbosum* L. (in low wet places), and *Chenolea diffusa* Thunb. towards H.W.S.

The succession of salt marsh plants is terminated a short way above H.W.S. by *Limonium scabrum* (Thunb.)O.K. (Dyer, 1961) which gives way to mesophytic and xerophytic grasses, shrubs and trees.

In the Lagoons, except at Little Beach, whose banks are devoid of vegetation, the zonation of plants is similar to that found along the river. The large spring tidal range in Lagoon 4 (Fig.2.) and the flatness of the banks of the eastern lagoons, which allows water to remain on the surface for some time at very high tides, causes the succession of

Fig. 3. A view across Lagoon 4 at low tide. Dense *Spartina* occupies the foreground, and halfway across the lagoon is a low-lying *Spartina* covered island. Note that on the steep opposite bank the plant succession is compressed and that mesophytic shrubs are growing only a short distance above the water.

salt marsh plants to become spread out. In some places, however, the banks slope steeply (e.g. the east bank of Lagoon 3) and here the zonation is often compressed.

In addition to the rooted vegetation outlined above Lagoon 4 contains masses of drifted algae. The chief of these is the slender, branched, brown alga, *Gracilaria verrucosa* (Huds.) Papenf.. A similar, smaller species present is *Stilophora flanagani* Kylin. The green alga *Codium tenue* Kützing is often found cast up on the lagoon banks. These floating algal masses occur also in Lagoon 3.

Notes on Spartina, Arthrocnemum and Chenolea.

Spartina capensis, found throughout the estuary, grows in coarse tufts to a height of 25-80 centimetres. As Macnae (1957a) has observed, members of the genus often lay down subterranean, soil -holding mats with their roots and stolons, and Dyer (1937) notes that a *Spartina* colony may so consolidate the substratum as to form an island. In Lagoon 4 there are several islands which have been established in this way (Fig.3.) and along the river banks *S.capensis* has formed many small promontories. The rigid spiky plants are yellowish in colour for most of their length and green near the roots.

Arthrocnemum pillansii Moss was the species of *Arthrocnemum* most commonly found. This plant possesses the jointed green fleshy stems and rudimentary leaves characteristic of the genus. *A.pillansii* differs from other species in having long stems (approximately 30 cm) prostrate and woody at the base, with erect green tips. Where the plants grow closely together there is a dense mat of stems covering the ground, while the ramifying root systems stabilize the soil (Dyer 1937). The plants growing near water are usually bright green, but in drier areas they become purplish and shrivelled in appearance.

Chenolea diffusa, which occurs near the high spring tide mark, has short stems and succulent, hairy leaves. Dyer (1937) suggests that Chenolea colonies are also responsible for the consolidation of mud banks. The plant requires less water than do Spartina and Arthrocnemum.

4. Salinity Variation within the Estuary.

Animals inhabiting an estuary must be able to withstand the salinity changes accompanying the semi-diurnal tidal flow of water. In order to gain an idea of the extent and duration of the salinity fluctuations, samples of water were collected during spring and neap tidal cycles, when maximum and minimum fluctuations occur.

Methods: Water samples were taken at hourly intervals at each of the first 16 stations on 3.iii.1963 and 10.iii.1963. The first series corresponded to neap, the second to spring tides. Heavy rain on 10.iii.63 interfered with sampling at Station Q and only 8 samples could be collected. On 8.viii. 1963 (spring tide) and 14.viii.63 (neap tide) samples were taken (in the upper reaches) at stations S and T. No water sampling was carried out at Station R.

Each sample was collected in a labelled 500 ml. bottle from just below the water surface a few inches from the shore. This method of sampling is at variance with that advocated by Redfield (1948), who contends that in estuaries, with the density stratification due to variations in salinity, a false picture of salinity is obtained by surface sampling. Surface sampling is adequate in the present case however. The animals concerned inhabit the river banks, and not its bed, and even at very high tides their burrows are covered to a depth of only a few inches.

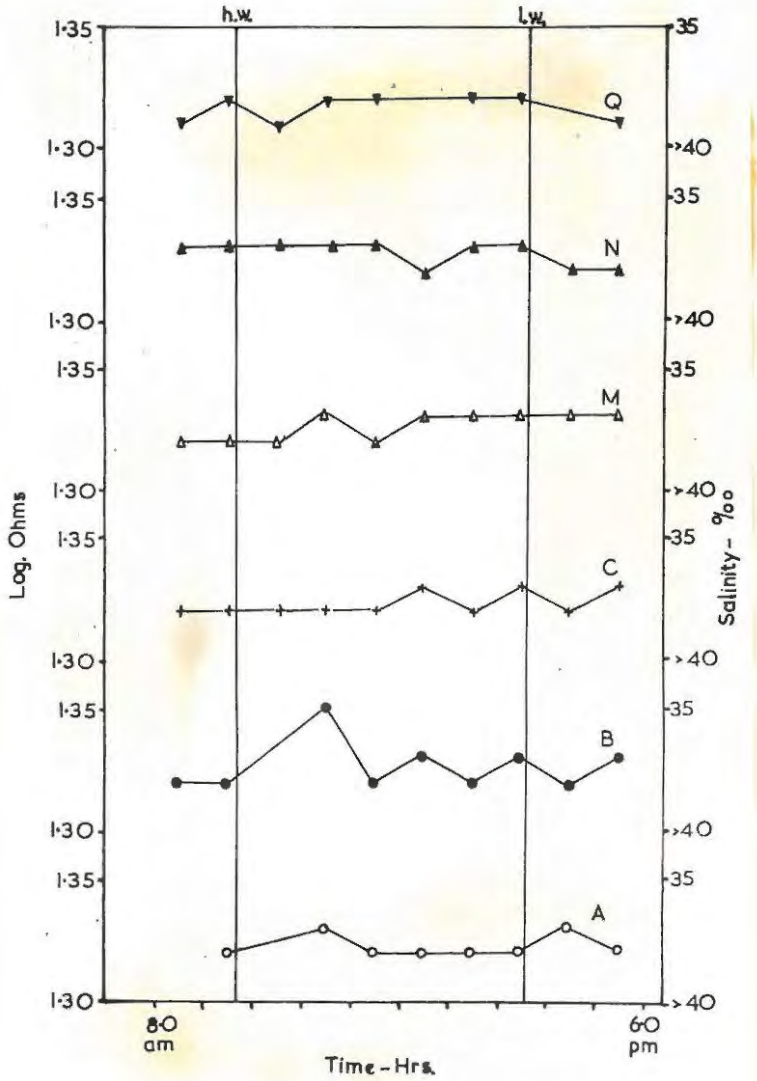


Fig.4. Curves of salinity change produced at neap tide in the open river over the first two miles of the estuary. The logarithm of the resistance (Ohms) is compared with time of sampling on 3.iii.1963. The curves for the six sampling stations, A,B,C,M,N and Q, have been separated for the sake of clarity, and an approximate salinity scale in parts per thousand is given on the right.
h.w. = time of high water at the seashore.
l.w. = time of low water at the seashore.

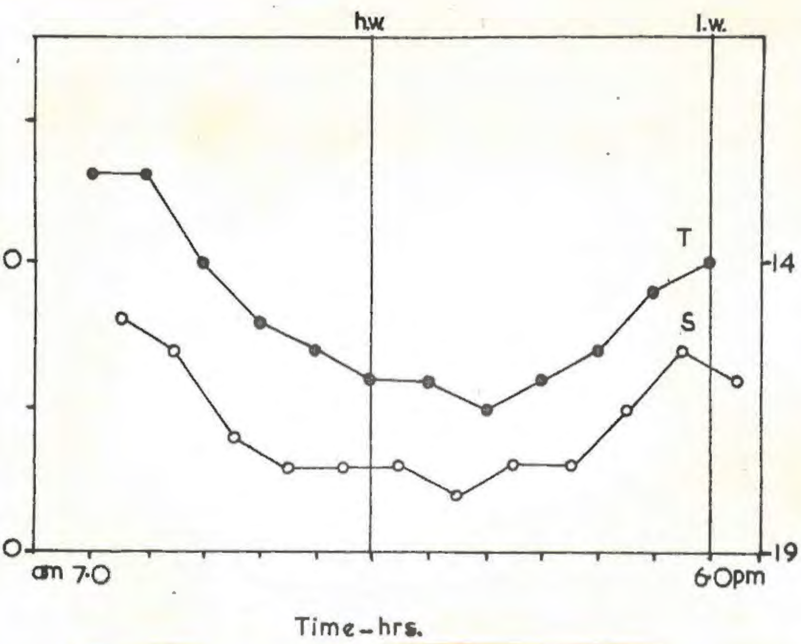


Fig.5. Curves of salinity change produced at the two upper reach stations, S & T, during neap tide on 14.viii.1963. The curves have not been separated as in Fig.4. Note that the resistance increases with salinity drop.

As soon as the water samples had been brought into the laboratory, three crystals of Thymol were added to each as a preservative to prevent the decay of any organic matter. Because of the large number of samples, it was not practicable to determine the salinity of all of them by titration. Instead, conductiometric methods were used. A "Doran" conductivity meter was employed to measure the resistence of the water. The platinum electrodes were immersed in the filtered samples, and the mean of two readings was taken. As a check on the accuracy of the instrument the specific gravities of the samples were found using a hydrometer, reading from 1.000-1.050. These results corresponded well with the resistances obtained. Finally, certain samples whose resistances covered a wide range, and a series of standard NaCl solutions, were titrated with $Ag\ NO_3$ in the manner described by Harvey (1928). The salinities were calculated using Knudsen's formula:

$$S^o/oo = 0.30 + 1.8050\ Cl'$$

Where S = salinity and Cl'= chlorinity.

These data were then compared graphically with the resistances and the salinity of any water whose resistance lay within the range could be estimated from the graph. Unfortunately, as the meter was graduated on a logarithmic scale, it was not very sensitive, especially for higher salinities.

Results: Figs. 4 & 5 show the curves of salinity change produced at neap tides in the river. Fig 4 represents the changes at Stations A,B,C,M,N & Q on 3.iii.1963 and Fig. 5. those at the two upper reach stations S & T on 14.viii.1963. Near the mouth there is little fluctuation in salinity during the neap tidal cycle, even as far as two miles up stream (Station Q) and the salinities over this area remain close to that of sea water (Station A). During

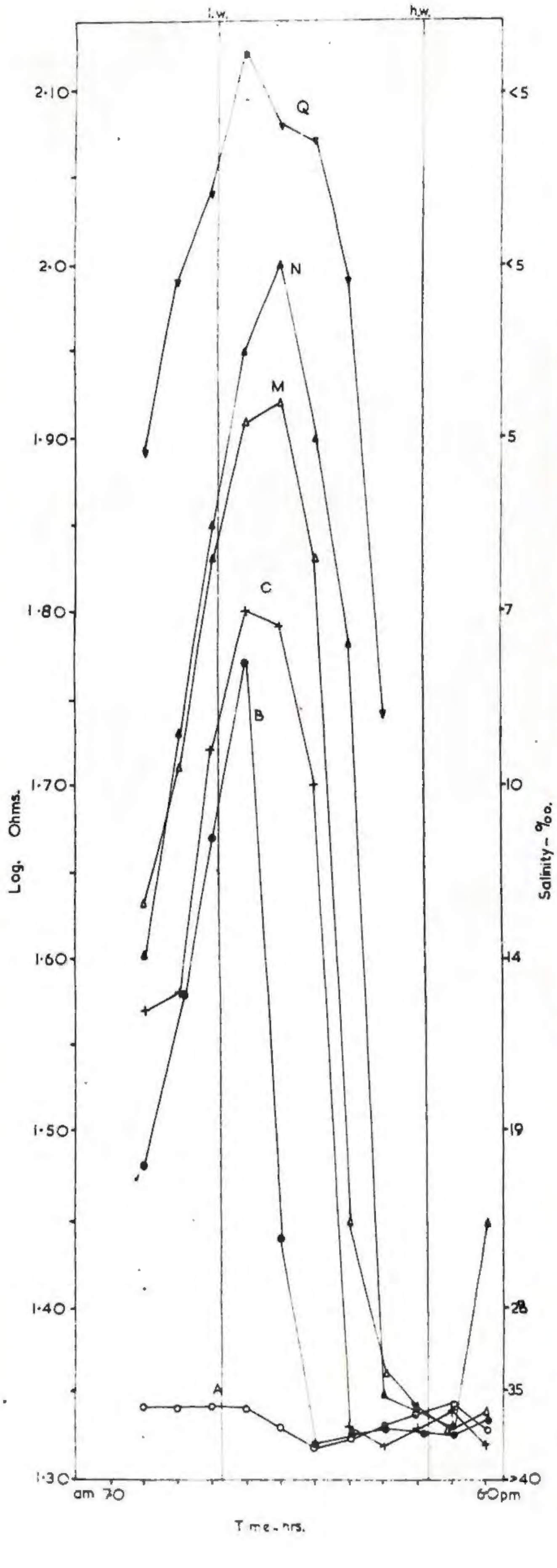


Fig.6. Curves of salinity change produced at the lower reach river stations (A,B,C, M,N & Q) during spring tide on 10.iii.1963.

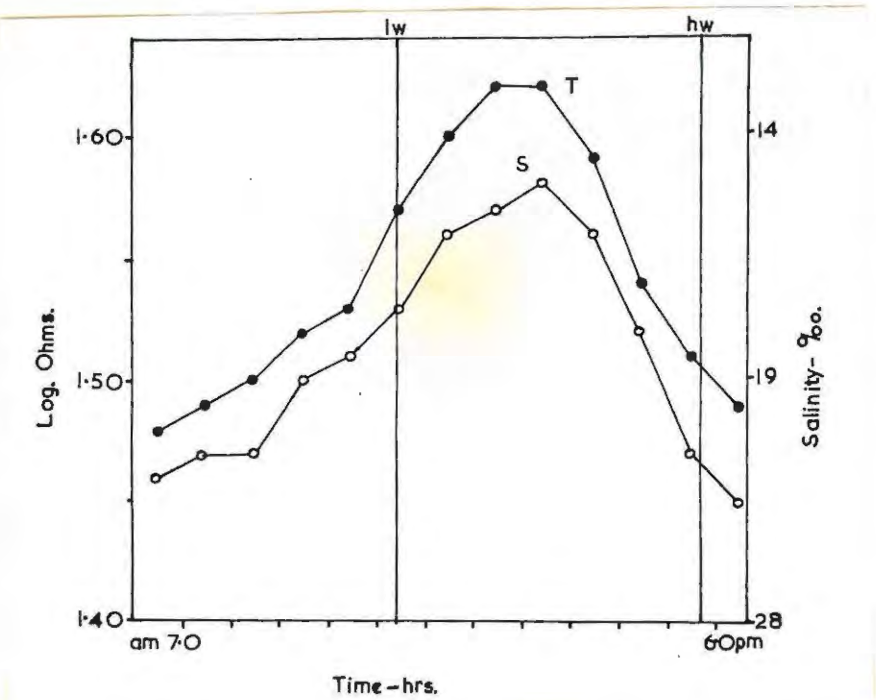


Fig.7. Curves of salinity change produced during spring tide at the two upper reach stations, S & T, on 8.viii.1963.

neap tide in the upper reaches there is considerable salinity change, and the inflow of fresh river water maintains the salinity below that of sea water. In Figs. 6 & 7 salinity changes during spring tides are given. In the lower reaches the salinity drop at low tide was accentuated due to the heavy rain, which caused flooding of the river, but at high tide the salinities at stations B,C,M and N returned to levels close to that of sea water. Unfortunately samples were not collected at Station Q during high tide. The salinity curves for spring tide in the upper reaches (Fig.7.) show that at stations S and T changes in salinity were greater than at neap tide (Fig.5.) and that at low tide the fall in salinity increased with distance from the sea. On both sampling trips the water at station T, a mile nearer to the tidal limit than Station S, was of lower salinity.

According to Ketchum (1953), there must be a net seaward water transport in an estuary to eliminate the fresh water flowing in from the upper reaches. After heavy rain the fresh water fraction is far greater than usual and at such times Ketchum suggests that the elimination of this water involves a combination of two factors:-

1. More rapid circulation with no change in overall salinity pattern.

2. An increase of the fresh water fraction throughout the estuary, resulting in a temporary downstream movement of the whole salinity pattern.

In Fig. 8 the salinity ranges (in parts per thousand) at each station during spring and neap tides are given for the first two miles of the estuary. These values were estimated from the standard graph prepared earlier, with a range from 5-40 parts per thousand.

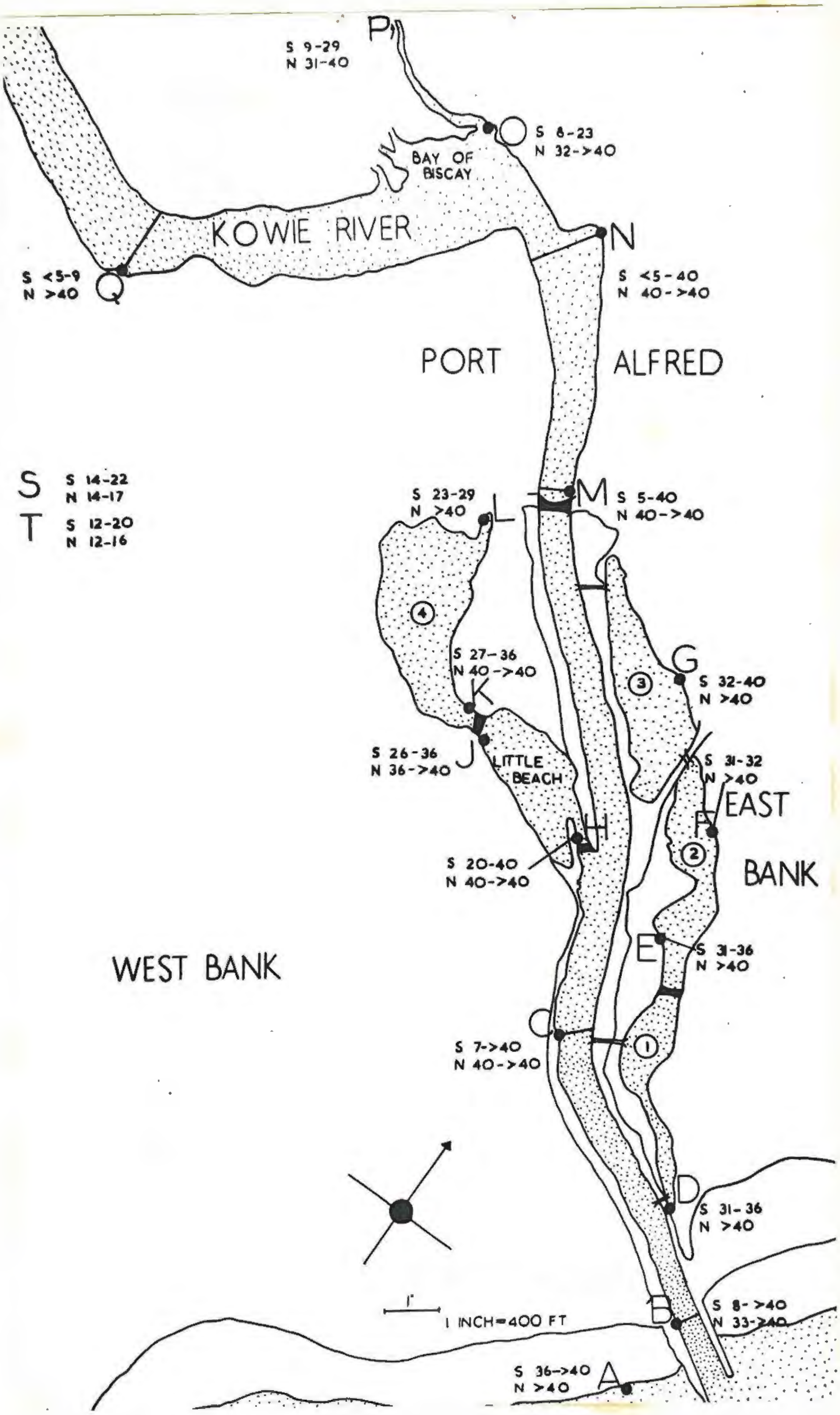


Fig.8. Map of the lower reaches of the Kowie estuary showing the approximate salinity ranges (in parts per thousand) at each of the sampling stations during spring (S) and neap (N) tidal cycles. The ranges at the upper reach stations have been inserted on the left.

The salinities at stations A,B,C,M,N and Q corresponding to spring tide indicate that Ketchum's theory may be applied at least to the lower reaches of the Kowie estuary. With the ebb of the tide the salinity pattern did indeed move seawards. As the tide re-entered the river the salinity pattern was re-established.

The western lagoons (Stations H,J,K and L) form a blind branch of the estuary. Curves of salinity change produced at neap tide on 3rd March 1963 are given on Fig.9a. The narrow range at all four stations (see also Fig.8) as well as the small deviations from sea water salinity, were to be expected in a system of this kind.

The increased range and generally lower salinities found at spring tide, (Fig.9b), are due both to tidal effects and dilution of the shallow waters by rain.

The isolation of the eastern lagoons accounts for the constantly high salinities found during neap tide (Fig. 10a, Fig.8), as these shallow bodies of water are subjected to evaporation in dry weather. At spring tides water seeps through the dykes into the lagoons and this, together with dilution because of rain, was responsible for the general lowering of salinity and a certain amount of fluctuation at stations D,E,F, and G (Fig.10b).

Graphs of salinity change in the tributary have not been included. Water movements here are complicated by the tides, the outflow of fresh water from the source and the water travelling past the mouth (Station O) from upriver. The ranges of salinity at Stations O & P on the sampling days have been given in Fig.8. These ranges were fairly large on both occasions, but the water was more dilute on 10.iii.63.

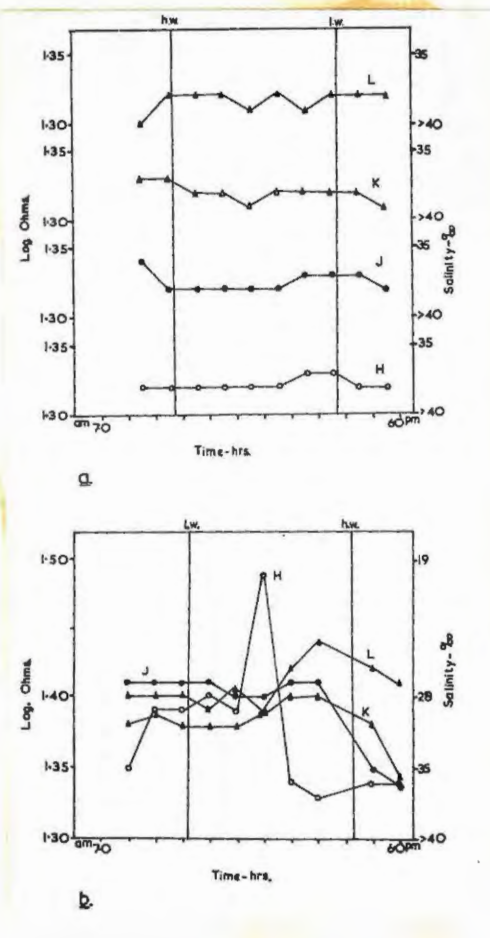


Fig.9. a & b. Curves of salinity change produced at the four western lagoon stations H,J,K & L, during neap (3.iii.1963) & spring (10.iii.1963) tides respectively. In Fig. 9a the curves have been drawn separately.

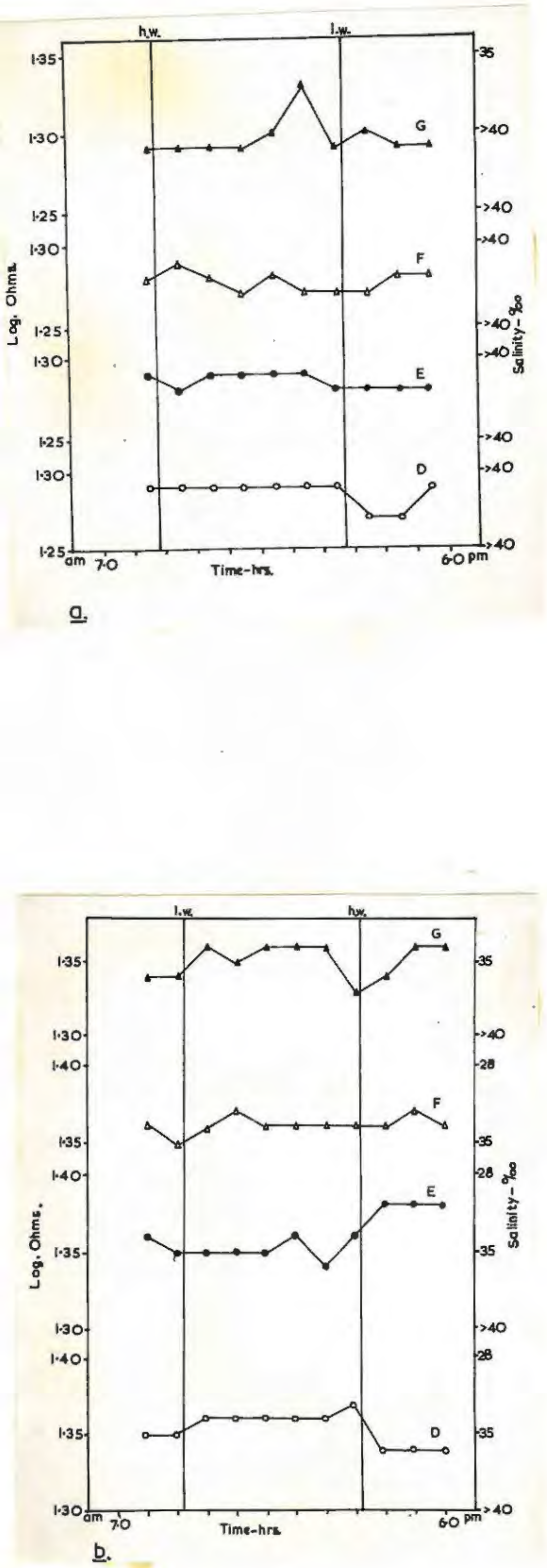


Fig. 10, a & b. Curves of salinity change produced at the eastern lagoon sampling stations, D,E,F & G during neap (3.iii.1963) and spring (10.iii.1963) tides respectively. All of the curves have been drawn separately.

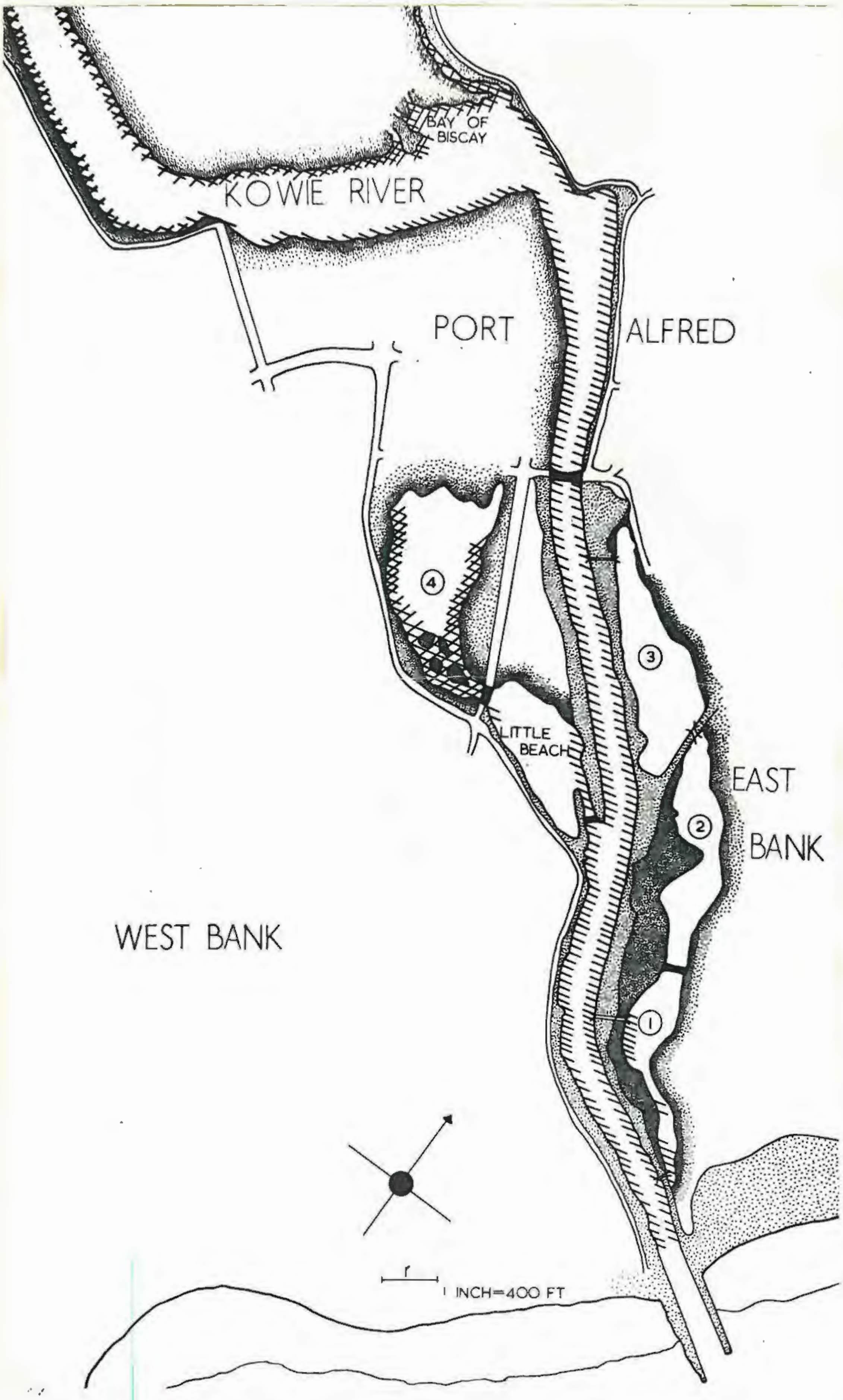


Fig.11. Map of the lower estuary showing the distribution of the crabs *Cyclograpsus punctatus* & *Sesarma catenata*. Cross hatching = Both crabs present; Single hatching = *C.punctatus* only.

IIB. THE DISTRIBUTION OF THE CRABS CYCLOGRAPSUS PUNCTATUS AND SESARMA CATENATA.

In the previous section an attempt was made to describe the variations in the estuarine substrate, plant cover and water salinity. In section B it is hoped to contribute to our understanding of the ways in which these environmental factors determine the horizontal and vertical distribution of the two grapsoid crabs. Whereever possible field observations have been supported by experimental work in an endeavour to relate cause and effect.

1. In Relation to Substratum.

In the lower reaches observations were made at twenty-yard intervals along the river banks. Farther upstream the banks were investigated wherever they were accessible. The distribution of the lower reach populations is shown in Fig. 11.

C.punctatus: This species is adapted to living under stones, as well as to burrowing. Many animals inhabit the stony dykes near the mouth, and do not construct burrows in this region. They are also only found under the stones on the sandy banks of Little Beach. Cyclograpsus populations extend upriver for a distance of eight miles from the mouth (Station S). Although they burrow in the muddy banks, where stones or other objects lie upon the surface the crabs frequently shelter beneath them. If the substrate is not wet or sandy, such objects may act as 'roofs' for shallow burrows. The banks and islands of Lagoon 4 are heavily populated with C.punctatus, but the crabs are found only in Lagoon 1 on the east bank of the river. They are present in small numbers in burrows and under stones at the seepage points.

S.catenata: No members of this species inhabit the rocky dykes or Little Beach. They are found only in places which are not very sandy or stony. The mudbanks of the river beyond the "Bay of Biscay" are honeycombed with the burrows of *S.catenata* and large colonies of the animals are to be found more than nine miles from the river mouth. In the upper reaches *S.catenata* mingles for a short distance with two other grapsoid crabs, *Sesarma eulimene* de Man & *Metopograpsus messor* (Forskal). These crabs are superficially similar to *S.catenata* and inhabit the banks from a mile below the tidal limit for some four miles downstream. No crabs were present at the tidal limit itself, but a little way beyond this point the river crab *Potamon perlatus* (M.Edw.) was found. *S.catenata* is abundant in Lagoon 4. One specimen was seen in October 1962 near Lagoon 1, but none were subsequently found in any of the three eastern lagoons.

2. Vertical Distribution with Relation to Height below High Water of Springs, to Vegetation and Resistance to Desiccation.

To see whether or not the vertical distribution of the crabs is affected by the degree to which their habitats are covered at high tides, this distribution was examined in relation to H.W.S. Level. Because the two species live so closely together, often inhabiting the same burrows, no distinction could be made between them, except near the river mouth, where only *C.punctatus* is present. Vegetation growing in the vicinity of the habitats was noted in an attempt to discover whether this bears any relation to the location of the burrows. Experiments to test the resistance of the two species to desiccation were also carried out.

Methods: Belt transects of the banks were made in the lower and middle reaches of the estuary at Lagoon 4 near

Station K. The belts were one yard (0.92 metres) in width and stretched from H.W.S. to the mud flats below. They were marked off in square yards. The number of burrows with mouths greater than 1cm in diameter was counted in each square and the type of vegetation was noted. This criterion was based on observations which strongly suggested that burrows with mouths less than 1cm in diameter belonged to mud prawns, worms or the small crabs Cleistostoma edwardsii McLeay and not to the grapsoid crabs. Profiles of the banks were obtained in the usual way employing an Abney level situated at H.W.S. level, a graduated stick and a field tape measure.

The best and most accessible places for the collection of animals were Lagoon 4 in the lower reaches and Stations S and T up river. Dull or wet days were the most profitable as many crabs were to be seen running about over the mudbanks. Cyclograpsus often sheltered under objects such as stones, logs or old tins which could easily be turned over. A knife or trowel was useful for digging the crabs out of their burrows. Crabs were transported to the laboratory in buckets, each containing a maximum of about twenty animals, which had been washed free of mud. They were transported dry.

In the laboratory the two species were kept together in porcelain sinks, covered with well-fitting gauze lids to prevent escape. The sinks were tilted at a slight angle and contained a few inches of sea water or sea water diluted with tapwater to 60% sea water salinity in the case of crabs from the upper reaches. The water was renewed every two or three days and was not aerated. Feeding was unnecessary as animals were used in experiments within a week after collection.

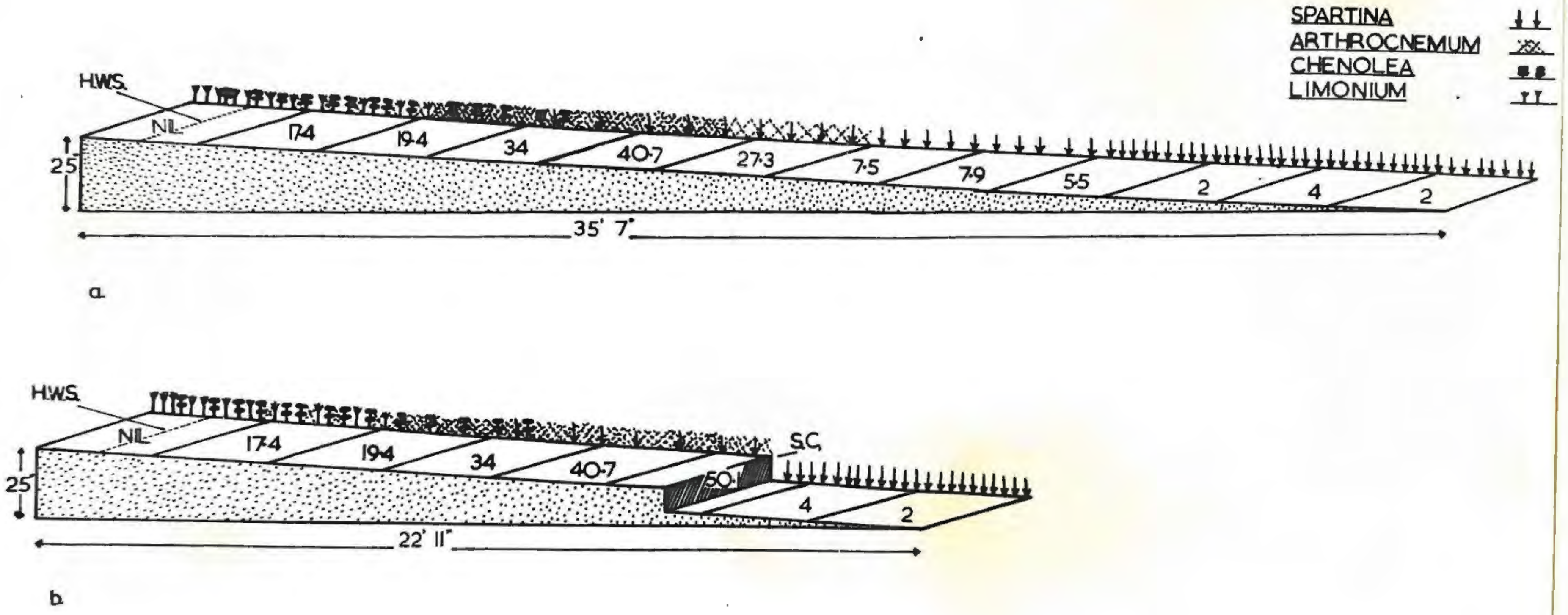


Fig. 12 a & b. Profiles showing the mean burrow density distribution on the banks of Lagoon 4, and the zonation of the vegetation. Both have been drawn to the same scale. H.W.S. = Level of High Water of Springs. S.C. = Salting Cliff.

The desiccation tolerance and resistance experiments were carried out as follows:- Crabs of both species were removed from their tanks, dried with a towel and placed separately in clean dry 1000 ml beakers on the laboratory bench, away from direct sunlight. The animals were left undisturbed, and mortality was recorded every 12 hours. The experiments were concluded when all the crabs were dead. The maximum day time temperature was noted for each experiment.

The first experiment was conducted during summer, using crabs from the lower reach population (Lagoon 4). Two other experiments were done in winter, using animals from Lagoon 4, and from the upper reaches (Stations S & T). Maximum carapace width was recorded in each experiment.

Vertical Distribution: In Fig. 12a the mean number of burrows per square yard from 7 transects taken in Lagoon 4 is given in relation to H.W.S. level and vegetation type. The following observations can be made from these data.

1. No burrows occur at or above H.W.S.
2. At a vertical distance of 2 inches below H.W.S. burrows are found and increase in number down the slope until a maximum number is reached 8 inches below H.W.S. The numbers of burrows then diminish and end 24 inches below H.W.S.
3. The maximum number of burrows occurs where *Arthrocnemum* is most dense. There are no burrows where only *Limonium* is present, but holes are found as soon as *Arthrocnemum* mingles with this plant, and also in the *Arthrocnemum*-*Chenolea* zone. Sparsely distributed burrows continue throughout the *Spartina* field.

Table II. Data from 6 Transects of River Banks taken in the Middle Reaches (Near Station 2).

Vertical Height Below H.W.S. (inches)	Mean No. of Burrows/Sq. Yd.	Vegetation.
2	0	Af
4	8.5	Ac Cp Sp
6	3.7	Ap Sp
8	0	Sp
10	0	Nil
12	0	Nil
14	17.5	Sp
16	0	Nil
18	11.3	Sc
20	12	Sf
22	0	Nil
24	10.5	Sf
26	3	Sf
28	10.7	Sc
30	0	Nil

A = *Arthrocnemum* f = frequent) Symbols of Plant
C = *Chenolea* c = common) Density from
S = *Spartina* p = present) Stephenson, (1944).

In Fig. 12a mean burrow density in relation to height below H.W.S. level down an even slope is represented, but there is no indication of the way in which this distribution may be altered by changes in the shore profile. Because of this, data were re-interpreted so as to produce a profile more like those which occurred at Lagoon 4. The salting cliffs present at normal high tide level in many places were examined and found to contain large numbers of burrows. The majority of the cliff faces were devoid of vegetation.

In order to represent the burrow density distribution over a profile possessing a salting cliff face, the mean height below H.W.S. of a large number of cliffs was determined. From this datum a "typical profile" (Fig. 12b) has been constructed and the burrow distribution of Fig 12a inserted with the assumption that the total number of burrows over the tidal range will be the same. For comparison the vertical burrow distribution obtained from the river bank transects near Station R is given in Table II.

From these data several facts can be clearly seen.

1. Most burrows occur between 14 and 20 inches below H.W.S., that is, at the level of the salting cliffs, despite the absence of Arthrocnemum.
2. Burrows are present as far as 28 inches below H.W.S. but do not continue beyond the end of the Spartina fields.
3. There is a definite correlation between burrow distribution and the presence or absence of vegetation.
4. In the places investigated, the river bank populations are more sparsely distributed than those in Lagoon 4.

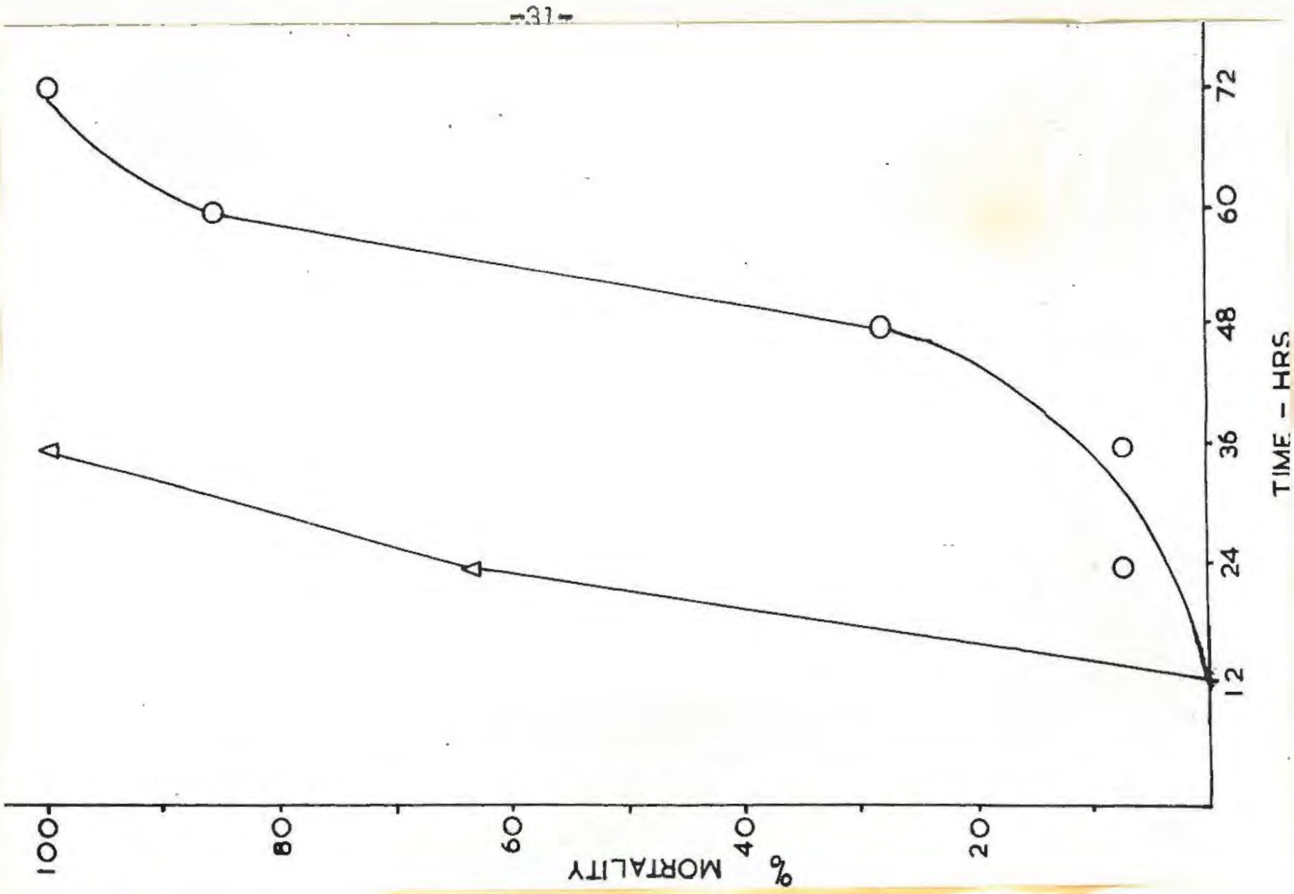


Fig. 13. *Cyclograpsus punctatus* and *Sesarma catenata*: Curves of percentage mortality with time for members of the lower reach population (Lagoon 4) kept out of water during summer. Circles = *C.punctatus*; Triangles = *S.catenata.*

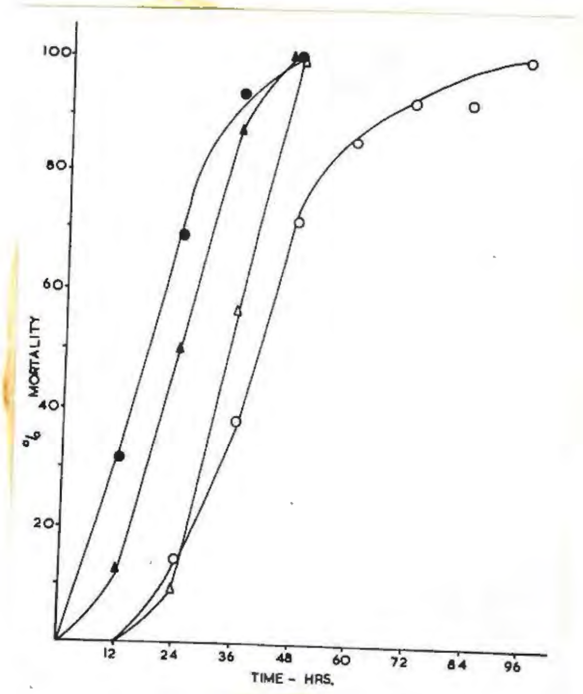


Fig.14. *Cyclograpsus punctatus* & *Sesarma catenata*: Curves of percentage mortality of crabs from the upper and lower reach populations, kept out of water during winter.
Open circles = Lower Reach *C.punctatus*;
Closed circles = Upper Reach *C.punctatus.*
Open triangles = Lower Reach *S.catenata.*
Closed triangles = Upper Reach *S.catenata.*

The nature of the dykes near the river mouth prevented quantitative surveys from being made. Here and in Little Reach C.punctatus lived under the stones in moist areas. Few were present below the water line, and none where the substrate was dry.

Desiccation Resistance: Curves of percentage mortality with time (Fig.13), for crabs from the lower reaches (Lagoon 4) during summer, show that C.punctatus from this region is apparently able to withstand desiccation better than S.catenata. Mortality curves for animals of both upper and lower reaches during winter have been plotted in Fig. 14. The resistance of members of the lower reach population at this time of the year was very similar to that found in summer although 100% mortality for S.catenata and C.punctatus occurred 12 and 24 hours later respectively.

The median times of survival were obtained by probit-log time plots for each experiment and are recorded in Table III.

Table III. Median times of survival of crabs out of water.

Season	Locality	Species	No. of Crabs	M.T.S. (Hrs)	Max. Daytime Temperature (°C)
Summer	Lagoon 4	C.punctatus	14	47	21
		S.catenata	11	22	
Winter	Lagoon 4	C.punctatus	21	39	16
		S.catenata	21	35	
Winter	Stations S & T	C.punctatus	16	17	16
		S.catenata	16	22	

On the basis of these figures it may be concluded that the crabs from the upper reaches are less resistant to

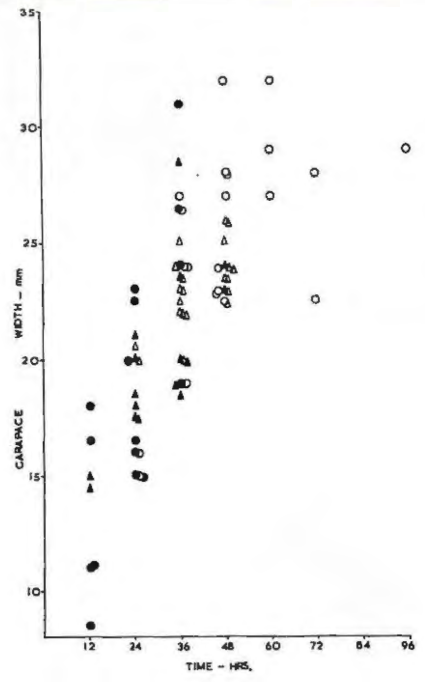


Fig.15a. *Cyclograpsus punctatus* and *Sesarma catenata*:

Graphic comparison of the carapace widths of winter individuals from both populations with time of death during exposure to air. Notation as in Fig. 14.

desiccation, while S.catenata from Stations S and T appear to be more resistant than C.punctatus. Furthermore, when summer and winter figures are compared, it appears that at the lower, winter temperature the M.T.S. of S.catenata is greater and that of C.punctatus less.

The ability of animals to resist desiccation is usually a function of their surface area. If the size range in different samples differs, then so too will their M.T.S. In Fig. 15a the carapace widths of the winter crabs are compared graphically with time of death and in Figs. 15b & c the same data are replotted showing the mean values of carapace breadth at different times of death. Regression lines have been drawn through these points and in each case control limits placed at two Standard Errors of Estimate for one of the regression lines. It is clear that, when the relatively small size of the samples is considered, it is not legitimate to conclude that there is any difference between the populations from the upper and lower reaches other than size. When the results from the two species are compared, however, as with the data for the upper reaches shown in Fig. 15d, the slopes of the regression lines are very different, so that for large specimens, the resistance of S.catenata will be greater than that of C.punctatus.

It may thus be concluded:-

1. That the animals of both species belonging to the upper reach population are on the whole smaller in size than those from Lagoon 4, provided the sampling was random.
2. That there is no evidence for a significant difference between resistance to desiccation of crabs from the two levels of the river.
3. That since time of survival varies directly with carapace width mortality rate is related to the surface to volume

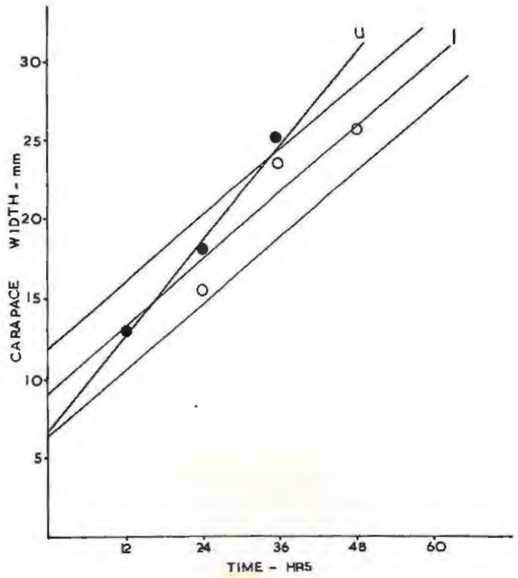


Fig. 15b.

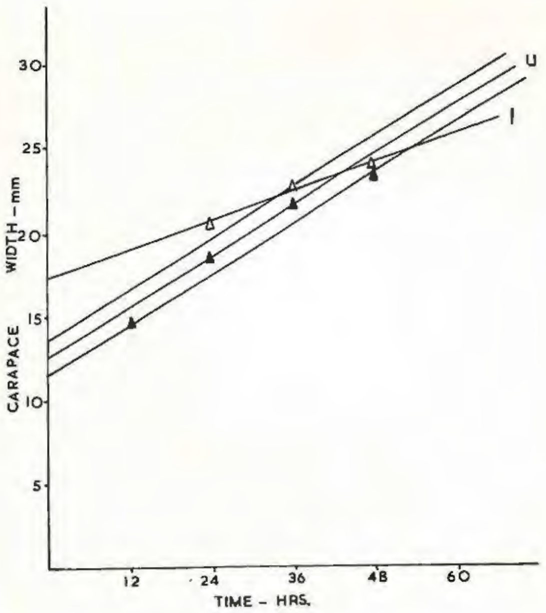


Fig. 15c.

Fig.15b. Cyclograpsus punctatus: Graph showing the mean carapace widths of animals from the upper (u) and lower (l) populations at different times of death during exposure to air. Regression lines have been drawn through these points and control lines have been drawn on either side of the lower reach regression line. Control lines for the upper reaches have not been drawn because the lower reach lines almost include the values for the upper reaches.

Fig.15c. Sesarma catenata: As Fig.15b. For S.catenata control lines have been drawn about the regression line for the upper reach population only. Notation for Fig. 15b and c as in Fig. 14.

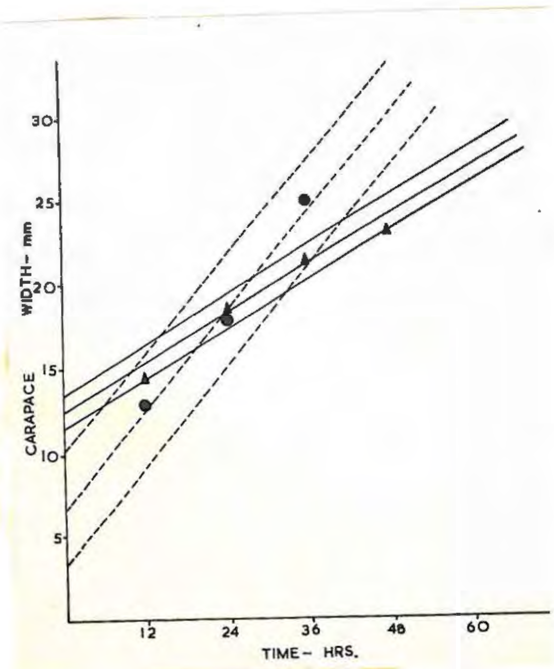


Fig. 15d. *Cyclograpsus punctatus* and *Sesarma catenata*. Graph comparing the data for the upper reach populations of the two species, taken from Fig. 15b and c. Control lines have been drawn on either side of both regression lines.

(The control limits in Fig. 15b, c & d are probably conservative in value. Regression lines have here been calculated in the usual way with such data, the variances of the means of the arrays around the grand mean being used rather than the variance of the individual data. The values of the Standard Errors of Estimates have been computed in the same manner and this will reduce the apparent variability of the population.)

ratio, although the exponent of this relationship is different for the two species.

4. That the long survival times observed for C.punctatus are due to the fact that the lagoon population includes exceptionally large individuals of this species.

3. Distribution in relation to Salinity.

General Methods and Limitations:

Resistance of the crabs to water of different salinities was investigated in three ways.

1. Rapid transferences of crabs into water of salinity lower than that of sea water.
2. Exposure to water of low salinity for periods of 12 or 24 hours followed by transference to sea water.
3. Exposure to water of progressively diminishing salinity.

The general design of these experiments entailing the transference of crabs from one salinity to another was such that two unforseen difficulties arose which necessitated the rejection of many observations. As a result an orthodox statistical analysis using probit technique cannot be undertaken, although probit-log time plots have been used to determine median times of survival.

The first difficulty was that crabs in water of low salinity, especially large C.punctatus, often fouled the water, either by regurgitation of liquefied gut contents or by excessive micturition. The water became yellow and gave off a sweetish odour, and the animals died within a few hours. In the early stages of the experiments the initial signs of this pollution went unrecognised, and this led to the death and subsequent discarding of many animals. It was later found that if the water was changed as soon as a yellow tinge appeared, as well as regularly every 12 hours, the effects of the pollution were successfully combated.

A further trouble was that in a few experiments the crabs reacted to the stress of low salinities by autotomising numerous walking legs. Since this caused extensive mortality, presumably owing to loss of blood, such experiments were immediately terminated.

Lest previous experimentation should have impaired the resistance of the crabs in any way, no crab was tested more than once. Similarly no specimen of sea water or diluted sea water was used more than once in case contamination might have occurred.

1. Rapid Transference.

These experiments were designed to determine whether or not the crabs are euryhaline and the extent of the salinity range which they will tolerate. Because of their estuarine environment, they are unlikely to encounter salinities exceeding that of sea water, and no experiments using highly concentrated water were attempted. Sea water collected from the Port Alfred sea front was diluted with tap water to produce solutions equivalent to 80%, 60%, 40% and 20% sea water. Taking the salinity of sea water to be 40‰ (it varies between 36 and 40^{0}/oo during the year) these are equivalent to 32, 24, 16 and 8^{0}/oo respectively.

The experiments were conducted using crabs both from the lower reaches (Lagoon4) and upper reaches (Stations S & T) of the estuary. Animals were kept in the water of their tanks (100% or 60% sea water, depending on locality) for several days and then transferred to clean 1000 ml beakers containing 600 ml of the diluted water or 0% sea water (tapwater). Controls were kept in 100% sea water. The results of experiments using crabs from stations S & T made it unnecessary to test the resistance of these animals to water of salinities other than 0%, 20% and 100% sea water.

Mortality was recorded every 12 hours and the experiments were terminated after 96 hours. The maximum carapace width of each animal was measured.

2. Exposure to Low Salinities followed by transferance to sea water.

Since the animals must be accustomed to the tidal alternations of low andhigh salinities, these experiments, with their exaggeration of natural conditions, were designed to show the ability of crabs to recover in sea water after exposure to water of lower salinity. Animals from Lagoon 4 only were used. After being placed as before in 0%, 20% and 40% sea water for 12 or 24 hours, the crabs were immersed in 100% sea water. Mortality was recorded every 12 hours and the duration of each experiment was 48 hours. The variability of the number of crabs used prevents the assessment of the significance of apparent interspecific differences, but where there were fairly large numbers of crabs exposed it is possible to note trends in the degrees of recovery of the two species.

3. Exposure to water of progressively diminished salinity.

A few simple experiments were performed, using animals from Lagoon 4 only, to see whether or not gradual decrease in salinity would have any effect upon the rate of their mortality in fresh water, as opposed to the rate when crabs were initially placed in fresh water. That is, it was proposed to investigate whether or not the two species could acclimate to water of low salinity.

After being for several days in sea water, crabs were immersed in 600 ml of 100% sea water, which was replaced after 12 hours by 80% sea water, after a further 12 hours by

Table IV Survival in Diluted Sea Water.

Locality.	Sea Water conc.%	No. of Crabs		Max. Survival Time (Hrs).		% Survival at 96 hrs.	
		C.punctatus	*S.catenata*	*C.punctatus*	*S.catenata*	*C.punctatus*	*S.catenata*
Lower Reaches (Lagoon 4)	0	18	18	36	36	0	0
	20	15	18	> 36	> 36	47	17
	40	12	14	> 36	> 36	92	36
	60	6	6	> 36	> 36	100	100
	80	6	6	> 36	> 36	100	100
	100	6	6	> 36	> 36	100	100
Upper Reaches (S & T)	0	14	16	72	60	0	0
	20	18	19	> 72	> 60	88	100
	100	9	11	> 72	> 60	100	100

60% sea water and so on until 0% sea water was reached. The experiments were terminated after 100% mortality had occurred. An additional experiment was conducted similarly using C.punctatus only, starting in 60% sea water.

Results.

1. Rapid transferences.

The results are recorded in Table IV and graphically, as percentage mortality with time (Figs. 16 & 17). These data show that of the two species C.punctatus from the lower reaches is more resistant to dilute sea water than S.catenata, which starts to die at least twelve hours before the former in salinities from 0-40%. Only in 0% sea water was there 100% mortality during the course of the experiments. It appears that for these crabs the critical salinity for C.punctatus lies between 20% and 40% sea water, while that for S.catenata is between 40% and 60%. Of the crabs from the lower reaches, C.punctatus is the more euryhaline, although both species can tolerate a wide range of salinities.

The crabs from the upper reaches, (stations S & T) (Table IV,Fig.17) where the water is always of lower salinity than sea water, show not only greater tolerance towards fresh and dilute water than their counterparts near the sea but also a greater range of tolerance, as they survive in 100% sea water. Table IV shows that lower reach samples of C.punctatus all die within 36 hours in 0% sea water, while those from the upper reaches survive for 72 hours.

Further analysis of the data given in Table IV involving the estimation of the median time of survival (M.T.S) from probit-logtime plots offers support for this view. Table V shows the M.T.S. of the crabs in low salinities.

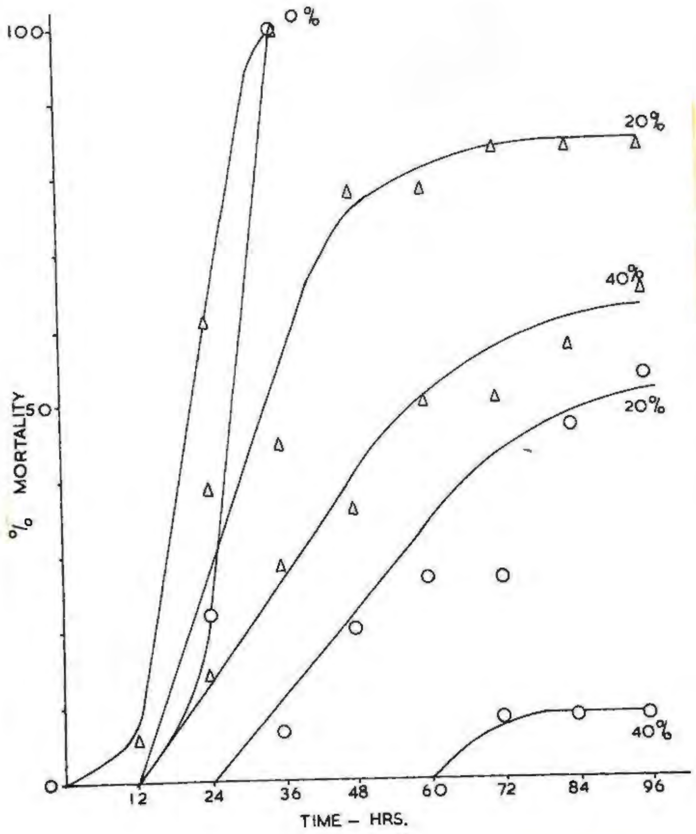


Fig. 16. *Cyclograpsus punctatus* and *Sesarma catenata*: Curves of percentage mortality with time for lower reach crabs exposed to salinities of 0%, 20% and 40% sea water. Notation as in Fig. 13.

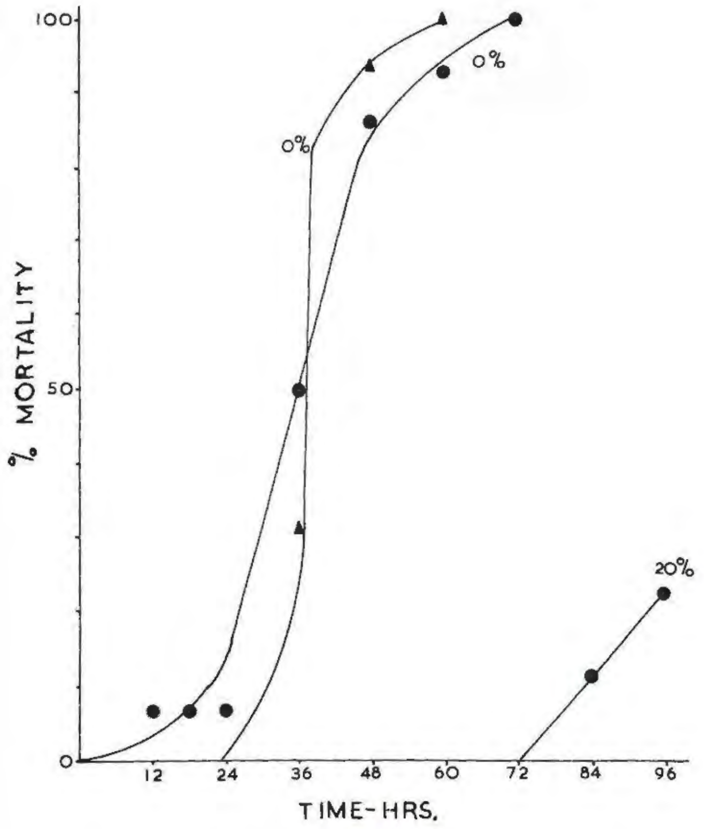


Fig.17. *Cyclograpsus punctatus* and *Sesarma catenata*: Curves of percentage mortality with time for upper reach crabs exposed to salinities of 0% and 20% sea water. Notation as in Fig. 14. During the course of the experiments no mortality was recorded for *S.catenata* kept in 20% sea water.

Table V. M.T.S. (hours) of the Crabs in low Salinities.

Salinity %	Lower Estuary (Lagoon 4)		Upper Estuary (St. S & T)	
	C.punctatus	S.catenata	C.punctatus	S.catenata
0	26	20	34	39
20	89	34	-	-
40	-	66	-	-

The blanks in Table V indicate that there was less than 50% mortality in the particular experiments. The data in Table V and the graph (Fig. 17) show that of the crabs from stations S & T, S.catenata appears to be the more resistant, the reverse of the situation found using members of the lower reach populations. This is in accordance with the observation that the colonies of S.catenata continue farther towards the tidal limit than those of C.punctatus.

Fig. 18, which is a graph of carapace width (in millimetres) against survival time, in 0% sea water, shows that there is little overall correlation between size and time of survival, although within each population there is a slight tendency for larger animals to survive longer.

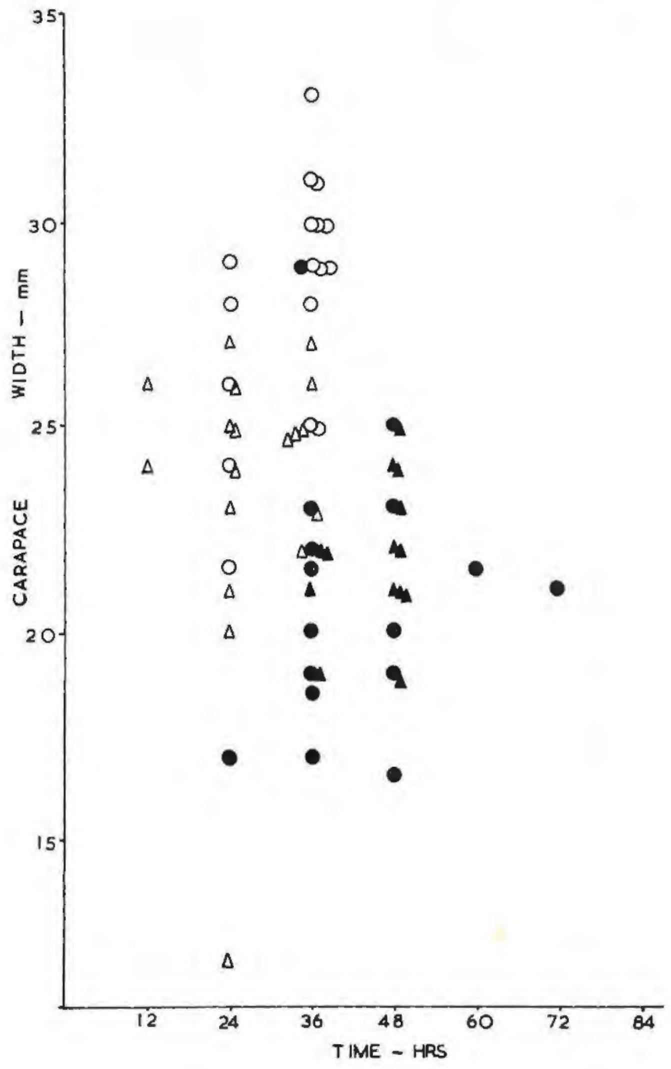


Fig. 18 *Cyclograpsus punctatus* & *Sesarma catenata*: Graph of carapace width with time to death in 0% sea water of crabs from both populations. Notation as for Fig. 14.

Table VI. Recovery after immersion in dilute water of members of the downstream population.

Initial Salinity %	Duration of initial Exposure (Hrs)	Species	No. of Animals	% Survival in Sea Water at end of Experiment (48 hrs).	% Survival in low Salinity after 48 hours, from rapid transference series.
0	12	*S.catenata* *C.punctatus*	39 16	31 75	0 0
20	12	*S.catenata* *C.punctatus*	10 10	100 80	22 80
40	12	*S.catenata* *C.punctatus*	10 5	70 100	64.5 100
0	24	*S.catenata* *C.punctatus*	16 35	0 31.5	0 0
20	24	*S.catenata* *C.punctatus*	13 23	77 66.5	22 80
40	24	*S.catenata* *C.punctatus*	15 9	74 83	64.5 100

2. Exposure to low Salinities for 12 or 24 hours followed by transference to sea water.

The results of these experiments are given in Table VI together with figures for mortality after 48 hours taken from the first rapid transference experiments for comparison. Graphs of percentage mortality against time have been plotted (Figs. 19 & 20).

These data show that after 12 hours' exposure to low salinities there is reasonable evidence of recovery in sea water and that even after 24 hours this evidence still persists, except for *S.catenata* started in 0% sea water. It is clear from the results of these experiments that both species should easily be able to withstand the more gradual and narrower salinity fluctuations imposed upon them by the tides in the natural habitat.

Little significance can be attached to apparent interspecific differences, but there seems to be a tendency for *C.punctatus* to recover more readily than *S.catenata.*

3. Exposure to water of progressively diminishing salinity.

Once the euryhalinity of the two species had been established, as well as the fact that the upriver crabs were adapted to low salinities without having lost the ability to survive in sea water, it was decided to test the adaptability of the down stream population.

The results have been plotted as before (Fig.21) and then, eliminating those animals which had died before being placed in 0% sea water, the curves of mortality in 0% have been drawn together with those from Fig. 13 for comparison (Fig. 22). The M.T.S. was obtained for each experiment. The data from these experiments are given in Table VII and the median times of survival from the first series of experiments are given for comparison.

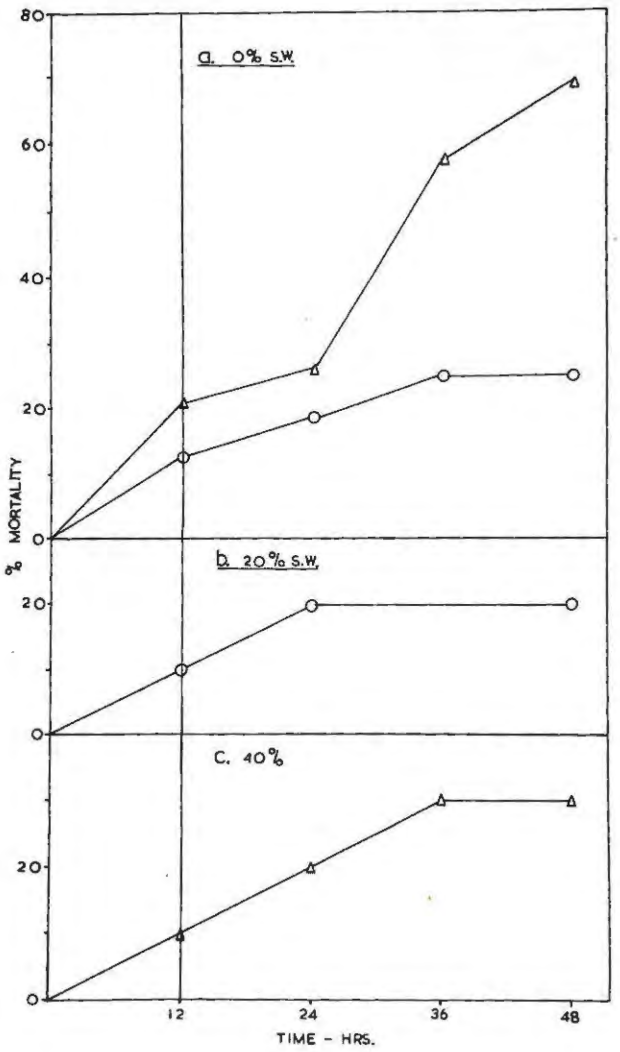


Fig. 19 a,b & c. *Cyclograpsus punctatus* & *Sesarma catenata*: Curves of percentage mortality with time of crabs transferred to sea water after 12 hours' exposure to water of low salinity. Fig. 19a,b & c show the curves produced using crabs initially immersed in 0%, 20% and 40% sea water respectively. Notation as in Fig. 13.

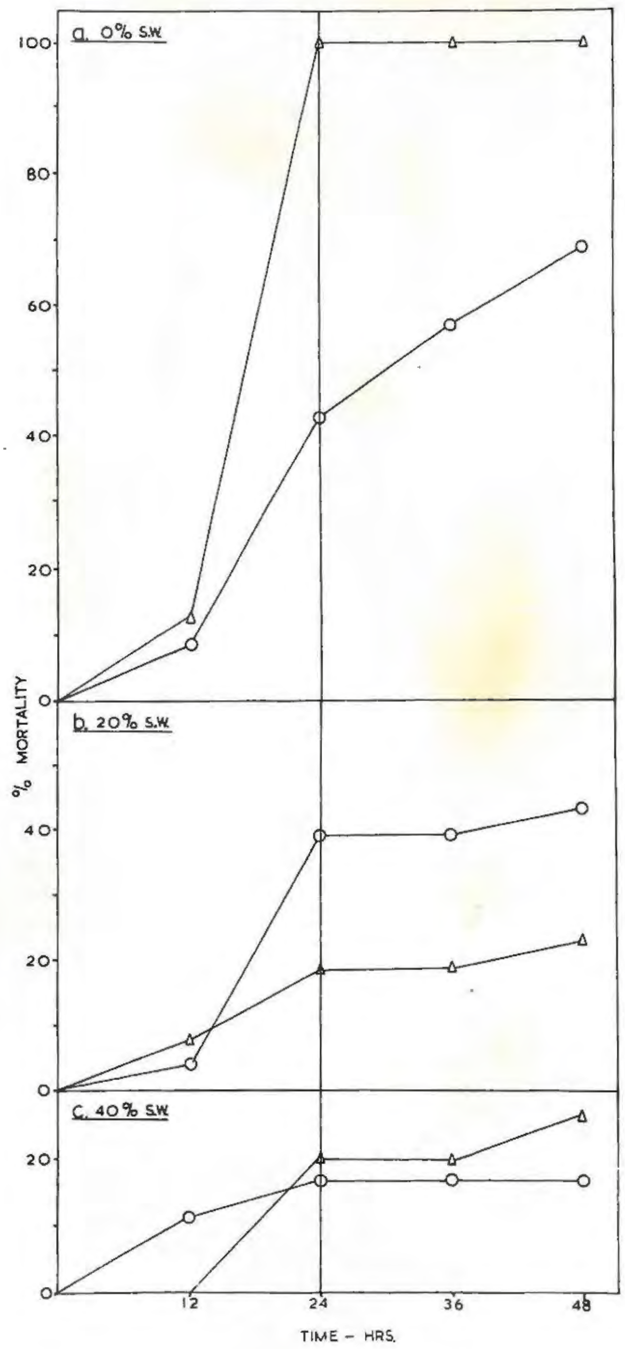


Fig. 20a, b & c. Cyclograpsus punctatus & Sesarma catenata. Curves of percentage mortality with time of crabs transferred to sea water after 24 hours' exposure to 0%, 20% and 40% sea water respectively. Notation as before.

Table VII. Data from third series of experiments.

Exp. Series.	Species.	No. of crabs.	Starting salinity %.	% Mortality Before Immersion in 0%.	Time before immersion in 0% sea water.	M.T.S (hrs.)
3	C.p.	15	60	6.7	36	22
3	C.p.	21	100	33.3	60	15
1	C.p.	18	0	-	-	26
3	S.c.	26	100	30.8	60	19
1	S.c.	18	0	-	-	20

The figures and graphs show fairly clearly that crabs in water which was diluted at twelve-hour intervals show no signs of acclimation to low salinities. Not only did they start to die before being placed in 0% sea water, but in 0% their mortality rates were similar to those of animals initially immersed in this salinity. At first sight it appears that the C.punctatus started in 60% sea water did in fact become acclimated. However, the M.T.S. leads to the conclusion that the increased survival time in this experiment may be due to an unusual degree of resistance in a few crabs and not to generalised acclimation.

Since the present study is not concerned with acclimation, further experiments on this phenomenon were not undertaken.

The facts suggested from these salinity resistance experiments are:

1. Both species are euryhaline.
2. In the lower reaches C.punctatus can tolerate a wider range of salinity than S.catenata.
3. In the upper reaches each has an increased range of tolerance, with that of S.catenata apparently exceeding that of C.punctatus.

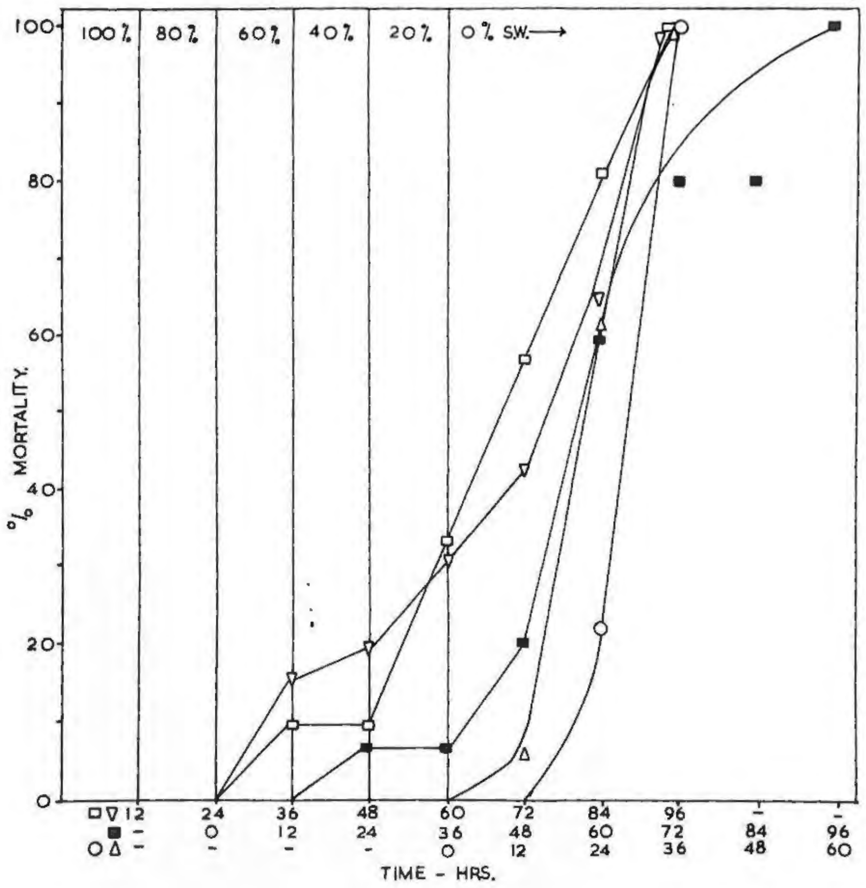


Fig. 21. *Cyclograpsus punctatus* and *Sesarma catenata*: Curves of percentage mortality with time of crabs immersed in water of progressively diminishing salinity. The mortality curves of animals started in 0% sea water have been taken from Fig.13 and included for comparison.
Circles = *C.punctatus* started in 0% sea water.
Triangles = *S.catenata* started in 0% sea water.
Open rectangles = *C.punctatus* started in 100% sea water.
Inverted triangles = *S.catenata* started in 100% sea water.
Closed rectangles = *C.punctatus* started in 60% sea water.

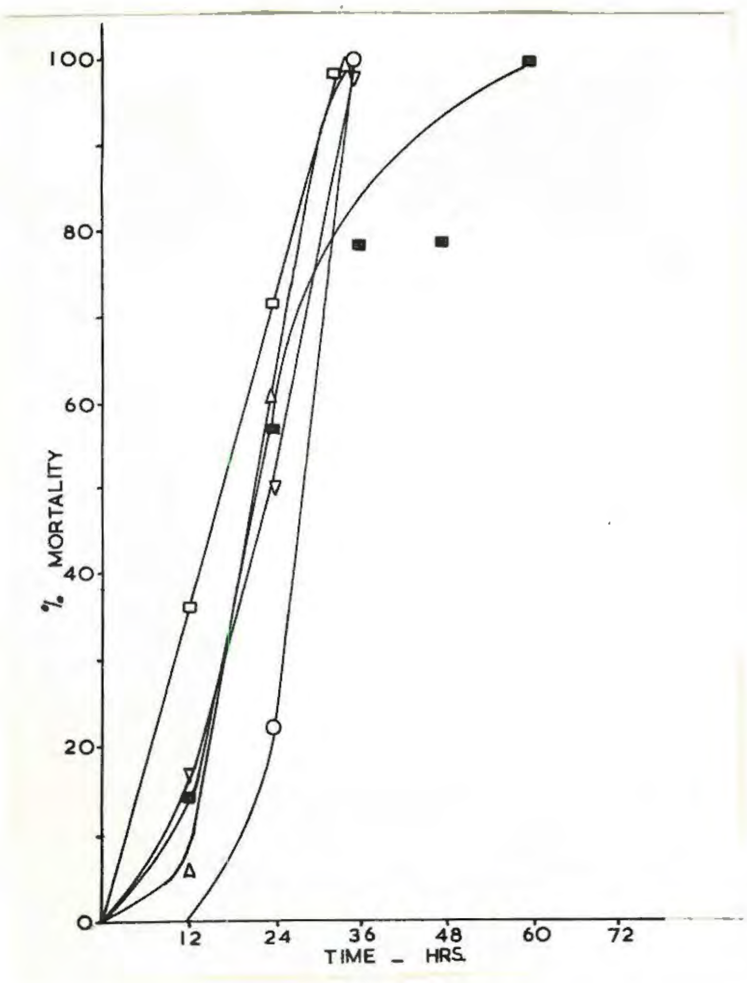


Fig. 22. *Cyclograpsus punctatus* & *Sesarma catenata*
The data in Fig. 21 have been replotted as if the animals had all been started in 0% sea water, i.e. those which had died before immersion in 0% sea water have been eliminated. Again, the curves from Fig. 13 have been included for comparison. Notation as for Fig. 21.

4. The ability of both species to withstand tidal salinity fluctuations has been established by exaggerating these fluctuations and noting that the crabs are able to recover in sea water.

III. DISCUSSION.

In Part I the distribution of the grapsoid crabs *Cyclograpsus punctatus* and *Sesarma catenata* in the Kowie River estuary has been examined in relation to certain major environmental conditions - terrain, vegetation, exposure at low tide (i.e. vertical height below H.W.S. level) and salinity. Field observations have been supported by experimental work wherever this was possible. In this study of the physical environment each factor was considered singly, but as Day (1951) has pointed out in a consideration of the distribution of a hypothetical burrowing animal, different factors may define the various limits of any habitat which contains well marked gradients. Thus the upper limit of vertical distribution of a burrowing creature may be set by exposure while the lower is determined by the quality of the substratum. In the analysis which follows an attempt is made to recognise the major factors which appear to limit the distribution of these grapsoid crabs, but it is important to realise that the analysis throws no light upon the relation between limitation and toleration. The analysis is concerned only with where the animals do live, not with where they are physiologically equipped to live. It must also be conceded that such an approach includes an element of speculation. It is possible to say for example, that an animal cannot extend beyond a certain vertical range because of exposure but to demonstrate the validity of this assertion beyond reasonable doubt is another matter. Furthermore it should be appreciated that the environmental factor which serves as a clue to the animal in limiting its vertical range may be related only indirectly to the stressful factor which is being avoided.

Barnard (1950) records that *S.catenata*, like the other members of the genus *Sesarma*, is adapted to a burrowing way of life, in estuaries, saltmarshes and mangroves. The work of Millard and Harrison (1954) and Day and Morgans (1956) confirm this. The present observations show burrowing to be extensive in the silty and sandy muds of the open river and Lagoon 4, but in the coarse, clean sand and rocky banks of Little Beach and the river mouth area S.catenata was never found.

C.punctatus, on the other hand, has been referred to in the literature as a "marine" crab able to invade estuaries and burrow there. Day and Morgans describe how it lives under stones and in crevices at the Durban Bay harbour entrance, and the species is present under stones on the beaches at Hermanus, Cape. (Scott, Harrison and Macnae, 1952).

Macnae (1957b) found C.punctatus inhabiting burrows in the Zwartkops River estuary, south of the Kowie River. In the Kowie estuary C.punctatus, as well as inhabiting burrows in the same places as S.catenata, also lives beneath rocks and stones lying on the substrate in the river mouth, Little Beach and farther upstream. Indeed, any object, such as a log or old tin may be utilized by the crabs as a shelter.

Holme (1949) has shown from his studies of the Exe estuary that coarse, bare sand supports a very impoverished fauna. Since neither of the two grapsoid crabs inhabits the sandy areas of Little Beach or the sea-shore, the presence of sand banks may act as a factor limiting distribution. This is supported by the observation that although C.punctatus digs holes under stones lying on mud, the sand beneath the stones at Little Beach and in the river mouth remains undisturbed by the animals living there. Apart from particle size, the moisture content of the sand and of the substrate in general may be of importance here. Reid (1932) maintains that differences in the level of soil saturation correspond with differences in the animal population. The sand at Little Beach is either very fluid where it becomes wetted, or dry and powdery above the water's edge. In neither condition is it favourable for the digging of burrows. Furthermore, observations in other parts of the estuary have revealed that most burrows occur where the mud is of a firm consistency and not soft and "slurry".

The following question now arises: Does the vertical distribution of the crabs depend merely upon the structure and consistency of the substratum, or is some other factor involved? The results of the desiccation resistance tests and vegetation surveys would seem to indicate that exposure to the atmosphere and plant cover are both important in this connection.

It has been found that resistance to desiccation in these crabs is largely governed by the surface/volume ratio, i.e. that survival time out of water increases with the size of the animals, irrespective of species. *C.punctatus* grows to a larger size than does *S.catenata*, and the maximal survival times recorded were for the largest specimens of C.punctatus. On this basis it is not unreasonable to suppose that were there any vertical zonation of the animals with respect to water level, such zonation might be correlated with size. No burrows occur above H.W.S. level, where the substrate is for the most part hard and dry. Maximum burrow density is usually in the vicinity of normal high tide level, although lower regions may be colonised on the broad, gently sloping mudbanks of the open river. Observations made in Lagoon 4, however, were of interest with regard to possible zonation. At and above the salting cliffs marking normal high water level the most common inhabitants of the banks were large *C.punctatus*, whose burrows were moist, but never contained free water.

At the bases of the salting cliffs and in the narrow mudbanks were holes containing water and medium to large sized members of both species, while a lowlying island in the lagoon which was completely submerged at every high tide possessed small, invariably water-logged holes which harboured very young crabs of the two species. Just as the plant succession on the banks of the lagoon was sharply defined in many places due to the narrowness of the mudbanks and the steep elevation above H.W.S., for the same reason, this zonation of the animals is more apparent here than in the open river.

At the places examined on the river banks the distribution was sparse as compared with that in Lagoon 4. When the breadth of the mudbanks exposed at low tide is considered, it is not surprising that zonation, if any, is obscured, and that most burrows are some distance below normal high tide level. Animals situated at high water level may have to endure far greater desiccation than their counterparts in Lagoon 4 (where the normal tidal range is relatively small) while the tide is low, whereas further down the tidal range the time of exposure is reduced between high tides. Although burrows on the river banks occur well below normal high tide level they are never so low on the banks that they would be covered to a depth of more than a few inches when the tide comes in.

It was noticed that these river bank burrows coincided very closely with the presence of Spartina fields, with their mats of roots and stolons consolidating the substratum. This supports the idea that burrows are not constructed where the terrain is unstable. Since, however, mudbanks devoid of vegetation are so rarely inhabited, even when they are of firm consistency, it is likely that the vegetation type also plays some part in determining distribution. The crabs can move about freely between the tufts of the *Spartina* and it may be that the camouflage and shelter which these afford contribute to this preference.

The most densely populated areas occur in the *Arthrocnemum* belt and on the salting cliff faces, which, though no vegetation grows upon them, are usually covered with an overhanging fringe of *Arthrocnemum*. Not only does this plant hold the substrate together with its ramifying root systems, but the mass of stems prostrate on the surface provides shade and helps prevent evaporation of the soil water. *Arthrocnemum* also offers excellent protection for the crabs, which, as they run to and from their burrows are completely hidden by the erect portions of the plants. Both species have been observed to feed upon *Arthrocnemum*. *C.punctatus* has also been seen feeding amid the drifted algae in Lagoon 4.

The experimental evidence shows clearly that salinity plays an important part in the horizontal distribution of the crabs. The upper and lower reach specimens represent two distinct populations with respect to salinity tolerance. At neap tide the salinity varies only slightly from that of sea water (about 40°/oo) in the lower reaches, while in the upper reaches salinities between 12-17°/oo were recorded. Salinity changes at spring tide were distorted by heavy rain in the lower reaches on 10th March, 1963, but although in some places the salinities dropped to below 5°/oo at low tide, e.g. at Station N, sea water salinity was re-established at high tide in the open river. Despite evidence of dilution by rain at certain lagoon stations, the salinities in the lagoons remained close to that of sea water. During spring tide the salinities at the two upper reach stations ranged between 12-22°/oo.

The salinity resistance tests showed that the critical salinity for lower reach *C.punctatus* lies between 20% and 40% sea water (8-16°/oo approx.) , while that for *S.catenata* is between 40% and 60% (16-24°/oo). The critical salinities for both species from upriver are near 20% sea water (16°/oo), and the results indicate that here *C.punctatus* is less resistant to low salinities than is *S.catenata.* The upper limit of *C.punctatus* is eight miles from the river mouth, at Station S, where the minimum and maximum salinities determined from the samples were 14°/oo and 22°/oo. *S.catenata* penetrates beyond Station T (12-20°/oo).

It is evident, therefore, that the range of salinity tolerance of lower reach crabs is more than adequate to cope with the salinities normally encountered in this region, and that the increased euryhalinity of upriver crabs is compatible with the salinities prevalent in the upper reaches at the times of sampling. It is moreover interesting to note that the results suggest that both species extend to the limits of their physiological tolerance, though clearly closer study is needed to define more exactly both the physiological and ecological boundaries.

There is the possibility that salinity affects vertical as well as horizontal distribution. The salinity of the environment at any level of the intertidal range is fairly constant between spring tide cycles, not only because the particular point is covered at each high tide by water of the same depth and therefore of the same salinity, but also because at ebb tide the water retained in the muddy foreshore is of higher salinity than the receding waters (Reid, 1932; Day, 1951). Alexander, Southgate and Bassindale (1933) found that the salinity change in the exposed mudbanks of the Tees and Tay estuaries lagged behind that of the outflowing water at the same distance from the sea. Since the water is of maximal salinity at high tide, animals inhabiting the banks at this level would encounter only this salinity. The two grapsoid crabs do exhibit a tendency to live near high tide level, but the rapid transference and recovery experiments show in effect that they are not of necessity confined to this more or less stable salinity level as they are well fitted physiologically to withstand the gross salinity changes encountered in the open tidal water, at least near the shore. The present observations and those of Macnae (1957b) in the Zwartkops estuary, point to the fact that the burrows are used only as shelters which the crabs leave when foraging for food. S.catenata especially is often to be seen running or basking on the mudflats and at the edge of the receding water. Salinity as a factor governing vertical distribution would seem to be of minor importance compared with the type and degree of saturation of the substrate and with the vegetation.

The rapid transference experiments show that, although all the animals eventually die in waters of low salinity, heavy mortality did not commence until after at least 12 hours' exposure to tap water. These figures contrast markedly with values for Pachygrapsus transversus obtained by Pearse (1929). This species, although it readily tolerated salinities greater than 30% sea water, died within less than three hours in fresh water. The ability of C.punctatus and S.catenata to withstand exposures to water of low salinity for longer periods, and to recover when returned to sea water, is an adaptation which might be extremely useful during heavy rains. Even so, such prolonged exposure to completely fresh water is a most unlikely occurrence, at any rate in the lower reaches where the usual salinity pattern is re-established at high tide.

The lagoon populations present something of a problem. Why is it that Lagoon 4 contains more animals per square yard than any other locality studied, while, apart from a few *C.punctatus* in Lagoon 1, the crabs are absent from the east lagoons?As Holme (1949) has remarked, sheltered areas of estuaries (such as these lagoons) are richly supplied with organic matter and the two species, especially *S.catenata*, held by Macnae (1957b) to be a detritus feeder, should flourish in these conditions. Organic matter is abundant in all four lagoons, the terrain is very similar and likewise the vegetation. The major difference between Lagoon 4 and the rest of the estuary is that although there is regular tidal circulation, its situation and blind nature permit little variation in salinity. Osmotic stresses are thus minimal and the plentiful food and the shelter afforded by plant cover can be used to best advantage.

The eastern lagoons, however, by virtue of their almost complete isolation, are subject to evaporation in dry weather and flooding in rainy periods. The presence of food would be of little use to animals unable to tolerate long spells of extremes in salinity. Experimentation has shown that of the lower reach population *C.punctatus* has a lower critical salinity than *S.catenata.* No experiments involving salinities higher than that of sea water were attempted, but it was observed that when crabs were left undisturbed in beakers containing 600 ml undiluted sea water, *S.catenata* died within a few days, while large specimens of *C.punctatus* were still active after three weeks, when at least one third of the water had evaporated. If this indeed presents a true picture, undistorted by mortality due to lack of oxygen, for there was no evidence of the pollution customary in low salinities, it indicates that *C.punctatus* is able to withstand the periods of high salinity produced at Lagoon 1 by evaporation.

This lagoon is the least isolated of the three and it may be that the longer periods of extremes in salinity prevalent in Lagoons 2 and 3 are beyond the range of tolerance of C. punctatus, thus accounting for the absence of this species. Undeniably this is largely a theoretical argument, and there is no reason to suppose that salinity is the only factor rendering the eastern lagoons unsuitable for habitation. The relations of the animals to temperature have not been investigated, but it was noted that crabs left out of water died more quickly when the maximum atmospheric temperature was 21°C than when it was cooler by 5°C. Both air and water temperatures at the low-lying east lagoons are considerably higher than over the open estuary during the summer months, while in Lagoon 1, where water exchanges with the river are the most marked, it is likely that temperatures are not so high as in Lagoons 2 and 3.

Still other factors prohibiting the colonisation of Lagoons 2 and 3, and to an extent, Lagoon 1, such as the chemical composition of the substrate, influenced by the decay of organic material and the stagnation of the water in various places, could be involved.

It can be concluded from this discussion that the distribution of the two grapsoid crabs in the Kowie River estuary is dependent upon a combination of ecological factors. All of the factors studied are of importance in determining this distribution, and others may be concerned to a greater or lesser degree.

Finally, it is possible to consider apparent evolutionary trends in the light of the work of other authors. Gross (1955) recognises a strong correlation between the ability of crabs to live on land and their ability to maintain the osmotic pressure of the blood more or less constant in environments of different salinity.

He and other workers (e.g. Jones, 1941) have found in their studies of semi-terrestrial sea shore crabs that these "transitional land forms" all display both hyper- and hypo-osmotic regulation. During the evolution of a semi-terrestrial habit it appears unlikely that such animals would have encountered dilute waters, and Gross could offer no explanation of their ability to maintain the internal concentration higher than that of the external medium. Hypo- osmotic regulation in these crabs also puzzled the two authors, for although both had observed crabs to evade predators by hiding in tide pools of higher salinity than sea water, one of the most prolific species, Pachygrapsus crassipes, showed a "strong dislike" of concentrated sea water and rarely entered pools with concentrations greater than observed blood values.

Jones (1941) suggested that hypo- osmotic regulation in terrestrial animals prevented the high salinities consequent upon evaporation at the gill surface from affecting the body fluids. Gross (1955) proved that this was not the case, however, as the volume of salt produced in this way was too small to be harmful, even if it were totally absorbed into the body fluids.

Water loss is the major problem assailing animals leaving an aquatic environment for a terrestrial one, and water conservation is of prime importance to these animals. In view of this Gross (1955) put forward the view that hypo- osmotic regulation in itself is not really concerned here because hypertonic media are rarely encountered in nature. He believed rather that the mechanisms involved were concerned with water conservation and that hypo-osmotic regulation is a "laboratory artefact" because it involves the same mechanisms - excretion of hypertonic fluids from kidney, gills or rectum. This view, however, encounters the difficulty that our knowledge of the mechanisms of hypo-osmotic regulation in crustaceans is limited.

In *Pachygrapsus crassipes* studied by Gross (1955) active uptake of water from a hypertonic medium can occur and this clearly cannot be regarded as a consequence of an adaptation to water conservation on land. Again, although the urine elaborated by *P.crassipes* living in a hypertonic medium is more concentrated than in normal sea water, the increase in osmotic pressure is less than 10% and this is largely due to an extensive removal of magnesium ions (Prosser, Green & Chow, 1955), an observation more suggestive of ionic regulation than water conservation.

Subsequent observations on populations of *P.crassipes* and *Hemigrapsus oregonensis* trapped in large numbers in a hypersaline lagoon temporarily cut off from the sea near San Diego, California, led Gross (1961) to the opposite view. He now suggested that lagoons of this kind might have afforded ideal conditions for the evolution of terrestrial crabs. Selective pressures would be present favouring the development of the abilities to regulate hypo-osmotically (high salinities during dry weather) and hyper-osmotically (lower salinities when the connection with the sea is re-established and during heavy rains), and to breathe air (when anaerobic conditions brought about by stagnation would force animals capable of so doing to leave the water). Gross (1961) thus postulates the existence during evolution of lagoons similar to the one described above, in which the ancestors of the present terrestrial and semi-terrestrial forms lived. He believes this to be the best explanation for the osmo-regulatory abilities of such crabs. Similarly, Edney (1960) has emphasized that the route to the land via the littoral zone directly is difficult because the problems of terrestrial adaptation are imposed at once, and from this it is clear that intermediate hypersaline pools would do much to alleviate the situation.

In an estuary two or possibly three pathways of terrestrial emergence are offered to a decapod. The one lies by way of the fresh waters, the route adopted by *Potamon.* As Dandy and Ewer (1961) have emphasized, this is not the way of success, for the requirements for water loading on land conflict directly with the requirements for osmotic regulation in fresh water. The second pathway is that of frontal attack. The semi-diurnal tidal salinity fluctuations and the possibility of being trapped in temporary hyper-saline lagoons will be forces not only selecting the development of both hyper- and hypo-osmotic regulation, but also probably a tissue tolerance to variations in the osmotic pressure of the blood which will enable the crabs to resist the most immediate physiological effects of water loss. In *C.punctatus* and *S.catenata* we have forms certainly capable of hyper-osmotic regulation, and, in *C.punctatus* at least, probably very considerable hypo-osmotic regulation. An estuary thus provides an excellent starting point for the invasion of the land and these two partially terrestrial grapsoid crabs may be said to have begun the journey away from the water.

Edney (1957) stresses the grave problems of this direct attack. There is, however, a third route to the land discussed by Alexander (1957) in relation to the evolution of the terrestrial Arachnida. She believes that some forms, instead of leaving the water and proceeding directly on to the land surface, initially burrowed into the banks and there, in greater protection, evolved further terrestrial adaptations before emerging to a place in the sun. Clearly from their habits this pathway is opened to the grapsoid crabs.

Three problems face terrestrial arthropods. The first is water conservation, which has been met in the most successful forms by the development of a fully impermeable cuticle. No terrestrial crustacean has yet satisfactorily solved this problem. The second is water loading. Ideally a terrestrial animal should be able to make good its water losses from transient sources of water. Crabs adapted to hyperosmotic conditions might, formally, be able to accomplish this feat as, insofar as it has been studied, they have the ability to absorb water actively through the integument. The site of this absorption has not been identified, however, and if, as is probable, it lies in the branchial or branchiostegal epithelium, then it does not profit the animal since it cannot exploit such important water sources as dew. Finally there is the problem of respiration. As will be shown in Part II of this thesis the Grapsidae and especially the Sesarminae, the small group to whichthe present species belong, have developed a form of aerial respiration. This type of respiration depends chiefly upon the re-oxygenation of water carried on to the land in the gill chambers, and as such exposes the animals to heightened water loss by evaporation. Plainly this is an unsuitable foundation on which to base a fully terrestrial life, and it is perhaps this factor which has prevented the Grapsidae from being as successful on land as the Gecarcinidae.

PART II

I. INTRODUCTION.

In Part I of this thesis the distribution of Cyclograpsus punctatus M.Edw. and Sesarma catenata Ort. in the Kowie River estuary was studied in relation to some environmental factors. It was found that the total population along the river banks has two extremes; at both ends one species lives without the other. S.catenata penetrates farther upstream than does C.punctatus, and vice versa. Between these extremes the two species occur together.

An aspect of the ecology of these two crabs which has not yet been considered is their relation to the animal community. In general terms this includes a complete survey of the estuary and all the animals present, as well as studies of food chains, predator-prey and parasite-host relationships. The present work does not pretend to deal with this enormous field, but instead it is hoped to throw some light on the close relationship of the two species to each other, for this in itself presents an interesting ecological problem.

It was felt that the nature of their relationship might become clear through a comparative study of some of the important facets of the life and habits of the two species. Three of these were selected for investigation: respiration, feeding and burrowing. It is obvious that biological work of this kind should be based on a thorough knowledge of the relevant morphology of the animals concerned, and for this reason the following report begins with an account of their general morphology and the detailed morphology of certain of their appendages. This and the succeeding sections (which cover the functional and behavioural aspects) are discussed fairly independently of one another. As a result the final discussion can be given over almost entirely to the broader problem of ecological interrelationships, and to an assessment of the significance of the biological work in this respect. To be at all meaningful it is essential that the ecological terminology used in such a consideration should be clearly understood, and it is proposed to deal with this here.

Some years ago a concept concerning closely related species living in the same locality was originated by Gause. Gilbert, Reynoldson and Hobart (1952) examined Gause's so called "theorem" and deplored the many different formulations (and hence interpretations) of it which have been made by various ecologists as somewhat misleading. Macfadyen (1957) takes the theorom to mean that "two animals with closely related habits cannot exist together in the same ecological 'niche'"., and remarks that "'Gause's theorem' is the term very widely used to signify the theme which was, perhaps, first enunciated by Darwin-' 'As the species of the same genus usually have, though by no means invariably, much similarity in habits and constitution and always in structure, the struggle will generally be more severe between them, if they come into competition with each other, than between the species of distinct genera.'"

It is unfortunate that the word niche has come to be used and misused in so many different ways. Elton (1927) used the term "to describe the status of an animal in its community, to indicate what it is doing and not merely what it looks like ... the niche of an animal means its place in the biotic environment, its relations to food and enemies." Thus the idea of a niche is a purely ecological one and not taxonomic.

Accepting Elton's broad concept of the "niche" it must be realised that any further analysis of this concept rests upon the way in which the niche is utilized by different animals. Elton (1927) acknowledges that the term can be used in a less all-embracing fashion. We can speak for example of the "carnivore niche", and this can be further subdivided into niches which give a more accurate definition of the feeding habits of the animals. Thus there is the niche occupied by carnivores which prey on small mammals as opposed to that occupied by predators on insects. On this basis, then, it might be considered that any two animals which do the same things occupy the same niche, and conversely, that any two animals doing slightly different things occupy different niches. It is in this latter sense that Macfadyen (1957) used the word in defining "Gause's theorem." Surely, however, we cannot use the term which originally had such vast connotations in such a limited way. If two closely related animals which are living in the same locality both prey on small mammals, for example, they occupy the same niche in accordance with Elton's principle. Should it be found on closer examination that one feeds on mice and the other on rats it could be said either that the niche has been divided into two smaller niches, or that the predators are using the same niche in different ways and in so doing have avoided competition for their food. This second interpretation would seem to be the more reasonable in view of the original definition.

It is in this way that the problem of the relationship between the two grapsoid crabs will be approached. These animals are closely related in that besides belonging to the same brachyuran family, they are both members of the small subfamily Sesarminae. They are similar in size and form and where they occur together on the banks of the Kowie River estuary every hole contains crabs of both species. Both are present in large numbers and their distribution with regard to those environmental factors studied is very much the same. Certain questions must therefore be answered in this connection:

1. Do these two species occupy the same niche - i.e. are they both herbivores or carnivores or can they otherwise

be distinguished in some equally definite way?

2. If they both occupy the same niche in this sense, are they feeding on the same food, thereby introducing the possibility of competition, or do they exploit the niche in different ways?

II. MORPHOLOGY & BIOLOGY.

1. Morphology.

(a) Aspects of general morphology and coloration.

Barnard (1950) has described the general morphology of *Cyclograpsus punctatus* M.Edw and *Sesarma catenata* Ort., and has defined the systematic position of these two species. Both are typical grapsoids, with the somewhat flattened carapace and the gap between the third maxillipeds common to the family Grapsidae. The oblique hairy ridge on the third maxilliped classifies them further as members of the sub-family Sesarminae.

C.punctatus has the lateral margins of the carapace rounded and the dorsal surface fairly smooth, while the carapace of *S.catenata* is squarish, the lateral margins are slightly convergent posteriorly, and the surface bears diagonal groovings laterally and various protuberances of which the most prominent are the four post-frontal lobes or bosses. Both species have seven well-defined abdominal segments.

It was noticed that colouration of *C.punctatus* from the Kowie River estuary was more or less constant and independent of habitat. This does not accord with Barnard's (1950) observation that brown, greenish and violaceous tints are common in mud-burrowers, while greys, buffs, oranges and pinks are consistent with the shore-dwelling habit. The usual colour pattern of the Kowie animals was as follows: carapace - dark grey to black, with white mottlings; upper surface of limbs-densely covered with reddish brown speckles; lower surfaces of body and limbs-deep cream. Markings were generally more distinct in large specimens than in young crabs, and appeared to become blurred and pale shortly before exuviation (cf. Broekhuysen,1941)

The widest part of the carapace of *C.punctatus* lies approximately half-way along its length. Measurements of the maximum carapace width of numerous large animals were made using vernier calipers and the greatest widths recorded for males and females were 36 and 32 mm respectively. Barnard (1950) states that male crabs may attain a breadth of 38 mm, but that the maximum breadth of females is only 26 mm.

The carapace of S.catenata was generally deep purplish black in colour and the upper surfaces of the chelipeds purple or maroon merging into the bright orange or yellow of the lower portions of the "hands". The walking legs were heavily mottled with dark grey or brown, and the upper surface of the body was pale grey. A few young crabs were paler, and speckled with grey or brown. This colouration rarely occurred, and would not account for Barnard's (1950) remark that the species as a whole is characterised by being brown in colour.

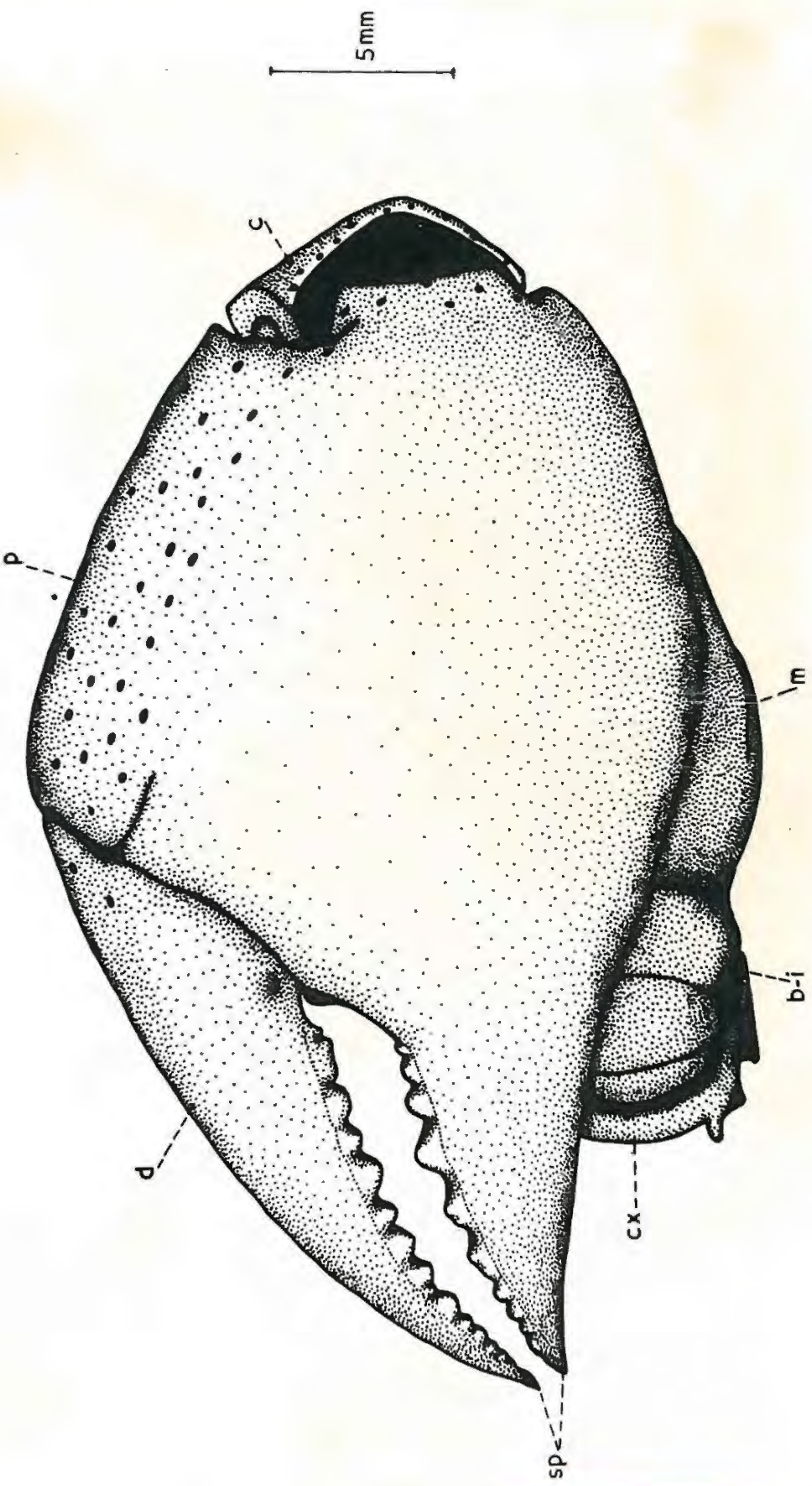
Measurements of maximum carapace width were taken anteriorly as the distance between the edges of the projecting post-orbital teeth. The largest male measured was 29.8 mm in width, and 26.7 mm was the greatest breadth found in a female. These figures are considerably larger than those quoted by Barnard - 25 mm and 17 mm respectively.

(b) Morphology of the Chelipeds and Mouthparts.

The chelipeds and mouthparts of a burrowing decapod crustacean are all concerned to a greater or lesser degree with feeding, respiration and the digging of the holes in which the animal lives. In order to obtain the clearest possible picture of these activities in the two grapsoid crabs, therefore, the morphology of the chelipeds and mouthparts of both species have been studied. The chelipeds were examined under a binocular microscope and drawings of different aspects of those of both male and female crabs were made. Before the mouthparts were removed the legs of crabs which had been preserved in 50% alcohol were cut off and discarded, and the crabs were boiled for an hour in 25%KOH. This was followed by a 30 minute rinse in running tap water. As a result of the potash treatment the cuticle was now soft and pliable, and the carapace and branchiostegite could be stripped away. The mouthparts and their delicate lobes and gills were thus exposed and were gently taken off, one by one. Smaller and more membranous appendages were progressively dehydrated in alcohol of increasing concentration, and after having passed from absolute alcohol to Xylene, were mounted in Canada balsam on glass slides. This method of mounting was not suitable for the large, heavily sclerotised third maxillipeds and mandibles. Semi-permanent preparations were made of these mouthparts. A little glycerine jelly, made up as described by Carleton and Drury (1957), was melted on a slide, the specimen was placed in the molten jelly and was covered with a cover slip. The jelly set within a few minutes, and the preparation was sealed with gold size. Since glycerine jelly mountant is an aqueous medium, there was no need for dehydration. None of the mouthparts was stained.

(i) The Chelipeds: In both species the chelipeds of the male are larger and more powerful than those of the female. Barnard (1950) describes the chelipeds as sub-equal, but present measurements of the chelae of numerous animals show that the right and left chelae are very often identical in size, and any marked difference between them is usually a reflection of the regeneration of a new limb after autotomization.

Pearson (1908), describes the form and modes of articulation of the segments of the cheliped of *Cancer pagurus*, and since these are similar for all Brachyura they will not be discussed here.



<u>Fig.23a.</u> <u>Cyclograpsus punctatus</u>. Outer view of the male cheliped in the flexed position.
d. = dactylus (finger); m. = merus.
p. = propus (hand); b-i. = basi-ischium;
c. = carpus (wrist joint); cx. = coxa;
sp. = spoon-shaped tips of finger and thumb.
Note pigmentation on upper surface of hand.

Fig. 23b. *Cyclograpsus punctatus.* Inner view of male cheliped in the extended position. Note the raised row of large tubercles on the concave "palm" of the hand, the curved row of bristles on the inner face of the merus (m.i.), the ridge separating this face from the ventral face (m.v.) and the sheet of coxal hair lying across the basi-ischium.

Cyclograpsus punctatus: The outer face of the "hand" of a male crab (35 mm carapace width) is shown in Fig. 23a. The hand is broad and smooth, and the gape between the strongly toothed finger and thumb is such that they meet only at the tips. The tips, which are hard and sharply pointed, are hollowed out into oblique "spoons", whose outer cutting edges come together when the chela is closed.

The inner surface of the cheliped in the extended position is represented in Fig. 23b. The dorsal surface of the coxa bears a fringe of stout, distally-pointing hairs, partially covering the basi-ischium. The merus is triangular in cross-section, with three laminarly expanded faces. The apex of the triangle is dorsal, and the inner face possesses a longitudinally curved row of short, stiff bristles. A longitudinal tuberculate ridge separates this face from the ventral face of the segment. The carpus is short, and the hinge-like articulations with merus and propus permit the chela to fold double but do not allow complete extension. The palm of the hand is concave, except for a strong median elevation bearing proximally a longitudinal row of three to five large blunt tubercles. The concave regions of the hand correspond to the positions of projections on the other segments when the limb is fully flexed.

In all the essential features the chelipeds of the female are extremely similar to those of the male. Outer and inner views of the cheliped of a female 28 mm in carapace width have been included for comparison (Fig. 24 a & b). The limb is smaller and less powerfully developed than that of the male, the teeth are weaker and more uniform in size, and the gape between finger and thumb is comparatively narrow. The wrist and hand are minutely pitted, and fairly large pits flank the outer edge of each tooth row (see Fig. 24a) and pits are scattered near the finger joint.

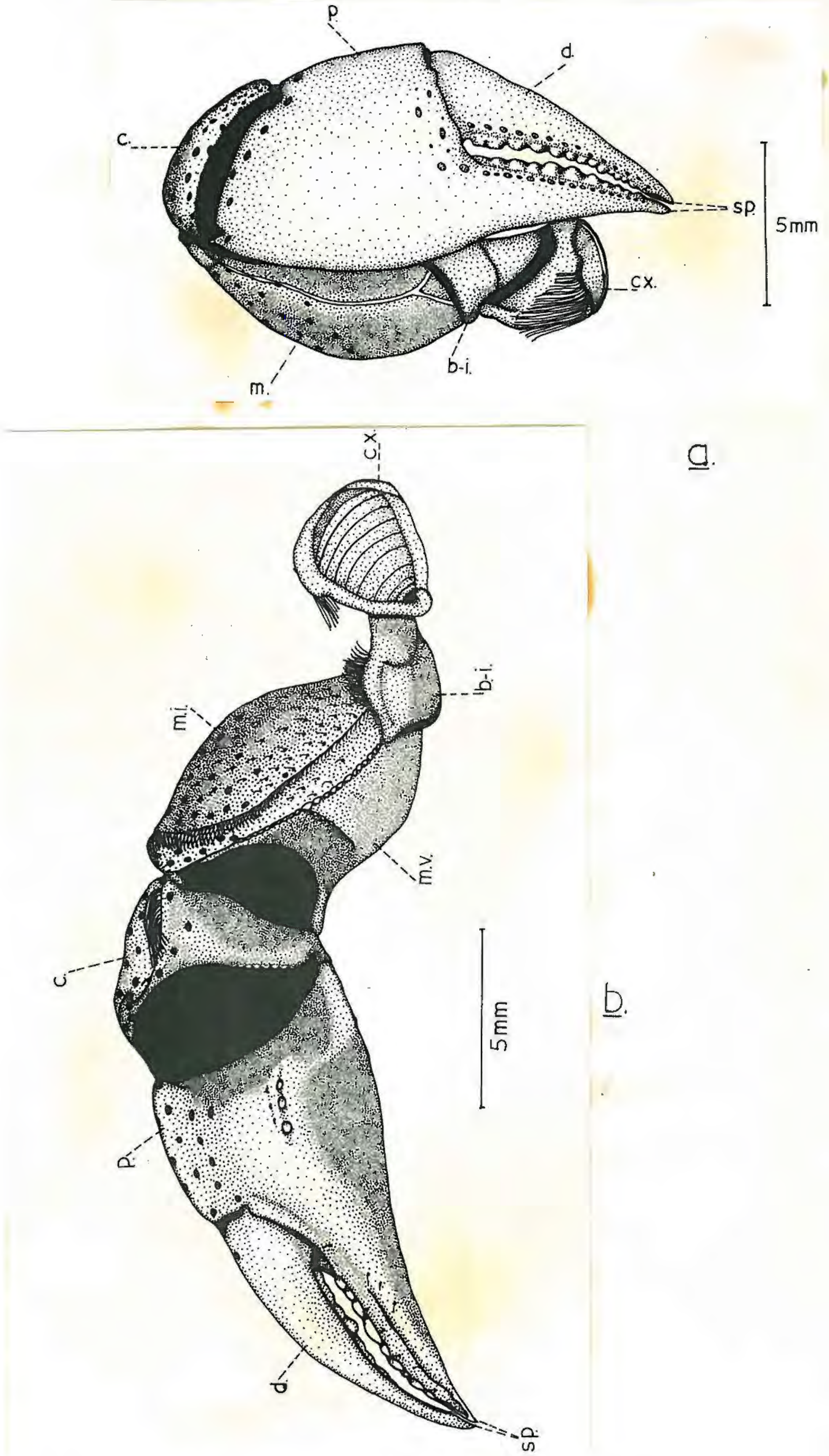


Fig. 24 a & b. *Cyclograpsus punctatus*: Outer and inner views of the female cheliped. Note the overall similarity to the male appendage. The female cheliped is relatively small and weak and the distribution of hair is slightly different from that of the male. Note pitting along the outer margins of finger and thumb.

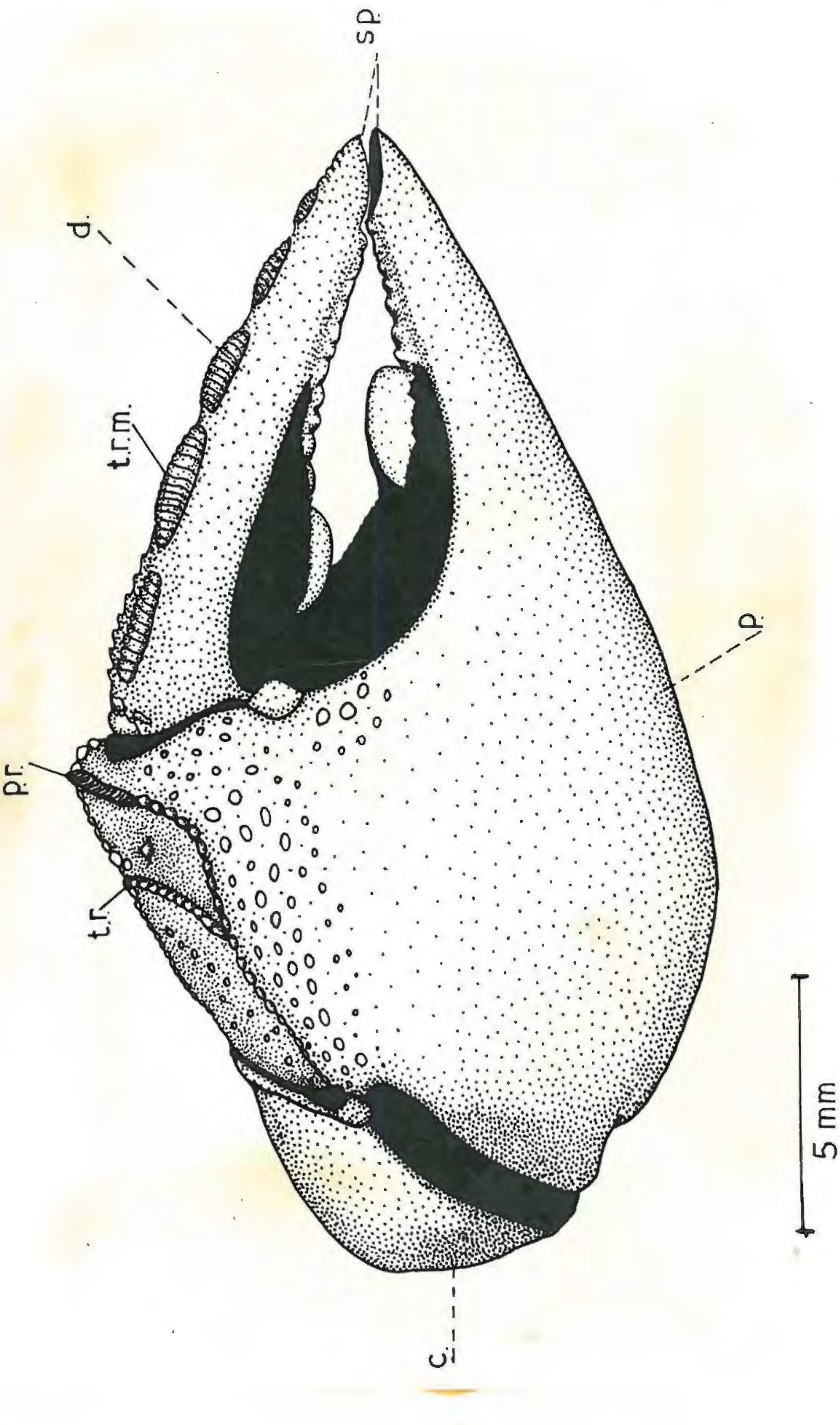


Fig. 25a. *Sesarma catenata.* Outer view of the male hand. Note the heavy sculpturing, the masses of hair on both finger and thumb at the hinge, and the rhomboidal area on the upper part of the hand, outlined by the pectinate (p.r.) and tuberculate (t.r.) ridges.
t.r.m. = milled tubercle on the upper surface of the dactylus.

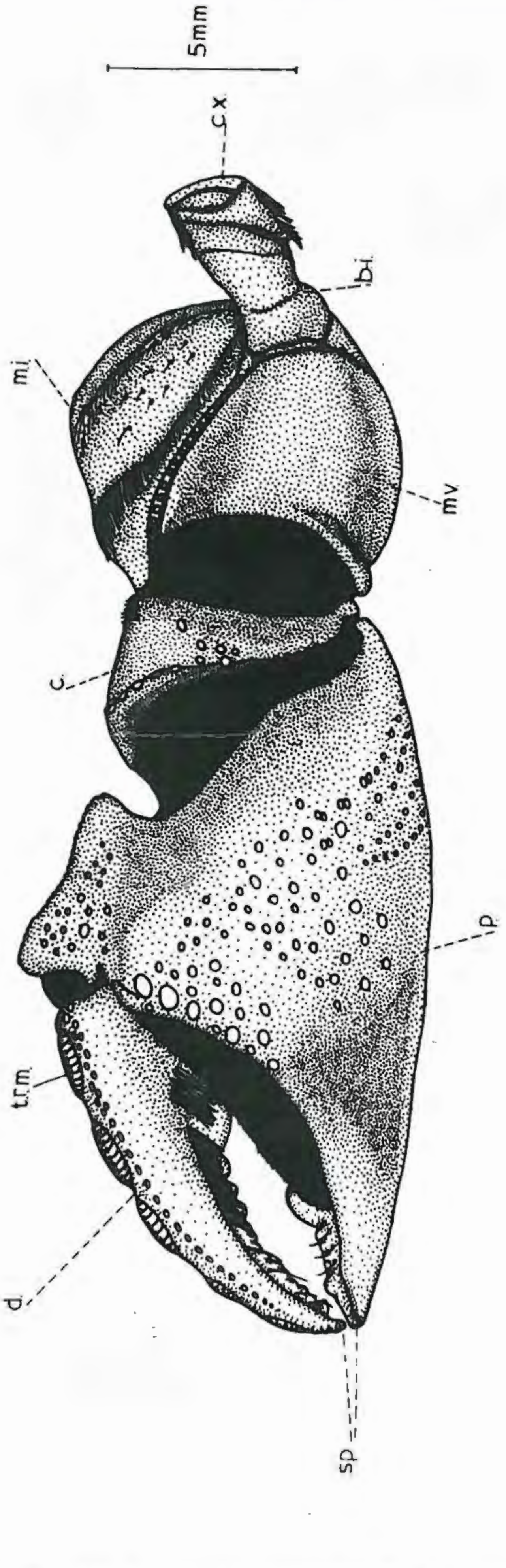


Fig.25b. *Sesarma catenata*: Inner view of the male cheliped, extended. Note the heavy tuberculation of the palm of the hand and the two rows of bristles on the inner face of the merus.

The remainder of the inner and upper surfaces are dotted with much smaller pits. The presence of these pits is contrary to Barnard's (1950) observation that the wrist and hand of the female are granulate. There is a poorly defined tuberculate ridge on the palm of the hand.

Sesarma catenata. The general structure of the chelipeds is very much like that found in *C.punctatus*, although there are numerous differences in sculpturing and the arrangement of hairs. There is in both male and female a coxal tuft of hair, and the inner face of the merus possesses a strong longitudinal band of stiff bristles and also a second, more diffuse row of short hairs towards the dorsal rim of the face (Figs. 25, 26). The lower portions of the outside of the thumb and hand of the male cheliped are smooth, and the median region is irregularly tuberculate (Fig.25a). One of the most obvious diagnostic characters of the species is the dense, black mass of hair which arises at the finger hinge of the male crab. Likewise peculiar to the species is the arrangement of ridges and tubercles on the upper surface of the propus and dactylus. Five well-defined longitudinally oval milled tubercles lie along the dorsal surface of the finger. The upper surface of the hand is flattened, and a rhomboidally shaped area is formed, bounded dorsally and ventrally by tuberculate ridges, and distally by a high, sharp pectinate ridge. The area is bisected medially by a high tuberculate ridge running parallel to the pectinate ridge. Small tubercles are scattered within the proximal half of the rhomboidal area. The gape between finger and thumb is wide, and the spoon-shaped tips are extremely sharp. The general dentition is rather weak, except for two teeth, one in each row, which are very large and almost hemispherical in shape, and which are possessed by most but not all male crabs. The palm of the hand (Fig. 25b) is generally tuberculate, and there is a ridge of granules

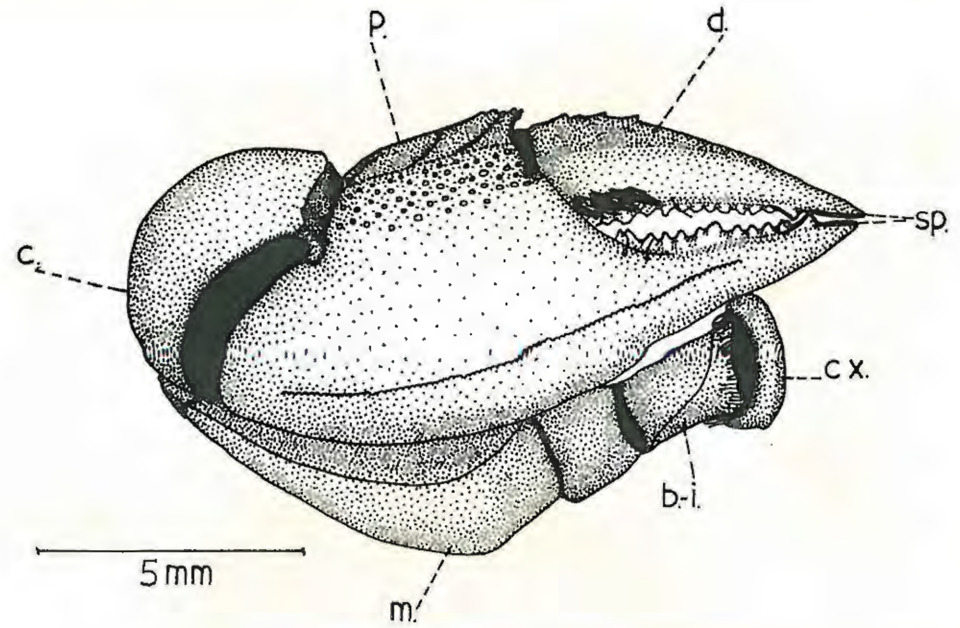


Fig. 26a.

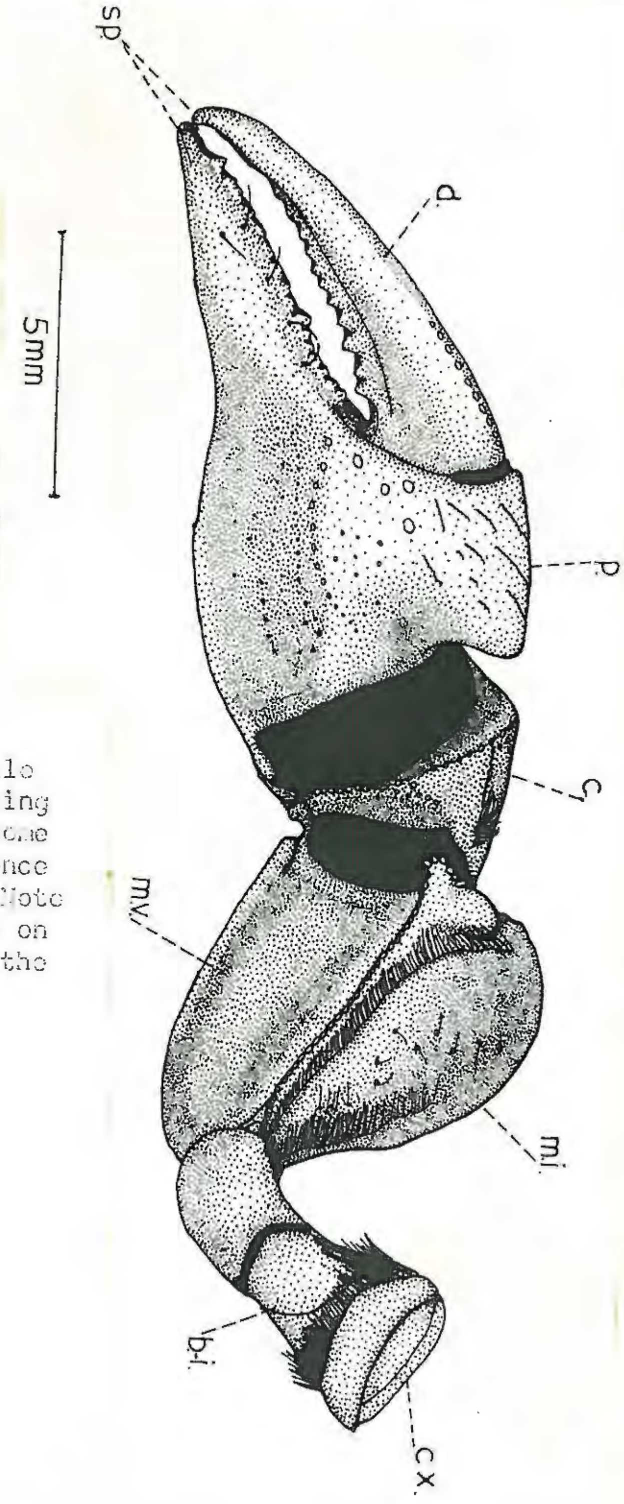


Fig. 26b

Fig. 26 a & b. *Sesarma catenata:* Outer and inner views of the female cheliped. The sculpturing is weak, but there is some indication of the presence of a rhomboidal area. Note the small patch of hair on the outer surface near the finger hinge.

flanking the milled tubercles on the inside of the finger.

In most respects the cheliped of the female is very similar to that of the male. Despite the indistinct sculpturing of the outer surface of the hand (Fig. 26a), there is the suggestion of the presence of a rhomboidal area on the propus, outlined by low granulate ridges. Barnard (1950) incorrectly denies the existence of the rhomboidal area in the female, and maintains further that the female of *S.catenata* is indistinguishable from that of *S.eulimene.* This is an erroneous observation, since not only are the colours of the chelipeds of the two species quite different (*S.eulimene* has greyish- white chelipeds), but the tuft of black hair on the dactylus of female *S.catenata*, easily visible to the naked eye in even the smallest specimens, renders female *S.catenata* immediately identifiable. The overall similarity to the male cheliped is shown in the drawing of the inner aspect of the female limb (Fig. 26b). The whole appendage is comparatively poorly armoured and sculptured, the dentition of finger and thumb is uniformly weak and the gape narrow.

(ii) The Mouthparts.

Pearson (1908) and Borradaile (1922), in their respective studies of the shore crabs *Cancer pagurus* and *Carcinus maenas*, describe the structure of the mouthparts- Pearson concerning himself more with the musculature and general morphology, Borradaile with the relation of form and function. From the work of these two authors, and of Verwey (1930) on the mangrove crab *Uca signatus*, it can be seen that the pattern of the construction of brachyuran mouthparts is constant throughout, a conclusion supported further by the present examination of the mouthparts of the grapsoid crabs *Cyclograpsus punctatus* and *Sesarma catenata*.

It is proposed therefore to give only a general description of mouthpart structure in these two species, emphasizing those features peculiar to species or family, or which may have some bearing on the habits of the animals. Details of structure or musculature not included here will be found in the above-mentioned publications.

In crabs the mouth is anterior, situated on the ventral surface. The six pairs of mouthparts are ranged one behind the other on either side of the mouth, with the heavily calcified mandibles, whose free cutting surfaces meet in the mid-line, followed by the first and second maxillae and the three pairs of maxillipeds. The region anterior to the mouth is composed of a broad, concave sclerite, the epistome, in which the upper portions of some of the larger mouthparts rest, and from which depends the labrum (which overhangs the mouth itself) and the lobed metastoma. These fleshy structures and the buccal aperture are hidden by the mandibles.

No sexual dimorphism in the mouthparts of the two species could be distinguished and the present study was made using male crabs of carapace width 26 mm (S.catenata) and 28 mm (C.punctatus). At the outset it may be noted that Borradaile's (1922) comments upon the hairs of Carcinus do not apply to the two grapsoid crabs. While some of the appendages are extremely hairy, these hairs are in every case simple in nature, whereas many of the hairs of Carcinus are compound, either feathered in some way, or serrated.

It is convenient to begin with description of the Third Maxillipeds, the largest of all the mouthparts, whose endopodites cover and conceal the majority of the underlying limbs. Figs. 27 and 28 show the outer (ventral) aspects of the third maxillipeds of C.punctatus and S.catenata respectively.

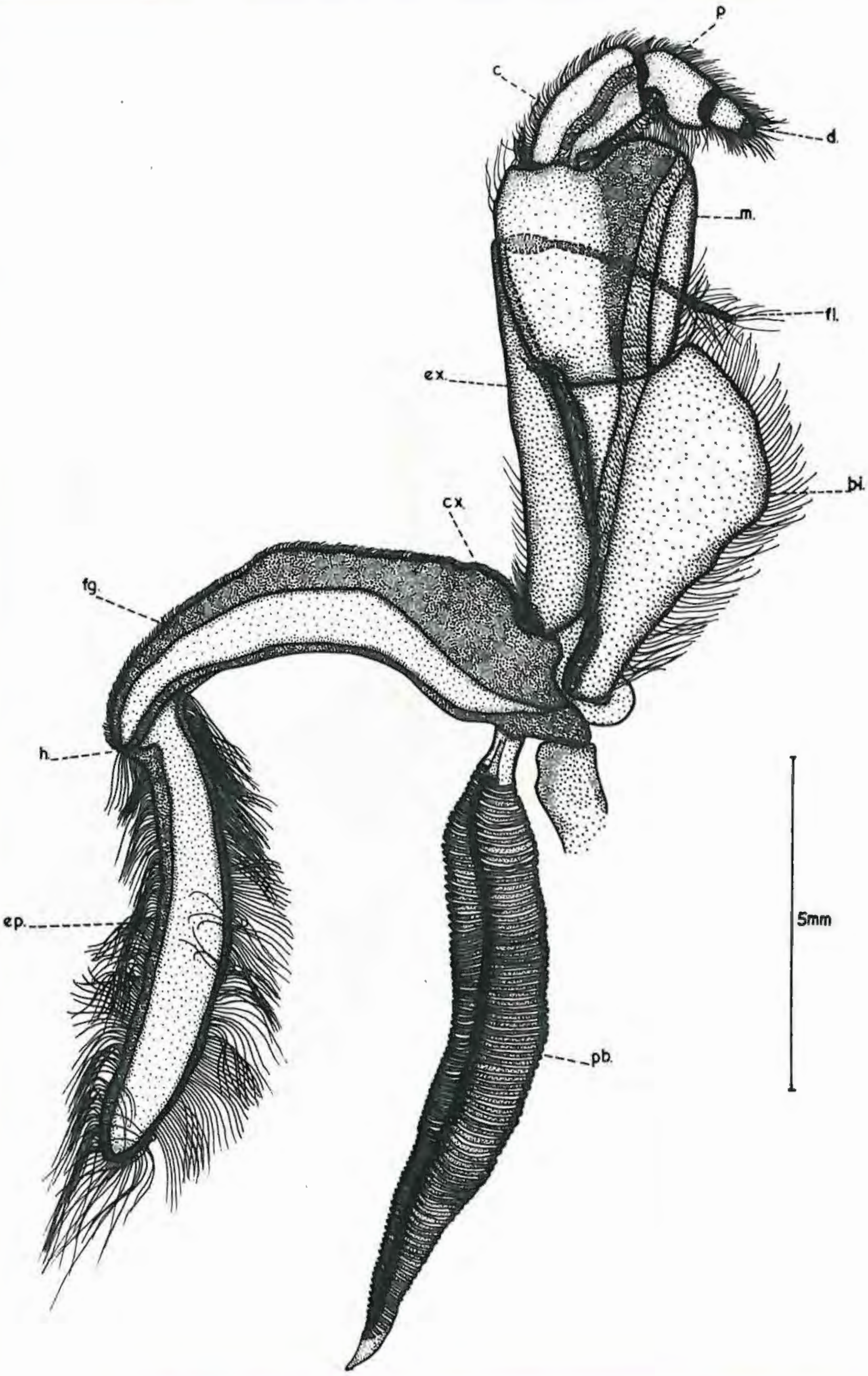


Fig. 27. *Cyclograpsus punctatus*: Outer view of the third maxilliped. (See text for description).

d. = dactylus;)
p. = propus;)
c. = carpus;)endopodite.
m. = merus;)
b.i. = basi-ischium.)

e. = expodite;
fl. = flagellum of exopodite;
cx. = coxa;
fg. = coxal flange;
h. = hinge;
ep. = epipodite;
pb. = podobranch.

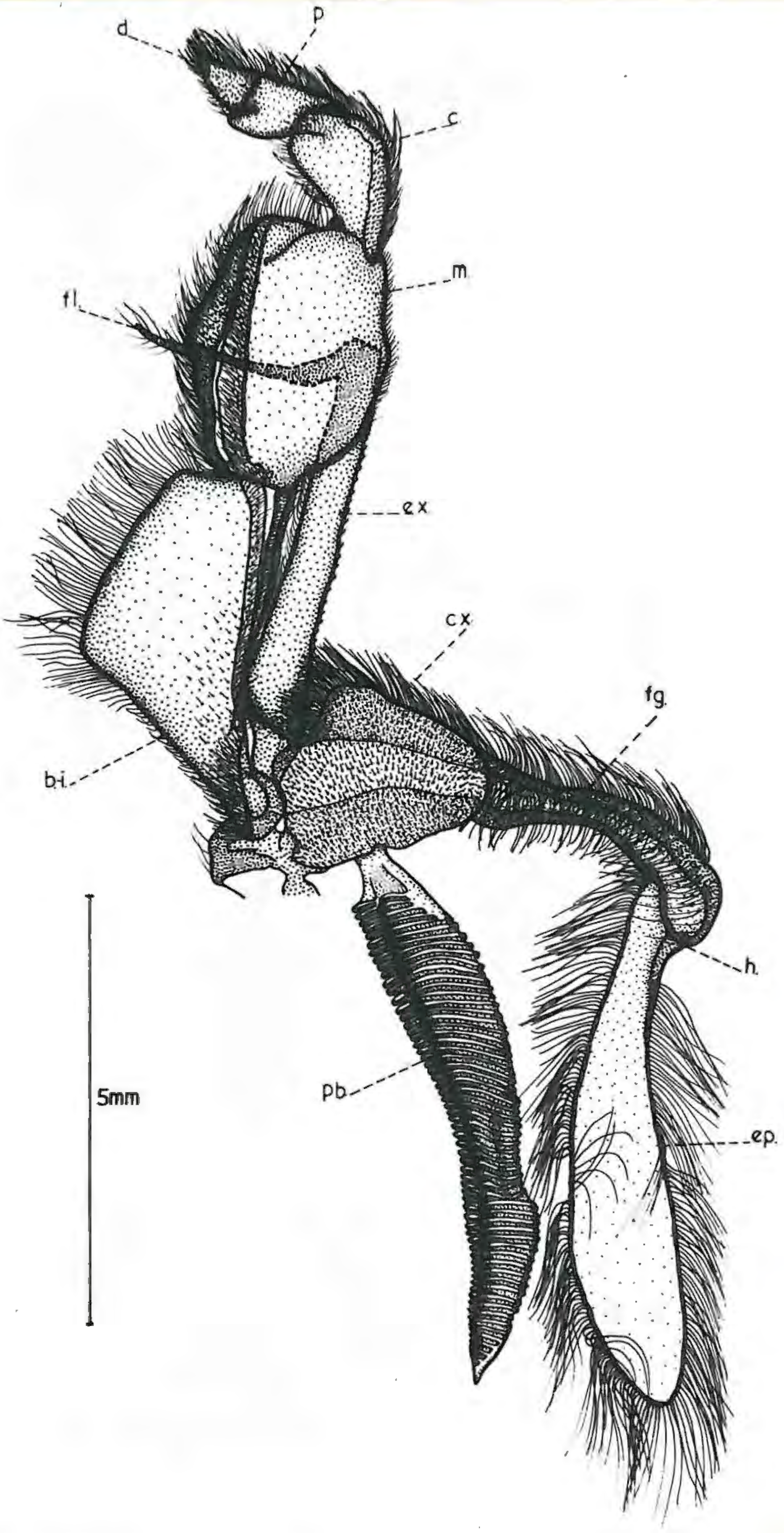


Fig. 28. *Sesarma catenata*: Outer view of third maxilliped (see text for description). Notation as for Fig. 27. Note that this appendage is very hairy in both species.

That of *S.catenata* is considerably the smaller, a difference apparent in almost all of the mouthparts, and unlikely to be completely accounted for by the slight difference in the overall sizes of the crabs. The diagonal ridge, covered with short, almost woolly bristles, can be seen running from the inner edge of the heart shaped merus to the opposite proximal edge of the flattened, heavily sclerotised basi-ischium, and acts as the chief diagnostic character of the sub-family Sesarminae, to which both species belong. The basi-ischium itself is sharply angled along the inner edge, and tapers proximally, so that a wide gap exists between the paired endopodites. The stiff hairy fringes on the inner edges of the limbs mesh in the midline, and partially serve to close the gap. This gap is common to the Family Grapsidae; the members of most other brachyuran families possess rectangular, door-like endopodites which completely hide the other mouthparts from view. In *C.punctatus* and *S.catenata* the endopodite is thickly edged with hairs. The three distal segments are slender and flexibly articulated, and the carpus bears a longitudinal band of short bristles on its outer surface.

The exopodite, composed of a flattish, tapering shaft and a many-jointed, whip-like flagellum or lash, is sparsely hairy, and is covered on the inner side by the endopodite and on the outer by the edge of the branchiostegite.

The endopodite and exopodite articulate with the coxa, a broad, sclerotised structure with a narrower lateral expansion or flange to the lower end of which is hinged the elongated, membranous, paddle-shaped epipodite. Short hairs occur along the upper margin of coxa and flange in *C.punctatus*, and in *S.catenata* these hairs, longer and more silky, are also present, as well as tracts of short bristles which cover the outer surface of the coxa itself, and a longitudinal row of longer hairs along the midline of the flange. The epipodites, which are especially sclerotized in *C.punctatus*, are outlined with hairs. On the dorsal surface of the coxa arises the podobranch, which is very large compared with those of *Cancer* and *Carcinus*, (Pearson, 1908; Borradaile, 1922).

As in other crabs, the third maxillipeds are maintained in a twisted position. The exopodite and endopodite lie in the horizontal plane over the mouth region, the coxa turns posteriorly, and is slanted so that the anterior edge points outwards, and the epipodite is orientated in the vertical plane, being directed backwards against the body wall within the branchial chamber, proximal to the gills.

The *Second Maxillipeds*, although very similar in construction to the third maxillipeds, are smaller, and the cuticle covering them is much thinner (Figs. 29 & 30). While the exopodite is almost identical in size and form to that of the third maxilliped, the endopodite is rather slender and of almost uniform width; and there appears to be some fusion of the coxa and basi-ischium. The podobranch arises on the coxal region between the exopodite and the broad, membranous epipodite, which is very hairy. Exopodite and endopodite are set farther apart in this appendage than in the third maxilliped, and according to Borradaile (1922) have greater powers of independent movement. Certain features of the structure of the dactylus are of interest inasmuch as they have not apparently been described for any other species. In *S.catenata* the distal two-thirds of this segment are covered with hairs, which give way at the tip to short, spiky, recurved hairs situated in deep pits. The surface of the dactylus in *C.punctatus* is not hairy, but the segment is fringed with silky hairs, and the tip bears upwards of twelve stout recurved projections, which might be termed spines or prongs rather than hairs because of their rigid, sharply

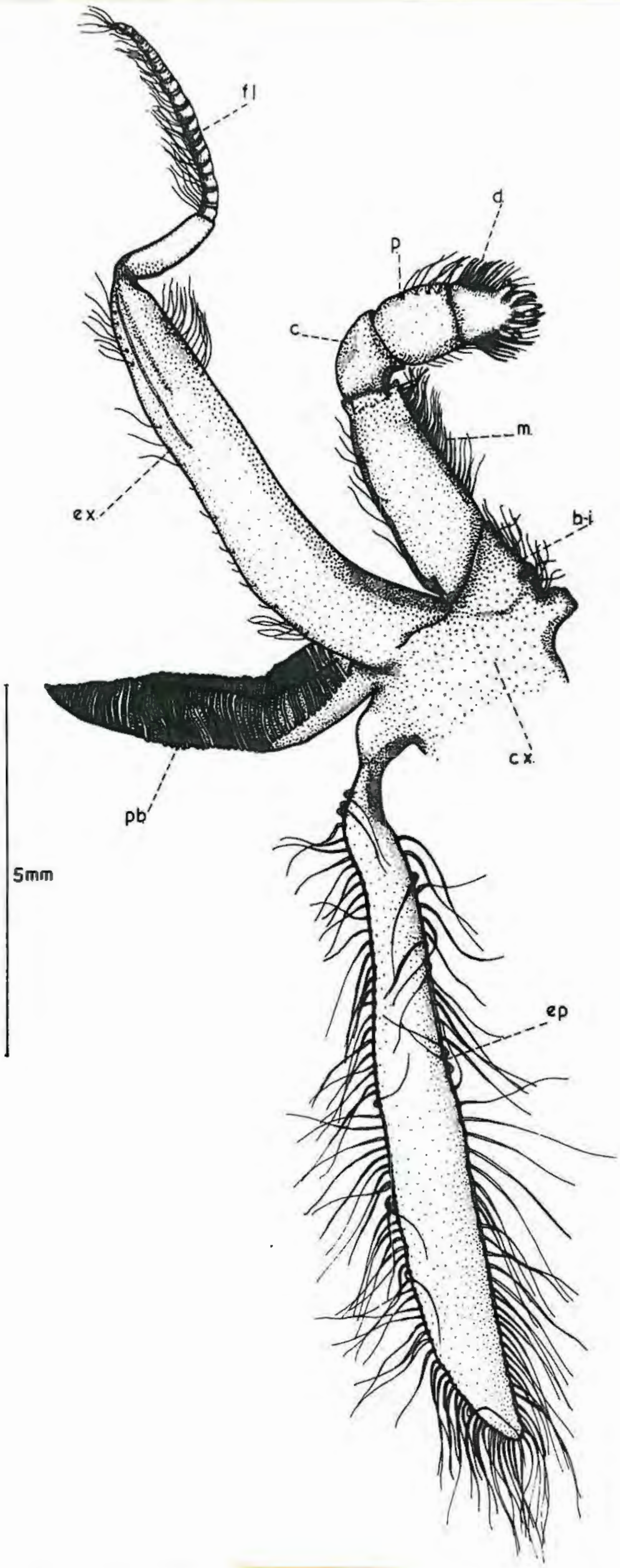


Fig. 26. *Cyclograpsus punctatus.* Outer view of the second maxilliped. This appendage is not as large, as heavily sclerotized or as hairy as the third maxilliped. Note the "prongs" on the dactylus (d). Notation as before.

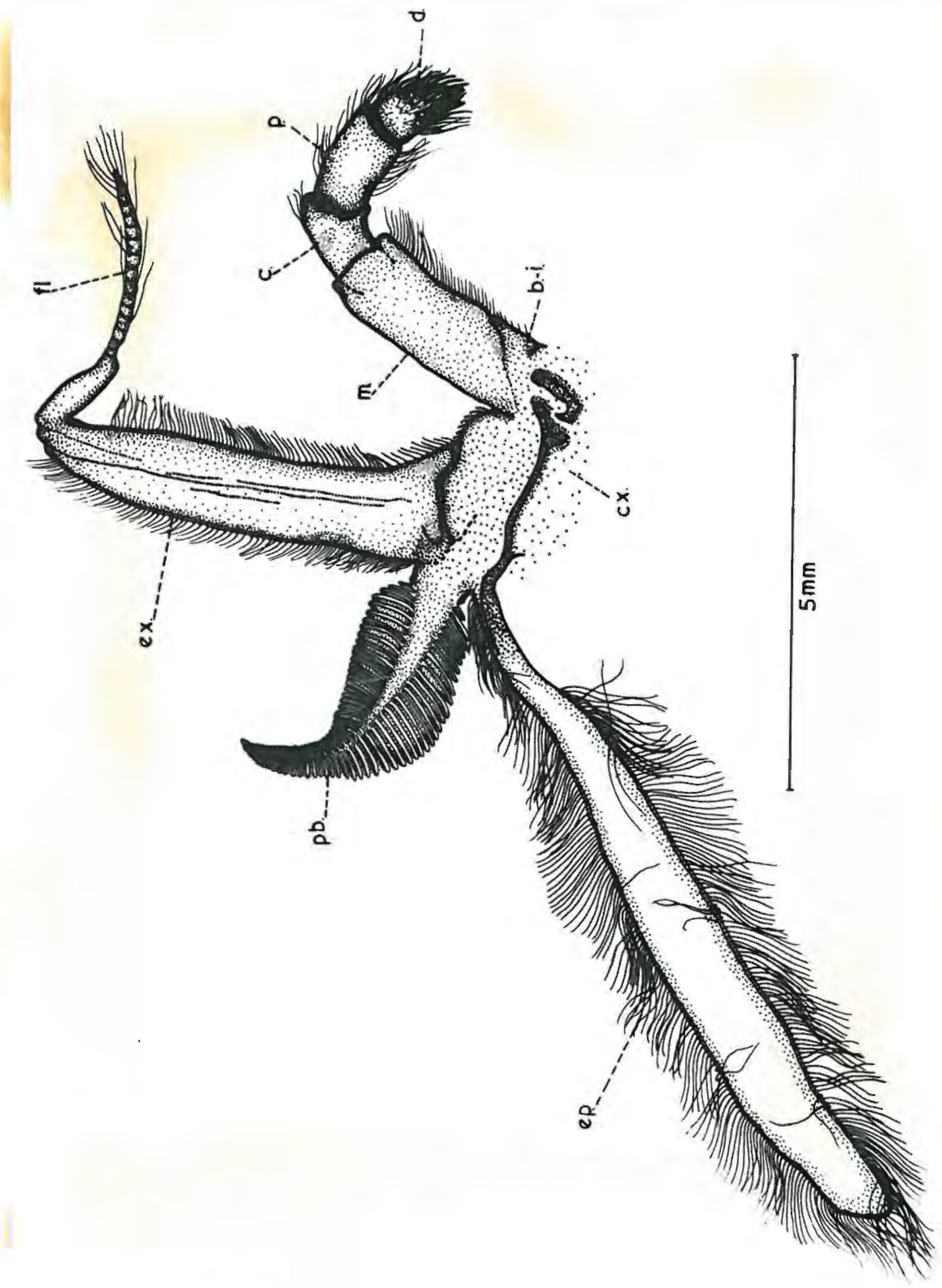


Fig.30. Sesarma catenata: Outer view of the second maxilliped. The dactylus is densely hairy but is not pronged like that of C.punctatus. Note that in both species the expodite is large relative to the endopodite.

pointed appearance. These are arranged alternately in two series, one on the inner, the other on the outer side of the tip, and curve in opposite directions so that they mesh like teeth. The second maxillipeds are orientated in the same way as the third maxillipeds, with the exopodite and endopodite in the horizontal plane and the epipodite twisted backwards to lie in the vertical plane in the gill chamber next to the inner branchiostegal wall.

The <u>First Maxillipeds</u> (Figs. 31 & 32) are flattened, delicate structures, covered with thin cuticle and lying proximal to the second maxillipeds. The exopodite is very much like those of the other maxillipeds, but the endopodite is more or less unsegmented and leaf-like, and is curved, facing obliquely inwards and outwards. There is a triangular, horizontally flattened expansion distally, which is thickened, separated from the main shaft by an inflexible suture, fringed with hairs, and rests in the hollow of the epistome above the mouth together with the flagella of all three of the maxillipeds. This expansion resembles that found by Borradaile (1922) in <u>Carcinus</u>, and in neither of the two grapsoid crabs is it hinged in the manner described by Verwey (1930) for <u>Uca</u> <u>signatus</u>.

Arising from the basi-ischial region is a large, hairy lobe or endite, which projects inwards and is ventrally convex, lying over the mandible. A proximal, heavily sclerotised endite originating on the coxa, curves over the area immediately posterior to the mandibles. This endite is the smaller of the two, and is rounded in outline, although hollowed out proximally in <u>S.catenata</u>. It is densely covered with hairs in both species, and possesses some degree of independent movement.

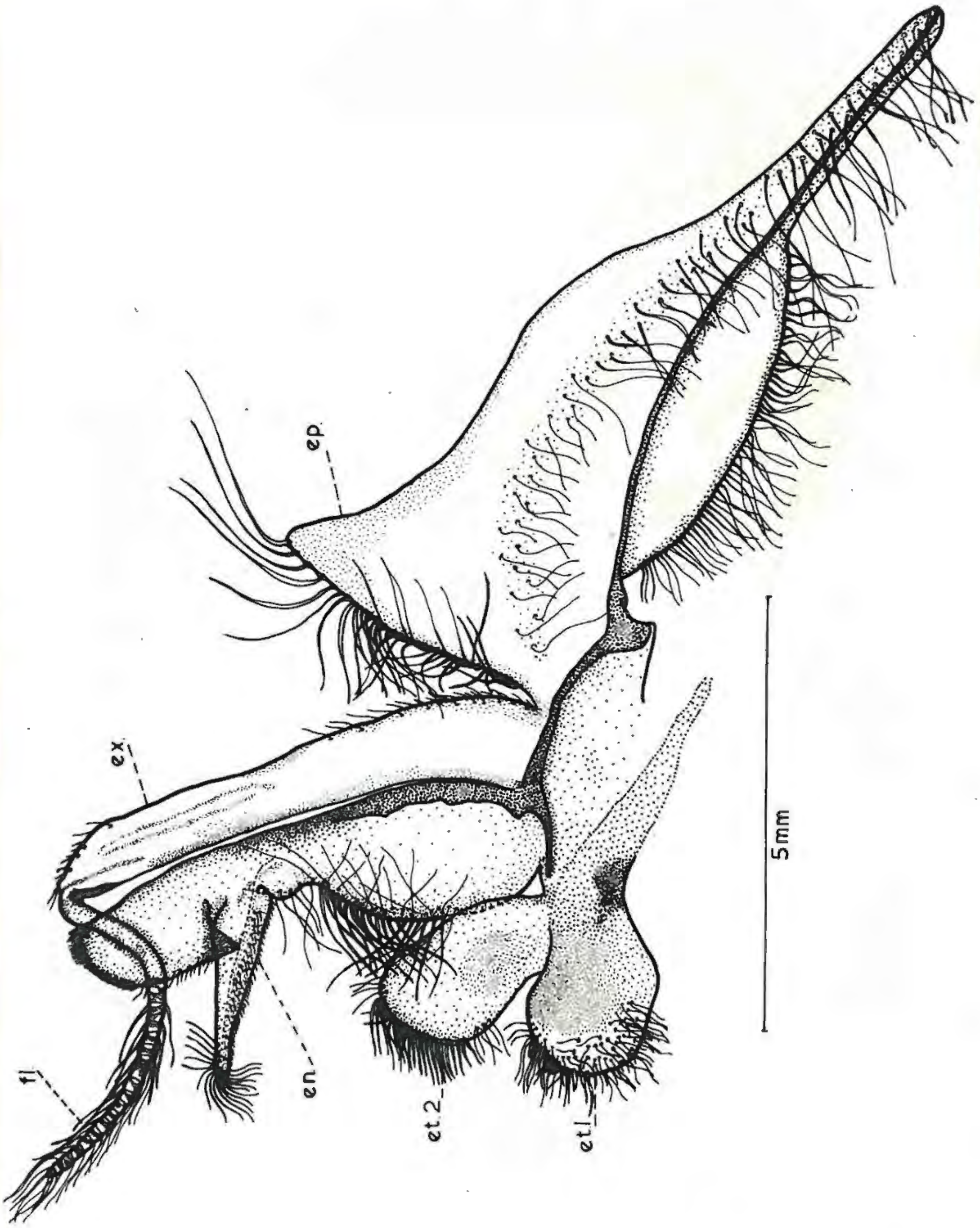


Fig.31. Cyclograpsus punctatus: Outer view of the first maxilliped. Note absence of gill, and the expansion of the epipodite to form a blade. The endopodite (en.) is fused and flattened, and the whole limb is poorly sclerotized apart from the two endites (et.1, et.2).

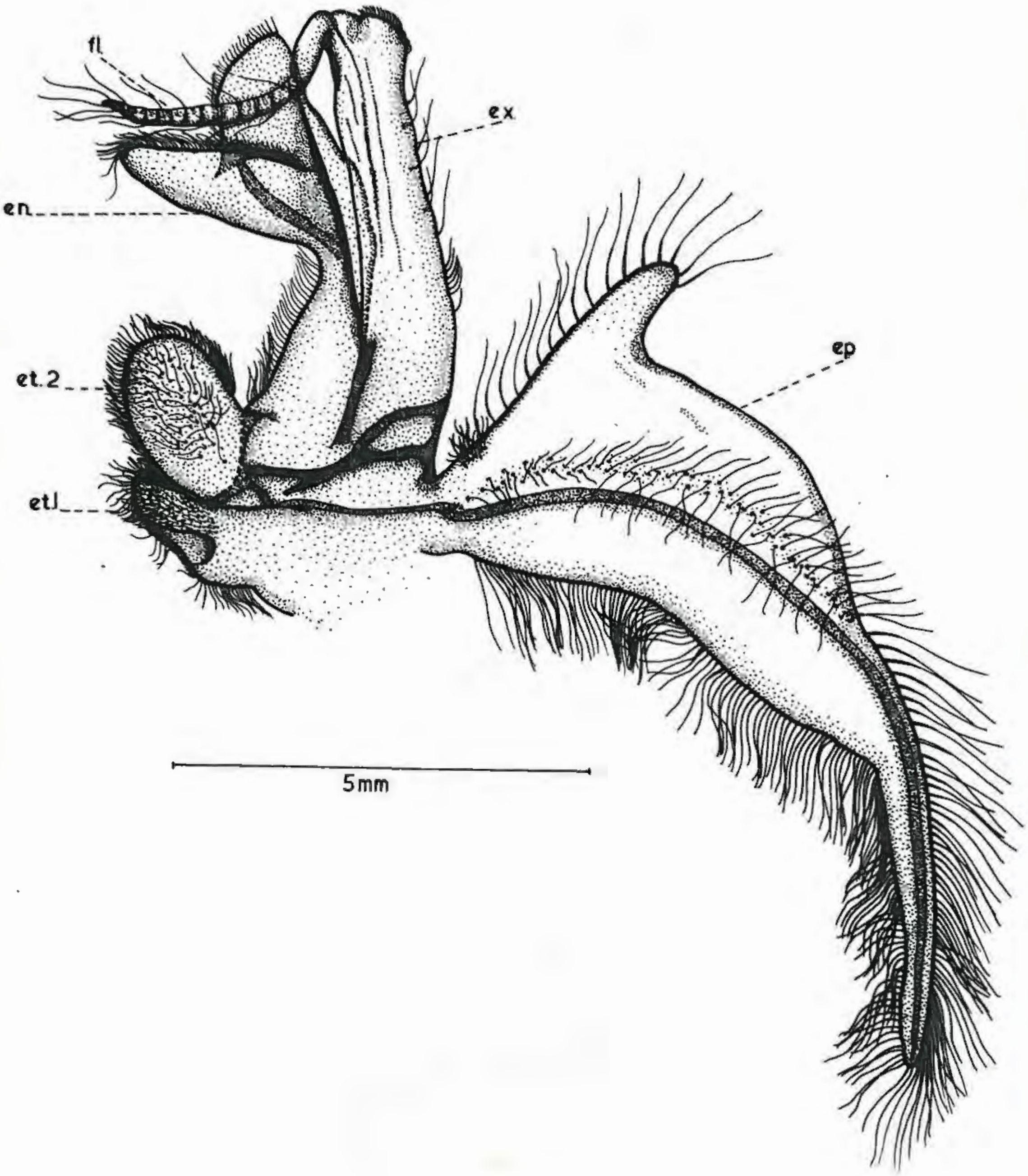


Fig. 32. Sesarma catenata: Outer view of the first maxilliped.

The epipodite is membranous, and is expanded proximally to form a triangular blade. The organ tapers distally and a sclerotised tendon runs along the entire length. A longitudinal hair tract runs parallel to the tendon, and the lower edge of the epipodite is densely hairy, while the inner side of the blade bears long, stout, widely-spaced hairs. The epipodite turns backwards into the branchiostegal cavity, and lies over the gills.

The *maxillae*, which are situated under the first maxillipeds, are tough, membranous appendages. There is a scaphognathite or "baler", composed of the fused exopodite and epipodite, and completely fringed with short, fine hair. The scaphognathite of *C.punctatus* (Fig.33) is very broad compared with that of *S.catenata* although the latter is the more heavily sclerotized (Fig. 34). The endopodite is reduced, and two large endites are present in the form of rounded cleft lobes, which are of the same order of size in the two species. There is considerable intergeneric variation in the form of these endites, which may be entire, except for a median notch at the tip, as in the distal endite of *Uca signatus* (Verwey 1930), incompletely cleft, as in *C.punctatus* and *S.catenata*, or deeply divided into narrow ribbon-like structures as in *Carcinus maenas* (Borradaile, 1922). In the two grapsoid crabs the large, curved distal endites are almost identical in shape, and lie across the mandibles. In *C.punctatus* the proximal endite is asymmetrically divided into two parts, the upper of which is the more slender. The same is true for the proximal endite of *S.catenata* but in this species the upper portion is minute and at first sight appears to be merely a slight protuberance, somewhat obscured by the dense hair of the larger lobe. The proximal endite of the maxilla is covered by the proximal endite of the first maxilliped.

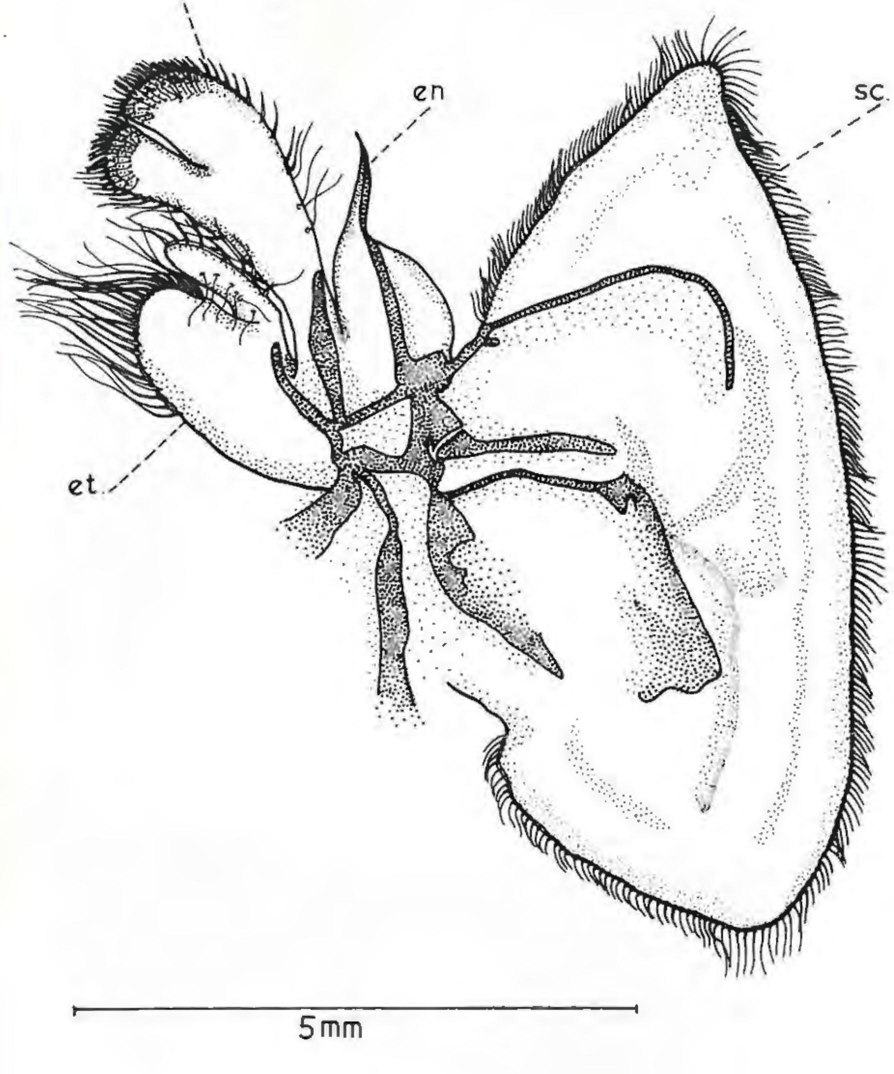


Fig.39. Cyclograpsus punctatus. Outer view of the maxilla. This appendage is membranous and the exopodite and endopodite have become fused to form the broad scaphognathite (sc.). The endopodite is tiny compared with the two broad, cleft endites (et).

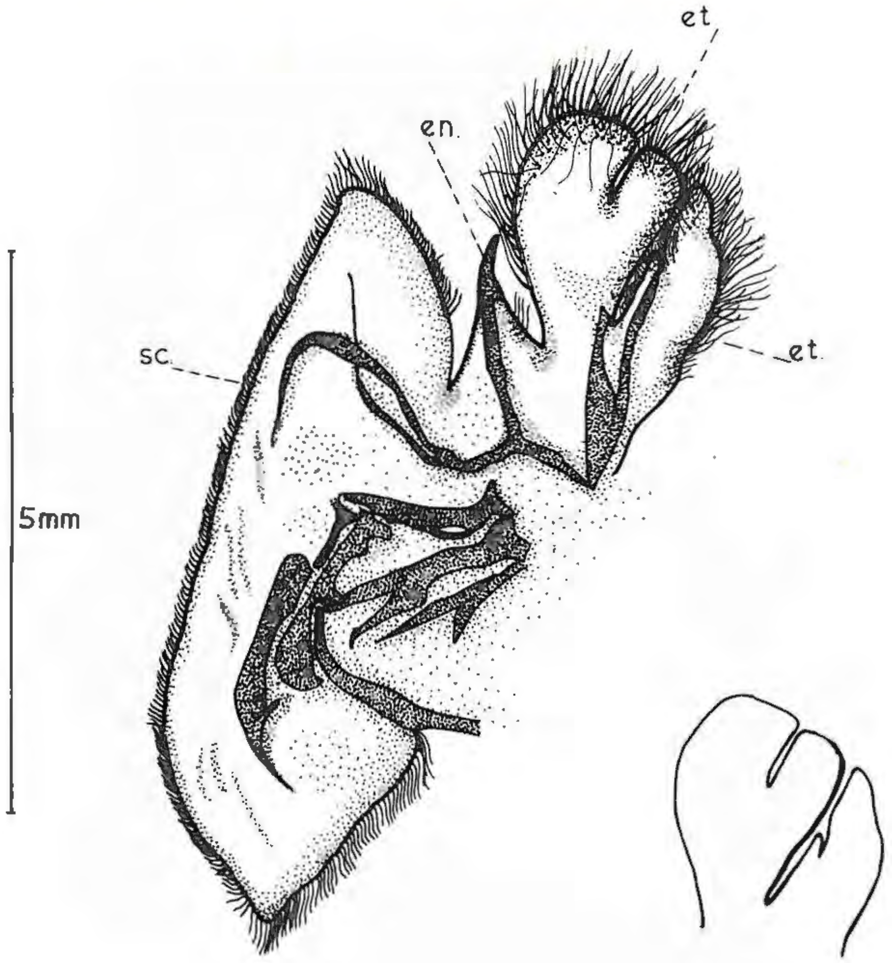


Fig. 34. *Sesarma catenata.* Outer view of the maxilla. Note that while the scaphognathite is small compared with that of *C. punctatus*, the endites are very large, and the supporting skeletal rods are strong. The endites have been drawn in outline at the right to show the shape of the proximal lobe which is only partly divided into two by a notch so that the upper portion is minute.

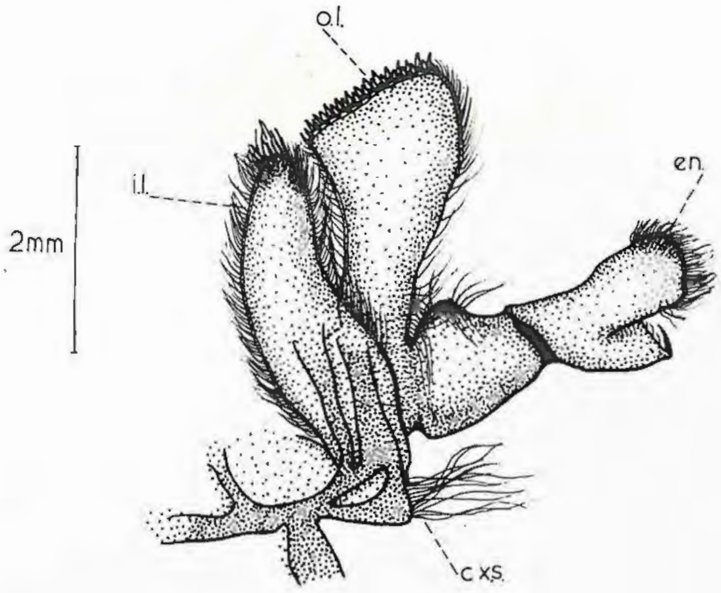


Fig.35. *Cyclograpsus punctatus*: Outer view of the maxillule. There is no exopodite, and the appendage is very small and delicate. Note the broad outer (o.l.) and inner (i.l.) laciniae which lie immediately over the mandibles. The outer lacinia bears spines on its distal edge. cx.s = coxopoditic setae.

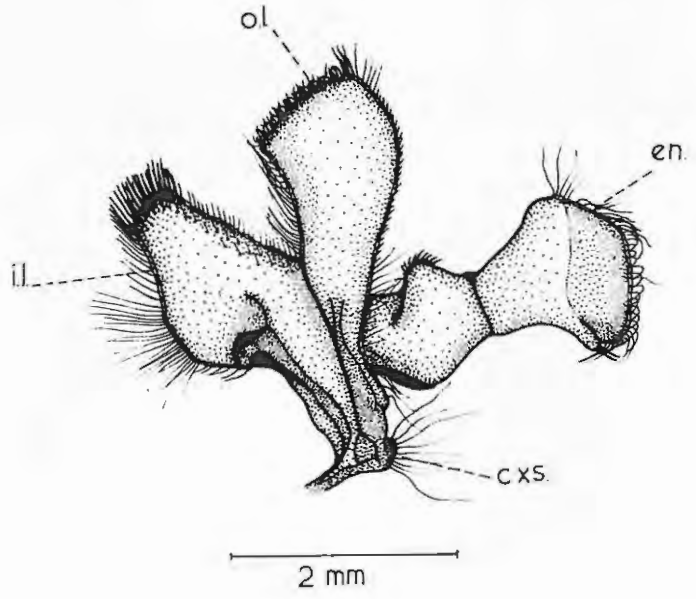


Fig. 36. *Sesarma catenata*: Outer view of the maxillule. The limb is similar in basic plan to that of *C.punctatus*, but is smaller and shaped slightly differently.

The *Maxillules* are the smallest and most fragile of all the mouthparts. They arise posterior and lateral to the heads of the mandibles. Their structure is very similar in both species (Figs. 35 & 36) although those of *C.punctatus* are rather larger. They do not appear to be as complicated as the maxillules of *Carcinus* (Borradaile, 1922), but are built upon the same basic plan and lie in the same position. Borradaile suggests that the endite-like lobes of these appendages should be called lacineae rather than coxa and basis, hitherto the accepted nomenclature. His reasons for this change, involving a consideration of the origin of the two lobes, seemed to warrant the use of these terms in the present instance.

The proximal lobe or inner lacinea, tapering in *C.punctatus* and irregularly shaped in *S.catenata*, is outlined with hairs, and lies under the proximal endites of the maxilla and first maxilliped. The outer lacinea is shaped like the distal endite of the maxilla, and lies beneath it and the distal endite of the first maxilliped. There are fringes of hairs along the sides of the lobe, but the tip is truncated, and bears a row of very short, curved, blunt spines. Both lacineae are attached to a sclerotized knob, the vestigial coxa, which has on its outer rim a tuft of long silky hairs (Borradaile's "coxopoditic setae"). The endopodite is directed antero-laterally and passes across the mandible. It is divided into two segments by a suture, and the swollen, spoon shaped tip of the more distal segment is tucked under the mandible in a groove next to the mandibular palp. In both species the tip of the endopodite possesses one or two curved spines on the inner lip of the spoon-shaped process, and in *S.catenata* the long outer lip is flexed dorsally. The exopodite is absent in the maxillule.

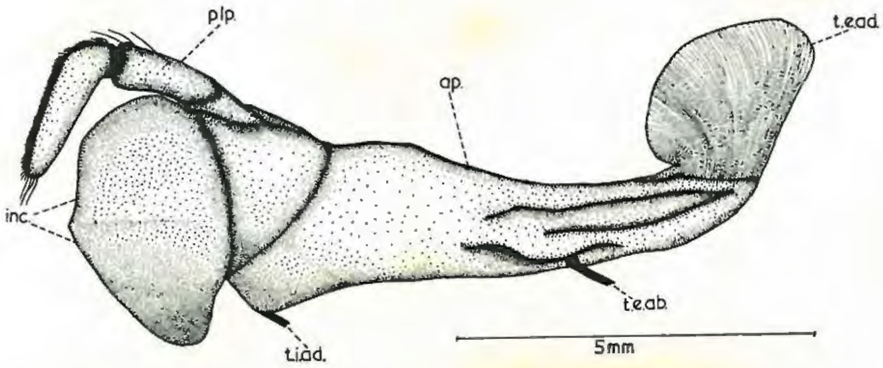


Fig. 37a. *Cyclograpsus punctatus*: Outer view of mandible. The limb is heavily sclerotized, and the sutures are rigid. The head is broad and curved and joined to the elongated apophysis (ap.). The membranous tendon of the external adductor muscle (t.e.ad.) is attached to the end of the apophysis, and the tendon of the external abductor muscle (t.e.ab.) is attached to the outer face of the apophysis.

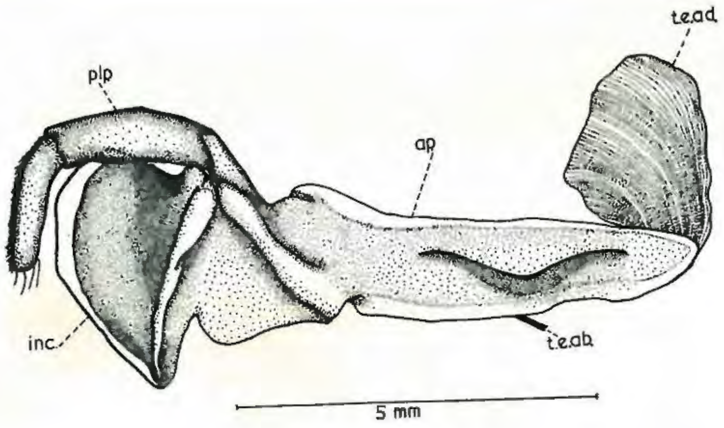


Fig.37b. *Cyclograpsus punctatus*: Inner view of the mandible. The head is concave and its edge is raised and sharp, forming the incisor area. The 3-segmented palp curves down and fits into the hollow of the head when at rest. Note the heavy strutting between head and apophysis. The tendon of the internal adductor muscle (t.i.ad. - see Fig. 37a) is attached at the junction of the struts and has not been drawn.

The *Mandibles* or jaws are very heavily calcified, and consist of the ventrally convex head and the long, tapering apophysis, upon which are inserted three tendons- the exterior adductor muscle tendon, which is a membranous structure at the end of the apophysis, the exterior abductor muscle tendon, attached to the posterior ventral face of the apophysis, and the interior adductor muscle tendon, on the anterior dorsal face.

Fig. 37 a & b are ventral and dorsal views of the mandible of *C.punctatus* respectively. The limb is stout and rigid, for the two sutures separating the head from the apophysis are inflexible. It can be seen that the dorsal surface of the head is markedly concave, and bounded by a flattened rim which is edged by extremely hard cuticle of knife-edge thinness - the incisor or cutting edge of the mandible. At the junction of head and apophysis is a high, rounded transverse ridge. A diagonal strut crosses the apophysis and meets the transverse ridge on the anterior side, and it is here that the tendon of the internal adductor muscle is attached. Here, too, arises the large, mobile palp which consists of three distinct segments. When the mandibles are at rest the apices of the incisor areas lie close together and may even overlap, and the palps are curved downwards, fitting into the hollow heads so that they cannot be seen from the ventral surface. The endopodite of the maxillule passes behind the palp where there is a notch formed at the second suture.

The structure of the mandible of *S.catenata* is very similar to that of *C.punctatus*. The major differences between the mandibles of the two species are in the relative sizes - that of *S.catenata* is the more slender of the two, and the strutting on its dorsal surface is more complex, as can be seen from Fig. 38 a & b.

Fig. 38a.

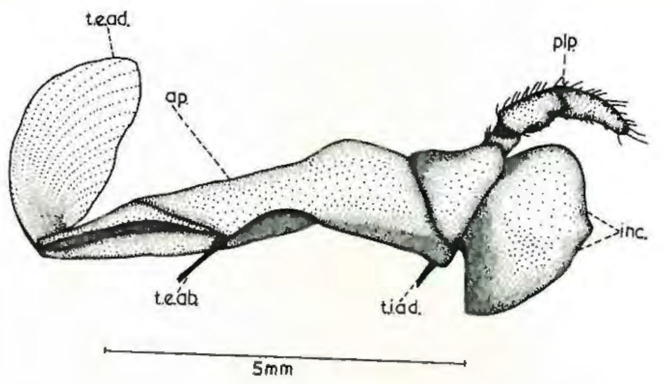


Fig. 38b.

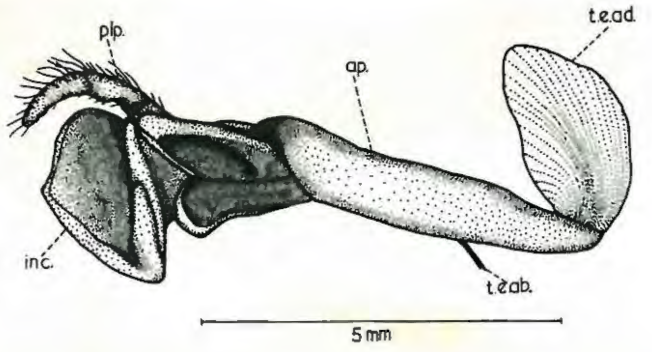


Fig. 38 a & b. Sesarma catenata. Outer and inner views of the mandible. Note small size and slenderness as compared with that of C. punctatus. Note the complex, arched strutting on the inner surface between the head and apophysis.

2. Respiration.

When animals forsake the aquatic environment in favour of a terrestrial or partly terrestrial existence they must of necessity develop some means of using the atmospheric oxygen which is so abundant in their new habitat. Although there are differences between aerial and aquatic respiration there is one basic mechanism which is common to both. This, as Carter (1931) explains in his review of the subject, is the diffusion through the respiratory epithelia of gases which have been dissolved in the layer of moisture covering the respiratory surfaces. In aquatic animals this layer is of indefinite thickness, but it is extremely thin in terrestrial species. Carter points out that to expedite diffusion respiratory epithelia must be of great thinness, and that respiratory surfaces are usually much enlarged. It is obvious that such organs would be highly susceptible to evaporation if exposed to the atmosphere. Advanced terrestrial forms have overcome this problem by developing internal respiratory organs and elaborate arrangements for keeping the epithelia moist.

For animals taking the first step from the water on to land the need to combat evaporation is, however, an urgent one, and some form of action must be taken immediately if the species is to survive. The water covering the respiratory surfaces of aquatic animals requires constant changing to prevent stagnation, and there is often some active mechanism of water circulation over the respiratory organs which may be completely external or at least partly exposed. These animals are thus particularly vulnerable in air, for the rapid evaporation affects not only the concentration of the body fluids, but will prevent oxygen uptake if the respiratory organs are dried out.

Certain Decapoda which lead a terrestrial or semi-terrestrial existence possess adaptations permitting them varying degrees of independence of the aquatic environment. These adaptations are summarised by Carter (1931), and range from the ability to reoxygenate water retained within the gill chamber to the development of accessory respiratory structures, such as the vascular "lung" on the roof of the branchial cavity of *Birgus latro* (the "robber crab"), and the unique lung on the ventral surface of the body of the hermit crab *Coenobita.* Finally, Carter mentions that some species of crabs are able to take air into the gill chamber via special posterior openings.

The grapsoid crabs *Cyclograpsus punctatus* and *Sesarma catenata* are both more or less amphibious, and, as was clearly demonstrated in Part I of this thesis, can survive for prolonged periods in air and clean water. A consideration of their respiratory processes therefore involves studies of the circulatory mechanisms employed under water, as well as the structural, mechanical and behavioural adaptations which allow aerial respiration.

(a) Aquatic Respiration.

The branchial chambers of the two species are similar in construction to that of *Carcinus maenas* (Borradaile, 1922). The eight gills on each side are distributed in a manner very like that of the nine gills of *Carcinus*, being closely applied to one another, and, except for the podobranchs of the maxillipeds which are directed horizontally and ventrally, are turned upwards and inwards. Borradaile's drawings and diagrams show this arrangement very clearly, as well as the positions of the epipodites of the maxillipeds: those of the second and third maxillipeds occupy the shallow hypobranchial space between the gills and the body wall, while the epipodite of maxilliped I lies over the gills in the epibranchial space, beneath the branchiostegite.

The branchial chamber itself consists of two sharply defined regions, the large "true gill chamber" and, in the cephalic region, the narrower "prebranchial chamber". This smaller cavity is really a passage leading to the exhalent opening, which is anterior, and is covered by the tops of the exopodite and endopodite of the third maxilliped. Between the anterior ventral edge of the branchiostegite and the coxa of the cheliped is a wide slit - the inhalent orifice of the branchial chamber.

Borradaile (1922), in describing the directions and modes of entryand egress of the stream of water pumped in and out of the gill chamber, cites the work of various authors. Milne-Edwards' (1839) classical account of the process states that the water is drawn in by way of the main inhalent opening only, but Bell (1853) Giard and Bonnier (1887) and Bohn (1897, 1907) believed that water entered above the walking legs along the length of the carapace. Pearson (1908) discovered besides the main inhalent opening (known by many workers as the "opening of Milne-Edwards") a posterior aperture above the last walking leg of *Cancer*, and Borradaile's work on *Carcinus* revealed the presence of an opening above each of the legs. Borradaile's observations led him to reason that water entering the gill chamber passes under the gills, i.e. within the hypo-branchial space, spreading upwards and backwards. The water then collects in the spaces above and posterior to the gills and overflows onto the outer gill surfaces, where it is joined by water which has travelled outwards between the gill leaflets from the hypobranchial space. The stream is then borne anteriorly to the exhalent passage, and expelled. Verwey (1930) was able to confirm these opinions by his work on the river crab, *Potamon granulatus*. Through a window, which he cut in the roof of the branchiostegite and sealed with a glass square, he could view the path taken by carmine particles introduced at the opening of Milne-Edwards. *P.granulatus* possesses a vaulted branchiostegite and the gill chamber is spacious, so that the window could be made without fear of damage to the delicate under-lying structures. The typically flattened carapace of the grapsoid crabs, their small size and the relatively thin cuticle, which cracks irregularly under pressure, rendered an investigation of this kind impossible in the present instance.

The characteristics of the inhalent and exhalent currents could be determined, however. Crabs were laid ventral surface uppermost on rectangular metal plates, covered with white paper. The animals were bound to the plates by strong elastic bands pinioning the legs and chelipeds on each side. They were then placed in white plastic dishes and covered with water to a depth of about half an inch. A drop of Indian ink was introduced into the openings of Milne-Edwards by means of a pipette, and the ink was drawn into the branchial chambers and pumped out at the exhalent openings in two streams, which tended to converge in the midline. No ink was taken up over the walking legs or at the back of the carapace, either in the spreadeagled position or when the crabs were moving normally under water, and no openings other than that of Milne-Edwards could be seen at the periphery of the branchiostegite when this was examined under the microscope. In both species the coxal joints of the walking legs and the adjacent branchiostegal rim are densely hairy, and in *C.punctatus* the back of the carapace is closely applied to the base of the first abdominal segment. The carapace of *S.catenata*, on the other hand, has some slight dorso-ventral movement, and can be raised posteriorly for about a millimetre, exposing the arthrodial membranes between the thorax and first abdominal segment and between the coxa of the last walking leg and the body. In none of the numerous crabs tested was Indian ink drawn in posteriorly even when the carapace was thus raised.

When the crabs are immersed in water, respiration is carried on continuously, but varies in intensity, as indicated by the strength of the exhalent current and the movements of the mouthparts. These are most marked in animals which have been placed in water after a few hours' exposure to the atmosphere. Upon entering the water the crabs expel air bubbles from the gill chambers, and lie at the bottoms of their containers with the legs and chelipeds loosely extended. If they are not completely submerged the animals lower their bodies so that only the eyes remain above water, and the vigorous exhalent currents produce ripples across the surface.

Even the largest specimens are really not big enough for detailed observations to be made of the activities of individual mouthparts during respiration, and this work was further hampered by the attitude of the chelipeds, which are held across the front of the animals. They were viewed through the sides of glass beakers, and several external movements could be discerned, despite some distortion caused by refraction and the fact that the animals were wary, retreating on approach and raising the chelipeds, thereby obscuring the mouthparts further.

The following activities were nonetheless observed:

1. The endopodites of the third maxillipeds are held downwards, away from the body. These organs generally do not move, but may sometimes beat gently up and down. The endopodite of one side may beat in this way for a few minutes at a time and then cease, when the beating is taken up by the endopodite of the other side. Should both endopodites beat at once, they do so alternately.

2. There is a rhythmic in and out shovelling movement of the coxae and flanges of the third maxillipeds, which

project from Milne-Edwards' opening. This does not necessarily coincide with the beating of the endopodites (although it proceeds with a similar frequency) as it is more or less continuous.

3. When the exhalent current is so strong as to form ripples in the water, it is always accompanied by the energetic flickering to and fro of the flagella of the maxillipeds. These are held outwards in the region of the epistome in front of the exhalent orifice, and although it was impossible to distinguish one from another it appeared that they were not moving simultaneously in the same direction, but were out of phase. Borradaile (1922) believes that this lashing of the flagella reinforces the current and turns it outwards. This conclusion is strongly supported by present observations. In animals which have been immersed in water for some time the flagella beat only intermittently, at intervals of a few seconds. If a drop of Indian ink is deposited near the epistome it can be seen that during what may be termed the "active phase" of the flagella, the water surface is disturbed by their rapid motion and by the powerful twin exhalent streams which initially converge in the midline and are then driven away from each other laterally and posteriorly, so that after a short time the crab is flanked by two half-ellipses of moving water. The pattern made by the Indian ink is comparable to the configuration of the field surrounding a bar magnet lying along the midline of the animal.

During the inactive phase of the flagella, the exhalent streams again converge, and there is a certain amount of mingling in the midline. The streams move rather sluggishly forward, parallel to each other, and eventually diverge, turning back until they reach the anterior rim of the carapace.

Occasionally a crab produces a current on one side only. During the active phase of the flagella the water is driven with the same force and in the same direction as if both sides were functional, but in the inactive phase, the rather slow current travels diagonally forwards across the front of the animal. These diagonal currents are to be expected from the position and direction of the exhalent passages on either side of the epistome. It is clear that when they are produced on both sides simultaneously the currents will, despite some mingling of the expelled water, ultimately repel each other. This in fact does occur during the inactive phase of the flagella. The greater force of propulsion and wider divergence during the active phase can only mean that the flagella are directly responsible. Borradaile (1922) remarks that "... these (flagella) exert their force more on the outward stroke when they are drawn by their extensors in the direction of their concavity as a cilium moves than when they are returning by their own elasticity in the direction of their convex sides". In view of this it might be of advantage to have the flagella beating out of phase for the sake of the continuity of the stream, although greater force would be achieved if all three were in phase. The strength and rapidity of their movements combined with differences in timing should, however, cause a current both powerful and continuous.

The function of this augmentation of the exhalent current strength is probably the removal of de-oxygenated water as far as possible from the inhalent opening. When the flagella are inactive, Indian ink suspended in the exhaled water is allowed to sink down towards Milne-Edwards' opening, as the currents are not strong enough to drive it all away from the animal. A second function has been suggested by Borradaile (1922), namely the deflection of particles of foreign matter which might otherwise lodge upon the organs of special sense. Finally there is the possibility that the turbulence caused by the flickering of the flagella would be advantageous to animals confined to small volumes of water, for instance the free water at the bottoms of burrows, as it could facilitate reoxygenation. This idea is supported by the work of Gameson and Truesdale (1959) on the re-oxygenation of water. They found that the exchange coefficient (cm. per hour) of stagnant water is 0.4 - 0.6, while that of water moving even very sluggishly is considerably higher. For example, the value of the coefficient for sluggishly flowing water about 2 inches deep is 4, and the re-aeration rate increases with speed of flow, so that water flowing down a 30° slope has a maximum exchange coefficient of 300.

Observations on the two grapsoid crabs correlate with these hypotheses. If animals are transferred from one container of clean water to another the flagellar activity is at first vigorous, but settles within a few minutes to the intermittent beating described above. Should they be transferred to organically contaminated water, however, the flagella flicker continuously, and do so even when the crabs are moribund. In water containing a suspension of mud particles there is similar prolonged flagellar activity, accompanied by elaborate cleaning and grooming behaviour.

The important part played by the exopodites of the maxillipeds in maintaining the welfare of the crabs thus explains the positions of the endopodites of the third maxillipeds during respiration. These move away from the other mouthparts, permitting the flagella freedom of movement. The identical activities of the three exopodites provide a reason for their similarity in size and form.

As yet we have considered only the external manifestations of respiration in the two species; no mention has been made of the mechanism which pumps the water in and out of the gill chamber with or without the assistance of the flagella.

Crabs were fastened to metal plates and immersed in water as before. The flagella of such crabs were always completely inactive, but the endopodites of the third maxillipeds were held away from the other mouthparts. In *C.punctatus* the endopodites showed little signs of movement, but in *S.catenata* they were sometimes shuffled slowly to and fro. Indian ink was again used to indicate the direction and strength of current flow. In *S.catenata* the exhalent streams were feeble, the ink being expelled in "puffs", while the currents produced by *C.punctatus* were stronger and uninterrupted. If the endopodites of the third maxillipeds were removed, the endites of the maxillae were plainly visible, sliding rapidly back and forth across the mandibles. This was found to coincide exactly with the powerful, undulating beat of the scaphognathite, situated behind the inhalent aperture. In order to expose the scaphognathite, the anterior branchiostegal wall, i.e. the pterygostome, of one side was carefully cut away, the operation being performed under water to prevent the interference of air bubbles. Borradaile (1922) explains clearly the movements of the scaphognathite which cause the water circulation. In specimens of *C.punctatus* and *S.catenata* whose branchiostegites had been partially removed, the directions of the water currents were unchanged. Water was drawn in over the coxa of the cheliped and pumped out anteriorly, but the exhaled water became rather diffusely distributed round the front of the animals as it was not being forced through the narrow exhalent opening or directed by the flagella. After about five minutes the flapping of the scaphognathite slowed considerably, as did the passive sliding movement of the endites.

According to Borradaile (1922) the major function of the epipodites of the maxillipeds is the cleaning of the gills. In the present species it was noticed that although removal of the pterygostome retarded the scaphognathite, there was an acceleration of the movements of the epipodite of the first maxilliped. The triangular blade of this organ lies antero-dorsal to the scaphognathite, over the front of the gill mound, and beats up and down so that the pointed tip describes an arc over the posterior gills. Fragments of tissue from the soft branchiostegal lining were collected by the hairy blade, and carried away with the exhalent stream.

The activity of the epipodites of the second and third maxillipeds, concealed under the gills, could not be seen, and in view of the size of the animals, no attempt was made to remove the gills lest the epipodites or other structures should be damaged in the process. The nature and situation of all three epipodites leads to the assumption that they travel up and down across the surfaces of the gills, raking the leaflets with their long, flexible hairs. They are able to move independently of the external portions of the appendages which bear them, but manipulation of the mouthparts of dead animals showed that every movement of the endopodites of the maxillipeds produces the passive sweep of the epipodites. Borradaile (1922) states that variations in the sizes of the exhalent and inhalent openings, and hence in the currents, depend upon the positions of the epipodite of maxilliped I and the expanded coxa of maxilliped III respectively.

This discussion of the aquatic respiration of the two grapsoid crabs has served to confirm and extend the work of other authors on the Brachyura. Although there may be slight variations from species to species, the circulatory system is essentially the same throughout the group, and the respiratory currents are initiated and controlled by the combined activities of specialised portions of the mouthparts.

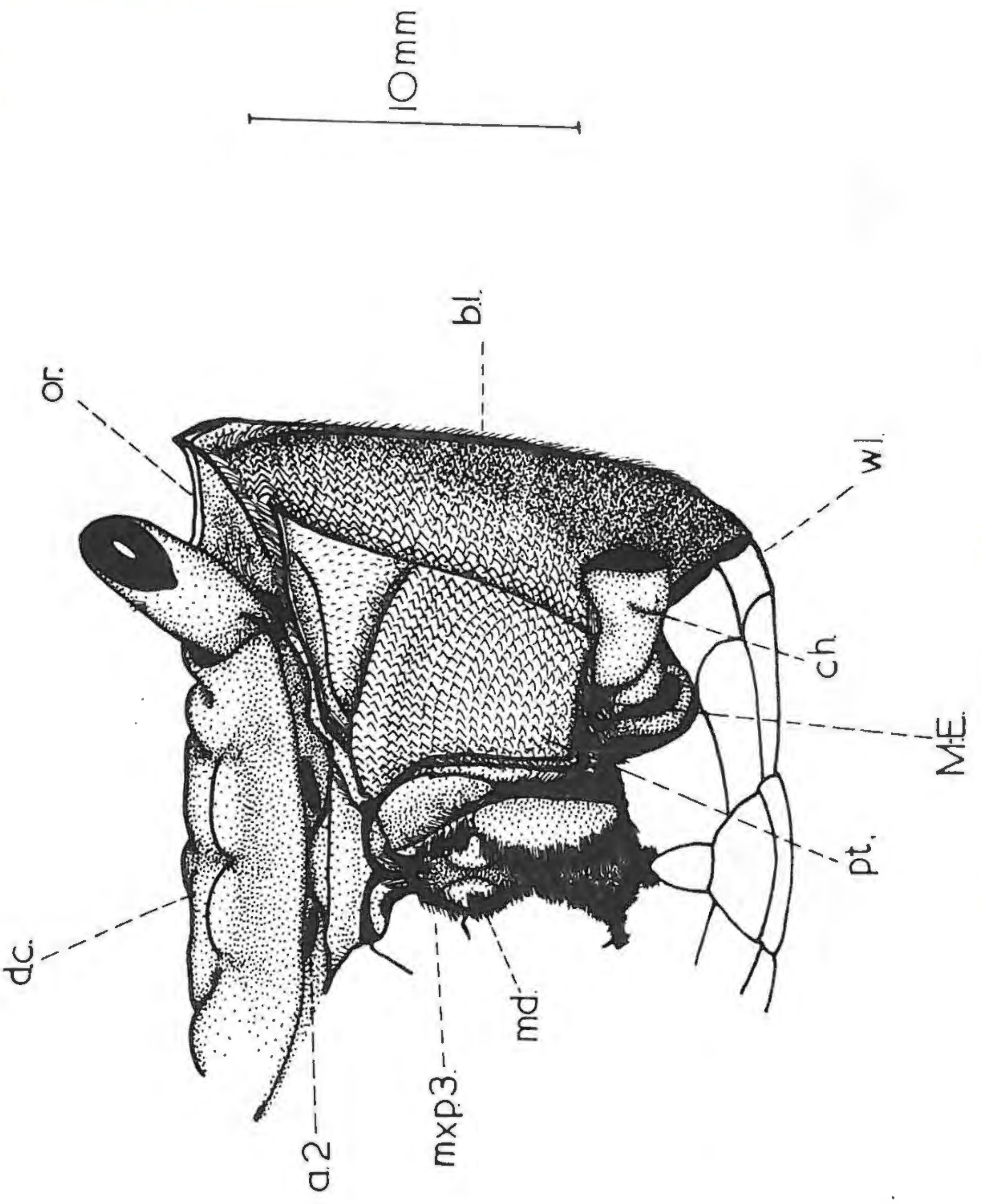


Fig. 39. Sesarma catenata Antero-ventral view of one side of an animal from which the legs and chelipeds have been removed. Note the gap between the third maxillipeds (mxp.3) under which lie the other mouthparts. The mandibles (md.) protrude towards the midline. Note the rows of geniculate hairs on the pterygostome (pt.) which is outlined by grooves dorsally and laterally, and on the lateral wall (b.l.) of the branchiostegite. There is a diagonal ridge on the third maxilliped.

d.c. = dorsal carapace (note bosses);
or. = orbit;
M-E. = opening of Milne-Edwards;
ch. = basal portion of cheliped;
w.l. = basal portion of walking leg;
a2. = second antenna, folded into its pit.

(b) Aerial Respiration.

It has already been stressed that the Sesarminae are semi-terrestrial or amphibious in habit, and that C.punctatus and S.catenata are capable of surviving out of water for lengthy periods. The Sesarminae are in fact said to possess a mechanism permitting them to utilize atmospheric oxygen for respiration - a mechanism which is practically identical in all Sesarma species, and extremely similar in other genera belonging to the taxon. This device is believed to consist in the animals' leaving the water with full branchial chambers and subsequently pumping the retained water over specialised areas of the carapace which guide and disperse the water so that it can be reoxygenated and drawn back into the branchial cavity to pass once more over the gills. In this way the same water can be used for respiration over and over again.

Fig. 39 shows the antero-ventral surface of a specimen of S.catenata from which the distal portions of the legs and chelipeds have been removed. The inner edges of the mandibles can be seen in the midline, projecting from under the widely separated, hairy third maxillipeds, which conceal the other mouthparts. Anterior to the mouthparts is a horizontally concave sclerite, fused dorsally with the carapace, and ventro-laterally with the pterygostome. In the angle formed between the sclerite and the pterygostome (i.e. the anterior wall of the branchiostegite) lies the exhalent opening, partially covered by the top of the third maxilliped. The pterygostome possesses a series of elongated, narrow grooves. The deepest of these runs diagonally from the exhalent angle across to the eye, where it becomes the lower margin of the orbit. It is joined there by a vertical groove, marking the boundary of the pterygostomial region and travelling down towards the inhalent aperture.

A short distance from the exhalent corner the diagonal groove bifurcates, and a horizontal channel traverses the pterygostome and unites with the vertical groove. A fourth groove, fairly short, but broad and shallow, arises from the horizontal groove, runs below and parallel to the diagonal groove and terminates under the orbit. The outer edge of each groove bears a fringe of short, stiff hairs.

The area enclosed by the horizontal and vertical channels and the free edges of the branchiostegite is patterned or reticulated with regular rows of curious geniculate hairs. These have been illustrated in a detailed drawing by Cott (1929a), who worked on *S.meinerti*, the largest of the *Sesarma* species. The cuticle of this area is tuberculate and the rounded, identical tubercles are also arranged in rows and occur in pairs. Each of the hairs arises between two pairs of tubercles, so that even lines of hairs and tubercles are formed. Every hair consists of two portions: a proximal portion at right angles to the pterygostome, and a distal portion which curves sharply inwards and downwards in the direction of the opening of Milne-Edwards, the whole structure being in the shape of a figure 7. The proximal portion bears on either side a 'barb' which consists of a flattened, pointed tuft of tiny hairs; distally the hair is smooth and tapering.

Behind the pterygostome, the lateral wall of the branchiostegite is similarly reticulated with slightly longer hairs.

When a small drop of Indian ink was placed anywhere on the reticulations of a dead animal, the fluid was immediately dispersed over a wide area and moved rapidly down towards the edge of the branchiostegite. Live crabs upon being removed from water began at once to pump copious steams from the exhalent openings. Although some of the water issuing from the gill chamber ran down over the mouthparts and was lost, **the** greater proportion flowed sideways into the diagonal and associated grooves, and thence downwards, wetting the entire reticulated area. At the same time the endopodites of the third maxillipeds, pressed firmly over the other mouthparts, were jerked to and from the midline by the brisk and powerful movements of the coxae in the opening of Milne-Edwards, exactly as described for *Sesarma nodulifera* by Verwey (1930). The animals adopted a somewhat elevated stance exposing the sides of the carapace.

After a few minutes water ceased to pour down over the mouthparts, but continued to run into the grooves and over the endopodites of the third maxillipeds, and the reticulations remained very moist. The pumping and the coxal activity were maintained generally for two to three hours. As time passed, however, the water leaving the gill chamber decreased in volume and contained air bubbles, and eventually the reticulated branchiostegal wall began to dry out, beginning posteriorly, until finally, when no water emerged from the exhalent orifice, the pterygostome was no longer damp and the coxae of the maxillipeds stopped their beating. During this time the body was gradually lowered and a hunched posture was assumed, with the walking legs and chelipeds drawn up very closely to each other and to the sides of carapace. This quiescent position was usually maintained until death supervened, but nocturnal activity was observed in some animals.

It is clear that in order to be able to pump water out over the branchiostegite for as long as three hours the crabs must possess some means whereby water can be collected from this surface and circulated again. If it could be proved that the water is repeatedly drawn from the branchiostegite back over the gills, it would automatically follow that there must be a good reason for the elaborate pumping mechanism and the dispersal of the water over the reticulated area. The nature of the reticulations serves to spread the water widely as a thin broken layer, and this would certainly increase the volume of oxygen taken into solution from the atmosphere, while the water is guided by the hairs towards the edge of the branchiostegite.

It was found by placing carmine particles near one of the exhalent openings of a crab which had been removed from water that the entire reticulated area became tinged with pink within a fraction of a second. Carmine was collected on the hairy ridges of the third maxilliped and on the bristles fringing the edge of the branchiostegite as well as the surface of the expanded coxa of maxilliped III in the opening of Milne-Edwards. If the carmine was alternatively deposited at Milne-Edwards' opening some of it was drawn into the branchial chamber, and reappeared at the exhalent opening, to course with the exhaled water over the branchiostegite. This process commonly occurred within one second, but occasionally three or four seconds elapsed before the pterygostome became suffused with pink. The length of time taken probably depended on the extent of circulation, for Borradaile (1922) reports that particles of foreign matter introduced via Milne-Edwards' opening are usually **whisked** upwards and out through the exhalent orifice without passing into the gill chamber proper, and rarely follow the main circulatory route.

This work indicates, therefore, that the reticulations and grooving on the branchiostegite of *S. catenata* indeed function in the way originally postulated by Milne-Edwards (1873) for other *Sesarma* species, and quoted by Stebbing (1893). Cott (1929a) concluded from his examination of dead specimens of *S. meinerti* that although he had never witnessed it such a mechanism would appear to be quite feasible in this species, and described the reticulated structure as "a device by means of which water, having been used for respiration in the gills, is made to circulate over the network, where it can take up fresh oxygen after which it re-enters the branchial chamber." Milne-Edwards had already commented that the mechanism was "de telle sorte que la même quantité de liquide peut servir pendant fort longtemps aux besoins de l'animal".

In Stebbing's (1893) opinion the movements of the coxae of the third maxillipeds are responsible for carrying the water back into the branchial chamber, and the ridges on the endopodites of these appendages act as breakwaters which also direct the stream onto the pterygostome. An additional function has been attributed to the coxae by Verwey (1930), who worked on several East Indian species of *Sesarma*. He found that particles of dirt accumulated on the hairy surfaces of the coxae as they moved to and fro in Milne-Edwards' opening, and that the particles were transferred to the midline. At the bases of the third maxillipeds of *S. catenata* there are tufts of hair, similar to those of other species. During the experiments using carmine it was noticed that particles were immediately collected on the branchiostegal fringes and on the coxae and breakwater ridges of the third maxillipeds only. The basal tufts adjacent to the coxae became reddened shortly afterwards, but the densely hairy mouthparts were unstained. In view of this it is probable that Verwey's observations also apply to *S.catenata*, but the actual process of the transference of particles is still unclear.

During aquatic respiration Milne-Edwards' opening was shown to be the only inhalent aperture. If this were still the case when the animals emerged on to land, the presence of reticulations posterior to the pterygostome would not only be pointless, but detrimental, since the water passing over them would be lost. It was nevertheless found that a powerful suction current comes into operation along the entire edge of the branchiostegite over the walking legs when the crabs are out of water. Drops of Indian ink were placed on the lateral reticulated surface at varying distances from the pterygostome, and each time the ink ran down and under the branchiostegite, and inky water issued from the exhalent orifice almost immediately.

Dorsally within the gill chamber of *S.catenata* near to the posterior border of the carapace and beneath the membranous branchiostegal lining, is a soft, lobular structure, identical in shape and relative size to the "vascular tuft" described by Cott (1929a) for *S.meinerti*. Cott maintained that this acted as a lung when the animals were on land since its proximity to the back of the carapace, which could be raised to make a slit up to four millimetres in width, would give the tuft direct access to the air. As long ago as 1879, Müller (as quoted by Stebbing, 1893), while holding in his hand the small *Sesarma (Aratus) pisonii*, noticed that the carapace was raised " ... and that by this means a wide slit was opened upon each side over the last pair of feet, affording a view into the branchial cavity". Müller observed this in other species of *Sesarma* and of *Cyclograpsus* and thought that when the elevation of the carapace occurred the animals automatically closed off the opening of Milne-Edwards, and took air in posteriorly. Verwey (1930) was able to refute the latter statement with respect to the East Indian mangrove crabs, but he too describes the formation of slits in *S.meinerti*, *S.nodulifera*, *S.taeniolata* and *S.bataviana*, and ascribed to the posterior openings the function of air uptake.

It has already been mentioned that the lifting of the carapace of *S.catenata* is limited, and is in no case sufficient to "afford a view" into the gill chamber. Manipulation of live and freshly killed animals produced no increase in the movement without tearing the internal organs.

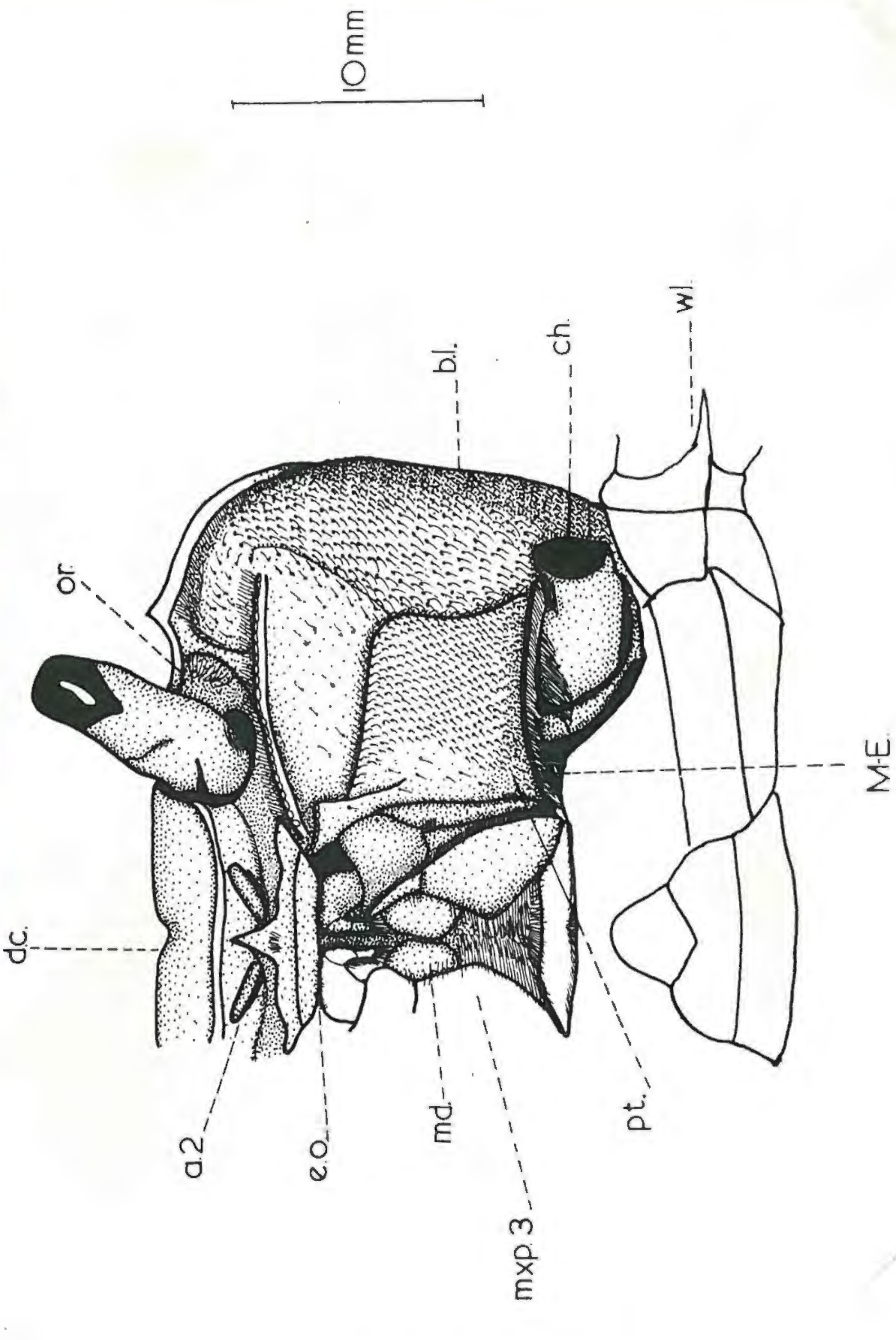


Fig. 40. Cyclograpsus punctatus: Ventro-lateral view of one side of an animal from which the cheliped and walking legs have been partially removed. Note the wide gap between the diagonally ridged third maxillipeds (mxp.3), and the rows of simple hairs on the pterygostome (pt.) and lateral wall of the branchiostegite (b.l.) The grooving on the pterygostome is not as complicated as that of S.catenata. d.c. = dorsal carapace;
a.2 = second antenna;
M.E. = opening of Milne-Edwards;
Ch. & w.l. = basal portions of chelipeds and walking legs;
e.o. = position of exhalent opening;
or. = orbit.

In *S.meinerti*, *S.taeniolata* and *S.bataviana* Verwey found that the posterior slits were formed when the water was very shallow, and that the crabs sucked water in posteriorly, whence it passed over the gills and was then circulated by way of the reticulations in the normal manner. This continued until all the water had been used up. Such elaborate behaviour has never been observed in *S.catenata*, and even crabs which have remained out of water for several hours cannot be induced to take up water at the back of the carapace.

The pterygostomial region and lateral branchiostegal walls of *C.punctatus* are similar in general structure to those of *S.catenata*, as can be seen from Fig. 40. There is a single diagonal groove running from the exhalent corner of the pterygostome to the orbit, and a broken vertical groove runs down the side of the pterygostome, which is traversed by a horizontal channel. The simple, down-curving hairs on the branchiostegite are more or less regularly arranged in rows, but are not as densely distributed as the geniculate hairs of *S.catenata* and the few tubercles on the cuticle are sparsely scattered. It was found by performing the same experiments with carmine and Indian ink that the circulatory processes out of water were identical in the two species. No posterior slit formation was ever observed in *C.punctatus*, and there are no "vascular tufts" within the gill chambers. In this species, however, the dorsal branchiostegal lining is thickened and spongy, and although there is as yet no histological evidence that it is vascular, it may well be so. Assuming this to be the case it is not improbable that the functions of the tufts of *S.catenata* and the roof of the branchial chamber of *C.punctatus* are the same.

From the studies of those species of *Sesarma* which raise the dorsal shield most noticeably, other authors appear to agree that this occurs only when pumping has ceased. The carapace is not raised prior to this presumably because while there is still sufficient water for circulation it must not be allowed to go to waste by running out at the back of the branchial chamber. Most of the workers consider the posterior openings to be used for air uptake, as the vascular tufts are so close to the hind end of the gill chamber.

Verwey (1930) believes that when *S.meinerti* is in very shallow water, the posterior slits primarily draw in water, and that air is taken in at the same time at the opening of Milne-Edwards, and only secondarily at the back of the carapace. Verwey also states that when all the available water has been used up and the carapace is finally lowered, air is still inhaled anteriorly. Whether or not Verwey's observations are wholly correct is of little import here. What emerges from his work and that of others, is that *Sesarma* species can breathe air during and after they have stopped circulating water externally, by means of their "lungs". Cott (1929a) felt that the circulatory mechanism, despite its usefulness, would expedite desiccation, thereby limiting progress on to land. This is probably true, and it might be thought that to take air into the branchial chambers when they no longer contained free water would simply make matters worse. Nonetheless it is the circulatory mechanism which has provided these crabs with access to land, and the ability to breathe by means of lungs allows them additional independence of the water. After all, even when there is insufficient water left to be pumped out of the gill chamber, the humidity within must be extremely **high** due to the moisture retained on the expanded respiratory surfaces.

In these terms, then, it can be postulated that of animals possessing these adaptations, the largest would be the most terrestrial in habit. The bigger the crab, the smaller the surface to volume ratio, and the greater the capacity of the gill chambers. These crabs would thus be the most resistant to desiccation, and would be able to circulate water and breathe air longest. Verwey (1930) has proved this to be true for the *Sesarma* species he studied. *S. meinerti*, the largest member of the genus, burrows high up on the banks and generally moves away from the water as the tide comes in. *S.taeniolata*, which is also fairly large, lives a little below *S.meinerti* and behaves in the same way. This species can pump water over the branchiostegite for at least nine hours. Two small species, *S.eumolpe* and *S.bataviana*, live much nearer to the water, and *S.bataviana* can pump for only about an hour. Neither of these two crabs shows any avoidance of water. All four species can survive immersion in water for indefinite periods, however, as can *S.catenata* and *C.punctatus*.

The fact that *C.punctatus* and *S.catenata* have never been seen to raise the dorsal shield sufficiently to draw in air or water posteriorly does not preclude them from having truly aerial respiration. As the volume of water circulating over the branchiostegite diminishes air bubbles are carried in the exhalent stream, and must be taken in under the edges of the branchiostegite at the same time as the water. There is furthermore no evidence against the continuation of air uptake after water circulation has ceased. If the vascular tufts of *S.catenata* and the spongy branchial roof of *C.punctatus* actually function as lungs, there is plenty of opportunity for them to do so during the latter stages of circulation and possibly when it has stopped altogether. Even so, the crabs do guard themselves against evaporation from the edges of the branchiostegite by assuming the characteristic hunched position when no more water is circulating. The legs and chelipeds, pressed closely to one another and to the sides of the body, must serve to reduce the size of the inhalent openings, and produce an area of high humidity immediately adjacent to the branchiostegite.

Similarly a high internal humidity level would be maintained for as long as possible.

Some comments on the behaviour of the two species are of note as far as their respective affinities for water are concerned. Observations on the crabs in the laboratory indicate that there is some avoidance of water in C.punctatus, irrespective of size, but more apparent in larger specimens, while S.catenata shows no "dislike" of the aquatic environment. In the field this distinction was not so marked, but throughout the course of the work done in the natural habitat, S.catenata was found in wet localities more often and in far greater numbers than C.punctatus.

Two of the sinks in which the animals were kept in the laboratory had cracked, roughened sides, and were large enough to contain more than a hundred crabs without overcrowding. Since both species could scale the sides with ease it was necessary to cover the sinks with heavy, well fitting lids. At first the sinks were not tilted, and were half filled with water, which was aerated. Although it was later found that the two species would survive indefinitely when immersed in clean water, interesting interspecific differences in their behaviour appeared in these particular crabs. Both species climbed nimbly up and down the sides of the sinks during the night, but in the daytime they were less active and S.catenata generally remained under water, hiding under stones and other objects on the bottom. C.punctatus, however, climbed up the sides of the sinks and clung to them by means of the sharply pointed walking legs. They often remained in this position for hours at a time, long after pumping had ceased, and returned within a few minutes if dislodged. On one occasion several of the crabs were discovered suspended over the water, having climbed backwards up one of the rubber aeration tubes made accessible by a nearby stone.

Once it had been established that the animals would survive without aeration provided they could leave the water, the sinks were tilted so that there was water at one end only. Again, *C.punctatus* seemed to show a preference for being out of water, while *S.ortmanni* stayed at the lower end of the sinks, making brief, infrequent excursions up to the dry end. *C.punctatus* congregated in the upper corners, climbing on top of one another so that pyramids were formed which sometimes consisted of about twenty crabs and reached well up the sides of the sinks. If one of these clumps was dispersed it was found that crabs which were completely covered by their fellows, and which had initiated the clump, were still circulating water over the branchiostegite after the outer animals had given up pumping. Clumping in *C.punctatus* is probably analogous to the bunching of land Isopoda, shown by Allee (1926) to reduce water loss, and by A.J. Miller, in a personal communication to Edney (1960), to increase survival in dry air. Quantitative experiments would of course be necessary to prove whether or not this is really the case.

Finally, certain grooming activities are closely associated with respiration. In order to make an investigation of these the mouthparts and pterygostomial regions of crabs which had just been removed from water were painted with fairly dry mud. The stream of water which poured down over the mouthparts to begin with washed away a large proportion of the mud in this area, and subsequently the endopodites of the third maxillipeds began to clean the underlying mouthparts by pulling and stroking them with their hairy, prehensile distal segments. Special attention was paid to the flagella and the endopodites of the second maxillipeds. At the same time the chelipeds were employed in various ways:

1. There was an up and down movement with the limb extended,

held closely against the body and describing an arc of about 90° between the horizontal position and the orbit. By imitating this with dead animals it was discovered that the bristles on the inner laminar face of the merus swept across the pterygostomial hairs. The bristles on the merus (one row in *C.punctatus*, two in *S.catenata*) thus act as combs, as Milne-Edwards first noticed in 1873. Cott (1929a) observed that in *S.meinerti* the curve of the merus fits exactly over the convex surface of the pterygostome, as it does also in *C.punctatus* and *S.catenata*. The function of the bristles was further confirmed by Cott, who noted that the reticulations of specimens of *S.meinerti* lacking one or other of the chelipeds were clogged with mud. Support is added by the fact that the bristles of the two present species became coated with mud, Indian ink or carmine particles which had been applied to the pterygostome during the course of various experiments.

2. The second activity of the chelipeds is really an enlargement of the first. When the limb is extended, its backward sweep against the body is limited by the propus, which catches on the post-orbital tooth. When the propus is flexed, the cheliped can move through an angle of 180° by virtue of the rotatory joint between the coxa and the body. As it sweeps backwards, the combs are dragged over the hairs of the entire lateral wall of the branchiostegite, while the tufts and tubercles of the carpus are brought into contact with the anterior regions. Even when the merus is farthest from the pterygostome, this important region is not neglected, for the tubercles of the palm of the hand rub against it.

3. The palms of the chelae are rubbed vigorously over the mouthparts. This activity may be carried out by the chela of each side alternately, or by both together, pointing downwards with the upper surfaces meeting in the midline. Every movement allows contact between

the pterygostome and the merus.

4. Frequently the finger and thumb "peck" at the mouthparts, at the pterygostomial regions of opposite sides and at each other. Probably this indicates the removal of lumps of mud or other foreign material hindering the passage of the respiratory currents and may be followed by the rubbing together of the hands, the palm of one over the outer surface of the other, presumably to dispose of accumulated dirt.

5. It has not been ascertained exactly how the combs of the merus are cleaned, but it is thought that the outer surfaces of the hands are responsible, since on numerous occasions the cheliped of one side was held forwards away from the body, while the other was carried across and the back of the hand drawn repeatedly over the inner face of the merus.

Figs. 23 - 26 show the sheet of long hair which arises on the coxa of the cheliped. With every movement of the limb the coxa rotates past Milne-Edwards' opening, and the hairs are dragged back and forth through those on the branchiostegal rim and the coxa of the third maxilliped. It is assumed that dirt collected on the coxal hair of the chelipeds is "pecked" off as described above. The similar bunches of hair on the walking legs may function in the same way with regard to the lateral edges of the branchiostegite, but the spheres of movement of these appendages are small compared with that of the cheliped.

The respiratory habits of these two grapsoid crabs coincide with those of the members of the Sesarminae which have been studied by other authors. On land the animals can use the water in the gill chamber many times by repeatedly pumping it over the hairy network on the branchiostegite, where it is re-oxygenated, and drawing it back into the branchial cavity. The importance of the network is emphasized by the complexity of the mechanisms for keeping it clean.

It is doubtful whether or not S.catenata and C.punctatus possess the ability to take in water and air posteriorly as described by Verwey (1930), but a suggestion as to the possible function of what appear to be accessory respiratory organs within the gill chamber has been put forward.

3. Feeding Habits.

Very little is known of the feeding habits of grapsoid crabs. According to Verwey (1930) *Sesarma* species are chiefly herbivorous and although they will take animal food, the diet generally consists of semi-decayed twigs, leaves, roots and other vegetable matter. Macnae (1957b) classifies *S.catenata* as a detritus feeder. Broekhuysen's (1941) paper on the breeding and growth of *Cyclograpsus punctatus* is uninformative as regards feeding.

The following account of the feeding habits of the two species is unfortunately rather superficial. It is practically impossible to see the actions of the mouthparts of such small animals, especially as the chelipeds and third maxillipeds obscure the underlying appendages. It is proposed to describe observations made in the field and the laboratory on the food and feeding of the animals and to try to correlate anatomical differences in the feeding apparatus with these.

(a) *Sesarma catenata.*

Mud was brought into the laboratory from the field and a small "terrarium" was set up in a deep container. The mud was packed down and thoroughly moistened with sea water. Crabs were placed in the terrarium and presented with fresh sprigs of *Arthrocnemum.* This was apparently recognised and the animals began to feed upon it in the following way.

1. The tip of a succulent stem was gripped with one of the chelipeds.

2. Tiny pieces of the flesh of the plant ~~was~~ were torn off by the other cheliped and pushed towards the mouth.

3. As the crab worked its way along the stem the chelipeds alternated in gripping and tearing the food. Only the

soft parts of the plant were taken, and the central vascular tissue was deftly cleaned and left behind as a slender strand.

4. The stem was relinquished every so often, usually after a short series of six or more "bites", and the animals commenced alternately touching the substrate with their chelipeds and moving these appendages to the mouth.

Partially dry *Arthrocnemum* was not accepted by the crabs, and as *Arthrocnemum* travelled best and remained succulent longer than any of the other salt marsh plants it was the only plant which could be used for these observations. It would be of interest to see whether or not *S.catenata* feeds on *Spartina.* Crichton (1960) records that *S.reticulatum* crops *Spartina alterniflora*, leaving only a few inches of stubble and eating the blades "in the same manner as we eat celery". *S.catenata* does not seem to eat *Spartina* capensis, for the tufts of grass near their burrows are not cropped, and no leaves were ever found in their holes. *S.reticulatum* habitually drags its food into its hole before commencing to feed.

This type of feeding appears to be rather different from that described for *S.catenata* by Macnae (1957b), who states that the animals collect surface deposits and filter them through the mouthparts, discarding unwanted material as pseudofaecal pellets, cemented with saliva. Verwey (1930) showed that *Uca signatus* fed in this way, sifting organic matter from mud collected by its chelipeds and returning the discarded mud to the substratum in small lumps.

On fine days *S.catenata* basks on the mudbanks or sits at the mouth of its burrow. The crabs emerge as the tide recedes, and move slowly over the surface of the damp mud and sometimes along the edge of the water. They are extremely sharp sighted and the movements of an intruder at least thirty yards away effectively put a stop to their activities, and they "freeze", poised for flight to the nearest burrow. They are especially disturbed by shadows falling on them and by movements above them, and were best approached slowly and stealthily from behind, as low down on the banks as possible. In places where the shadow of the observer was directed away from the crabs, it was possible to come to within ten feet of them. Although the animals are so watchful and are swift runners, they are not timid creatures, and even when approached very closely will sit outside their holes until the last moment before vanishing within. After a few seconds they reappear in what can only be termed an inquisitive manner and perch half in and half out of their burrows, ready to dart back into hiding.

In these conditions no details of their feeding in the natural habitat could be obtained, but some general information was gathered. When *S.catenata* runs at speed the body is elevated and the chelipeds are held up away from the ground. While foraging on the banks or in the water, locomotion is slow and the chelipeds are used as walking legs. Every so often one of the chelipeds is lifted to the mouth in a way reminiscent of the "tasting" performed by the land crab *Cardisoma* (Herreid, 1963). After a time the crab settles down to feed, usually in a damp, muddy spot or at the edge of the water. The body is held up so that the movements of the chelipeds and the field of vision are unimpeded, and the chelipeds swing from the substrate to the mouth and back again, either alternately or one at a time. This may proceed for some minutes before the animal goes on to a new area or scampers away to a burrow or to bask on the bank. As the crab feeds mud is scooped up in the spoonshaped tips of the chelipeds and transferred to the mouth appendages which work actively to and fro.

At intervals the procedure is reversed - one of the chelipeds brushes over the mouthparts and is then wiped on the surface mud in one swift movement. It would seem, therefore, that Macnae (1957b) is correct as regards the rejection of unwanted material, a conclusion substantiated further by examinations of the stomach contents of crabs killed in the field. The major constituents were minute fragments of plant material, which occasionally included algal spores. The appendages of tiny crustaceans were sometimes present, but mud or sand grains were very rarely found, as were tough woody or epidermal plant tissues.

It was at first thought that while the animals were feeding in the laboratory they were doing so in two ways - sifting the mud for detritus in between taking "bites" of the Arthrocnemum. This alteration of bouts of two different types of feeding hardly seemed reasonable. If the animals were not picking up surface particles however, but were removing unwanted material from the mouthparts (an activity involving similar movements of the chelipeds), the meaning of their changes in behaviour becomes clear, and analogous to the rejection of pellets containing bits of Spartina by Sesarma reticulatum (Crichton, 1960). There is also the possibility that between the periods of feeding upon Arthrocnemum the mouthparts require to be moistened, and the chelipeds may carry drops of water from the wet surface of the mud to the mouth region, picking them up in the same way as the closed tips of a pair of forceps This could be combined with the removal of pellets of debris. The possible need for moisture during feeding may provide one reason for the fact that the crabs always feed in damp places - on the recently wetted river banks at low tide and often under the water.

In reality the two types of feeding, i.e. that observed in the natural habitat and that seen in the laboratory, may not be very different. We know that *S.catenata* feeds by collecting mud and by picking off pieces of living plant tissue. We also know that very few mud or sand grains or pieces of tough plant material find their way into the alimentary canal, and that the chelipeds reject the vascular portions of *Arthrocnemum.* Both types of feeding thus consist of the uptake of vegetable matter, while hard or gritty substances are discarded. It is difficult to determine which is either of the two types is the more important. The presence of spores and the remains of small animals in the gut may be indicative of detritus feeding, but since the other fragments of plant material are unrecognisable there is no way of telling the type of feeding by which they have been obtained. The process of sorting out organic matter from lumps of mud must indeed be extremely complicated if it in fact occurs, for individual mud particles are on the whole considerably smaller than the pieces of food found in the gut. It is unlikely that this selection could be achieved by simply sifting the mud through the hairs of the mouthparts. This makes the evidence for detritus sifting seem rather unconvincing, and suggests that *S.catenata* does not filter or sieve mud for pieces of detritus, but instead has some means of extracting micronutrients from the mud, which is then discarded, while any bits of plant or animal material and a few mud and sand grains are taken up incidentally. Perhaps the final proof will come only as a result of future studies of the cohesive properties of mud particles, and the relation of crumb size to the sizes of pieces of organic detritus.

S.catenata will readily accept meat, especially if the crabs have been starved for a few days beforehand. In the laboratory animals were given 1 cm. cubes of sheep's lung, which is rather fibrous. When a piece of meat was deposited near a crab immersed in water, the antennae began to flick rapidly in all directions, and the animal advanced upon the meat, casting about with the chelipeds until they grasped the food and brought it up to the front of the body. The meat was dealt with in the same way by all the crabs, irrespective of size and sex and whether or not they were under water. The meat was held firmly with one chela while the other pulled off tiny pieces and transferred them to the mouth where they were engulfed by the vigorously moving mouthparts. In some cases the meat was so tough that considerable force was obviously being exerted to detach shreds from it.

The crabs ate watchfully, never abandoning hold on the meat and raising the unoccupied cheliped threateningly if approached by an animal which was not feeding. If another crab attempted to take the meat, the owner would retreat a little way before continuing to feed. The meat was entirely consumed, except for thick pieces of skin or fibre, which were picked clean and then discarded. Once the meat had been eaten, the crabs did not move away, but cast about with their chelipeds in search of more food. Often the chelipeds reached unerringly for fragments of the meat which had been scattered in front of and under the animals. This activity continued after all such fragments had been eaten, especially in crabs immersed in water, and any movable object in the immediate neighbourhood was picked up. Anything hard such as a small stone was immediately dropped, but softer substances were conveyed to the mouth to be tasted. On several occasions crabs were seen to taste pieces of their own faeces in this way, only to discard them at once with some violence.

The general pattern of feeding in S.catenata thus involves two stages. There is an initial stage in which material is tested by the chelipeds, which appear to be able to distinguish hardness and softness, and then a tasting of softer substances which leads to rejection or ingestion. In the event of the latter there is probably further sorting of the food by the mouthparts themselves.

(b) Cyclograpsus punctatus.

Practically no field observations were made of the feeding habits of C.punctatus. The crabs remain in their burrows for the greater part of the day but apparently do not feed there. They emerge in the evenings to forage.

When starved C.punctatus was given pieces of meat these were immediately accepted, especially by animals immersed in water. Both chelipeds grasped the food, pulled it towards the mouth and held it there, forcing it between the mandibles, until the whole of it had been eaten. If a piece of meat was too large to be dealt with all at once it was torn in two by the chelae, and one piece was tucked protectively under the body until the other had been eaten, when the first was retrieved and eaten in turn. The chelae then cast about to find stray fragments of food. All of the crabs fed in the same way, but now and then smaller specimens behaved like S.catenata, picking off shreds of meat between periods of chewing. Large male crabs which had not been fed "prowled" slowly about in pursuit of smaller animals which either fled, sometimes abandoning their meat, or had the meat wrested from them.

The stomach contents of C.punctatus reveals that the species is mainly herbivorous. There were generally rather large pieces of woody plant material, epidermal tissue, some of which appeared to be grass-like, and slices of Arthrocnemum stems. The remains of small Crustacea were extremely rare, and no mud particles were ever found. This indicates that C.punctatus is a coarse feeder, chewing off pieces of vegetable matter with its mouthparts, without first shredding or sifting the food.

In the terrarium the crabs devoured *Arthrocnemum* stems, and one animal siezed a very woody portion which was lying on the surface, and rushed with it to a sheltered corner where it proceeded to feed, holding the food endways on towards the mouth and making audible "crunching" noises as the mandibles cut through it. One evening at dusk as the tide rose in Lagoon 4, numerous large crabs were found amid the drifted algae, feeding actively upon the strands of *Gracilaria* and associated plants in an identical manner.

Of the two species *C.punctatus* is the more inclined to cannibalism when unfed. Large males will sit quietly watching unwary smaller crabs wandering nearby. Sometimes a small crab, particularly *S.catenata*, may walk under the elevated body of the larger *C.punctatus* or scramble over its back without being attacked. As soon as it comes within reach of the chelipeds, however, one of these darts out with great swiftness and grips the front of the small animal, bringing it nearer the mouthparts. The grip is intensified and cracks the carapace of the small crab, and pieces of the internal organs of the stil struggling victim are torn out and eaten. The presence of food is soon detected by other *C.punctatus*, which gather in the vicinity and descend on the corpse once it has been relinquished by its killer. Large males occasionally advance and try to snatch the little crab away.

Because almost nothing is known of the rôles played by the mouthparts during feeding, few comments can be made concerning a correlation between differences in form and function. The mouthparts of both species are very hairy and similar in construction, and there is no striking difference which might indicate how *S.catenata* can extract certain constituents of the substances brought towards the mouth while rejecting unwanted material. The chewing endites or gnathobases are practically identical in size and degree of mobility and calcification. On the whole, however, the endopodites of *C.punctatus* are larger than those of *S.catenata*.

The major structural differences are found in the second maxillipeds and the mandibles. The tip of the dactylus of the second maxilliped of *C.punctatus* is pronged (see Fig.29) while that of *S.catenata* bears stout hairs (Fig. 30). This may reflect the greater need for grasping and guiding large pieces of food to the mouth in *C.punctatus*.

The mandibles of *C.punctatus* are massive compared with those of *S.catenata*, and the incisor edge is longer. In *C.punctatus* the whole appendage is very solid, the apophysis is well calcified and there is heavy strutting on the inner surface (Fig. 37). This strutting presumably acts as a shock absorber as the mandibles cut the food, and though it is more complex in *S.catenata*, the struts in this species are slender and arched and the apophysis is poorly sclerotized (Fig. 38).

These morphological differences and the differences observed in the feeding habits of the two grapsoid crabs confirm that *C.punctatus* is a coarse, unselective feeder, chewing off pieces of food with its mouthparts and using the chelipeds to guide and push the food into the mouth. *S.catenata* is unable to cut up hard substances with its more delicate mandibles, and possesses some means of sorting out its food after shredding it with its chelipeds. It is not unlikely that this type of feeding arose from the need to deal with large pieces of food. Once the ability to sort out edible, and reject unwanted material had been established it could be improved and extended to include the absorption of nutriment from the surface mud.

Fig. 41a

Fig. 41b.

Fig. 41 a & b. Two heavily populated salting cliffs. Note the numerous holes in the salting cliff faces. In the upper picture the vegetation can be clearly seen as it hangs down over the cliff. The two major plants are Arthrocnemum (jointed stems at the right) and Chenolea (stems with whorls of fleshy leaves.)

4. Burrowing.

The burrowing habits of some semi-terrestrial crabs are very easy to study in the field because the animals live on open beaches. Many workers have been able to watch animals for hours using binoculars, and excellent sketches and photographs of burrowing in certain species have been made. The burrowing habits of species of *Uca* (Pearse, 1914; Verwey 1930) and *Ocypoda* (Cowles, 1908; Cott, 1929b) are particularly well documented.

S.catenata and *C.punctatus* live in areas with extensive plant cover, however, and for this reason no field observations on their burrowing habits could be made. Even in places where their burrows are somewhat exposed, the banks are so honey-combed with passages that there is probably little necessity for surface digging. At any rate there were never any signs of recent digging. Fig. 41 a & b are photographs of two heavily populated salting cliffs with numerous well established burrows, and serve to illustrate this point.

Verwey (1930) mentions in passing that *Sesarma* digs with the walking legs and makes perpendicular or slanting burrows which may have a side entrance. *S.reticulatum*, the marsh crab of the eastern United States, has been studied by Crichton (1960). Crichton does not describe how this species digs but shows clearly the form of the passages constructed. Each burrow or nest has several openings leading to more or less level, twisting corridors, which may interconnect before joining a deep vertical shaft, often descending to a depth of thirty inches and nearly always containing free water. A nest is usually inhabited by several crabs, of which only one or two are males.

It is well known that *S.catenata* is a burrower. In South African estuaries, for example at Knysna, these are in many places the only crabs living in the mudbanks near the high water mark (Day, Millard & Harrison, 1952).

Barnard (1950) takes *C.punctatus* to be an estuarine burrowing form, as well as being adapted to living under stones, but before the present observations were made it was felt that the work of more recent authors did not really support Barnard's statement. Day and his co-workers (1951-1959) found during their studies of the ecology of

South African estuaries that the species occured only on rocky shores. In the Zwartkops estuary Macnae (1957b) recorded the presence of C.punctatus and S.catenata in the Spartina zone on the mudbanks, and remarks that "Cyclograpsus punctatus is conspicuous making burrows among those of Sesarma and also sheltering under any available logs or boulders".

In the Kowie River estuary, however, C.punctatus has never been seen burrowing. It is certainly found living in the same places as S.catenata, but in these localities every hole contains a number of crabs of both species. It is likely that at Zwartkops this is also the case and that the observations of Macnae, whose work did not entail an investigation of the habits of the crabs, were not sufficiently detailed to give a true picture of the situation. For the reasons outlined above it is at least improbable that he in fact saw crabs burrowing. In consequence, three questions now arise:

1. Does C.punctatus really burrow, or does it use the holes made by S.catenata as shelters in the same way as stones or logs?

2. It is possible that C.punctatus will burrow only as a result of the burrowing activities of nearby S.catenata?

3. If C.punctatus does dig holes, which species constructs those burrows inhabited by both species?

Specimens of C.punctatus were placed in a glass sided terrarium containing moist, firmly packed mud, sloped so as to produce a miniature salting cliff with water at the bottom. The crabs were left undisturbed for several days. On inspection it was found that both males and females had been digging at the upper corners of the mud as far from the water as possible. Some of the holes sloped gently down into the mud, and in certain cases several crabs had been digging near one another, and had made small nests with two or three entrance passages. This provides answers to the first two questions: C.punctatus does burrow, and will do so in the absence of S.catenata. In reality, of course, this is merely a verification of a conclusion already reached during the field work. C.punctatus inhabits burrows on the banks of the somewhat isolated Lagoon 1, the only place of its kind where the species is apparently not associated with S.catenata.

When both species live together in the same hole, *S.catenata* clusters near the entrance while *C.punctatus* sits at the bottom, and there is frequently not more than one specimen of the latter in each burrow. These particular burrows are nearly all in low-lying places inundated during most high tides, e.g. mudflats and the *Spartina*-covered islands in Lagoon 4. Higher up on the banks are burrows in which live numerous *C.punctatus* but very few *S.catenata*.

Crabs of both species were allowed to make burrows in a terrarium in the laboratory, and in every case *C.punctatus* did so at the top of the mound as before, but *S.catenata* always dug lower down in the wetter mud at the base of the "salting cliff". This evidence leads to the suggestion that the low-lying burrows are constructed by *S.catenata* and are used as shelters by *C.punctatus* which happen to be in the vicinity, much as they will use any hollow object such as an old tin, while the burrows higher up on the banks belong to *C.punctatus* and are shared by the occasional specimen of *S.catenata*.

(a) Types of Burrows.

The work of Crichton (1960) indicates that the shafts described by Verwey (1930) for *Sesarma* species are probably greatly simplified. Certainly the burrows of the two grapsoid crabs at present under consideration are scarcely as simple.

Sesarma catenata: In places inhabited by *S.catenata* alone, for instance, the upper reaches of the estuary, two types of burrows are found.

(1) The salting cliffs are much eroded by their daily tidal inundation and are riddled with holes (see Fig. 41 a & b). The openings on the salting cliff faces are broad and cavernous, and lead back into hundreds of short interconnecting passages which run in all directions. It was discovered by digging along a bank for some yards that there were no discrete nests or deep vertical shafts, but that the tunnels formed a network, extending along the bank over the depth of the salting cliff, and reaching back into the bank for about eighteen inches. Crabs living within this network would be able to move for considerable distances along the banks at almost any level without coming to the surface. It was impossible to collect many animals from these burrows, since they afford such easy means of escape. Sometimes a

crab would vanish within the passages to reappear at an opening a few inches away, and if pursued would continue to do this, darting in and out of various holes and finally evading capture by disappearing completely. Prolonged digging with a spade or trowel was often of no avail as far as catching these crabs was concerned. Free water generally stands at the lower levels in these systems of holes, and the walls consist of smooth, firm, rather sticky mud throughout.

(ii) The second type of burrow occurs on the mudflats below the salting cliffs. These are simpler in construction, and are similar to those of *S.reticulatum* (Crichton, 1960). There is usually a wide, more or less vertical shaft which may open to the surface directly but frequently has several side entrances. Although the density of the holes over a given area may be high, each group of holes represents the openings to an individual system and there is no complex universal network. When crabs were being collected from this type of burrow they would at first try to escape by running to the bottom of the shaft. Nevertheless, they were seldom trapped in this way, but were so agile that they could dodge the hand of the collector by moving speedily up and down the passages until they had the opportunity to break away and run to a neighbouring burrow.

Nests of this kind are chiefly found in softish mud, contain a good deal of free water and are inhabited by a maximum of about six crabs, of which one or two are males. The males show a tendency to remain near the mouths of their holes, and the females congregate just below the surface. The openings are approximately 2-4cm in diameter.

The burrows of very young crabs are constructed according to the same plan, with a vertical shaft and occasionally a side entrance. They are narrow, and lie near

Fig.42. Upper region of a salting cliff face in Lagoon 4. The wide holes lead back into the entrance caverns of a C.punctatus nest. The vegetation in the foreground is a mixture of Arthrocnemum and small tufts of Spartina. The upper plant is Limonium. Note that the burrows do not continue up as far as the Limonium.

water in soft, wet mud. The openings may be flush with the surface, as are those of the larger burrows, but are often situated at the tops of small hillocks.

Cyclograpsus punctatus: Evidence has already been given which indicates that the burrows highest on the mudbanks belong to *C.punctatus.* These burrows are different from those known to have been made by *S.catenata* and are moreover inhabited by extremely large numbers of *C.punctatus.* In addition, the burrows inhabited by *C.punctatus* in Lagoon 1 are also of the type found at the top of the salting cliffs, but as the population here is comparatively small they contain fewer crabs than those in Lagoon 4 and are not as complicated.

Fig. 42 is a photograph of the upper region of a salting cliff face in Lagoon 4. The vegetation lying over the surface has been pulled away to disclose the mouths of crab burrows. Although the substrate is wetted only at high spring tides, the hard, sticky mud is nearly always moist. Each of the broad main entrances leads back into a cave, and the shapes of these caves and the passages connected with them were investigated by carefully cutting away part of one of the banks with a spade.

The entrance caverns are large, and the salting cliff faces covering them are in reality very thin, being hollowed out to form overhanging roofs. Numerous gently sloping galleries lead away from the caves, and run parallel to the face of the cliff, ending blindly or linking with galleries from neighbouring entrance caverns. In each gallery there were often many large *C.punctatus*, and as the galleries were not wide enough to permit the crabs to pass one another, they were usually standing close together, facing outwards. It was noted that these crabs never attempted to escape by running away. The majority crouched where they were or edged slowly into nearby tunnels where they clung with tenacity to the substrate, whereas the odd specimen of S.catenata sheltering in the galleries always ran out into the open and sought to hide elsewhere.

Winding passages lead from the entrance caverns back into the banks, and corridors descend from the top of the salting cliff where there are openings as far as two feet from the edge amid the vegetation. A complex system of runways is thus formed consisting of twisting tunnels which join here and there and have short, blind-ending offshoots. A shallow, more or less circular chamber lies some way behind and a little below the base of the salting cliff. The lowest entrances open directly into the chamber and the upper passages unite and run into it as two or three wide shafts.

A system of this kind constitutes a single nest, which may have fifteen to twenty entrances and large numbers of corridors and galleries, unconnected with those of adjacent nests. Although the mud remains moist between high spring tides there is very rarely free water standing at the lower levels. Apart from these burrows, C.punctatus makes short, shallow channels at the edges of stones and other heavy objects on the surface of the banks, and the holes made by young animals are similar to those dug by young S.catenata. There is insufficient information at present about the low-lying burrows occupied by both species. Even if these are initiated by S.catenata, there is nothing to indicate whether or not C.punctatus takes part in the digging activities.

(b) Methods of Digging.

Some observations were made in the laboratory to determine whether or not the two species dig their burrows in the same way.

A terrarium was set up as before, but this time had opaque sides and was covered with a sheet of thick plate glass. Animals were placed in the terrarium which was kept in a darkened room. The terrarium was illu~~str~~minated from above so that the plate glass lid acted as a mirror on the inside, preventing the animals from seeing movements in the room but giving an unrestricted view of their activities from the outside. Unfortunately the sharp-eyed S.catenata was still able to detect movements within close range, and immediately ceased to burrow when disturbed. This, coupled with the fact that these crabs always burrowed at the lower end of the terrarium and became obscured by the soft mud there, rendered the observations on S.catenata rather less detailed than those on C.punctatus, which was less watchful and burrowed in the drier mud at the top.

Cyclograpsus punctatus: Crabs were placed in the terrarium during the late afternoon and were left more or less undisturbed for 24 hours. Their first reaction on entering the terrarium was to hide themselves at the bottom of the "salting cliff" under the water, which was about an inch deep. They were able to camouflage themselves by trampling the soft mud with energetic movements of the walking legs, displacing some of the mud which rose in suspension, leaving a shallow depression into which each crab sank. At first the crabs were invisible in the muddy water, and as the mud settled some of it landed on them and they could often be located only by following the ripples of their respiratory currents.

The terrarium was generally inspected early the next morning, when signs of digging which had occurred during the night were found at the top corners of the mound. As a rule crabs which had dug holes large enough to hide them completely spent the greater part of the day concealed within. During the first night male crabs often managed to burrow this far into the mud, whereas females had usually not yet reached this stage, and either hid under water or shared the burrows of other crabs during the day.

The crabs emerged in the evenings at about 8.30 p.m. or a little later. They stood outside their holes for some time, clearing surplus mud from the surfaces of their bodies, and then ran down to the water. After this they generally wandered about in the region of the burrows for an hour or more before settling down to enlarge their own holes. During the wandering period they sometimes dug for a few minutes in places where burrows had apparently been started and abandoned, but eventually each returned to its own site.

Both males and females dig in an identical manner, and the same method is used for digging vertical, sloping and horizontal burrows. The actual movements were best seen in animals just beginning to dig holes. The chelipeds were held forwards and downwards on the substrate to brace the crab and the tips of the walking legs of one side were firmly embedded in the surface mud. In the meantime the walking legs of the other side deliberately trampled the mud, so that a considerable quantity was loosened. After several minutes the trampling stopped and the crab moved away and dragged with it over the surface some of the mud, which partly adhered to the digging legs. This mud was scraped from under the body and legs by the cheliped of the other side, which as it did so rolled small lumps over the surface and stuck them onto the substrate by patting them down with the hand. Three or four of these pellets were deposited near the entrance of the hole before digging was recommenced. In every case the excavated mud was dragged over the surface by the legs, and there was no indication that certain legs or one of the chelipeds were modified or used for carrying "armfuls" of mud as in *Ocypode* (Cowles, 1908; Cott, 1929b) and *Uca* (Pearse, 1914; Verwey 1930).

The slope of the burrow once the entrance has been made depends on the angle of the body and of the digging legs with respect to the surface. The legs of either side can be used for digging but an animal nearly always approaches its particular burrow from one direction and so does most of its digging with the legs of one side only. When digging proceeds below the surface the mud is dragged up and deposited next to the opening. Elaborate cleaning activities punctuate the digging, and the crabs run to the water from time to time to "wash". An actively digging crab can remove a quantity of mud equal to two to three times its own volume during one night. Males on the whole dig faster than females of the same size, probably because the male chelipeds are so much larger and capable of moving more mud at a time than those of the females.

In the laboratory the burrows of *C.punctatus* were never very long or deep and the crabs stopped digging after one or two nights' work, when their holes were large enough to conceal them completely. Where digging was still in progress the burrow entrances were surrounded by heaped pellets of mud for a distance of at least two inches, but the mud at the mouths of finished burrows soon became flattened by the movements of their owners.

Sesarma catenata: Males and females were placed in a terrarium and immediately sought cover under water. This species also camouflages itself with mud, but does so not by trampling the wet mud with its legs but with movements of the body. The tips of the legs are buried in the substrate and the body is swung upwards and forwards and then rapidly downwards and backwards so that the mud is pushed away posteriorly. By repeating this several times a crab makes a deep, broad trough under the water. At first the animal is hidden by the mud particles thrown into suspension, and later, as the mud settles on the carapace, it merges very effectively with its surroundings.

To start with, both males and females remained in the water, sitting at the edges of the troughs with their eyes above the surface and subsiding backwards into their troughs when approached. In the laboratory the females hardly deviated from this pattern, and evinced no signs of burrowing activities. In the natural habitat the behaviour of females is timid compared with that of the males. The females cluster within the burrows and rarely bask on open banks, probably because they must rely solely upon agility and swiftness to escape predators owing to the weakness of their tiny chelipeds. It is possible that this timidity restrained them from burrowing in the artificial habitats provided in the laboratory. The females were never seen to leave their troughs during the day, and spent the greater part of the night there as well, making brief excursions over the mound, and rushing back to the water if disturbed. On the other hand, they may not dig at all, since the females kept in the terrarium would feed on *Arthrocnemum* placed at the top of the mound and were not deterred by its exposed position. It is not impossible that they simply share the burrows constructed by males and take no part in the digging.

After 24 hours most males had begun to dig holes in the wet mud slightly above the water at the lower end of the terrarium. During the day they hid in their holes and displayed little of the exploratory behaviour observed in the field. At about 8.30p.m. the crabs emerged. They did not linger outside their burrows cleaning themselves but immediately entered the water, leaving it glistening wet after a few minutes to wander up and down over the bank. An hour later the crabs were generally at work on their burrows, but as has already been emphasized, it was very difficult to see their movements with any clarity. As far as could be determined, their digging is very like that of C.punctatus but in addition considerable use is made of the chelipeds as spades. This was often observed in animals enlarging the mouths of their holes. The crab stood outside its burrow, sideways on to the opening, with the legs widely spread out and the body elevated. The chelae were held in front of the crab, away from the substrate. Then, with finger and thumb touching, the cheliped nearest the hole was swept down to the rim and a lump of mud the size of a small pea was scooped up. The concave inner surface of the hand was used as a spoon, which carried the mud across the front of the crab, scraped it off into the substrate and patted it into place.

Burrowing in S.catenata was discontinued when the holes were deep enough to hide the crabs, and since the mud was fairly soft excavated pellets soon settled into the surrounding mud and the signs of digging were obliterated.

(c) Cleaning Behaviour.

Intimately connected with burrowing is the elaborate cleaning behaviour which is very similar in both species. In order to make a study of this behaviour the burrows of the crabs in the terrarium were plugged with mud a short while before the nocturnal activity was to begin. As the crabs left their burrows, breaking through the plugs, the sticky mud adhered to their bodies. S.catenata seldom embarked on cleaning activities straight away, but entered the water. C.punctatus usually cleaned itself for at least 15 minutes, however, and its movements could be observed in some detail. Both C.punctatus and S.catenata stop digging every so often to perform at least part of the cleaning ritual. The work of cleaning is carried out by all of the appendages, of which the most important are the chelipeds and the third maxillipeds.

1. The "hands" are rubbed over and under each other and lumps of mud on their surfaces are scraped off on to the substrate.

2. The reticulated areas are frequently brushed with the combs on the chelipeds, and the chelae pick off mud particles in the pterygostomial region.

3. The eyes, antennae and mouthparts are carefully cleaned, (i) By the chelipeds, which pick off mud in the anterior regions of the crab and which rub their inner tuberculate ridges over the mouthparts and sense organs. Any lumps of mud removed in this way by one chela are generally picked off with the finger and thumb of the other and pushed firmly onto the substrate with a quick, short movement, although S.catenata may pass mud to the mouth instead.

(ii) By their own activities and additional activities of the third maxillipeds. The eyes are rapidly raised and lowered in the orbits, the second antennae are extended and rubbed together in the midline and the endopodites of the third maxillipeds clean each other and the underlying mouthparts with pulling and stroking movements made by the three distal segments. These three segments, the dactylus, propus and carpus (which together can be called the "palp" of the third maxilliped) intermittently abandon the mouthparts to clean the eyes and antennae. The endopodites are moved away from the body like french doors, and the palps are extended and used in three ways. The joint between the merus and carpus allows a wide lateral rocking movement of the palp to and from the midline. When the palps are swung as far to the sides as possible, they reach up to and behind the eyes which are invariably lowered at the same time, so that on the return stroke the palps curve over them, gripping and brushing the eyes with their hairy inner edges. These movements may continue for some time before the palps are cleaned in their turn by the chelipeds.

The first and second antennae are cleaned in much the same way as the eyes. A smaller swing of the palps is required to clean the first antennae, which are very short and lie at the inner side of the orbit. The longer second antennae are more ventral and nearer the midline, and the palps flick over them when they are held out laterally, but when the antennae point anteriorly away from the body they are pulled and stroked and sometimes gently but briskly rubbed together by the palps. Again, particles accumulating on the endopodites are removed by the chelipeds.

4. After the greater part of the mud on the anterior regions of the body has been removed the chelipeds begin to clean the under surface, picking lumps of mud from the abdomen andthe bases of the walking legs and transferring the mud to the substrate or to the mouth as before.

5. Finally, the walking legs, if they are very muddy, are flexed and extended in adjacent pairs and rubbed vigorously against one another. The first walking leg is rubbed not only against the second, but also against the cheliped of the same side, while the opposite chela reaches underneath to pick off particles as the legs are drawn towards the body.

None of the appendages is able to reach the roof of the carapace, which may be heavily coated with mud, but at this stage the animals enter the water. In the water the anterior cleaning movements continue, but the animals remain immersed only until the mud on the shield has been washed off.

Although the cleaning ritual is identical in the two species, C.punctatus has longer periods of cleaning activity than S.catenata and spends a correspondingly shorter time under water than the latter.

Finally a few comments can be made concerning the burrows as they occur in the natural habitat, and the behaviour of the crabs with respect to the water which daily moves back and forth over the mudbanks containing their burrows.

The well established burrow systems on the banks of the Kowie estuary never show signs of recent digging. Presumably once passages have been made by colonies of crabs little further digging is required apart from repairs to reopen or enlarge tunnels damaged by flooding or some similar cause. In any case water movements and the numerous crabs running in and out of the holes must soon smoothe the surface mud, effectively removing any traces of digging. Quite possibly burrow systems may be inhabited by succeeding generations of animals without the necessity for any digging at all.

The differences in the water affinities of the two species are reflected in the zonation of their burrows, but neither shows the "dislike" of water found in some other crabs. Sesarma meinerti and S.taeniolata vacate their burrows when the tide comes in and run up to drier regions. S.taeniolata may even climb trees to escape inundation (Verwey, 1930). This reaction has never been observed in S.catenata and C.punctatus which also do not plug up their holes in the face of the encroaching water like Uca (Pearse, 1914; Verwey, 1930) and Ocypoda (Cowles, 1908; Cott, 1929b). On the other hand there is no special tendency for the two present species to follow the water as the tide recedes and to stay close to it throughout the tidal cycle as do *S.bataviana* and *S.cumolpe* (Verwey, 1930). It appears, therefore, that *S.catenata* and *C.punctatus* are truly semi-terrestrial and occupy a position on the landward path intermediate between those of "water-lovers" and "water-haters".

5. Some Additional Observations.

Certain additional observations of the life and habits of the two grapsoid crabs were made during the course of the field work and the studies in the laboratory. No quantitative or detailed analyses were carried out but a report is given here because it is felt that these observations are relevant to the main theme. It should be appreciated that most of the aspects described were noticed incidentally, and that because of this an element of speculation is introduced into a consideration of their precise meaning.

Reproduction: Broekhuysen (1941) records that C.punctatus has its breeding season during the winter months, from May to November. Present observations agree with Broekhuysen's statement, although a few berried females were found at other times of the year. Nothing is apparently known of the breeding habits of S.catenata, but during the period August 1962 to December 1963 it was noticed that most females were in berry during summer, i.e. from mid November to January, while females carrying eggs at other times were extremely rare.

Diurnal Rhythms. We have already seen that in the laboratory the crabs are active at night but remain more or less quiescent during the day. This evidently reflects the presence of an innate activity pattern. In the section dealing with aerial respiration it was shown that the animals adopt a hunched posture once water has ceased to circulate over the branchiostegite and gills, and it was assumed that this was a means of reducing further water loss. At night, however, even crabs deprived of water often became extremely active. This was particularly noticeable during the desiccation resistance experiments. While the crabs were still capable of movement they wandered about in their containers during the night, despite the inevitable acceleration of desiccation which must have taken place, and returned to the hunched position in the daytime.

There is some indication of a difference between the two species with regard to degree of rhythmicity. In the natural habitat *S.catenata* is fairly active during the day, moving over the substrate, foraging, sometimes stopping to bask, running in and out of burrows and to and from the water. On rainy days especially, these crabs spend much of the time scuttling apparently at random over the banks. In the laboratory the animals seldom remain at rest for long periods. In contrast is the behaviour of *C.punctatus*, which rarely emerges from its burrow before nightfall while in the tanks in the laboratory the crabs spend much of the day in clumps without moving at all.

Thus it would seem that although both species are nocturnal, *C.punctatus* has a definite diurnal activity rhythm while *S.catenata* is simply more active at night than it is during the day.

Responses to Light and Dark: *C.punctatus* appears to show a negative response to light. During the daytime it not only remains in hiding, but in those burrows which contain both species, *C.punctatus* is always to be found at the very bottom, while the crabs in the nests high on the banks are completely concealed within the galleries and passages. In the tanks in the laboratory this species congregated in clumps at the dry ends, but the clumps were largest when the upper ends of the tanks were shaded. If the lower ends were in shadow, many of the animals remained in the water, and the clumps at the upper ends consisted of only a few crabs. Although female *S.catenata* generally stay in their burrows for the greater part of the day, they are most often found very near to the surface, while the males and a few of the females move freely over the substrate. This species showed no particular preference for light or dark, but in the laboratory the animals generally remained in the water at the lower ends of their tanks, whether they were in shadow or not.

Flight, Warning and Threats On the whole *C.punctatus* is easier to capture than *S.catenata*. This seems to be accounted for by the fact that *C.punctatus* reacts more slowly to external stimuli, and crabs of this species may be approached very closely before they are disturbed by shadows or movements. Because of their small, weak chelipeds the females of both species must rely solely upon speed and agility to escape an attacker. Certainly female *S.catenata* run swiftly into hiding when an intruder is sighted, but *C.punctatus* females usually crouch where they are, clinging to the substrate, or try to creep into some nearby cranny. Once they have been caught, however, the females of this species are generally more active than the males in trying to escape, and if released will run for considerable distances in search of shelter.

S.catenata males run for cover when approached, but if they are driven into a corner a specialized behaviour pattern comes into play. The chelae are immediately brought across the front of the body so that the broad, orange outer surfaces of the hands with their black patches of hair are in full view, and look like a pair of eyes (Fig. 43). Further stimulation with a stick or a finger of the observer results in some adroit dodging by the crabs, with the chelae always facing the source of attack. If an animal is still unable to escape, a counter attack may be launched during which the chelae reach out to grip the "assailant", often dealing out some prolonged and painful nips. Sometimes the warning display may be accompanied by a rubbing together of the heavily ridged and tuberculate upper portions of the hands, which still face outwards but point downwards so that the

Fig. 43. *Sesarma catenata*: A male caught amid *Spartina*, giving its warning display by holding the conspicuously marked chelipeds in front of its body. One chela is about to sieze a twig with which the animal is being stimulated (not shown). Note the rhomboidal areas on the upper surfaces of the hands and the milled tubercles on the fingers.

Fig. 44. *Cyclograpsus punctatus*: Threat posture of male, chelipeds flung wide apart, fingers and thumbs gaping. Note that although the mud is crumbling, the animal is standing on "tip-toe".

upper edges meet in the midline. *S.eumolpe* and *S.quadrata* males have sculpturing on the chelae which is very similar to that of *S.catenata*, with milled tubercles on the dactylus and a rhomboidal area on the hand outlined by pectinate and granulate ridges. Tweedie (1954) watched *S.eumolpe* rubbing the dactyli together and remarked, "I heard nothing, but am convinced that the crab was stridulating." Stridulation is a well known device used by some arthropods either to warn off an enemy or to warn other members of the same species of impending danger. Guinot-Dumortier and Dumortier (1960) discuss the possibility of the presence of stridulation in the Sesarminae and agree that if *S.eumolpe* and *S.quadrata* do stridulate this can occur only in male crabs since the sculpturing of the hands of the females is so indistinct. They point out that stridulation in the Sesarminae had not been envisaged by workers prior to Tweedie, largely because Ortmann (1901) had said that as he had observed nothing of the kind in *Sesarma* species he did not believe that the sculptured areas were used for this purpose. The French authors suggest, moreover, that certain of the hairs on the bodies of the crabs may act as auditory organs in the same way as the hairs of some insects.

If a male specimen of *C.punctatus* is cornered, the response is very different from that shown by *S.catenata* males. The crab stands on "tip-toe" and throws the chelipeds wide apart in an intimidating threat posture (Fig. 44). This is rarely followed by any aggressive action, however. In fact the more an animal is stimulated, the more extreme becomes the posture, until the crab overbalances and lies rigidly on its back with the chelipeds and walking legs stretched wide, and it is often several seconds before recovery is sufficient for the threatening attitude to be resumed. While *C.punctatus* was being collected in the field the differences in the behaviour of males and females was especially marked.

As we have already seen, the females made energetic attempts to escape, but the males immediately assumed the threat posture and did not try to scramble up the sides of the buckets. If one of these males was released it generally adopted the posture again for a short while before running in search of a hiding place.

As would be expected in heavily populated areas, dead crabs of both species were often found. It was striking that dead *S.catenata* were usually entire, while *C.punctatus* was often mutilated in a way strongly suggesting predation by birds. This may of course not be the case, since the mutilation might be the work of a scavenger which for some reason feeds only upon *C.punctatus.* On the other hand it is not impossible that because of its slower reaction to attack, and particularly because of the curious retarding effect of the threat display upon flight in the males *C.punctatus* is more vulnerable to predation than the speedier *S.catenata.* Mutilated bodies of *C.punctatus* were nearly always found in exposed places, where the rather light colouration of the crabs contrasted with the darker mud. Amid the vegetation, where they were either covered or camouflaged, e.g. among the yellowish *Spartina* tufts, the animals were rarely found to have been damaged. Although *S.catenata* frequents exposed mudbanks, the dark colouration blends very well with the surrounding.

Territorial Behaviour: Neither species exhibits any signs of territorial behaviour. Both are truly gregarious since those holes or nests inhabited by one species only contain several to many crabs, and dozens of *C. punctatus* may share the shelter afforded by a large boulder. Although the animals do dig their own holes, it is apparently immaterial whether or not a particular hole is always inhabited by particular crabs.

S.catenata wanders far and wide on the mudbanks and simply makes for the nearest burrow if attacked. If a nest belonging to this species is destroyed, the inhabitants scatter to hide in other holes, without any signs of antagonism from the crabs whose holes have been invaded. Furthermore, the well established salting cliff burrows made by *S.catenata* are networks of tunnels in which no crab is restricted to any one area or set of passages. Thus there is not intraspecific display of ownership.

It has already been stated that the two species share each other's burrows, probably making use of them as shelters. This applies especially to *C.punctatus* which will use any form of cover in this way. In the laboratory the two species were kept in the same tanks, and neither showed any indication of being disturbed by the presence of the other. The crabs moved about freely, sometimes climbing over one another, and no warning or threat behaviour was observed in the males. It would seem, therefore, that the lack of territorial behaviour does not merely reflect the relationship of animals to members of their own species, but extends towards all of the grapsoid crabs living in the community. The presence of the other species is apparently not only tolerated, but virtually ignored.

III. DISCUSSION.

Part II of this thesis was directed towards an understanding of the relationship between the crabs Cyclograpsus punctatus and Sesarma catenata when they occur together in the same area of the banks of the Kowie River estuary. It was hoped that the nature of this relationship would be made clear by comparing some aspects of the biology of the two species, and three of these, respiration, feeding and burrowing were selected for study. This work included morphological investigations, experiments and numerous observations carried out in the field and the laboratory. It was not possible to examine any one aspect in great detail, but the author feels that even these slight glimpses into the lives of the two animals may be of some value. The grapsoid crabs as a whole have not been studied to any great extent, and less still is known about the members of the subfamily Sesarminae. As for these two South African species, our knowledge is limited to Broekhuysen's (1941) paper on the breeding and growth of C.punctatus, for besides this neither of them appears to be **mentioned** in the literature except as a name in the lists compiled during ecological surveys. The author found the present work most absorbing and believes that further studies of the habits of these crabs would help to bridge a considerable gap in the information we have about the animals living in South African estuaries, and about grapsoid crabs in general.

It is customary when speaking of a relationship between two rather similar things to emphasize their affinity or otherwise by assessing the extent to which they differ. No important differences appear to exist between the respiratory activities of C.punctatus and S.catenata and for this reason respiration can have no part in this discussion. In this case the similarity of the respiratory habits simply reflect a close taxonomic affinity. If their respiratory activities had instead been markedly different this might have been an indication of some ecological disparity between the species.

Initially two questions were asked with regard to the ecological relationship of the crabs. The first of these concerned the problem of their niche or niches. Do they in fact occupy the same niche? Using "niche" in the broad Eltonian sense the answer is that they do. Not only are both species herbivores, but they are also burrowing animals living on the banks of an estuary at approximately the same vertical level and in identical climatic conditions. Thus, both of them may be said to occupy the same sub-division of the great "herbivore niche".

Before analysing this situation further we must examine critically the controversial "Gause's theorem", together with the opinions of other authors regarding the problems surrounding occupancy of the same niche.

If we accept "Gause's theorem" at its face value as enunciated by Macfadyen (1957) - "two animals with closely related habits cannot exist together in the same ecological 'niche'", our first conclusion would seem to be erroneous. It has already been agreed, however, that "niche" when used in this way implies that the habits of the animals concerned are identical. Even so, it must be appreciated that the theorem as it stands only applies in very specialized conditions, for as Macfadyen himself states, such associations of animals can and do exist in nature. One of the major requirements of the theorem is that there must be some factor which is shared by both species and which limits increase in the populations because it governs the density of the animals in the area they occupy. Gause's own experiments (e.g. Gause, 1934) were done in the laboratory, where food and living space were limited, and Crombie (1945), whose experiments were rather like those of Gause, stresses the fact that "Gause's theorem" cannot be accepted without reservation. In the presence of a density dependent limiting factor competition between the species may develop, with the increase of the population of one species at the expense of the other. The end result of such competition is often the elimination of the unsuccessful competitor.

We know therefore that competition can arise, albeit in highly specialized conditions. Surely then it would be of advantage to animals which occupy the same niche to exploit it in different ways. In so doing these animals would reduce the likelihood of competition ever arising between them, thus solving a problem which, according to Darwin, is most severe for nearly related animals living in close physical proximity. Lack (1945) has proved this to be the case with respect to some predatory sea birds. He found in his studies of the cormorant and shag (*Phalacrocorax* species) that although both are fish predators and nest on the same cliffs, they do not eat the same fish or have their nesting sites in the same areas of the cliffs. Lack (1946) discovered that this type of relationship prevailed among many other related species of predatory birds; hence it may be said that the animals can and do inhabit the same niche, even when they are closely allied and are in close physical proximity to each other. Furthermore, it is true that such animals can exploit the common niche differently - thereby reducing the possibility of competition.

Thus we may now put the second question concerning the relationship between the two grapsoid crabs. How are they using their niche? They must be doing one of two things. Either they are both using the niche in the same way and will continue to do so until competition occurs with all its implications, or they have avoided the possibility of competition like Lack's birds.

Elton (1927, 1953) claims that the food and feeding habits of animals constitute the most important aspects of the "niche" concept. Here too the crux of the matter rests upon these aspects. *C.punctatus* is a coarse feeder, chewing off pieces of food with its heavy mandibles and guiding the food towards its mouth with the chelipeds and feeding appendages. *S.catenata*, despite the fact that it may feed on the same type of vegetation as *C.punctatus*, does so in a completely different way, rejecting tough material which presumably cannot be masticated with its more delicate mandibles. In addition the evidence we have suggests that the vast stores of nutriment contained in the surface mud are available to this species because of its ability to sort its food. In this way the possibility of competition for food has almost certainly been reduced. We have no definite proof that the difference between the food and feeding habits of the two species is very striking, however, and it might be thought that this conclusion should not be based upon so flimsy a foundation. It must nevertheless be realised that the dense plant cover and constant renewal of organic deposits in the estuarine environment provide an enormous food supply for the animals. Because of this the likelihood of their being forced to compete for the same food is very small, and there is probably little necessity for their feeding habits to differ markedly.

One other mechanism should be mentioned in connection with the problem of avoiding competition for food. The animals might come into competition not so much by feeding on the same things, but because the presence of one species in some way interferes with the feeding of the other. This possibility (if it indeed exists) may have been reduced to some extent by the fact that *C.punctatus* appears to have the more definite diurnal rhythm. *S.catenata* does much of its feeding during the day, while *C.punctatus* remains quiescent in dark places in the day time, emerging to feed only at night.

We are thus able to provide an answer to the second question regarding the utilization of the niche by these two closely related species living in the same locality. The feeding habits and behaviour patterns of the two species may be said at least partially to have separated them ecologically. Furthermore, although their utilization of the niche may be only slightly different, the food resources of their environment are so rich that at present they serve to reduce the possibility of competition instead of acting as a density dependent limiting factor promoting it.

The work of Pearse (1929) has contributed much towards the understanding of the relationships between semi-terrestrial Decapoda living on the same shores. From his studies of the animals inhabiting the beaches and reefs at Tortugas Pearse concluded that animals do not start the journey to land indiscriminately as it were, but solve the problem of competition first. Once this has been successfully achieved those animals potentially able to overcome the general problems of terrestrial existence are free to continue on their way. If we subscribe to this view, which is certainly a reasonable one, it is clear that each of the present species must have differed, at least in their feeding habits and probably in other ways as well, long before the evolution of their semi-terrestrial habit.

Pearse (1929) was particularly interested in evolution, and included in his work a consideration of the problem of competition for living space. The crabs and hermit crabs at Tortugas, he found, had separated into distinct zones on the shores. Closely related species, even if they lived the same distance from the water, inhabited completely different localities or occupied different places in the same locality.

In this way the animals had simply avoided one another and in so doing had avoided competition.

Pearse and other workers have analysed this aspect in more detail with respect to *Ocypoda* and *Uca*, two genera belonging to the Ocypodidae, the most advanced of the brachyuran families. These animals often live in crowded colonies on tropical beaches. Here, every crab possesses an individual burrow, and because of this the animals cannot be regarded as fully gregarious in habit. The colonies are in the form of mosaics, divided into territories belonging to individual crabs and which extend for a short distance about the mouth of each hole. *Ocypoda* species nearly all warn intruders away by stridulating loudly from the depths of their burrows, while the fiddler crabs stand within their territories near the mouths of their holes, and the males adopt threatening postures or dart out to attack strange animals wandering in the neighbourhood. Pearse (1914) noted that fighting is not only confined to males, but that "each individual jealously guards the area about his own burrow". Both of these crabs thus have some means of advertising "their possession of a token property", (Wynne-Edwards, 1962). *Uca* especially appears to show a preference for particular localities, and if removed from its territory may spend days trying to return. A fiddler crab may occupy the same burrow for days or even weeks without changing the location of the mouth by so much as half an inch (Crane,1941).

All this introduces a new element - the avoidance of competition for living space by the members of a single species. In single-species colonies of *Ocypoda arenaria* (Cowles, 1908) and *O.ceratophthalma* (Cott, 1929b) it has been noticed that crabs rarely approach the burrows of others in the community. An animal entering the wrong hole, if it is undeterred by the warning of the owner, may endeavour to take possession of the hole, but is always met with strong resistance. In mixed crowded colonies of *Uca* species Crane (1941) observed that male crabs of one species were extremely intolerant of the presence of crabs of their own kind, and showed far greater tolerance towards members of other species. For example, *U.beebei* and *U.stenodactyla* sometimes lived only one and a half inches apart, "whereas adult males of the same species will tolerate each other's burrows not less than three inches apart and generally more."

In contrast with the method of avoiding inter- and intra- specific competition which has been evolved by the Ocypodidae is that which has been adopted by *S.catenata* and *C.punctatus.* It is true that there is some indication of vertical zonation in the habitat, since the species tend to separate according to their respective affinites for water - *S.catenata* burrows where the terrain is inundated at every high tide, while the largest specimens of *C.punctatus* make their holes higher up on the banks. It is also possible that the difference in the breeding seasons of the two species may be of importance at another level. The crabs produce large numbers of pelagic larvae, and it is not unlikely that in shallow bodies of water such as lagoons larval mortality is less extensive when one species breeds at a time than if both were to deposit their egg masses at the same season of the year.

Intermediate between the largest *C.punctatus* and the newly hatched larvae are the small to medium sized adults which inhabit the lower regions of the banks. Unlike the ocypodid crabs, the two grapsoids are fully gregarious in that the burrows constructed by one species or the other are inhabited by more than one member of the particular species.

Furthermore every burrow in this area often contains several crabs of both species. As we have seen neither shows any signs of territorial behaviour within the species or towards crabs of the other species, and the owners or tenants of a nest appear to ignore the presence of any crab entering in search of shelter. In this way there is evidently no competition for living space either intra- or interspecifically, since all the crabs are able to share all the available space.

It can be suggested that an association of this kind has many other advantages. One is that it allows the animals considerable freedom of movement away from their holes while foraging or making excursions to the water, since they can simply make for the nearest hole when danger is imminent. Another advantage might derive from the possible stridulation of S.catenata males. If these crabs do in fact stridulate, and if both species can "hear" the vibrations produced, this could serve as a warning device for all the crabs in the vicinity at the approach of danger.

It is a great pity that so little consideration has been given to the ecological relationships between the genera and species of the Sesarminae by other authors. Verwey (1930) shows clearly that the East Indian species of Sesarma occupy zones correlated with their size and the degree to which they are terrestrial, These zones overlap fairly widely, however, and it would be of interest to find out whether or not the animals have solved the problem of competition for space in the same way as have the two present species.

Finally, let us consider the origin of territorial behaviour from the point of view of feeding. There are two ways in which this could have come about. If C.punctatus lived exclusively on Arthrocnemum and S.catenata obtained all its nutriment from the surface mud several consequences might arise. Initially the two species might separate so that each was living close to its own food supply, and it is conceivable that each species would guard its home area against intruders. In this way interspecific territorial behaviour could come into being. The next step might be the division of the habitat into individual territories, like those of many mammals and birds. This is not really likely in a temperate estuarine environment because although the food resources are vast and are constantly replenished, replenishment is rather slow. In temperate regions organic decomposition takes place much less rapidly than it does in the tropics and vegetation does not grow as quickly or luxuriantly. An animal confined to a small area in these conditions might easily exhaust its available food within a short time so that intraspecific territorial behaviour would be of no benefit.

If the feeding habits of the two species were instead exactly the same, this could also lead to the development of territorial behaviour. *Uca* species all feed in the same way on organic detritus (Verwey, 1930) and live in tropical regions. The climate ensures that food is plentiful, and because of this the animals can afford to live in individual burrows, however crowded the colony, without needing to wander far from their holes to forage.

Thus, if animals need to feed either on completely different or on identical foods to be territorial, , it can be suggested that *C.punctatus* and *S.catenata* are prohibited from dividing the habitat in this way. First of all, the feeding habits of the two species overlap. Secondly the climate is such that an animal confined to a small area might use up its food supply, and this necessitates foraging over a wide area. Lastly it is clear that as they move about in search of food the two species and the individuals of a species must come into contact with one another. Division of the habitat into territories thus becomes an impossibility. The gregarious habit as we have seen, is of advantage in that all of the animals can share the available space without competing for it. It is postulated, however, that this is an advantage gained as a result of the food requirements and feeding habits of the crabs. It is there factors, and the environmental conditions upon which they depend, which have forced C.punctatus and S.catenata to be gregarious and to mingle so closely with each other in the areas which both species occupy together.

GENERAL SUMMARY.

1. The semi-terrestrial grapsoid crabs *Cyclograpsus punctatus* and *Sesarma catenata* have been studied in two ways. Part I of this thesis gives an account of their distribution in the Kowie River estuary in relation to certain environmental factors. Part II deals with further aspects of their biology as well as the ecological relationship between the two species.

2. A description of the estuary is given, together with a report of studies of the types of substratum and vegetation and of the salinity variations which are produced at spring and neap tides in the upper and lower reaches.

3. The distribution of the animals in the estuary is described, as well as the results obtained from determinations of burrow density in relation to H.W.S. level and vegetation type, desiccation resistance experiments and tests to investigate resistance to variations in salinity.

4. The results are discussed and it is shown that the vertical distribution of both species is dependent upon the stability of the substratum and the presence or absence of vegetation as well as the ability of the animals to withstand exposure. Horizontal distribution is largely dependent upon salinity and the type of terrain. It is suggested that other factors probably play a part in determining distribution. The problem of the evolution of the terrestrial and semi-terrestrial habit is discussed, with special reference to the two grapsoid crabs.

5. The ecological relationship between the species in the places which they inhabit together is considered, and it is pointed out that an understanding of this problem may be reached through a comparison of certain morphological and biological aspects.

6. A description of general morphology and coloration and the detailed morphology of the chelipeds and mouthparts of the two species is given, and it is concluded that the major interspecific differences between the mouthparts lie in their relative sizes and strengths.

7. Observations and the results of experiments concerning aquatic and aerial respiration are discussed, and it is shown that the aquatic respiratory activities of both species are similar to those of other Brachyura. The animals are able to respire on land by pumping water retained in the gill chambers over the ridges and hair tracts on the branchiostegite, where it is reoxygenated and then reused. The semi-terrestrial habit is discussed in relation to respiration and associated behaviour patterns, and a possible function for special structures within the gill chambers is suggested.

8. The feeding habits are described and evidence for the presence of some differences in the food and feeding of the two species is presented. It is shown that both will feed upon macroscopic vegetation, and that the ability of S.catenata to sift nutriment from the surface mud (which has not as yet been conclusively proved) might stem from the more obvious rejection of unwanted material.

9. The types of burrows inhabited, digging activities and associated cleaning behaviour are described and discussed.

10. Various additional observations of the life and habits of the two species are commented upon. These include breeding seasons, diurnal rhythms, light and dark responses, flight, warning and threat, and territorial behaviour.

11. In the discussion the ecological relationship of the species to each other is considered in the light of their morphology and biology. It is concluded that although the animals both occupy the same ecological niche in the broad sense,

the possibility of competition arising between them for food and living space is a remote one for several reasons:-

(a) The feeding habits are at least slightly different.

(b) The differences in their diurnal rhythms may help to prevent the feeding of one species interfering with that of the other.

(c) The food resources of the estuarine environment are vast.

(d) Their different breeding seasons may serve to prevent larval competition for space in shallow water, and there is some evidence of vertical zonation on the banks which is correlated with the sizes of the adult animals.

(e) Both species are gregarious and there is neither inter- nor intraspecific territorial behaviour, so that all individuals are able to share all the available space.

12. Finally it is postulated that the nature of the environment (and hence the nature of the food supply) and the feeding habits and food requirements of the two species, have not only forced them to be gregarious but have also prevented them from developing inter- or intraspecific territorial behaviour.

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* = Not seen in the original.