A COMPARATIVE STUDY OF SOME ASPECTS OF THE BIOLOGY AND ECOLOGY OF *SESARMA CATENATA* ORT. AND *CYCLOGRAPSUS PUNCTATUS* M. EDW., WITH ADDITIONAL OBSERVATIONS ON *SESARMA MEINERTI* DE MAN

by

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In the estuary of the Kowie River in the Eastern Cape Province there occur two amphibious grapsoid crabs, *Sesarma catenata* Ort. and *Cyclograpsus punctatus* M. Edw. They live together in many places, commonly inhabiting the same burrows in the muddy banks of the river. The present exploratory study of these two species has been undertaken to enhance our knowledge of their biology as well as our understanding of the relations between these two very similar animals which live in such close proximity one to another.

THE HABITAT

The Kowie River empties into the sea at Port Alfred, and is broad, winding and shallow. The tidal limit lies 13 miles from the mouth and over most of this length extensive, gently sloping mudbanks are left exposed at low tide. The level of mean high tide is marked by a low salting cliff which is surmounted with vegetation. At Port Alfred itself the river runs between steep, stony, artificial dykes and on either side lie lagoons (Fig. 1). The lagoons on the East Bank (1, 2 and 3) are almost completely cut off from the river although an exchange of water does take place via seepage points in the dyke. The two western lagoons (4 and 5) are fully tidal.

Large areas of the intertidal zone in the estuary are colonised by the tall, coarse marsh grass *Spartina capensis* Nees (*S. stricta* Roth.). This usually disappears about the level of High Water Neaps (HWN), to be replaced by a zone of typical salt marsh plants, dominated by *Arthrocnemum*, especially *A. pillansii* Moss, which has long stems, prostrate and woody at the base and terminating in erect green succulent tips. With the *Arthrocnemum* there may be mingled *Spartina* and *Triglochin bulbosum* L., particularly in low wet situations, and towards High Water Springs (HWS) *Chenolea diffusa* Thunb. A short distance below HWS *Limonium scabrum* (Thunb.) O.K. appears and spreads upwards, presently to give way to grasses, shrubs and trees. The zonation of plants on the banks of four of the five lagoons is very much the same as that along the river banks. The banks of Lagoon 4 (known locally as Little Beach) are sandy and devoid of vegetation. The two lagoons which lie furthest from the sea (3 and 5) contain masses of drifted algae, in particular the slender, branched brown alga *Gracilaria verrucosa* (Huds.) Papenf.

The distribution of the two crabs in the area round Port Alfred is shown in Fig. 1. Beyond the town, where the river is not restrained by artificial dykes, the two species occur together

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living in burrows in the muddy banks along the shore line. In many areas of Port Alfred *C. punctatus* occurs alone. Unlike *S. catenata* this crab is adapted for living under stones or other shelter, as well as in burrows. It has therefore been able to establish itself amid the stony walls

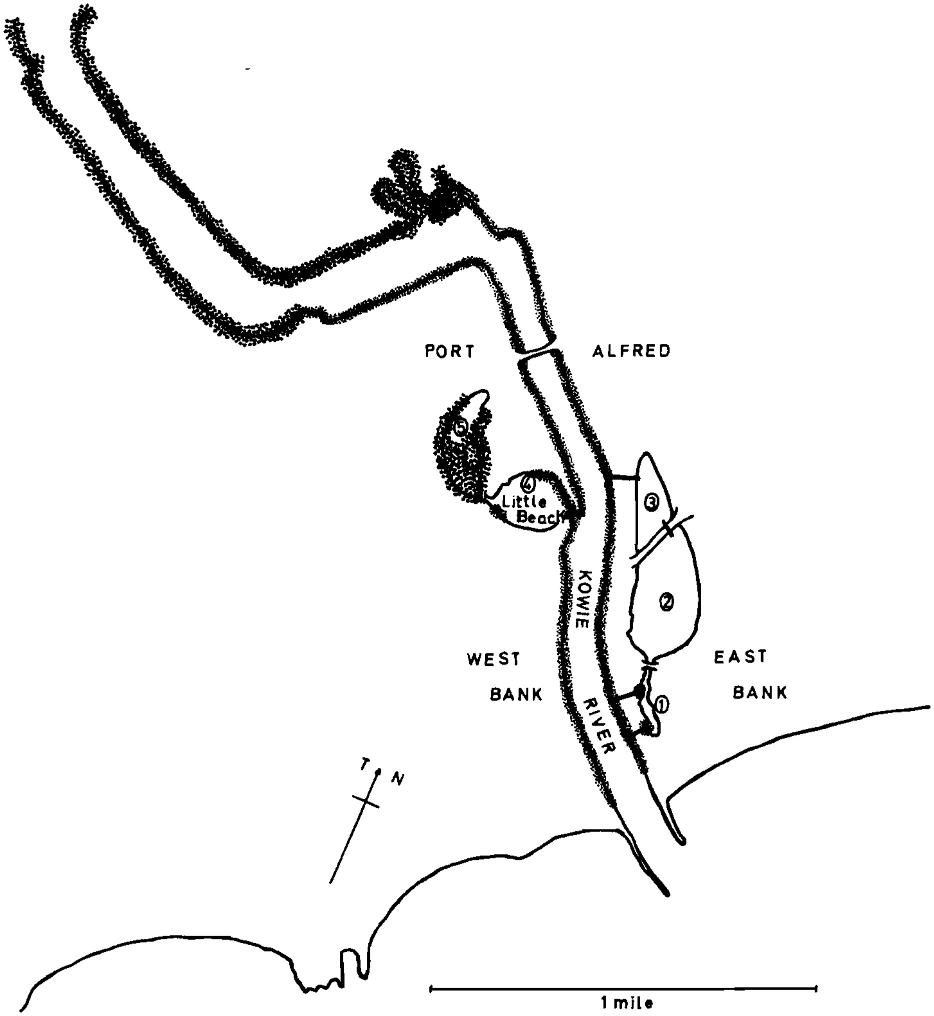


Figure 1. Map of the first three miles of the Kowie River estuary. The course of the river has been straightened near the mouth by the erection of stony dykes, and there is a series of lagoons on either side of the main water course. Those on the east bank (Lagoons 1, 2 and 3) are connected to the river via seepage points in the dykes (black bars); Lagoons 1 and 2 are confluent, and there is a seepage point in the bank which separates Lagoons 2 and 3. The lagoons on the west bank (Lagoons 4 and 5) are fully tidal. The distribution of *Cyclograpsus punctatus* and *Sesarma catenata* in the lower reaches of the estuary is shown. Fine stippling = *C. punctatus* only; Heavy stippling = both species present.

of the dykes lining the river and also in Lagoon 4 where it finds adequate shelter under stones. Small numbers are also found in Lagoon 1 where they live in burrows or beneath stones at the seepage points along the east bank.

ON BURROWS AND BURROWING

In the muddy banks of the river the two species live closely together, often inhabiting the same burrows. Belt transects of one yard width were made at seven points along the shore of Lagoon 5 and a further six transects were made at a station up the river about three miles from its mouth. The number of burrow entrances in each square yard was counted and the nature of the vegetation recorded. An analysis of the results of these transects shows that the burrow mouths extend up the banks to a vertical level about two inches below HWS; below this they increase in numbers, so that the greatest density is at the level of the salting cliff, and then decrease again until they end about 24 to 28 inches vertically below the level of HWS.

The distribution of burrow entrances is markedly affected by the presence and type of vegetation. They are particularly abundant where *Arthrocnemum* is most dense, and appear also where this plant is mingled with *Chenolea* and/or *Limonium*. They are never found where *Limonium* alone is present. At the lower levels the burrows occur as far as the outer margin of the *Spartina* fields but no further. These findings are illustrated diagrammatically in Fig. 2, which is based upon data obtained in Lagoon 5. It would seem probable that burrow distribution is determined not only by the level of water at high tide, but also by the type of plant cover and the suitability of the substratum for digging. As Dyer (1937) reports, *Arthrocnemum*, *Chenolea* and *Spartina* all possess ramifying root systems which consolidate the soil. Although the *Spartina* fields are always inundated at high tide the mud between the tufts remains firm, while that farther out is soft and fluid. Both *Spartina* and *Arthrocnemum* provide excellent cover without restricting freedom of movement: the animals can scuttle rapidly between the

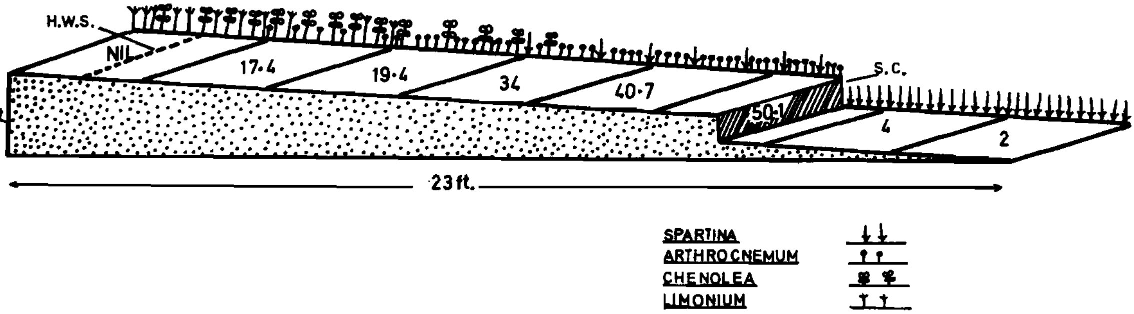


Figure 2. Diagram of a belt transect of one yard width, based upon data obtained from the shore of Lagoon 5. The density of burrows in each square yard is given, as well as the distribution of the plants *Spartina capensis*, *Arthrocnemum*, *Chenolea diffusa* and *Limonium scabrum*.
H.W.S. = High Water Springs; S.C. = Salting Cliff.

tufts of yellowish grass, and those living in the *Arthrocnemum* zone are invisible as they run about beneath the mat of woody stems. The numerous burrow mouths on the more or less vertical salting cliff faces, which are themselves devoid of vegetation, are generally concealed by an overhanging fringe of *Arthrocnemum* stems.

The results of these transects make no distinction between burrows excavated by the two species. While it is clear that *S. catenata* can dig burrows for itself as these are found in regions where the species occurs alone, both in the upper reaches of the Kowie estuary and at Knysna (Day, Millard and Harrison 1952), the evidence that *C. punctatus* can burrow is less certain. Scott, Harrison and Macnae (1952) report that it is sometimes found in shallow burrows in the estuary of the Klein River at Hermanus, and in the present investigation it was found inhabiting burrows in an isolated region in which *S. catenata* did not occur. It could not, however, be excluded that such burrows had been excavated by *S. catenata* at some earlier time, more especially as *Cyclograpsus* was never observed actually burrowing in the field.

To resolve this point crabs of the two species were placed in separate glass terraria containing moist, firmly packed mud sloped so as to produce a salting cliff with water at the bottom. The animals were allowed to remain undisturbed for several days and the terraria were then inspected. Both species had constructed burrows. It was most striking that without exception *C. punctatus* had constructed burrows at the top of the mound, whereas *S. catenata* had done so in the wetter mud at the base of the artificial salting cliff and nearer the water level. It would thus appear likely that in any area where the two species occur together the burrows nearer the water line have been made by *S. catenata*, those higher by *C. punctatus*. Some support for this is found in the relative distribution of the two species where there is a mixed population. In the burrows in low-lying situations inundated during most high tides many specimens of *S. catenata* are present in each burrow, and usually not more than one *C. punctatus*. Higher up the banks the position is reversed as *C. punctatus* is numerous and *S. catenata* scarce. With this information it is possible to study the types of burrow constructed in the field by the two species.

Two types of burrow appear to be inhabited by *S. catenata* (Fig. 3a). The first, which is to be found in the mudflats below the salting cliffs, consists of a more or less vertical shaft running downwards for 15-20 cm. This shaft may open directly to the surface, but usually has one or more side entrances with openings of 2-4 cm. in diameter. Each of these shafts represents an individual burrow and there is no evidence of any connections between neighbouring shafts or their approach corridors. These nests are found in softish mud, contain a good deal of free water and are inhabited by a maximum of about six crabs of which only one or two will be males. In general structure they resemble those of *Sesarma reticulatum* Say described by Crichton (1960).

The second type of burrow is found in the salting cliff faces. Here the openings are far wider and lead into a network of interconnecting tunnels, containing free water at the lower levels, which may reach back 40-50 cm. from the cliff face. The system of tunnels spreads for long distances; excavation showed one such system to run for several metres along the bank. There was no evidence of separate nests.

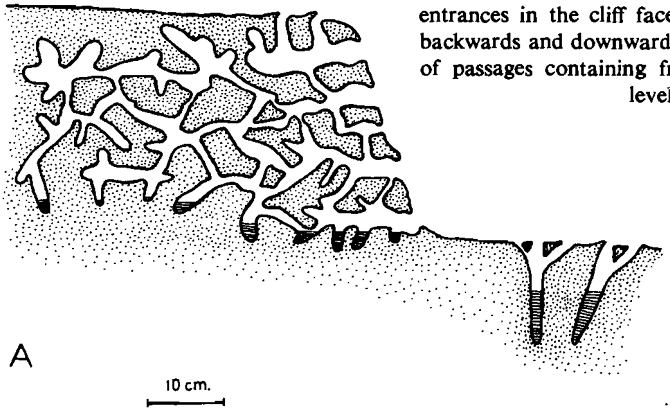
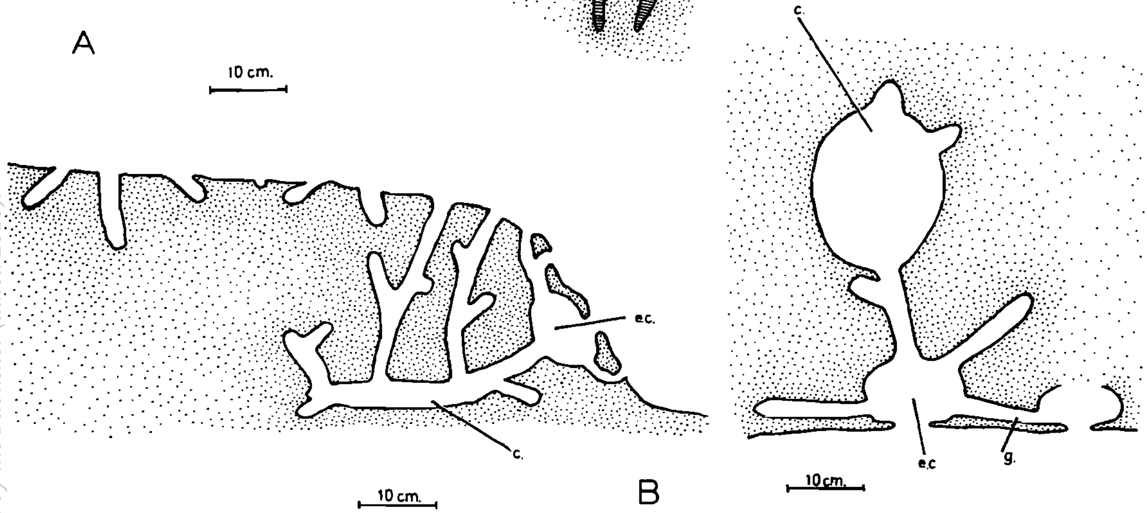


Figure 3a. Diagram of a vertical section through a mudbank to show the structure of the burrows excavated by *Sesarma catenata*. On the right are examples of nests found in the mudflats below the salting cliffs, i.e. vertical shafts containing considerable free water and having one or more side entrances. To the left is the salting cliff with wide entrances in the cliff face and above it, leading backwards and downwards to a complex network of passages containing free water at the lower levels.



3b. Diagrams to show the structure of burrows excavated by *Cyclograpsus punctatus*. The one on the left represents a somewhat simplified vertical section through a mudbank. Note the short, simple "bolt-holes" in the bank above the salting cliff and the more elaborate nest with entrances in the salting cliff face. One main entrance and several subsidiary ones lead to the entrance chamber (e.c.) immediately behind the salting cliff face, and a passage leading backwards and downwards into the bank opening into the oval chamber (c.) below. From this chamber a number of passages arise, some of which lead as almost vertical shafts to the surface while others end blindly. The diagram on the right shows the same nest in horizontal section, and illustrates the manner in which lateral galleries (g.) arise from the entrance chamber as well as the oval shape of the lower chamber.

The burrows excavated by *C. punctatus* (Fig. 3b) differ from those of *S. catenata* in several particulars. Again two different types can be distinguished. The simpler of the two consists of holes which appear to serve merely as temporary shelters for animals wandering amid the vegetation above the salting cliffs. The narrow entrances (3-4 cm.) are nearly always concealed by overlying stems and foliage, and are often found as much as 100 cm from the edge of a cliff. These holes, which penetrate the dryish mud at all angles, are simply straight tunnels about 5-10 cm. in length. They are thus not capacious enough to accommodate more than one or two animals at a time and never contain free water.

Burrows excavated nearer to the edges of the salting cliffs have a more elaborate structure and generally contain a dozen or more crabs. The entrances, which are large, lead to wide chambers immediately behind the surface of the salting cliff. From these chambers arise several gently sloping galleries which run parallel to the cliff face and may end blindly or connect with similar galleries from other entrances. Vertical shafts with openings at the cliff's edge may lead down to the entrance chamber. One or two passages from the rear of the entrance chamber run backwards and downwards into the bank for 5-10 cm. and open into a shallow, more or less oval chamber which lies approximately level with the base of the cliff. This chamber gives rise to more passages, most of which end blindly, although one or more may lead up as wide shafts to open at the surface amid the vegetation above the salting cliff. A system of this kind, with many separate entrances and numerous corridors, constitutes a single nest which is independent of those adjacent. Within these burrows there is rarely free water standing even at the lower levels, a condition which contrasts with the cliff tunnels of *S. catenata.*

Specimens were isolated in terraria with sloping mudbanks to observe their patterns of digging. The activities of *C. punctatus* may be fairly easily observed since they excavate at or near the top of the mudpile. The movements of *S. catenata* are far harder to see both because digging occurs near the water's edge and because this species is much more easily disturbed. The method used by *C. punctatus* in digging is the same in the two sexes, although the males are more effective than the females. The chelipeds are held forwards and downwards to support the crab which then tramples the mud with the legs of one side. This activity is continued for several minutes and a considerable quantity of mud is loosened. The crab then moves out of the burrow or away from the place where it has started to dig, using the digging legs to drag with it some of the mud, which is sticky and adheres in part to the legs and the ventral body surface. The mud is now scraped off both ventral surfaces and legs by the cheliped of the opposite side, being rolled up into small lumps which are then stuck to the substrate by patting them down with the hand. Some three or four such pellets are deposited near the entrance of the burrow before digging is recommenced. Elaborate cleaning activities punctuate the digging and at intervals the crabs run down to the water to wash away adhering mud. There is no indication that the chelipeds or certain specialised limbs are used for carrying away the mud as is the case in *Ocypode* (Cowles 1908, Cott 1929b) and *Uca* (Pearse 1914, Verwey 1930). While digging is still in progress the entrance to the burrow is surrounded by heaped up mud pellets, but these are rapidly flattened by the movements of the occupant of the burrow. A crab may remove a quantity of mud equal to twice or three times its own volume during one night's digging.

Only males of *S. catenata* have been observed to dig when males and females are placed in a terrarium together. Isolated females do show some digging activity but this seems to be restricted to the excavation of shallow open trenches which are quite ineffectual as shelters. It thus appears probable that in the field females simply use burrows which have been constructed by the males, unless perhaps the two sexes play specific roles at different stages of the excavation. The pattern of digging is very much the same as that observed in *Cyclograpsus*, but *Sesarma* further uses its chelipeds as spades. This action was most easily observed in animals enlarging the entrances to their burrows. A crab will stand outside the burrow, sideways on to the opening and facing outwards, with the legs spread out and the body elevated. The chelae are held in front of the crab away from the substratum. The cheliped nearest the hole is then extended and swept down to the rim and a small lump of mud about the size of a pea scooped up on the lower edge of the hand. The cheliped is then carried back in front of the animal and with a short, backward movement the little pellet is scraped off onto the substratum and patted into place. It is possible that this procedure is more effective in working in soft mud than is the use of the legs alone.

ON RESPIRATION AND DESICCATION

Both *Cyclograpsus* and *Sesarma* are amphibious. They feed above the water's edge when the tide is low, and *Sesarma* is often to be seen basking on the mudbanks on sunny days; *Cyclograpsus*, though less inclined to leave its burrows during the day, may be found wandering amid the vegetation above the mudbanks. Such a habit inevitably calls for respiratory adaptations and it might further be expected that *Cyclograpsus*, because its burrows lie higher up the mudbanks, would be more resistant to desiccation than *Sesarma*.

Müller (1864) appears to have been the first author to describe the aerial respiratory adaptations of grapsoid crabs. His account of observations of live *Sesarma*, *Grapsus* and*Cyclograpsus* species were quoted more or less verbatim by a number of later authors in various texts, and it was not until Verwey (1930) studied the mangrove crabs of the East Indies that the problem was re-examined and much of Müller's work confirmed and extended. By great good fortune it was possible during the present investigation to obtain a number of specimens of the largest and most terrestrial of the species studied by Verwey, *Sesarma meinerti* de Man, which is a mangrove crab abundant on the Natal coast. We were thus able to compare the respiratory adaptations of this species with those of *C. punctatus* and *S. catenata*, and at the same time check some of the observations reported by Verwey.

"PUMPING"

When any of these crabs emerge from the water they carry water in the branchial chambers. The movements of the scaphognathites drive this fluid out of the exhalent openings and over the antero-lateral surfaces of the branchiostegite. In *S. catenata* the movements of this fluid have been observed by placing tiny drops of carmine suspension at various sites on the body. On issuing from the exhalent opening the fluid passes along a deep groove fringed with short stiff hairs; this runs out laterally from the exhalent opening and shortly bifurcates (Fig. 4).

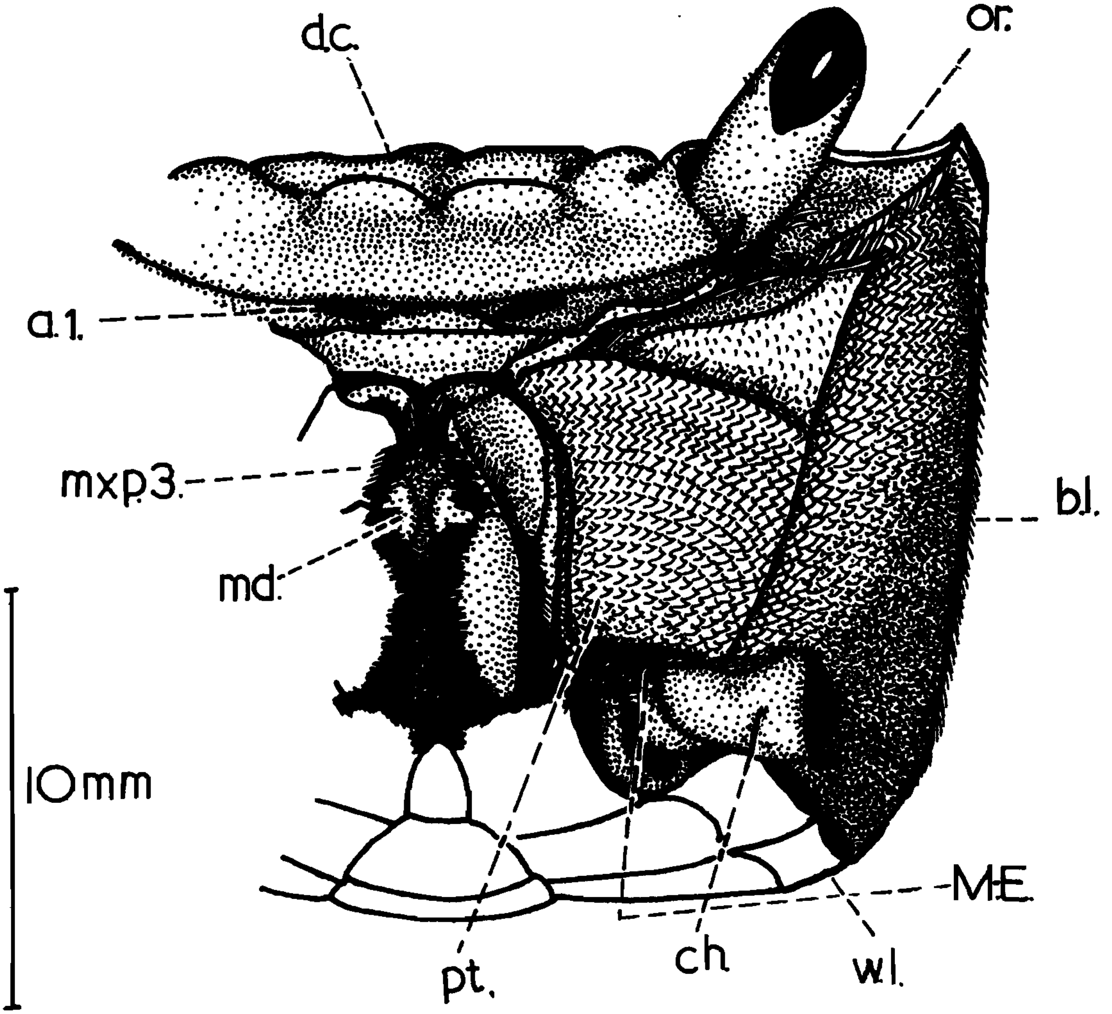


Figure 4. Anterior view of *Sesarma catenata* showing details of grooves and distribution of geniculate hairs on the antero-lateral surface of the left side of the branchiostegite. Note the broad groove leading away from the exhalent opening (this cannot be seen as it is concealed behind the top of maxilliped 3), and branching into two grooves, one of which travels on towards the orbit while the other goes more or less horizontally across the pterygostome. A third groove runs almost vertically down and terminates at the edge of the branchiostegite over Milne Edwards' opening above the cheliped. There is an anterior field of hairs as well as a postero-lateral field which extends backwards as far as the last pair of walking legs. a.l. = antennule; b.l. = lateral wall of branchiostegite; ch. = stump of cheliped; d.c. = roof of carapace; md. = mandible (partially concealed by maxilliped 3); M.E. = opening of Milne Edwards; mxp. 3. = maxilliped 3; or. = orbit; pt. = pterygostome; w.l. = stump of walking leg.

The more dorsal fork runs towards the lower margin of the orbit, the more ventral almost horizontally, demarcating the upper limit of an extensive reticulate area of tubercles between which stand geniculate hairs; the detailed structure thus agrees with that in *S. meinerti*, described by Cott (1929a). This area extends over the ventral half of the anterior face of the branchiostegite, the pterygostome. A similar reticulation and field of geniculate hairs occurs on the lateral surface of the branchiostegite. The water, carried laterally in the two grooves flows as a thin film over the fields of geniculate hairs and re-enters the gill chamber, anteriorly, by way of the opening of Milne Edwards (a third, more or less vertical groove assists in guiding it in this direction), and laterally beneath the edge of the branchiostegite above the walking legs. In this manner water is constantly circulated through the branchial chamber and effectively aerated by being spread as a thin sheet beneath the hairs on the branchiostegite. The system may be regarded as an inverted plastron, the geniculate hairs recalling, on a grosser scale, those of *Aphelocheirus aestivalis* Fab. (Thorpe and Crisp 1947 a and b).

The rate of circulation of water in this manner can be very rapid. If a droplet of carmine suspension is placed near one of the exhalent openings, the entire reticulate area is suffused with pink in less than one second, while carmine placed at the opening of Milne Edwards will commonly reappear at the exhalent opening in less than one second, but may occasionally take three or four seconds to complete the circuit. This value is perhaps deceptively small, for Borradaile (1922) has reported that particles of foreign material introduced into the branchial cavity by way of the opening of Milne Edwards are often driven rapidly upwards and out through the exhalent opening without passing through the gill chamber proper.

These observations accord well with those of Verwey (1930) on *S. meinerti*, *S. taeniolata* White, *S. bataviana* de Man, *S. cumolpe* de Man and *S. nodulifera* de Man. Another grapsoid, *Eriocheir sinensis* H. Milne Edwards, was shown by Olthof (1936) to employ a similar method of aerial respiration. This animal is, however, unable to sustain the circulation for more than a few minutes since much of the water pumped out of the exhalent openings immediately runs down over the mouthparts and is lost ventrally. In *Sesarma* this is largely prevented by diagonal setose ridges on the third maxillipeds which act as breakwaters, as described by Stebbing (1893), and also assist in directing the fluid onto the pterygostome.

A similar circulation of water has been demonstrated in *C. punctatus*. The detailed organisation of the grooves over the pterygostome differs from that in *Sesarma* while the tubercles are fewer and the hairs simple. Here, too, "breakwaters" on the third maxillipeds aid in maintaining the circulatory flow.

It is worthwhile to emphasize here that the exhaled water is drawn in not only anteriorly but also along the whole length of the lateral edge of the branchiostegite. Although Verwey (1930) does not mention this, it seems most probable that it is also the rule for the species he studied. We have been able to demonstrate it clearly in *S. meinerti*, and it would seem that the same occurs at least in *S. taeniolata* and *S. bataviana* since examination of dead specimens of these two species showed that the reticulate areas on the branchiostegite continue posteriorly as far as the last pair of walking legs.

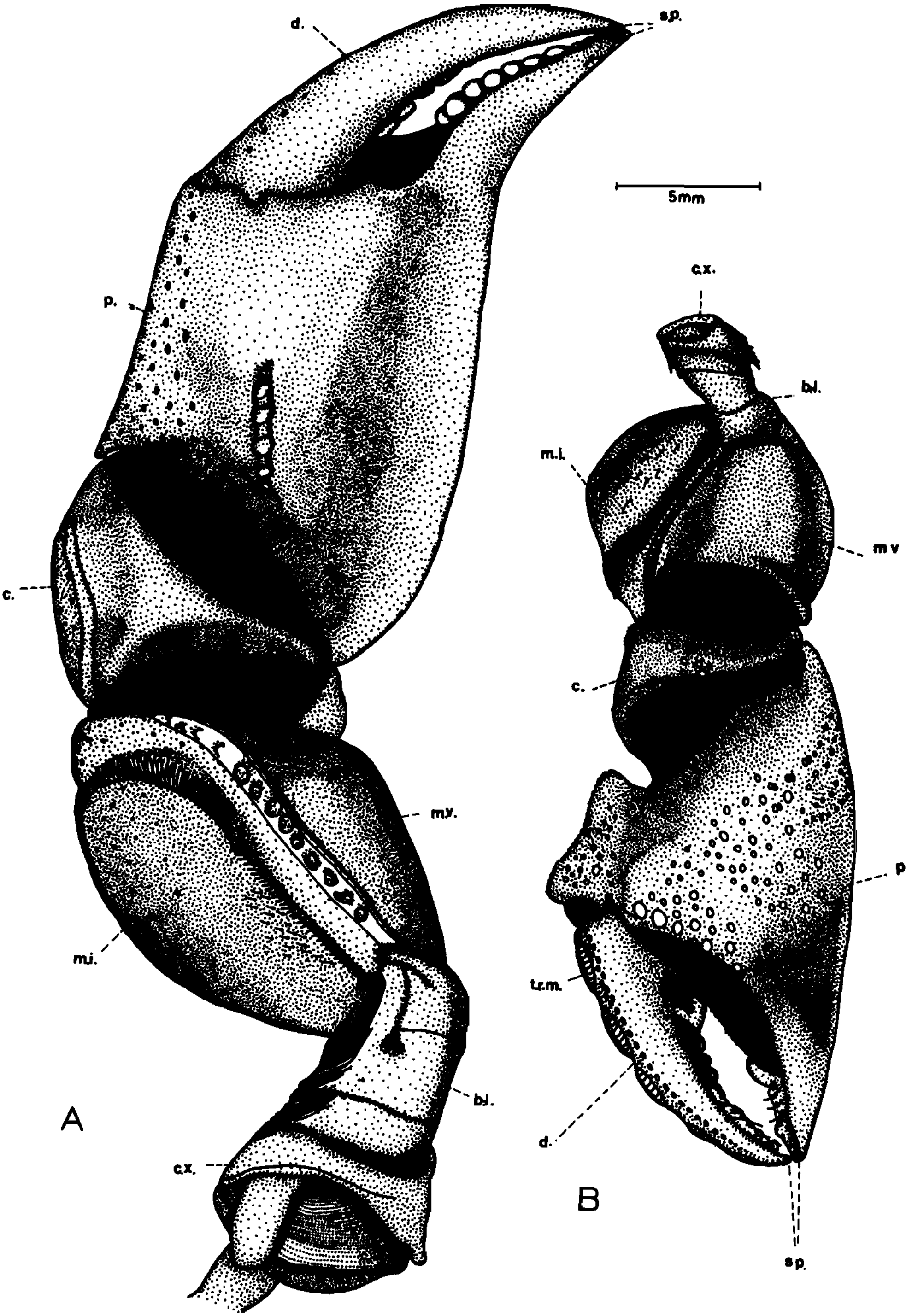
A further point concerned with the mechanics of this system of aerial respiration deserves comment. An examination of the respiratory currents of the animals when under water shows that the only functional inhalent opening is that of Milne Edwards. In fact as Verwey remarks, these crabs respire under water in the same way as do many fully aquatic crabs such as the Portunidae. Water is never drawn into the branchial cavity either at the lateral or the posterior margin of the branchiostegite. This therefore contrasts strongly with the situation during pumping for aerial respiration.

The importance of the reticulate areas in the life of these crabs is reflected in the special arrangements for their cleaning. Particles of carmine applied to the reticulate areas are washed down by the respiratory stream and many of them collect on the "breakwaters", on the long setae at the edge of the branchiostegite over the inhalent opening and on the stout bristles of the coxae of the third maxillipeds which oscillate in and out of the opening of Milne Edwards. Such accumulations of particles are speedily picked off by the chelae. Particles on the pterygostome and lateral wall of the branchiostegite are removed by the merus of the cheliped. As Cott (1929a) has already pointed out, the curve of this podomere fits exactly the convexity of this region and furthermore bears strong bristles in longitudinal rows. There is one row in *C. punctatus* (Fig. 5a), while *S. catenata* (Fig. 5b) has two, as does *S. meinerti* where there are in addition numerous bristles scattered between the rows. Any movement of the cheliped near to the body thus causes these bristles to be dragged through the hairs on the branchiostegite, and particles adhering to the reticulate areas are combed off. Large lumps of foreign material not removed in this manner are picked off by the chela of the opposite side, and the combs themselves are also cleaned by the chelae, being rubbed by the backs of the hands.

Crabs were fully submerged in water which was then gradually withdrawn so as to permit observation of the transition from aquatic to aerial respiration. As soon as the level of the water drops below that of the exhalent openings the fluid begins to run down over the reticulate areas. Some of this water is taken up again via the openings of Milne Edwards, but while the latter remain immersed most of the inhaled fluid is drawn from the surrounding water. As more and more water is removed the body is lowered so that Milne Edwards' openings remain covered. When all the available water has been removed, however, the animals adopt a somewhat elevated stance exposing both sides of the carapace, while water passes across the reticulate areas and is drawn under the edge of the branchiostegite. With time and evaporation the quantity of water leaving the gill chambers decreases and contains air bubbles; presently the reticulate areas begin to dry out. Eventually, after two to three hours in *S. catenata* and *C. punctatus*, and often more than twelve hours in *S. meinerti*, no further water emerges

Figure 5a. *Cyclograpsus punctatus:* Inner view of left cheliped of adult male. Note the single longitudinal row of bristles on the inner face of the merus. These bristles constitute the "comb" which is dragged through the hairs on the reticulate areas of the branchiostegal wall as the inner face of the merus is swept past this surface. The details of the arrangement of the bristles are identical in both sexes. b.-i. = basi-ischium; c. = carpus; cx. = coxa; d. = dactylus; m.i. = inner face of merus; m.v. = ventral face of merus; p. = propus; sp. = spatulate tips of dactylus and propus.

5b. *Sesarma catenata:* Inner view of right cheliped of adult male. In this species there are two longitudinal rows of bristles on the inner face of the merus which function as combs to clean the reticulate areas. Again the details of the arrangement of these bristles are identical in the two sexes. t.r.m. = milled tubercle on dactylus; other notation as in Figure 5a.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from the exhalent openings and the beating of the coxae of the third maxillipeds ceases. As this drying process is taking place the body is gradually lowered and a hunched posture is finally assumed with the walking legs and chelipeds drawn up closely to each other and to the sides of the carapace, a pose which probably reduces evaporative water loss.

CARAPACE MOVEMENTS

Both Müller (1864) and Verwey (1930) reported that the grapsoid crabs they studied were able to raise the carapace posteriorly so as to open a slit at the hind end of each branchial cavity. The details of the observations and interpretations of these two authors differed markedly, however. Müller stated that the opening occurred when animals were dry, and that the slits were wide enough to permit him to see directly into the branchial chambers. He concluded that the animals were breathing air, drawing it into the gill chambers posteriorly, and that the posterior elevation of the carapace, and its consequent lowering anteriorly, closed the openings of Milne Edwards during this process. In contrast Verwey asserted that carapace elevation never occurred once pumping had ceased, and that it always took place when the crabs were in a small quantity of water. He believed that water, not air, was drawn in via the posterior slits, and since the forward movement of the carapace was insufficient to close the openings of Milne Edwards, that this occurred at the same time as the circulation over the reticulate areas. The water taken in at the back of the carapace was, he claimed, derived from two sources, namely, the surrounding water and also water which, on emerging from the exhalent openings, was pumped not over the reticulate areas but dorsally over the carapace. This fluid ran posteriorly in two streams and was taken in through the slits when it reached the hind margin of the carapace, to be again expelled anteriorly and recirculated, either dorsally or ventrolaterally as before.

In an attempt to resolve the apparent conflict between these two sets of observations, specimens of *C. punctatus*, *S. catenata* and *S. meinerti* were subjected to various tests to discover whether or not they are all able to elevate the carapace, the conditions required to elicit this elevation and the function of the phenomenon where it occurs. The ability to pump water dorsally over the carapace and its relation to the formation of posterior slits was also investigated.

Despite the fact that Müller (1864) described the formation of slits in species of *Cyclograpsus*, saying that these were plainly visible when the animals moved about over mudbanks, it was found that there was no movement whatsoever of the carapace of *C. punctatus* in any conditions. The arthrodial membrane between the carapace and the first abdominal segment of this species is short and the carapace is firmly attached to the body. It proved impossible to produce any movement of the carapace of *C. punctatus* even by manipulating those of freshly killed animals. Furthermore all the water exhaled during aerial respiration runs ventrolaterally over the reticulate areas, since the frontal ridge between the orbits is too high to permit this fluid to spill over it and run backwards. *C. punctatus* does therefore not employ either of the aerial respiratory mechanisms described by Müller and Verwey. Very much the same may be said for *S. catenata*. In this crab, however, the carapace is more loosely attached posteriorly and can be very slightly raised (about 1 mm.). This movement occurs generally when the animals are submerged, although it has occasionally been observed to take place shortly after the crabs have been removed from water and are pumping. Experiments using dye suspensions nevertheless showed that the "slits" so formed play no part at all in external water circulation. Dorsal circulation is prevented, as in *C. punctatus*, by the height of the frontal ridge.

S. meinerti can raise the carapace considerably, and a fairly large specimen (carapace width 40 mm) may lift the posterior margin about 3 mm from the normal position. Even when elevation is maximal, however, it is insufficient to afford a view into the branchial chambers. Slight elevation occurs at irregular intervals when this species is under water, but this is unaccompanied by any change in the normal respiratory circulation. Maximal carapace movement takes place, as Verwey (1930) pointed out, when only a little water is available, and there is no movement at all when the crabs are on a dry substratum, either during pumping or after this has ceased. It is thus clear that the "slits" are not used, in this species at least, to draw in air.

One of the attributes of *S. meinerti* which fits it so well for the semi-terrestrial habit is the ease with which it makes use of very small sources of water to replenish the branchial fluid while on land. This can be shown most clearly in animals which have been desiccated for about 24 hours, by which time pumping is at an end and the reticulate areas are quite dry. If such an animal is provided with a thin film of sea water spread over the surface of a hard substratum (e.g., the bottom of a glass beaker) it immediately squats down until the ventral surface of the body touches the water and within a few seconds draws sufficient of it into the gill chambers for pumping to commence. This is likewise true for animals placed on firmly packed sand moistened with sea water—pumping begins within seconds of contact between the ventral body surface and the surface of the sand. It might be thought that posterior slits would be of advantage during this process as they would provide an additional area along the branchiostegal margin for water uptake. But crabs given a small supply of free water never raise the carapace until pumping is well-established, while those on sand show no carapace movement. Furthermore, since the bodies of the crabs are held more or less horizontally the posterior margin of the carapace is at no time in contact with either water or sand. The sites of water uptake are the posterolateral margins of the branchiostegites above the third, fourth and fifth pairs of walking legs. We were able to demonstrate this by repeating the experiments using a weak solution of light green in sea water, killing the animals as soon as pumping had begun and then examining the branchial chambers. The heaviest accumulation of the dye was between the bases of legs 3-5, which bear tufts of setae anteriorly and posteriorly, and on the setae fringing the edge of the branchiostegite above these legs. The posterior margin of the carapace had not taken up the dye and there was very little accumulation anteriorly. It seems very probable that the setose tufts and fringes assist in lifting the water to the gill chambers by capillary force; once it reaches the edge of the chamber the suction produced by the beating of the scaphognathites (which recommences as soon as the body makes contact with the moist surface) would be sufficient to draw it inwards and over the gills. The posterior slits might, of course, come into operation as sites of water uptake only when there is sufficient water available for them to be immersed, or it is possible that they may be used only to take up water pumped posteriorly over the carapace. The first suggestion may be eliminated at once. If the supply of free water is very gradually increased the behaviour of the crabs remains unaltered until a critical water level is reached, dependent on the size of the animal. At this level (about 4 mm for the largest specimen) the body is tilted forwards and downwards so that Milne Edwards' openings are below the water surface and are able to become once more the main inhalent openings, while the posterior end of the body is lifted even farther out of the water.

Only the dorsal pumping and possible uptake of this exhaled water via the slits remains to be considered. During the first stages of pumping, when the exhaled fluid is most copious, a portion of it does indeed pass dorsally over the carapace. It travels upwards over the rather low frontal ridge and forwardly sloping frontal bosses, and spreads out over the anterior third of the carapace, which is hairy. The spread is almost always limited to the setose region, however, (could it be that it acts as an evaporative cooling device?), and any excess fluid flows not backwards but sideways and down onto the lateral reticulate areas below. There are certainly never twin streams running down to the back of the carapace and it is impossible to induce even desiccated crabs to take up water posteriorly when droplets are placed at the posterior margin with a pipette.

It is thus abundantly clear that Verwey (1930) was incorrect in his interpretation of the function of posterior slit formation in *S. meinerti* and the other species he studied. Yet the fact that the phenomenon occurs during pumping when a little free water is available would appear to indicate some correlation between this and aerial respiration.

The gill chambers of Brachyura taper off immediately behind the last pair of gills and terminate as a pair of narrow channels above the last walking legs. In more aquatic crabs, such as *Scylla serrata* (Forskal) (an Indo-Pacific marine and estuarine form), *Cancer pagurus* L. (Pearson 1908) and *Carcinus maenas* (L.) (Borradaile 1922) the channel is short and shallow. However in semi-terrestrial forms we have examined, including, besides *S. meinerti*, *S. catenata* and *C. punctatus*, *Ocypode ceratophthalmus* (Pallas) and *O. kuhlii* de Haan, *Grapsus maculatus* (Catesby), *Potamon perlatus* (M. Edw.), *P. sidneyi* Rathbun and *P. depressus* (Krauss), the channel is longer and relatively deeper, and curves downwards posteriorly. *S. meinerti* in particular has the channel well-developed and fringed with posteriorly directed hairs. It would thus be expected if the carapace is elevated while the branchial chambers are filled with fluid that this fluid would escape from the chambers by running down the channels and out of the gill chambers via the slits. Three points should be noted here. Firstly, an animal removed from water and placed on a dry substratum can pump for a limited time only, as the continued passage of branchial fluid over the reticulate areas tends to accelerate evaporation. Secondly, a similar animal provided with a small supply of free water on which to draw will carry on pumping for much longer and frequently raises the carapace, while thirdly, a desiccated crab drawing water from damp sand will not raise the carapace at all.

Bearing these points in mind, we again desiccated crabs and placed them in glass beakers containing a film of light green-sea water solution spread over the bottom. The behaviour of each specimen was closely observed through the side of its beaker for a period of approximately one hour. The sequence of events in every case was as follows:

(1) The body was lowered until its ventral surface touched the surface of the water; at

once a film, which was held in place by the tufts of hair at the leg bases and on the thoracic and abdominal segments, was set up between the body and the water.

(2) Within a few seconds pumping had commenced, and after one or two minutes the coloured fluid was flowing strongly over the reticulate areas.

(3) After about 5 minutes the carapace was slowly raised and a stream of branchial fluid ran posteriorly out of the branchial chambers, down under the abdomen and rejoined the film beneath the animal.

(4) After about one minute the carapace was again lowered. The elevation and lowering recurred at irregular intervals of five to ten minutes throughout the period of observation, and with each elevation there was an outflux of branchial fluid.

The answer to the problem regarding the function of slit formation surely lies in the fact that the edges of the branchiostegite must be in direct contact with the supply of free surface water—hence the setting up of a film between the water and the ventral body surface. Were the crabs simply to continue drawing from the little reservoir beneath them as water evaporated from their reticulate areas the film would shortly be broken and it would be necessary to move on to another small puddle or to return to water to "reload". But if, at fairly frequent intervals, some of the water taken up were returned to the reservoir the film would remain intact, sustained use of one tiny source of surface water becomes possible and the ability to stay on land is thereby enhanced. This would hold good for the very firmly-packed muddy substrate on which they naturally occur, but would be disadvantageous on porous sand where any water lost would immediately be imbibed and might be irrecoverable. The slits thus function as a device for water conservation during excursions on to land instead of providing an additional surface along the branchiostegite for water uptake.

"LUNGS"

In all three of the species at present being studied, the circulation of water over the branchiostegite ends some hours after emergence from water, but the crabs are capable of surviving for far longer periods away from water. It might perhaps be expected that once the available water in the gill chamber had been expended the animals would return to water to "re-load". In *C. punctatus* this is not the case. In laboratory aquaria if these animals are offered a choice between air and water, specimens of *Cyclograpsus* will remain out of water for long periods after all pumping has ceased. The ability to remain out of water for extended periods has become so well-developed in two large species of *Sesarma*, *S. meinerti* and *S. taeniolata*, that Verwey (1930) has termed these animals "water-haters". The burrows of these two species are normally inundated only at high spring tides, and as the water begins to encroach on the mudbanks the crabs run inland away from it and may ultimately seek refuge in the branches of trees. It would therefore appear that some further mechanism of aerial respiration exists.

A number of terrestrial and partially terrestrial Brachyura show obvious specialisations of the gills and branchial chambers; these modifications may be easily correlated with the degree of terrestriality of the animals (Pearse 1929, Gray 1957, Edney 1960). Several groups, among them the Ocypodidae, have the branchial lining expanded into vascular folds and tufts providing a large surface for air breathing. While there are no striking modifications of the gills or the lining in grapsoid crabs Cott (1929a) has described what he calls a "vascular tuft" at the back of the branchial chamber in *S. meinerti*. Present studies show that this is a pericardial sac, arising not from the lining of the branchiostegite but ventrally from the pericardial sinus near the posterior border of the carapace. Cott suggests that it may be respiratory in function, its proximity to the posterior slit giving it direct access to the air. This may perhaps be true for *S. meinerti* where the slit is wide, but the fact that the slits are closed when the animals are no longer pumping renders it rather dubious. Moreover in *S. catenata* where carapace movement is only slight, and *C. punctatus* where there is no movement at all, the relative size of the pericardial sac on the floor of each branchial chamber is no less than in *S. meinerti*. In these two species the sacs can have no direct access to the air and it does not seem possible to attribute any respiratory function to these structures. It is to be noted that Drach (1939) and Bliss (1963) have suggested that the sacs play an important role in ecdysis and that, at least in highly specialised terrestrial crabs such as *Gecarcinus*, they may also be concerned with the uptake of surface water. It seems probable, therefore, that in *C. punctatus* and *Sesarma* the moisture retained within the branchial cavity is sufficient to allow respiratory exchange to occur across the gill surface after the cessation of pumping.

DESICCATION

Mention has already been made of the behaviour of *Cyclograpsus* in laboratory aquaria when offered a choice between land and water. The behaviour of *C. punctatus* and *S. catenata* in these conditions is markedly different. At night both are active, but in the daytime, unless disturbed, *Cyclograpsus* rests inactive out of the water while *S. catenata* remains submerged, hiding under stones and other suitable objects.

Some preliminary experiments have been made upon the survival time of specimens of the two crabs when out of water. This will be influenced not only by temperature, humidity and air movement, but also by body size. Small specimens of both species, of carapace width less than 15 mm., survived without water in the laboratory for less than 24 hours; large specimens of *C. punctatus* with a carapace width greater than 25 mm. would survive for two to three days. When allowance was made for the effect of carapace width, no significant difference was found between the survival time of the two species; certainly there was no effect of a magnitude comparable with their marked difference in behaviour.

ON THE AQUATIC MEDIUM AND DISTRIBUTION

The tidal flow of the Kowie estuary ceases about 13 miles from the sea. Neither *C. punctatus* nor *S. catenata* inhabits the whole length of the estuary. Populations of *C. punctatus* extend upriver for a distance of 8 miles from the mouth, while *S. catenata* spreads beyond this for a further mile and a half where it is found together with two other grapsoid crabs, *Sesarma eulimene* de Man and *Metopograpsus thukuar* (Owen 1839). The latter species is to be found in the banks about a mile from the tidal limit and spreads downstream for a distance of about 4 miles.

Conductivity measurements of the water at the upper limits of distribution were made hourly over a period of eleven hours both at a spring and a neap tide during the month of

August in order to get an idea of the fluctuations in concentraton of this medium. The results of these determinations showed that at the upper limit of the range of *Cyclograpsus* the concentration fell at low water to a value equivalent to about 37% sea water concentration and rose at high water to approximately 45% during the neap and 60% during the spring tide. Further upstream, at the limit of invasion of *S. catenata*, the concentration was equivalent to approximately 30% sea water concentration at low water, rising to 40% at HWN and 50% at HWS.

The two species have therefore established themselves over a wide range of concentrations. Their tolerance of media of different concentrations was tested in a preliminary experiment by determining their survival time in sea water diluted with fresh water to various concentrations. Samples were taken of the populations both from Lagoon 5, where the concentration of the water normally differs little from that of sea water, and also from the upstream limits of the two species. Animals from Lagoon 5 were kept in undiluted sea water and those from the upper reaches in 60% sea water for several days before use. They were then transferred individually to 1 litre beakers containing 600 ml of sea water, diluted sea water or fresh water. Between 20 and 40 animals were used for each of the following test media: 100%, 80%, 60%, 40%, 20% sea water, and fresh water. The media were renewed every 12 hours and at the same time mortality was recorded, the experiment being terminated after 96 hours. Animals which autotomised appendages during the experimental period were discarded, as were a number of specimens of *C. punctatus* which fouled the water with regurgitated gut contents. The experiment was carried out at a room temperature of 20° C.

All animals survived in media from 100% down to 60% sea water. In the more dilute media survival of these representatives of the two populations was different. With specimens from the lagoon some mortality occurred in 40% sea water and considerable mortality in 20%. No crab survived for 36 hours in fresh water. With specimens from the upper reaches all animals survived in 40% sea water, there was slight mortality of *Cyclograpsus* only in 20%, but neither species was capable of surviving in fresh water although survival times were longer than with specimens from Lagoon 5.

The results of this brief study show that animals in the upper reaches are well able to withstand the daily fluctuations in concentration of their natural medium. Furthermore they are tolerant of a wider range of medium concentrations than the Lagoon 5 population.

ON FEEDING

The feeding patterns of the two crabs are very distinct. This is most easily recognised if specimens which have been starved for a few days are offered small pieces of meat. If such food is placed beside an animal of either species in the water it is readily accepted. *S. catenata* will grasp the food with the chelipeds and bring it close to the mouthparts. The meat is then held in one chela and shredded by the other, each shred as it is torn off being conveyed to the mouthparts. Hold on the meat is seldom relinquished in the presence of other animals, but the use of the chelae as gripping and shredding implements may be alternated at irregular intervals. Full-grown *C. punctatus* behave very differently. The food is taken by the chelipeds, moved towards the mouth and held there, being forced between the mandibles until the whole fragment is eaten. If a piece of meat is too large to be dealt with all at once, it is torn in two by the chelae and one piece tucked under the body until the other has been eaten; the first fragment is then retrieved and devoured. As a result of this difference in behaviour, if *S. catenata* is offered meat which contains much connective tissue, it will finally discard a fibrous residue which has been picked clean, whereas *C. punctatus* will consume the whole fragment. In both cases, once the main lump is finished the crabs will not move away but cast about with their chelipeds in search of further food. Although there is this very marked difference in the behaviour of the adults, small specimens of *C. punctatus* were occasionally seen feeding in the same manner as *S. catenata.*

This same difference is to be seen in the behaviour of the two species towards fresh sprigs of *Arthrocnemum. S. catenata* will grasp a stem with one of the chelipeds and, with the other cheliped, tear off tiny pieces of the flesh of the plant which are conveyed to the mouth. As the flesh is gradually removed from the stem the chelae alternate in their roles of gripping and tearing, the process being continued until only the axial vascular tissue remains as a slender strand which is then discarded. During this process the stem may be laid down after six or more fragments have been pulled away, and movements made by the chelipeds, which touch the mouthparts and the substratum alternately. These movements, which may continue for two or three minutes at a time, will be discussed later. It will have been noticed that the pattern of feeding on *Arthrocnemum*, which takes place on land, is far more leisurely than that shown by animals eating pieces of meat in a laboratory aquarium. In the latter conditions it is important that the meat should be consumed as speedily as possible, since the juice diffuses into the surrounding water and soon attracts neighbouring animals to the spot. These will not only seize the meat if it is relinquished, but will attempt to wrest it from the grasp of the crab which is feeding. *Arthrocnemum* is plentiful on land, however, and competition for any individual sprig must be virtually non-existent. It is therefore possible for the whole ritual of the feeding behaviour to be carried out undisturbed.

C. punctatus will also feed on *Arthrocnemum*, grasping the stem with its chelipeds so as to present it endways to the mouthparts where it is sliced up by the mandibles. In laboratory terraria (consisting as before of a sloping mudbank with a pool of water at the bottom) this species always collects the sprigs placed on the bank and runs down to the pool to eat them in the water. It is not clear if all the food is taken to the water to be eaten, but on the only occasions when *C. punctatus* has been observed feeding in the field the animals were fully submerged and generally eating strands of *Gracilaria* in the manner described. Neither species has ever been seen to seek the shelter of its burrow during feeding, and remains of plant or animal material have never been found in any of the holes excavated and examined.

Macnae (1957) states, without citing evidence, that *S. catenata* feeds by collecting surface deposits and filtering these through the mouthparts, unwanted material being discarded as pseudofaecal pellets cemented with saliva. Field observations lend some support to this statement. While foraging the crabs move slowly, with the body held high and the chelipeds being used as walking legs. Perhaps this "walking" of the chelipeds represents a rhythmic searching pattern, for at intervals of half a dozen steps or so one or other of them is lifted to the mouth, a pattern resembling the "tasting" which Herreid (1963) has described in the land crab *Cardisoma guanhumi* (Latreille).

Presently a crab will settle down to feed, usually in a damp, muddy spot or at the edge of the water. The body remains elevated so that movements of the chelipeds and the field of vision are unimpeded. The chelipeds then swing alternately from the mouth to the substratum and back again, or the same type of movement is performed by one cheliped alone. This activity may proceed for some minutes before the animal moves off to a new area. The crab appears to be feeding in this manner, material being picked up in the spoon-shaped tips of the chelae and transferred to the mouthparts which are actively working. At intervals the procedure is reversed; in a single swift movement one of the chelipeds is brushed over the mouthparts and then wiped on the surface of the mud. It would seem that this is employed in the rejection of unwanted particles.

These observations do not demonstrate that mud is actually taken up by the chelipeds and that fine particles of food are sorted from the mud by the mouthparts. In fact, as will be shown later when discussing the gut contents of *S. catenata*, the role of the mouthparts as a filter must be negligible—if indeed they are used at all for such a purpose. It has unfortunately not been possible to evoke this type of feeding pattern in the laboratory where closer observations could be made, but it seems likely that the chelipeds select the relatively larger, soft particles from the surface of the mud. It is, however, to be noted that Verwey (1930) gives an account of the feeding of *Uca signatus* (Hess) in which he describes the sifting of organic particles by the mouthparts from mud collected by the chelipeds, the discarded mud being returned to the substratum in small pellets. Although the details of the process are unclear, it appears that it is common, at least among Ocypodidae living on mudbanks, for Verwey was able to review a large number of similar accounts of feeding which had been made by many earlier workers on species belonging to this family.

Our observations allow an interpretation of the behaviour described earlier in connection with feeding on stems of *Arthrocnemum*. It seems probably that the function of movements of the chelipeds to the mouthparts between periods of feeding is that of freeing the appendages of unwanted material, not necessarily the products of mouthpart-filtration but simply tough or unwieldy lumps of food and possibly adhering mud which clog the mouthparts and prevent them from operating efficiently. It may be added here that no evidence was found that *S. catenata* will eat *Spartina capensis*, for tufts of this grass near their burrows are never cropped, nor will the animals accept fresh blades of *Spartina* offered to them in the laboratory. No leaves were ever found in their holes. In this *S. catenata* differs from *S. reticulatum*, which Crichton (1960) reports as cropping the marsh grass (*Spartina* sp.) of Southern Florida so as to leave only a few inches of stubble, the leaves often being dragged into the animal's hole before being eaten.

From these observations it would appear that *S. catenata* is able to consume small particles only, whereas *C. punctatus* characteristically takes coarser material. This conclusion is amply supported by examination of the stomach contents of crabs freshly collected and killed in the field, as well as by comparative studies of the structure of the chelipeds, certain of the mouthparts and the gut armature.

The organic matter found in the stomachs of *S. catenata* consists mostly of minute fragments of plant material, with occasional algal spores, while appendages of small Crustacea are also sometimes present. Tough woody or epidermal plant tissues are very rarely found. The quantity of mud and sand grains in the gut varies. The stomachs of a few specimens contained only a few grains, whereas in others the cardiac and pyloric stomachs were almost completely full of mud and sand. Most animals had only food material in the cardiac foregut, while the pyloric foregut and/or the midgut were packed with fine mud and sand particles. This indicates that mud and sand are certainly collected by the chelipeds from the surface detritus while feeding, and that the sifting of food from this material takes place in the foregut of the animal. The role of the mouthparts in sorting would thus appear to be that of rejecting only the very coarsest particles, as was put forward earlier.

The diet of *C. punctatus* shows considerable seasonal variation. Senior students at Rhodes University, working under the supervision of Dr. J. C. van Hille, examined the stomach contents of this species during April (R. E. Boltt, personal communication). At this time of year the contents are mainly animal in origin, although a small quantity of algal material is present. Early zoaea larvae are found in large numbers, as well as the remains of isopods, entire crusta-

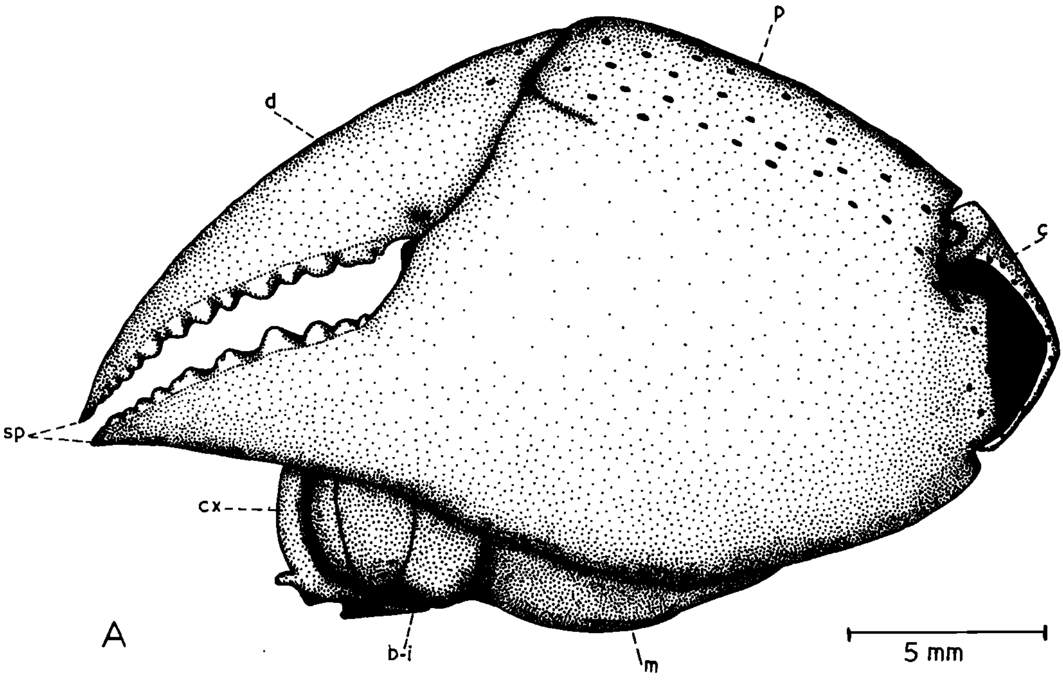
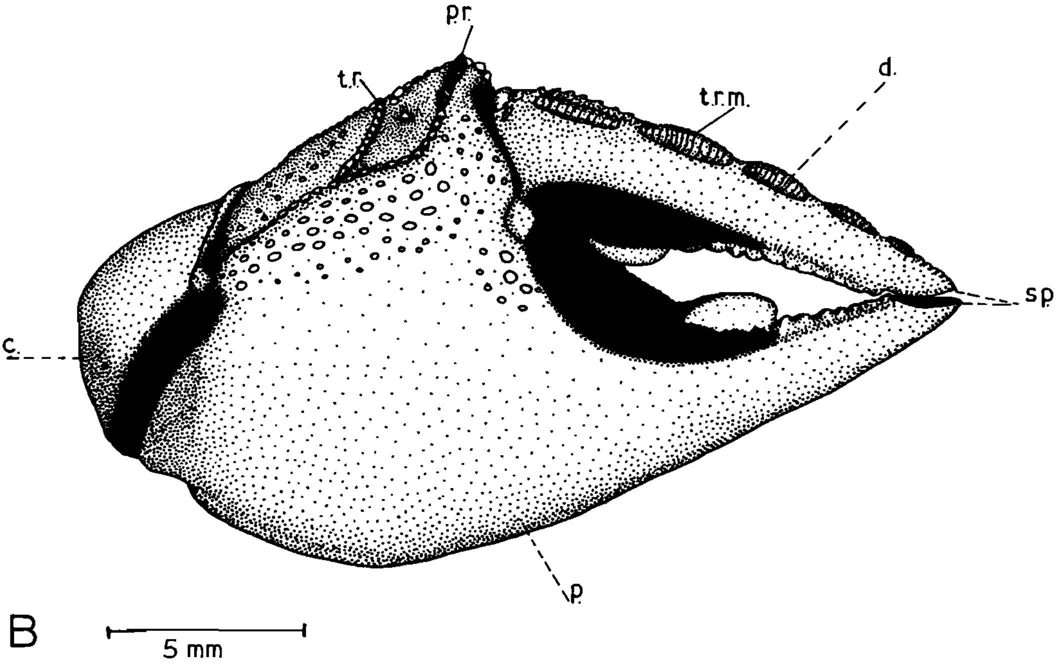


Figure 6a. *Cyclograpsus punctatus:* Outer view of left cheliped of adult male (flexed). Note that the area over which the spatulate tips of the finger and thumb appose is fairly narrow, and that the toothed areas of these two podomeres are able to come into close contact with each other for almost their entire length — i.e. the gape between them is narrow. b.-i. = basi-ischium; c. = carpus; cx. = coxa; m. = merus; p. = propus; sp. = spatulate tips of dactylus and propus.

cean limbs and sclerites and portions of polychaete worms. Our own investigations of the gut contents of animals collected during summer (December to February) show that vegetable matter forms the major part of the diet during this season. This consists of large pieces of woody plant material, epidermal tissue and slices of *Arthrocnemum* stems. Remains of Crustacea and other animals are extremely rare. No mud or sand particles have ever been found.

The difference in feeding habits of the two animals finds reflection in the structure of the chelipeds. In both species the tips of the dactylus and propus of these appendages meet to form small spatulate pincers (Fig. 6a and b; see also Fig. 5a and b). The spatulate platforms of *S. catenata* are, however, relatively larger and appose over a wider area than do those of *C. punctatus*, as might be expected from the greater emphasis in the former species upon a fine picking action using the tips of the chelipeds. Again the form of the propus differs, a character which is more particularly obvious in the larger chelipeds of the males. While in *C. punctatus*



6b. *Sesarma catenata:* Outer view of right cheliped of adult male (flexed). Note the wide area over which the spatulate platforms of the finger and thumb appose. The gape between these two podomeres is so wide that the tooth rows are unable to come into contact with each other, although it is possible that the enormous proximal teeth might be employed to grip a large lump of food while the other cheliped detaches small fragments from it. Note also the complex patterns of ridges and tubercles on the hand and the masses of thick setae at the hinge between finger and thumb. p.r. = high pectinate ridge on propus; t.r. = tuberculate ridge on propus; t.r.m. = milled tubercle on dactylus; other notation as in Figure 7a.

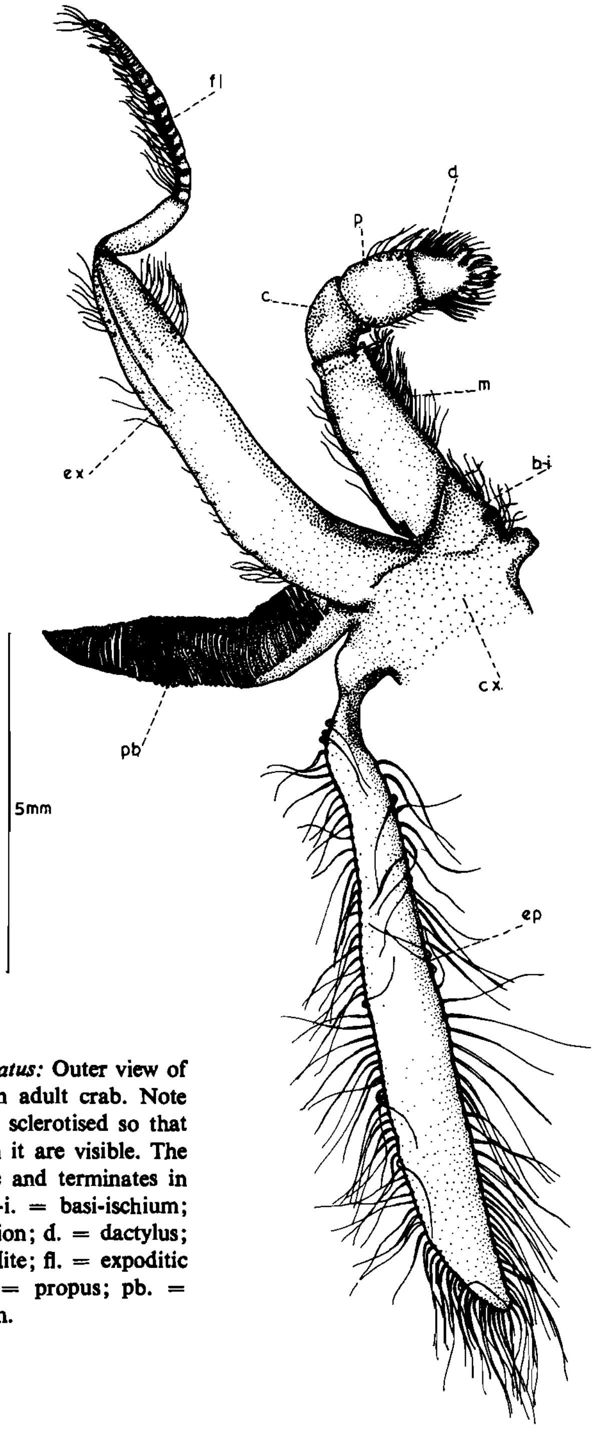


Figure 7a. *Cyclograpsus punctatus:* Outer view of right second maxilliped of an adult crab. Note that the appendage is heavily sclerotised so that no muscles or tendons within it are visible. The dactylus possesses stout setae and terminates in powerful, curved prongs. b.-i. = basi-ischium; c. = carpus; cx. = coxal region; d. = dactylus; ep. = epipodite; ex. = expodite; fl. = expoditic flagellum; m. = merus; p. = propus; pb. = podobranch.

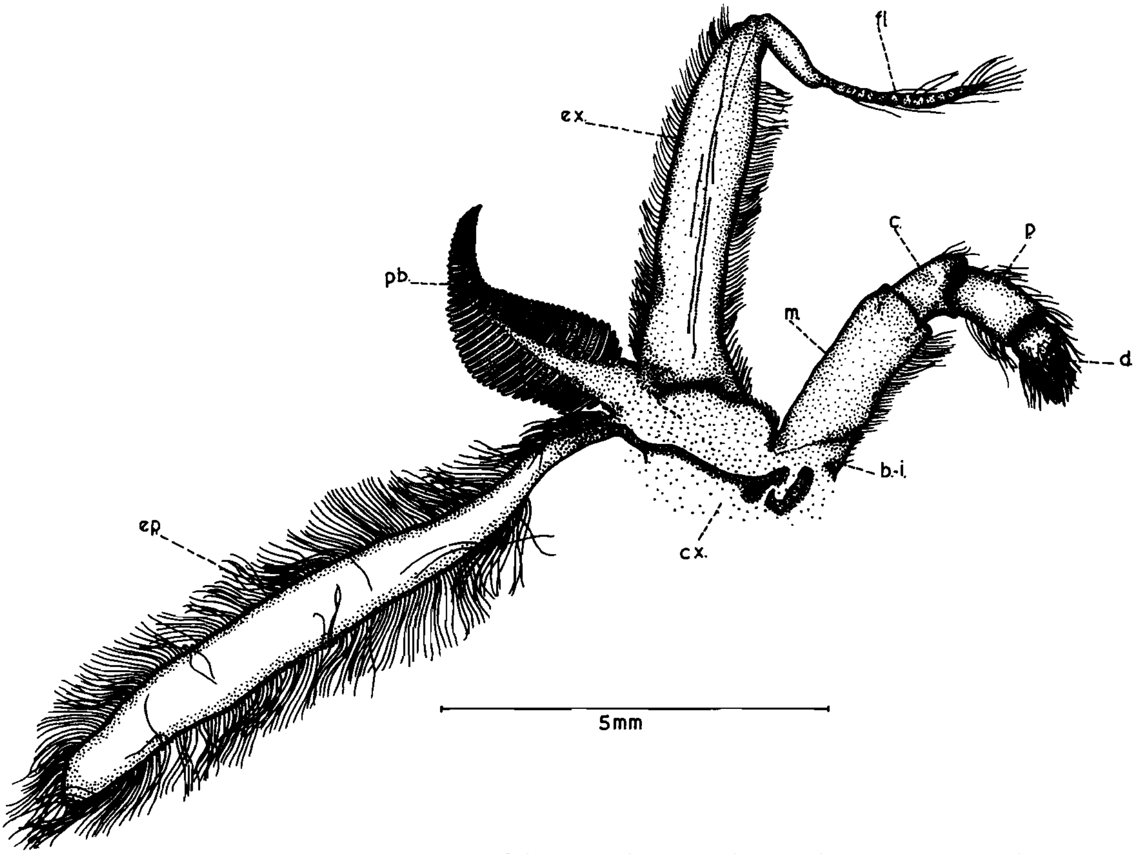
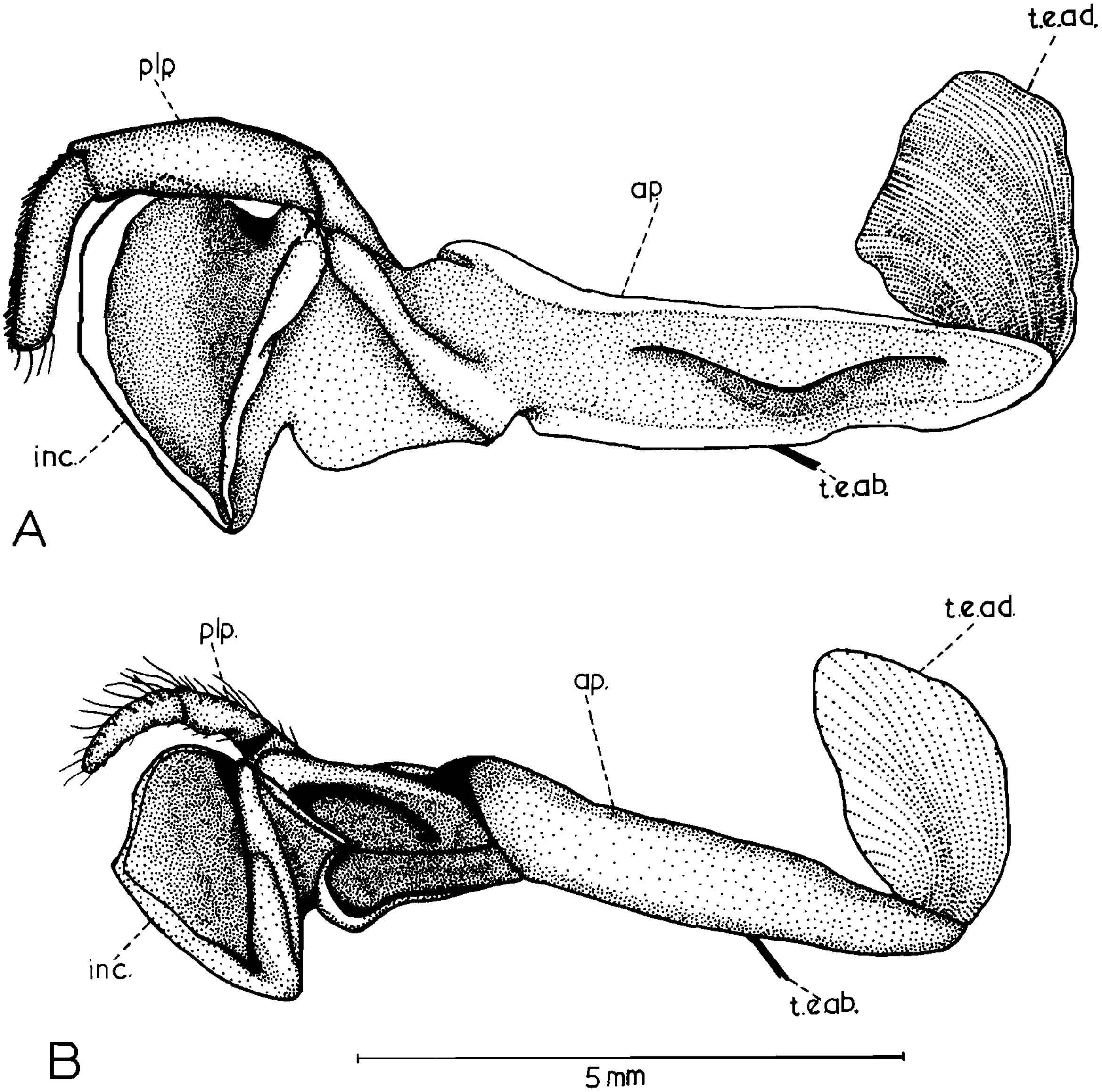


Figure 7b. *Sesarma catenata:* Outer view of right second maxilliped of an adult crab. The appendage in this species is relatively smaller and more delicate than that of *C. punctatus*. Tendons and some of the musculature are clearly visible through the outer cuticle. Here the dactylus is smooth in outline, and its setae are soft and flexible. Notation as for Figure 8a.

the toothed edge of the propus is convex and comes closely into contact over almost the entire toothed surface with the corresponding and concave edge of the dactylus, in *S. catenata* the toothed edge of the propus is strongly concave and does not touch the toothed margin of the dactylus which is only very slightly concave. The two claws might be compared, the one of *S. catenata* with the common pattern of bow-limbed forceps used in dissection, the other, that of *C. punctatus*, to a pair of long-nosed electrician's pliers.

A second and striking difference is to be noted in the form of the tip of the dactylus of the second maxilliped of the two species. In *C. punctatus* (Fig. 7a) there are powerful prongs which probably assist in gripping the food as it is forced between the mandibles, while in *S. catenata* (Fig. 7b) the tip, although densely setose, is smooth in outline. Again the mandible of *C. punctatus* is heavier than that of *S. catenata* with a longer incisor edge, a more heavily sclerotised apophysis and more powerfully developed struts in the distal region of the apophysis;



Figures 8a & b: Inner views of the mandibles of *C. punctatus* (Figure 8a) and *S. catenata* (Figure 8b). The mandible of *C. punctatus* is the larger and more heavily sclerotised of the two, and the struts behind the head of the appendage, as well as the apophysis, are far more powerfully developed. Although the strutting in *S. catenata* is relatively elaborate, it is arranged as a number of slender arches, rendering the structure less robust than in *C. punctatus* where the strutting is massive and simple. ap. = apophysis; inc. = incisor area; plp. = mandibular palp; t.e.ab. = tendon of the external abductor muscle; t.e.ad. = tendon of the external adductor muscle.

these struts will carry the thrusts developed in biting to the articulation of the mandible on the epistome, the strongly developed proximal strut allowing effective use of the lever-like action of the apophysis (Fig. 8a and b).

By analysing the gut contents and examining the structure of the gastric mill in a number of species of spider crabs from the Isle of Man, Hartnoll (1963) was able to show that differences in diet can be correlated with the nature of the gut armature. This is true also for the present two species. In general it is found that the sclerotisation of the gastric mill is far heavier in *C. punctatus* than in *S. catenata*, the ossicles of the former are powerfully developed, while those of the latter are more slender and delicate and the setae of *C. punctatus* are short, stubby and often spinose whereas in *S. catenata* they are elongated and fine. The most striking differences are to be seen in the structure of the median and lateral teeth. In *C. punctatus* (Fig. 9a) where the gut has to deal with coarse lumps of food, the median tooth is large and well-sclerotised and has a hard central ridged area on which the two lateral teeth "bite". These lateral teeth are strong, and bear anteriorly five broad rounded denticles. Posteriorly the denticles become sharply pointed, eventually fusing together almost completely to form a sharp cutting edge. The inner border of the tooth is traversed by a number of stout ridges. In contrast to this primarily masticatory apparatus, the three teeth in *S. catenata* form a sort of press, apparently used mainly for compacting the mud particles which have been separated from the small fragments of food. It will be seen from Fig. 9b that the median tooth bears three hard pads in the postero-median region which come into contact with the lateral teeth during "chewing". The lateral teeth have three large anterior denticles merging posteriorly into a cutting edge, the ridges are curved and slender and are free at their tips. The ridged inner face of the tooth is concave and the ridges are often found to be caked with mud particles, as is the smooth padded area on the median tooth. It would seem that the separation of food material from the ingested mass of mud and detritus takes place anteriorly within the foregut and that the main function of the three largest teeth is to deal with rejected particles which must then be transported to the hindgut. Certainly this would agree with the distribution of the gut contents in this species which has already been described.

CLEANING BEHAVIOUR

Mention has already been made of the patterns used in cleaning the anterior and lateral surfaces of the branchiostegite. In burrowing the crabs inevitably become muddy and have to clean themselves. Their behaviour was followed by plugging with soft mud the mouths of burrows they had made in terraria and then observing an occupant when it emerged. No significant difference was seen in the techniques of cleaning employed by the two species, but *C. punctatus* devotes more time to cleaning itself; a dirty *S. catenata* will usually walk directly into the water and thus wash off much adhering mud.

The hands of the chelipeds are cleaned by rubbing them against each other on both surfaces, while lumps of mud are scraped off onto the substratum. The chelipeds are used extensively as tweezers to remove fragments of mud from other parts of the body, from the mouthparts, the reticulate respiratory surfaces, the ventral surface of the body and the legs. Pellets of mud removed in this manner may be deposited on the substratum at once, or, in the case

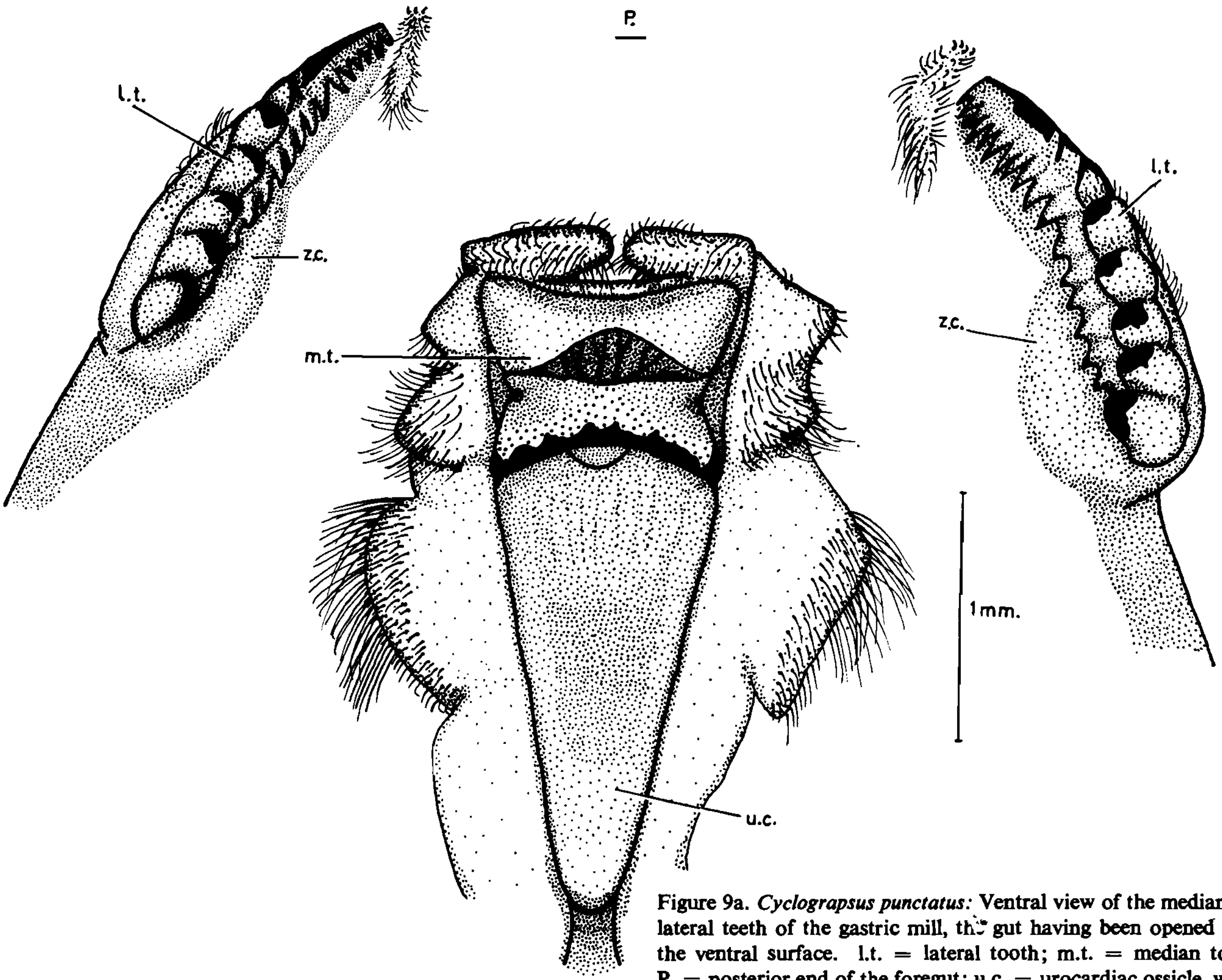


Figure 9a. *Cyclograpsus punctatus:* Ventral view of the median and lateral teeth of the gastric mill, the gut having been opened from the ventral surface. l.t. = lateral tooth; m.t. = median tooth; P. = posterior end of the foregut; u.c. = urocardiac ossicle, which bears the median tooth (the pterocardiac ossicle is not shown); z.c. = zygocardiac ossicle, bearing the lateral tooth.

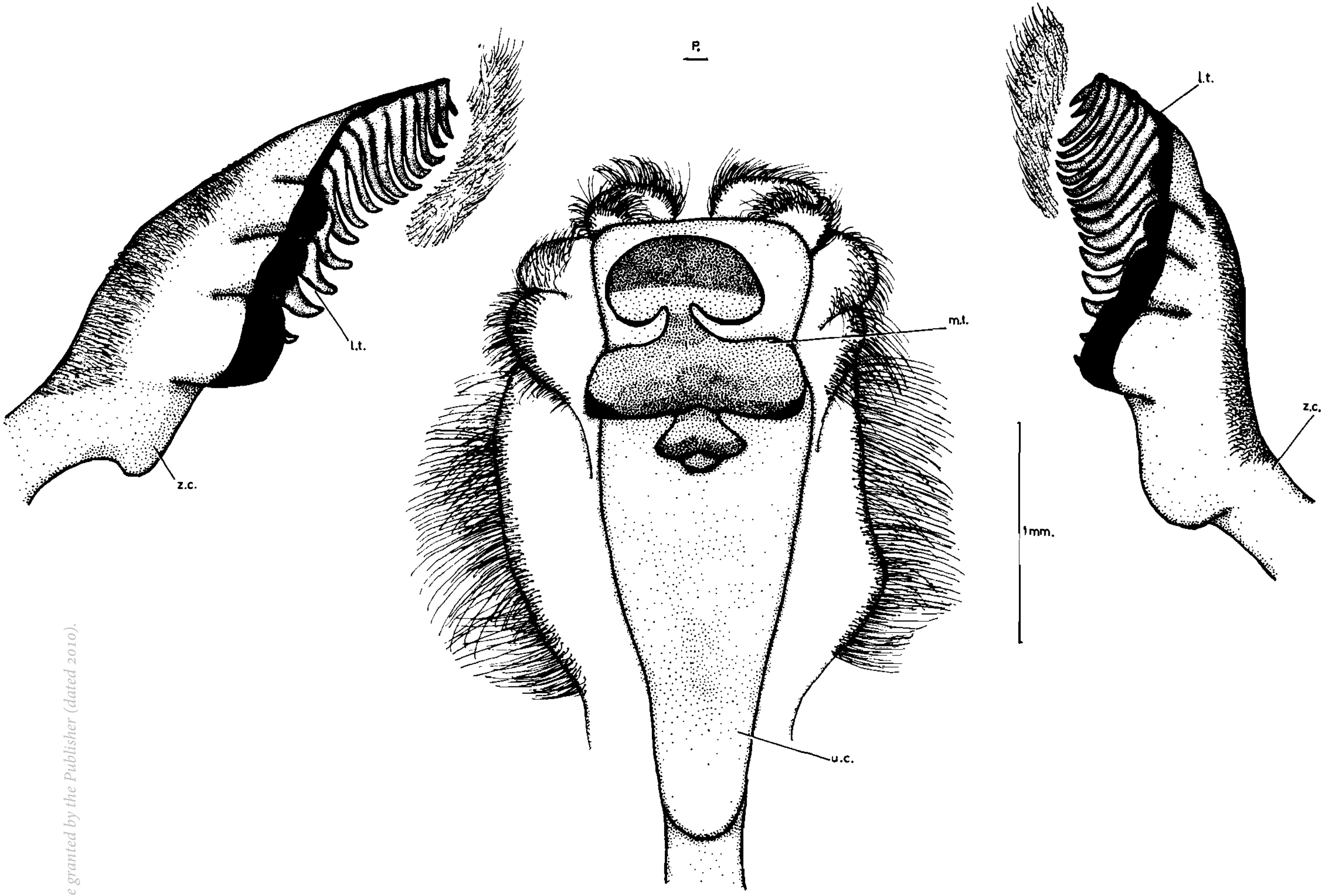


Figure 9b. *Sesarma catenata:* Ventral view of the median and lateral teeth of the gastric mill, the gut having been opened from the ventral surface. Notation as for Figure 9a.

of *S. catenata*, be first transferred to the mouthparts. The pellets, which are usually much smaller than those excavated during burrowing, are merely wiped off onto the substratum, and the animals then proceed with the business of cleaning without stopping to pat them into place.

The method of removing more closely adhering mud varies from one structure to another. The mouth parts, eyes and antennae may be burnished by the inner tuberculate ridges of the propus of the cheliped (Fig. 5a and b), but they are also brushed by the setae on the inner margin of the palp of the third maxilliped, mud transferred to these hairs being removed in turn by the chelipeds. Finally the walking legs are cleaned by rubbing adjacent pairs together, the first walking leg brushing itself against the cheliped as well as the second walking leg. The flexibility of the last walking leg allows it to be twisted over the third leg so that the posterior surface can be cleaned. None of the appendages can reach the roof of the carapace which is washed clean when the animals enter the water.

FLIGHT AND THREAT

If released in an aquarium tank with a muddy bottom but no other protection, both crabs will immediately bury themselves in the mud. Their methods of effecting this are, however, different. *C. punctatus* tramples vigorously with its legs, stirring up the mud which then sinks to cover the upper surface of the crab, now lying in a shallow depression which it has excavated. *S. catenata* buries the tips of its legs in the mud, and, having got a grip, the body is swung forwards and upwards and then rapidly backwards and downwards to drive the mud posteriorly. By repeating this movement several times the crab makes a deep, broad trough in which it rests, hidden by the particles of mud which, stirred up by its digging, gradually settle on its back.

Within the burrows their behaviour of the crabs is again distinct. The complex interconnecting galleries excavated in the faces of the salting cliffs by *S. catenata* have already been described. If disturbed within such a burrow, *Sesarma* escapes by flight and may reappear at another entrance only to retreat once more if pursued. The tunnels of *C. punctatus* are somewhat narrower on the whole and the crabs appear to be unable to pass one another. Their response to threat is to grip the sides of the burrow so that they are not readily removed.

In the open this difference in behaviour finds similar expression. *S. catenata* will run swiftly to shelter, while *C. punctatus* crouches, clinging to the substratum, or crawls slowly away. The latter species is less readily disturbed and can thus be far more easily approached and studied in the field.

A further reflection of their different behaviour is seen in their responses if driven into a corner from which they cannot easily retreat. *S. catenata* adopts what is basically a defensive attitude (Plate Ia); the chelae are abruptly brought together across the front of the body to display their broad, yellow and orange outer surfaces, the black patches of hair at the hinges of the dactylus on the propus recalling eyes. If further stimulated the crab will dodge sideways, still presenting its chelae towards the point of attack and ultimately, if unable to escape, will lunge out at the source of irritation with its claws. The display of the chelae is sometimes accompanied in the males by a rubbing together of the heavily tuberculate outer surfaces of

Plate Ia. Defensive posture of a male *Sesarma catenata*. The outer surfaces of the chelae are displayed, the black tufts of setae against the paler cuticle of the hands giving the appearance of eyes.

the dactylus and propus of the cheliped (Fig. 6b). Similar behaviour has been observed in *S. cumolpe* and *S. quadrata* (Fabricius) (Tweedie 1954, Guinot-Dumortier and Dumortier 1960). Tweedie has regarded this as a form of stridulation, but was unable to detect any noise being produced by *S. cumolpe*. No sound has been heard from specimens of *S. catenata* making these movements.

In a similar situation *C. punctatus* threatens, standing on tiptoe and throwing the chelipeds wide apart (Plate Ib). Such a response is very rarely followed by attack. If the intensity of stimulation is increased the pose becomes further exaggerated until finally the animal overbalances and falls upon its back with legs and chelipeds spread-eagled. It may be several seconds before the crab rights itself again to adopt once more its threatenting posture.

Some insight into these differences is perhaps provided by a consideration of the two species in the field. *S. catenata* forages by day although it is also active at night. In foraging in the open its chief security lies in flight to the shelter of a stone or burrow, and, in extreme

Plate Ib. Threat posture of a male *Cyclograpsus punctatus*. The body is elevated and the chelae are thrown wide apart.

danger, the sudden display of the chelae may serve to halt an enemy sufficiently long to allow the animal to escape. The safety of *S. catenata* really depends upon the gregarious nature of the species which usually ensures an abundance of burrows to which it may escape, and equally upon the fact that, unlike *Ocypode* (Cowles 1908, Cott 1929b) and *Uca* (Crane 1941), the two grapsoids show no territorial behaviour but live in a community in which a burrow of either species is any crab's shelter.

C. punctatus is, on the other hand, essentially nocturnal, rarely emerging from its burrows before nightfall. Further, as has been stated, retreat into the depths of a burrow in the face of danger may be blocked by other crabs. It cannot escape and depends for its safety upon a threat display which appears to have become so inflexible in performance as to be no more than a bluff.

It is striking that, of dead specimens of the two species collected in the field, those of *S. catenata* were usually intact, whereas those of *C. punctatus* were commonly mutilated, suggesting that they had been attacked by birds. Such an observation is in keeping with the ready and elusive flight of *S. catenata* and the poor adaptation for defence of *C. punctatus* outside the relative security of its burrow.

REPRODUCTION

No special observations have been made upon reproductive behaviour. Broekhuysen (1941) records that the breeding season of *C. punctatus* is during the winter months from May to November. This was confirmed during the present observations although a few berried females were found at other times of the year. *S. catenata* is a summer breeder, most females being in berry from mid-November to January; females carrying eggs at other times were extremely rare.

DISCUSSION

Verwey (1930) divided the *Sesarma* species of the East Indies into two types, "water-lovers" and "water-haters". Two of the smaller species, *S. bataviana* and *S. cumolpe* belong to the former category, avoiding exposure and following the water down as the tide recedes. The large *S. meinerti* and *S. taeniolata* on the other hand vacate their burrows and move to drier stations as the water rises, and may even climb trees if the tide is very high. The present two species show neither pattern and within the relatively narrow confines of their habitat between the tide marks appear to be truly amphibious.

Although the two crabs occur together over the greater part of their range in the Kowie estuary, their distribution does not fully overlap. As has been described, *C. punctatus* lives in the stony dykes which line the river in the town of Port Alfred. Whether the failure of *S. catenata* to extend into this area is due to the elimination of would-be invaders by some agency or whether the animal displays a behaviour pattern which restricts it to a soft substratum has yet to be determined.

At the other extremity of their range *S. catenata* spreads further up the estuary than does *C. punctatus* and both appear to exist in situations which are close to the limits of their osmotic tolerance. *C. punctatus* extends to a level where the concentration of the medium at low water is equivalent to about 37% sea water concentration and we have shown it capable of survival at 40% sea water concentration but to die from prolonged exposure to a concentration of 20% sea water. *S. catenata* experiences lower concentrations at low water and it has been found to be capable of prolonged survival in water of 20% sea water concentration. It is possible that we have here a case of a physiological limiting factor acting directly upon survival. It is to be noted, however, that neither species has been shown to extend to the absolute limit of its tolerance and without further investigation it cannot be excluded that a behavioural response towards the osmotic concentration of the water may not be the immediate cause which limits the upriver spread of the two species. The presence of a specific osmoreceptor has been demonstrated in the crawfish *Jasus lalandii* (Lam., M. Edw.) (Krijgsman and Krijgsman 1954), and active choice of a preferred salinity has been shown in *Pachygrapsus crassipes* Randal (Gross 1957) and in species of *Gammarus* (Lagerspetz and Mattila 1961).

It has further been shown that specimens of both species collected from the upper limits of their distribution are more tolerant of low concentrations than are those collected from near the mouth of the estuary. This recalls the condition found by Anderson and Prosser (1953) in *Callinectes*, where specimens collected from a low salinity habitat survived longer at extreme dilution than did those from a habitat of higher salinity. It could therefore be interpreted as the effect of acclimation to lower external concentrations in the individuals from the upper reaches of the estuary. Alternatively, the possibility exists that there is a genetical difference affecting aspects of their physiology between individuals from the upper and lower reaches: it may be noted incidentally that crabs from the lower reaches attain a greater size than those from nearer the tidal limit. Distinct races as far as osmotic control is concerned have been recognised in the isopods *Mesidotea entomon* (L.) (Lockwood and Croghan 1957) and *Cyathura polita* (Stimpson) (Segal and Burbanck 1963) and perhaps also in the amphipod *Gammarus duebeni* (Lilljeborg) (Beadle and Cragg 1940). It is possible to visualise a steady selection pressure being exerted on the population towards the top of the estuary, perhaps more especially upon the younger stages, which are known in some crabs to be less capable of withstanding osmotic stress than the adults. This is true, for example, in *Sesarma cinereum* (Bosc) and *Panopeus herbstii* Milne Edwards (Costlow, Bookhout and Monroe 1960, 1962) and also in *Carcinus maenas* (Lance 1964).

Finally in the river banks outside the town of Port Alfred the two crabs excavate burrows which stand in different relations to the tidal levels. This separation is effected by the difference in their choice of a site for burrowing, as has been demonstrated by studies in terraria; in this particular their different distribution appears to be determined by their behaviour and not directly by some limiting environmental factor.

It is now necessary to consider whether there exists any competition between these two species. Certainly there can be none between the young stages for the two species reproduce at different times of year. But inter-specific competition for food or space might exist between the adults. It has been emphasised that the feeding patterns of the two species are markedly distinct. *S. catenata* feeds upon small particles collected from the surface of the mud and shreds larger material before ingesting it; *C. punctatus* is a lump feeder. It seems probably that in nature these differences may find a sharper expression than they do with hungry specimens in the laboratory and that *Sesarma* feeds largely upon small particles and decaying matter on the surface of the mud, while *C. punctatus* eats vegetation rather higher up the tidal slope or beneath the water surface when food of animal origin is scarce. However, further field observations are required to verify or refute this surmise. Certainly there is ample food for both species in the estuary. There is also no evidence for inter-specific competition for burrow space since the areas selected by the two species are distinct. Indeed, rather than competition, it seems possible that there is an element of mutualism in their relation for they display a synoecy in the literal sense of the word. It has been stressed that the safety of both species very largely depends upon retreat into the burrow systems and, where the two crabs live together, a far wider band of soil between the tidal limits is excavated than would be the case should one species occur alone. To this extent, by offering, a greater area where shelter may be found, the two species possibly gain more from their close association than they lose from the effects of a yet undemonstrated inter-specific competition.

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SUMMARY

Two similar grapsoid crabs, *Cyclograpsus punctatus* M. Edw. and *Sesarma catenata* Ort., are found living closely together in the banks of the estuary of the Kowie River in the Eastern Cape Province of South Africa. They frequently share the same burrows. To enhance our knowledge of their biology and of the relations between them which permit these animals to live successfully in such close contact with each other, an exploratory study of certain biological and ecological aspects has been made. In the course of this work burrowing activities, salinity tolerance, aerial respiratory adaptations (with additional reference to those of *Sesarma meinerti* de Man), food and feeding and cleaning and other behaviour have been considered comparatively, while their distribution with relation to type of terrain, plant cover, the tide marks and salinity have been investigated.

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