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ASPECTS OF THE BIOLOGY AND ECOLOGY OF THE GENUS *TYLOS* LATREILLE

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(With 30 figures and 18 tables)

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CONTENTS

INTRODUCTION

sopod genus *Tylos* Latreille belongs to the suborder Oniscoidea which miscellany of more or less terrestrial forms. This group has been split eries by Vandel (1943), viz. the Tylienne and the Ligienne. The former wo families, the Tylidae and the Stenoniscidae, while the latter contains amilies, including all the true terrestrial isopods. After an exhaustive on into the anatomy and morphology of the Oniscoidea, Vandel me to the not surprising conclusion that this heterogeneous suborder yphyletic origin. The Tylienne series, which is not truly terrestrial and mostly halophilic species which are still dependent on the marine ent, is derived from the marine Valvifera group, having many structural s. The Ligienne series is derived from some marine family, possibly nidae. This group, which has occupied numerous terrestrial niches, most perfect adaptation to terrestrial life.

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The family Tylidae contains the single genus *Tylos* Latreille comprising at present 15 known species, the distribution of which may be seen in the following list, adapted from Vandel (1945).

Southern Group	*capensis* Krauss	South Africa
	granulatus Krauss	South Africa
	neozelanicus Chilton	New Zealand
	spinulosus Dana	South America
	wegeneri Van Name	Venezuela
West Pacific Group	*granuliferus* Budde-Lund	Borneo & Japan
	opercularis Budde-Lund	Philippines
Indian Ocean Group	*albidus* Budde-Lund	Nicobar Island
	minor Dollfus	Seychelles
	nudulus Budde-Lund	Christmas Island
Red Sea Group	*exiguus* Stebbing	Red Sea (possibly synonymous with *latreillei*)
Northern Group	*insularis* Van Name	Galapagos Island
	latreillei Audouin	Mediterranean, North and Central America
	niveus Budde-Lund	Florida, Cuba, Venezuela
	punctatus Holmes & Gray	California, Mexico

The similarities of the species of the southern group has led Vandel to suggest a Gondwana origin for this group, in which he includes the Venezuelan *wegeneri* for its similarities to *capensis*.

Since 1843, when the German naturalist Krauss described *T. granulatus* and *T. capensis* from the Cape, many records of these species have been made. Most of these merely mention the animals' occurrence, or are brief morphological notes with a view to their easy identification. Barnard, in three separate papers (1925, 1934, 1940), has written the most about these species, and while his descriptions of the structure are excellent, it is felt that some of his ideas regarding the reproduction and digestion might require revision.

As both species, by virtue of their large numbers, form an important part of many sandy beach ecosystems of South Africa, it was felt that an ecological study would be particularly interesting and would reveal both the similarities and differences of the two species. This study was thus undertaken in an attempt to document and explain the many observations made. Simultaneously, the work on the European *T. latreillei* by Mead (1968), Matzakis (1956), Soika (1954), and Arcangeli (1953), was borne in mind, and the similarities and differences noted.

DESCRIPTION OF SPECIES

As a complete description of the external morphology of both species has not yet been published, this has been done as a preliminary to the ecological descriptions. A list as complete as possible of all references to the two species is included.

Tylos granulatus Krauss, 1843

Tylos granulatus Krauss, 1843: 64, pl. 4, fig. 5. Budde-Lund, 1885: 275; 1906: 74, pl. 3, figs 21–24; 1909: 70. Dollfus, 1895: 352. Stebbing, 1910: 43. Barnard, 1924: 236; 1925: 29, fig. 3; 1932: 217. Panning, 1924: 172. Vandel, 1945: 227; 1943: 40. Brown, 1959: 470.

Pleistocene fossil: Haughton, 1931: 27.

Body oval—elongate, widest at fifth or sixth segment. Integument chitinous, transparent, thick, covered with numerous flattened roughly elliptical granules (Fig. 4c). Membranous subintegumental layer bearing branched chromatophores. Head (Fig. 1) evenly convex, bearing two compound eyes dorsolaterally, each composed of about 50 ommatidia. No distinct frontal line, but faint impressed line joining anterior margins of eyes, becoming obsolete mid-dorsally. Vertex narrowed antero-ventrally between first antennae, giving way to broadly rounded frontal process. Broad clypeus below frontal process, with labrum ventrally attached. Labrum asymmetrical due to underlying left mandible atop right mandible. Narrow gena situated lateral to second antennae, ventrally embracing mandibular bases.

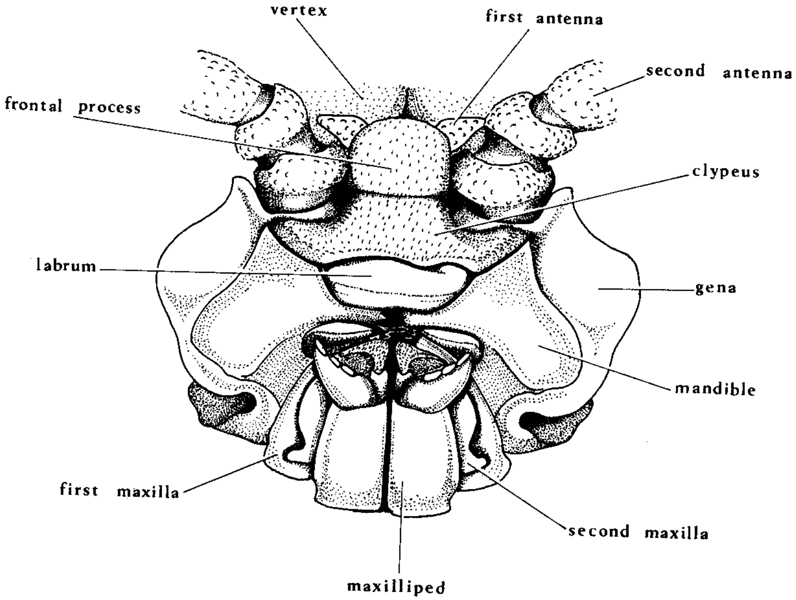

Fig. 1. *Tylos granulatus*. Anterior view of head.

Head appendages—first antenna consisting of single almost immobile segment medio-dorsal to second antenna, dorsally flattened, triangular, level with rest of vertex, ventrally with broad articulating area, with socket-like depression near apex of triangle, containing numerous aesthetascs. Second antenna (Fig. 2c) stout, elongate, consisting of five basal segments plus flagellum

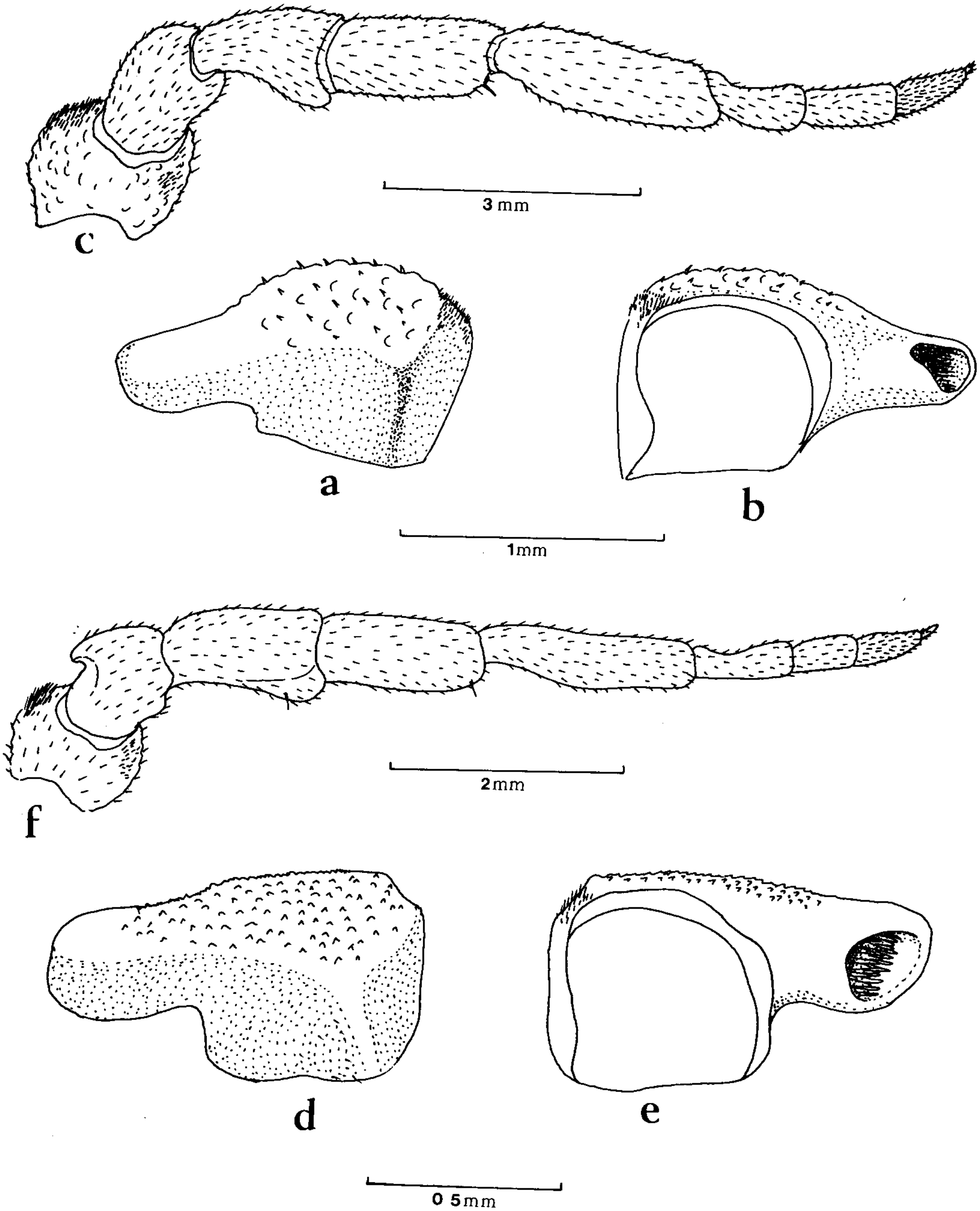

Fig. 2. a. *Tylos granulatus*. External view of first antenna. b. Internal view of first antenna. c. Second antenna. d. *Tylos capensis*. External view of first antenna. e. Internal view of first antenna. f. Second antenna.

of four smaller segments, terminal segment minute. Surface granular, with numerous setae, especially on terminal and subterminal segments. Mandibles powerful, heavily chitinised. Left mandible (Fig. 3a) with incisor process of three powerful teeth. Lacinia mobilis also strongly chitinized with three teeth,

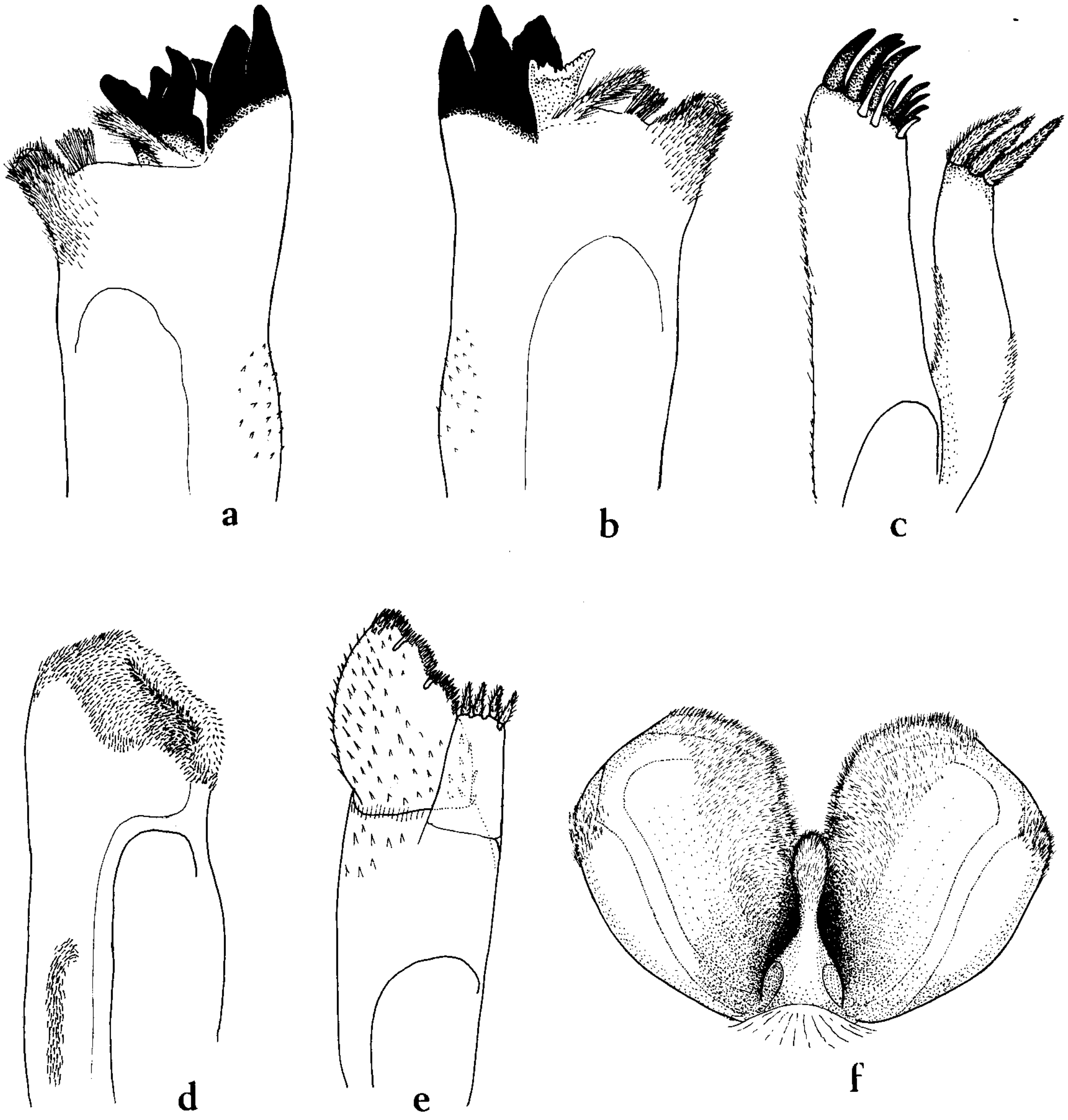

Fig. 3. *Tylos granulatus*. a. Left mandible. b. Right mandible. c. First maxilla. d. Second maxilla. e. Maxilliped. f. Labium.

with setose lobe at base. Latter followed by group of 10–12 penicillae, exterior to which, heavily setose molar process bearing terminal rasp-like process. Right mandible (Fig. 3b) similar to left, differing only in lacinia mobilis, which is very reduced, not heavily chitinized. Incisor process fits between lacinia mobilis and incisor process of left mandible. First maxilla (Fig. 3c) bilobed, consisting of two endites, outer lobe longer than inner, with setae along entire outer margin, bearing about 11 or 12 terminal hooked teeth of varying size, larger ones strongly chitinised. Inner lobe terminated with three stout setose penicillae. Second maxilla (Fig. 3d) consisting of single broad lamella, terminally heavily setose, bearing groove on inner face. Maxilliped (Fig. 3e) consisting of coxa, and basopodite bearing palp and endite. Broad strong palp with most of external surface armed with flattened blunt spines. Median edge divisible into three sections, reflecting fusion of three segments, each bearing numerous close-set blunt spines. Endite smaller than palp, terminated with five setose penicillae. Lobed lower lip (Fig. 3f) just ventral to mandibles, heavily setose on medio-dorsal surfaces. Tongue-like median setose lobe at base of outer lobes.

Pereion—consisting of seven segments, all except first having epimerites (Fig. 4a), those of segments six and seven being quadrate, large, those of other

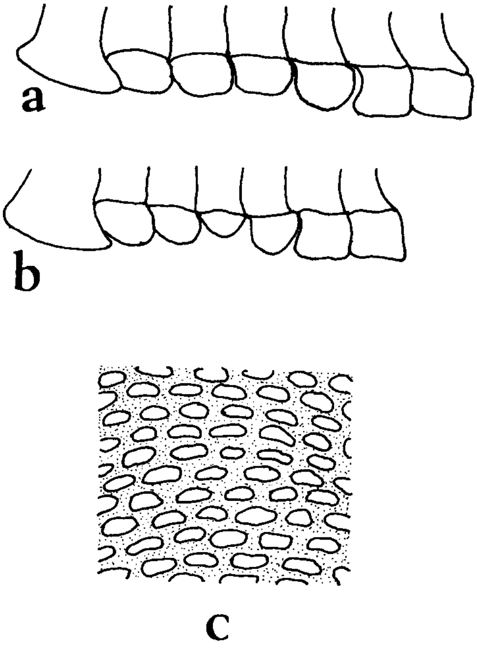

Fig. 4. a. *Tylos granulatus*. Pereion epimerites. b. *Tylos capensis*. Pereion epimerites. c. One square millimetre of exoskeleton surface, showing granulation.

segments being smaller, rectangular/triangular. Seven pairs of pereiopods present, first four pairs being forwardly directed, differing slightly from three posteriorly directed pairs. Each pereiopod consisting of six segments, basopodite largest. An obvious angle between basis and rest of leg. Anterior four pairs of pereiopods (Fig. 5a) with basis equal to ischium + carpus + merus in length. Merus with large rounded dorsal lobe. Carpus, propodus, and dactylus together forming a claw. Numerous spines and setae present on all segments, especially on more terminal ones. Posterior three pairs of pereiopods (Fig. 5b) with basis equal to ischium + merus in length. Dactylus small; propodus, carpus, and merus stout, with strong spination. In ovigerous females, lamellar oostegites present on all pereiopods.

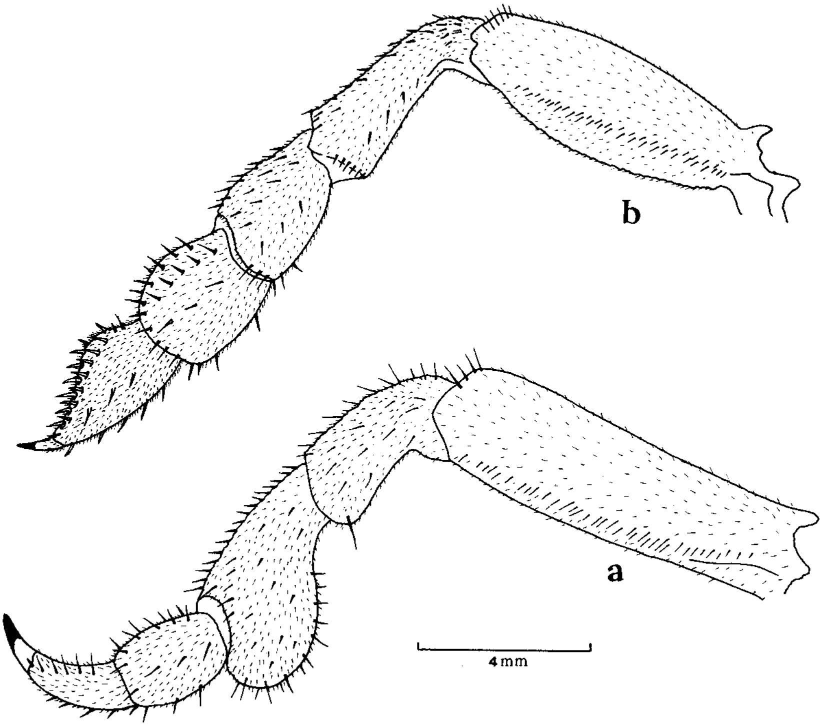

Fig. 5. *Tylos granulatus*. a. Second pereiopod. b. Fifth pereiopod.

Pleon—consisting of five free segments, plus rectangular telson. Latter twice broader than long. Five pairs pleopods present (Fig. 6), first pair reduced to slender lamella, posterior four pairs consisting of basis plus endo- and exopodite. Both latter lamellar, performing respiratory function. Exopod with numerous vertical folds, endopod with irregular folds. Second to fourth exopods with posterior pointed process medially. Endopod of second pleopod in male

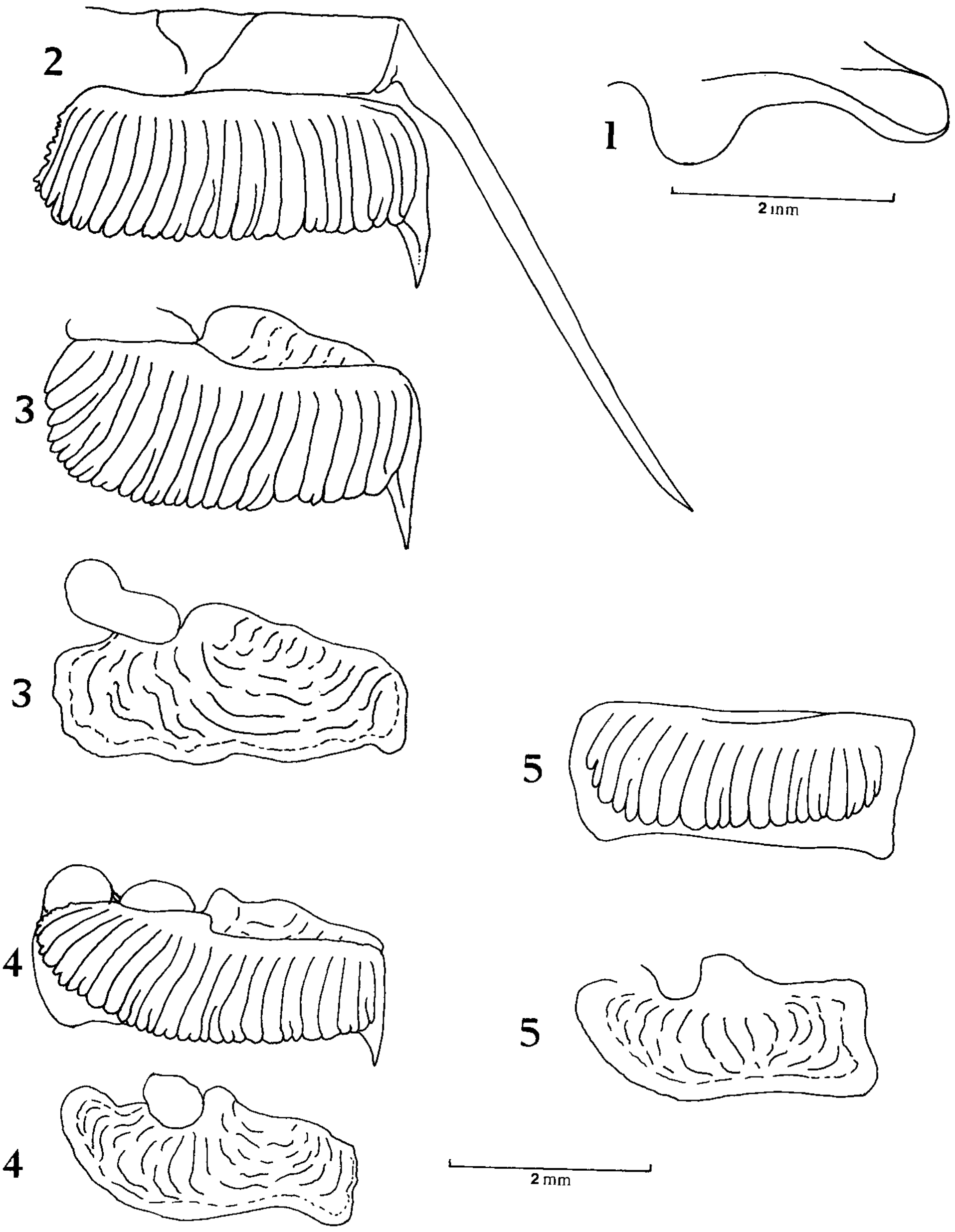

Fig. 6. *Tylos granulatus*. Pleopods one to five, male. (Two to five drawn to scale.)

modified to form long copulatory stylet medially, stretching posteriorly to level of fourth pleopods. Uropods valve-like, ventral, covering anal aperture, consisting of flattened basal portion with tiny setose endopod posteriorly. No sign of bilamellar uropod as mentioned by Stebbing (1910). Ventrally, segments three to five of pleon forming broad plates, those of segment five being antero-medially produced around the uropods, almost meeting in midline (Fig. 7a).

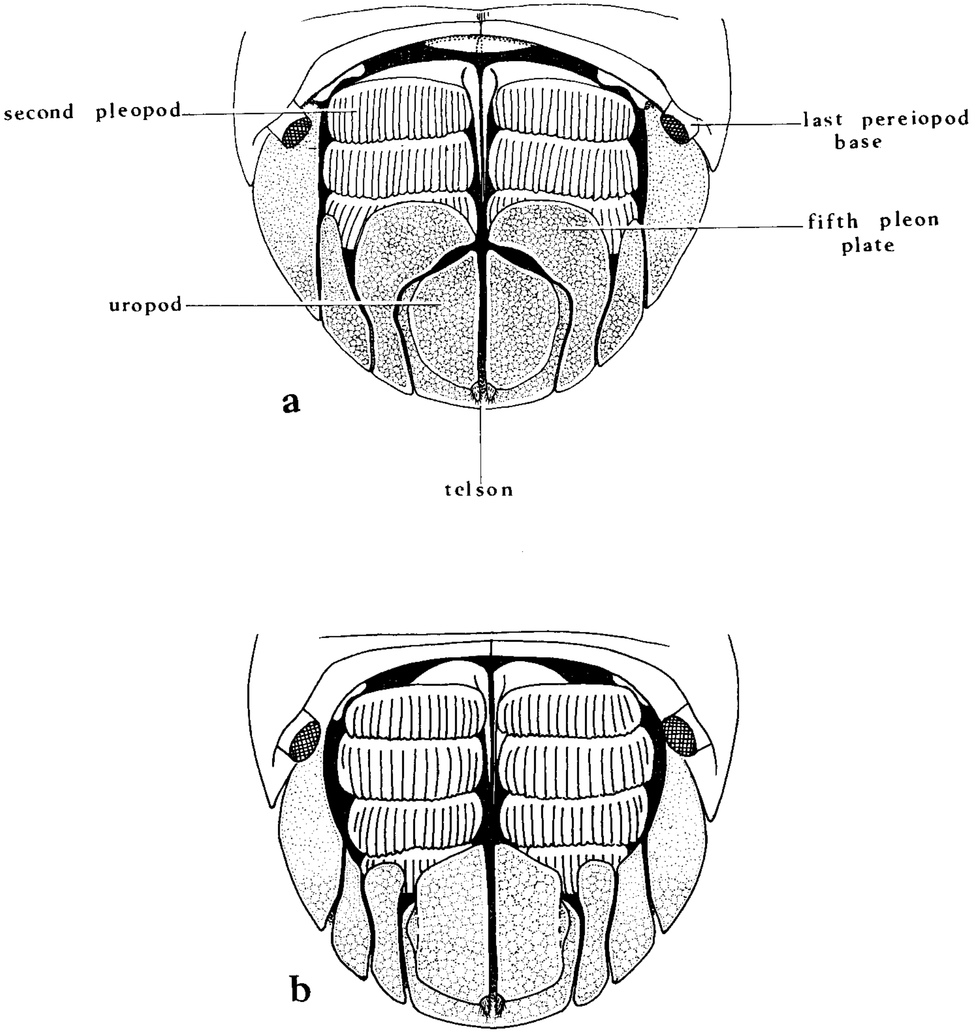

Fig. 7. Ventral view of pleon. a. *Tylos granulatus*. b. *Tylos capensis*.

Tylos capensis Krauss, 1843

Tylos capensis Krauss, 1843: 64, pl. 4, fig. 6. Budde-Lund, 1885: 276; 1906: 73. Dollfus, 1895: 352. Stebbing, 1910: 43. Barnard, 1932: 218, pl. 3, figs 14–18. Vandel, 1945: 227; 1952: 192.

Tylos granulatus (*non* Krauss), Collinge, 1945: 345.

Tylos incurvus Budde-Lund, 1906: 79, pl. 3, fig. 41.

Body oval-elongate, widest at fifth pereion segment. Integument chitinous, transparent, thick, minutely setulose, smooth. Membranous subintegumental layer bearing numerous branched chromatophores.

Head—evenly convex, bearing two compound eyes dorso-laterally, each composed of about 40 ommatidia. No distinct frontal line, but faint impressed line joining anterior margins of eyes, becoming obsolete medio-dorsally. Antero-ventrally the vertex narrowing between first antennae, giving way to broadly rounded frontal process, ventral to which, the broad clypeus, with labrum attached ventrally to it. Labrum not as asymmetrical as in *T. granulatus*. Narrow lateral genae embrace mandibular bases ventrally.

Head appendages—first antenna (Fig. 2d–e) consisting of single almost immobile segment, medio-dorsal to second antenna, dorsally flattened, roughly triangular, level with vertex surface, ventrally with broad articulating area, having socket-like depression near apex, containing numerous aesthetascs. Second antenna (Fig. 2f) stout, elongate, consisting of five basal segments plus flagellum of four smaller segments, terminal segment being proportionally larger than in *T. granulatus*. Second basal segment also differs from *T. granulatus*. Entire appendage setose. Mandibles powerful, heavily chitinized, left mandible (Fig. 8a) with incisor process consisting of three strong teeth, lacinia mobilis also of three powerful chitinous teeth, with setose lobe at base, followed by group of 10–12 penicillae, external to which, heavily setose molar process, terminated with rasp-like process. Right mandible (Fig. 8b) similar to left, differing only in lacinia mobilis, reduced, not heavily chitinized. Incisor process fits between lacinia mobilis and incisor process of left mandible. Labium bilobed and heavily setose, situated ventral to mandible, with median tongue-like setose lobe. First maxilla (Fig. 8c) bilobed, consisting of two endites. Outer lobe longer than inner, bearing setae on outer edge, with 10–12 curved terminal teeth of varying size, the larger teeth being heavily chitinized. Inner lobe terminated with three stout setose penicillae. Second maxilla (Fig. 8d) consisting of weakly chitinized broad plate, terminally heavily setose, with groove on inner face. Maxillipeds (Fig. 8e) meeting in mid-line, forming efficient lower lip, consisting of coxa and basopodite bearing broad palp and more slender endite. Palp with external surface scattered with blunt spines. Median edge divisible into three sections, reflecting fusion of three segments, each bearing numerous paddle-shaped modified spines. Endite smaller than palp, terminated with five setose penicillae.

Pereion—consisting of seven free segments, all except first bearing epimerites (Fig. 4b), those of segments six and seven quadrate, those of other segments smaller, ventrally rounded. Seven pairs of pereiopods present, first four

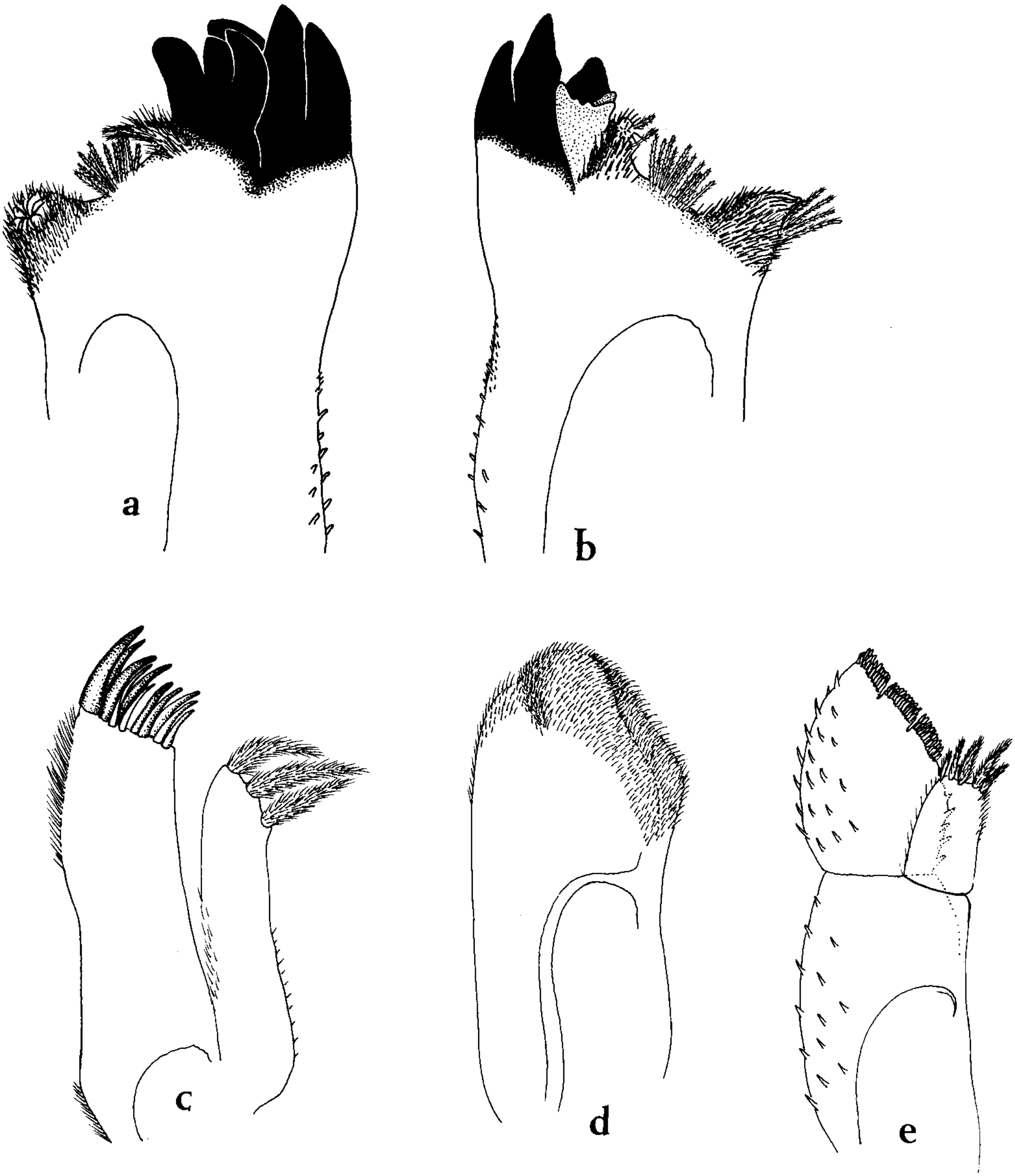

Fig. 8. *Tylos capensis*. a. Left mandible. b. Right mandible. c. First maxilla. d. Second maxilla. e. Maxilliped.

pairs forwardly directed, remaining three pairs posteriorly directed. Each pereiopod consisting of six segments, basopodite largest. Obvious angle between basis and rest of leg. Anterior four pairs with basis equal to merus + ischium + carpus in length. Merus with large dorsally rounded lobe. Carpus, propodus, and dactyl together forming a claw. Numerous spines and setae on all segments, especially on more terminal ones. Posterior three pairs with basis equal to ischium + merus in length. Dactyl small; propodus, carpus, and merus stout, with strong spination.

Pleon—consisting of five free segments plus rectangular telson, latter broader than long. Five pairs of pleopods present, first reduced to slender lamella. Posterior four pairs consisting of basis, endo- and exopodite. Latter lamellar with numerous vertical slits, unlike *T. granulatus*, which has numerous folds. Endopods with irregular folds. Endopod of second pleopod of male modified to form median copulatory stylet, stretching posteriorly to level of fourth pleopod (Fig. 9). Uropods valve-like, ventral, covering anal aperture, consisting of single flattened lamina, with thickened ring-like inner portion, bearing tiny setose endopod posteriorly. Ventrally, fifth segment of pleon not produced antero-medially as in *T. granulatus* (Fig. 7b).

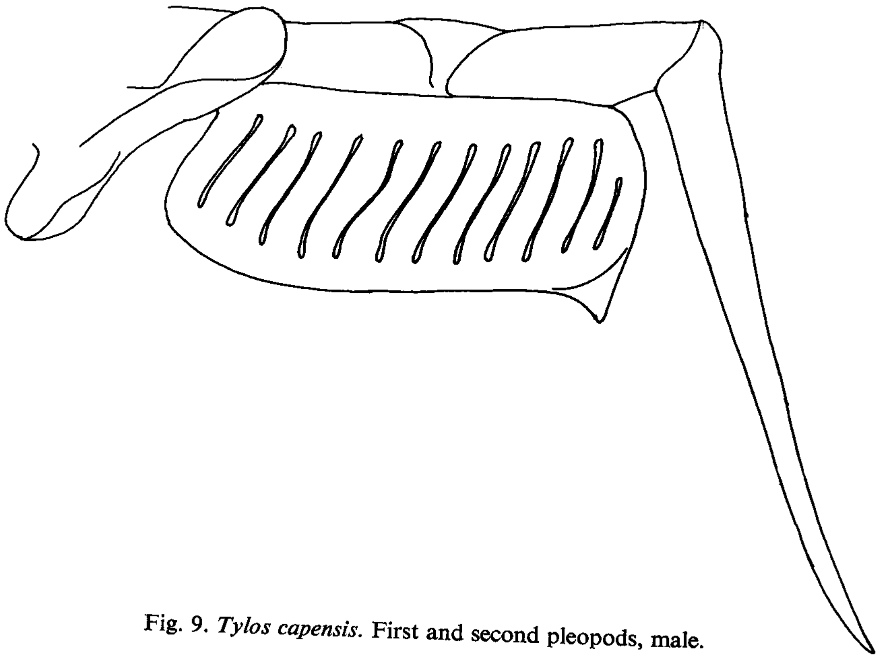

Fig. 9. *Tylos capensis*. First and second pleopods, male.

GEOGRAPHICAL DISTRIBUTION

Tylos granulatus

Krauss (1843) recorded his new species of *T. granulatus* from Table Bay. On the Cape Peninsula this species has been collected by the author at Hout Bay, Noordhoek, Olifantsbosch, Schuster's River mouth, and Witsandsbaai. Intensive collecting shows that the southern limit of the species is about 24 km from Cape

Point, and about 48–56 km from the first record of *T. capensis,* viz. Simon's Bay. Collecting along the coast of South West Africa has established the northern limit of the species to be in the region of the Ventura wreck site (19.10S., 12.37E.). This record extends the known range of the species by 480 km, the most northerly published record being Swakopmund (Panning 1924). Although the coast from this region north to the Kunene River was covered, as well as the southern coast of Angola, no further specimens were found. *T. granulatus* thus has a range of about 1 600 km. It was noted that towards the end of the northerly range the animals were not found on open beaches but were burrowing in the sand between rocks. A possible explanation for this was found in one of the limiting factors which prevent the northerly spread of the species. This is the ghost crab *Ocypode cursor* which inhabits sandy beaches and burrows into sand. This crab which occurs in large numbers, feeds voraciously on any organic material thrown ashore. Like the fiddler crabs of the same family, *O. cursor* seems to possess a tidal rhythm, and was observed to be active by day and at night. There can be little doubt that the presence of this crab presents a strong barrier to the isopods, feeding on the material which would normally form the food of *Tylos. O. cursor* occurs in the Mediterranean and along the entire west African coast. The southernmost record is 6,5 km north of Möwe Point, South West Africa. (19.23S., 12.42E.). The overlap of the two species is thus a matter of about 21 km, in which area neither is very abundant.

Haughton (1931), during a geological survey of the formations of the west coast, collected a fossil isopod from the oyster line of the diamondiferous deposit of Alexander Bay. The isopod was tentatively identified as *T. granulatus.* The hard matrix which concealed the ventral surface of the animal has now been drilled away. The granular surface together with the form of the ventral process of the fifth pereion segment establishes the first identification as being correct. The age of the oyster line is placed as mid Pleistocene. The species thus has a minimal age of 500 000 years. Taking rates of evolution into consideration it is probable that this species was already established at the start of the Pleistocene.

Tylos capensis

This species was first recorded by Krauss in 1843 from Table Bay, but this must have resulted from an error in labelling, as no record of *T. capensis* from the west coast has since been established. The species occurs eastward from False Bay. Budde-Lund (1906) records it from Simon's Bay, but this population has died out, perhaps due to naval and municipal development in the area. From Muizenberg eastward, the species occurs at most of the open beaches, including Strandfontein, Macassar Beach, Somerset Strand, Gordon's Bay, but is nowhere very plentiful. Along the south and east coasts the species occurs intermittently and is common in the Port Beaufort and Knysna areas. North of Port Elizabeth the occurrence could not be confirmed, but probably stops somewhere on the southern Natal coast. Barnard (1932: 219) makes the following statement: 'These animals form one of the most marked differences between the faunas of the west and the east sides of the Cape Peninsula. If this separation of the two species, one from Table Bay northward and the other from False Bay eastward is proved to be a fact by further and more intensive collecting, it leads to the interesting though perhaps fruitless speculation as to why there was no transgression of the one species into the area of the other, when the sea was continuous across the present Cape Flats between Table Bay and False Bay.'

Method of dispersion

The actual method of dispersion of the species is still under dispute. Two main possibilities exist, viz. by sea or over land. Sea dispersion does not seem at all impossible. The survival of various sizes of *T. granulatus* in sea water was tested. The results are given in the following table.

(Temperature of water—17°C. Juveniles—under 20 mm length)

			Comatose		Dead	
	No. Animals	Start	No.	Time	No.	Time
Adults	15	0850	11	1600	15	1900
			13	1700		
Juveniles	15	0850	6	2000	5	2000
			10	0800 (next day)	14	0900 (next day)

Although by no means conclusive, it would appear that the juveniles have a greater survival time than the adults in sea water. The death of the adults is probably due to oxygen starvation, as the area of the pleopods is insufficient to take enough oxygen from the water by diffusion. The pleopod area in the juveniles is proportionally much greater than in the adults. From observations on beaches, it was seen that juveniles tend to feed lower on the beach than adults. The juveniles are usually found on the debris lines, the adults only occasionally. On the debris lines there is the danger of powerful waves swamping the feeders. This was often seen at Blouberg (an area where intensive observations were carried out). The juveniles roll up into a ball when exposed to an incoming surf. This rolling encloses a bubble of air between the setose pereiopods, making them buoyant. The result of being caught in the surf is that they are deposited on the beach at the new debris line, along with pieces of food. This would seem to be a useful adaptation for food-finding. It is possible that with a very powerful wave, instead of being left behind on the sand, the juveniles are swept to sea. A survival of 12 hours at sea would give them a good chance of being thrown up on an adjacent beach. This would explain the distribution of the species in such places as Lüderitzbucht, where small sandy bays alternate with steep rocky outcrops, over which it would be impossible for the animals to climb. It is interesting to note that Menzies (1952) records having taken two almost adult specimens of *Tylos punctatus* in a surface plankton haul in Newport Harbour, California.

Menzies notes that *T. punctatus* has a very discontinuous distribution along the coast, being found around bays and estuaries, and never on open coasts. He concludes that this record may strengthen the hypothesis that such discontinuous distribution can be accounted for by the animals being carried by ocean currents.

The behaviour of adults caught in the surf is interesting. As the incoming surf sweeps over them, they 'flatten out', allowing the water to wash over them and then back. As soon as the water has receded, they can be seen to move rapidly up the beach, out of the reach of the waves.

Land dispersion is almost certainly used under certain conditions. The most obvious example is that of the Orange River mouth. Brown (1959) noted that when the river mouth was open to the sea *T. granulatus* was to be found in the sand on the southern bank. In March 1968 the mouth was completely blocked by an extensive sand bar, along the entire length of which the isopods were to be found. This sand bar had been in existence for two years since the last flooding of the river. This latter event occurs spasmodically, sometimes consecutively for several years, or more usually once every two or three years. Between floodings the sand bar is built up. Within two years, *Tylos* had thus colonized a sand bar about 3 km long. The most obvious method of colonization would be by moving in from the undisturbed banks of the mouth. Since the Orange River population is to be found on the landward side of a crest on the beach, it is unlikely that the alternate method of colonization occurs here.

HABITAT

Both *Tylos granulatus* and *T. capensis* inhabit sandy beaches of the coasts of southern Africa. On these beaches the animals are exposed to numerous environmental factors, the influence of each varying in importance to the animals. These factors include the sand itself, the sea and its tides, the water table in the sand, temperature fluctuations, humidity, light, precipitation, in addition to several extraneous factors. Although some of these factors are discussed separately below, it must be borne in mind that they all interact to produce the overall habitat.

TYPE OF BEACH

Tylos granulatus

After numerous observations, it can be said that this species frequents beaches which almost invariably are exposed to strong wave action, uninterrupted by rocks. This type of beach is common along the west coast, all the localities listed in the section on distribution being of this type. The preference for the exposed beach could clearly be seen in several places, particularly in Griffith's Bay, Lüderitzbucht, where there is a small exposed beach, as well as a long stretch of low rocks. Behind the latter in the HWS to HWN region, is a band of sand similar to that of the exposed portion. *Tylos* was found on the exposed part, up to the edge of the rocks but not in the sand behind the rocks.

The slope of the beach would also appear to be of some importance. The populations are spread out on flat beaches, where the high tide floods a large area. This was clearly seen at Groenriviermond and Stormvogelbucht. On beaches with a moderate gradient such as Blouberg (slope of 1/8) the population is still fairly outspread. At the mouth of the Orange River, where the population inhabits the sand bar at the actual mouth of the river, the beach has a slope of 1/4, and the animals are found on the landward side of the crest. The latter is at the HWN mark. Presumably to live on the seaward side of the crest would expose the animals to too much wave action.

Tylos capensis

Unlike *T. granulatus*, this species does not seem to be as selective in its choice of beach, being found on exposed as well as on sheltered beaches. At Strandfontein, an exposed beach with a very gentle slope (about 1/20), the population is spread out along the HWS region. At the mouth of the Breë River the population is found on a short steep beach (1/6) within the actual mouth of the river. Although quite sheltered, there is still some wave action, mostly due to wind on the open expanse of water. At Knysna the population is found at the lower reaches of the lagoon estuary, again on a short steep beach, but where the wave action was very slight.

SAND

Tylos granulatus

The actual type of sand in which *Tylos* burrows is very variable, and it would seem that the animal has a wide tolerance of sand grain size. At Griffith's Bay and Groenriviermond the sand is very fine, forming a soft mud when saturated with water. The Blouberg sand varies from fairly fine white quartz grains to layers of coarser mixed grains and shell fragments, very compacted. The sand at the mouth of the Orange River is dark brown, consisting of grains of garnet, amethyst, granite, fairly coarse and very friable. At Blouberg the area inhabited by *Tylos* ends with the start of a large reef of rock. In this area the beach consists of fine pebbles all about 2–3 mm in diameter. No animals are to be found here, but 20 animals transferred to this area all burrowed to a depth of about 120 mm. The most unusual substrate in which this species was found was observed at Griffith's Bay, where the upper 127 mm consisted of fine white sand. This gradually gave way to a 76 mm layer of grit and small pebbles. Below this was a 152 mm layer of limpet and mytilid shells, followed by large rocks and shells to a depth of 610 mm. Animals are found in this very coarse substrate to a depth of about 305 mm.

Tylos capensis

As in *T. granulatus* this species has been found in a variety of sand types, viz. very fine quartz sand with shell fragments at Strandfontein, friable fairly fine sand at the mouth of the Breë River, and uniformly fine sand at Knysna.

T. latreillei from the Mediterranean and North American coasts appears to be very different from both South African species in its choice of habitat. Arcangeli (1953) remarked that *T. latreillei* avoided beaches of fine sand, nor was it found at river mouths where the sand tended to mud, as its pereiopods impaired its progress. Instead, it inhabited crevices of rocks, or lived amongst stones and pebbles, or sometimes in coarse sand. *T. punctatus* of the North American west coast also differs from the southern African species in choice of habitat. Menzies (1952) notes that *T. punctatus* inhabits sandy beaches, but is found under logs and debris where the sand is usually dry and seldom inundated by the high tides.

TIDES AND THE WATER TABLE

Tylos capensis and *T. granulatus*

The importance of the tides is more fully discussed in the section dealing with rhythmicity. Arcangeli (1953) in his discussion of the ecology of *T. latreillei* remarks that this species is 'indifferent' to the tides—quite the opposite to the present species. The water table varies with the tides but is unlikely to have any direct effect on the animals. From Figure 17 of the transect of the Blouberg area studied, it can be seen that the water table is too far below the level to which the animals burrow to influence them.

WIND AND PRECIPITATION

Tylos capensis and *T. granulatus*

Light rain and mist have no apparent effect on the animals, while gale force winds do not seem to interfere with their feeding activities.

TEMPERATURE

Tylos capensis and *T. granulatus*

As can be seen from Figure 10, the temperature within the sand at the level of the high tide mark is subject to less fluctuation than the surface sand. As under normal conditions no extremes of temperature are experienced, it seems unlikely that the daily temperature changes have any influence on the animals. Seasonal temperature changes are of greater importance and are probably involved in the timing of the reproductive cycle.

HUMIDITY

Tylos capensis and *T. granulatus*

As *Tylos* breathes by diffusion of gases through modified pleopods which are exposed on the ventral portion of the pleon, humidity is of great importance. The habits of the animal thus preclude any serious exposure to desiccating conditions. The sand, even a few metres above the HWS mark, has a relative

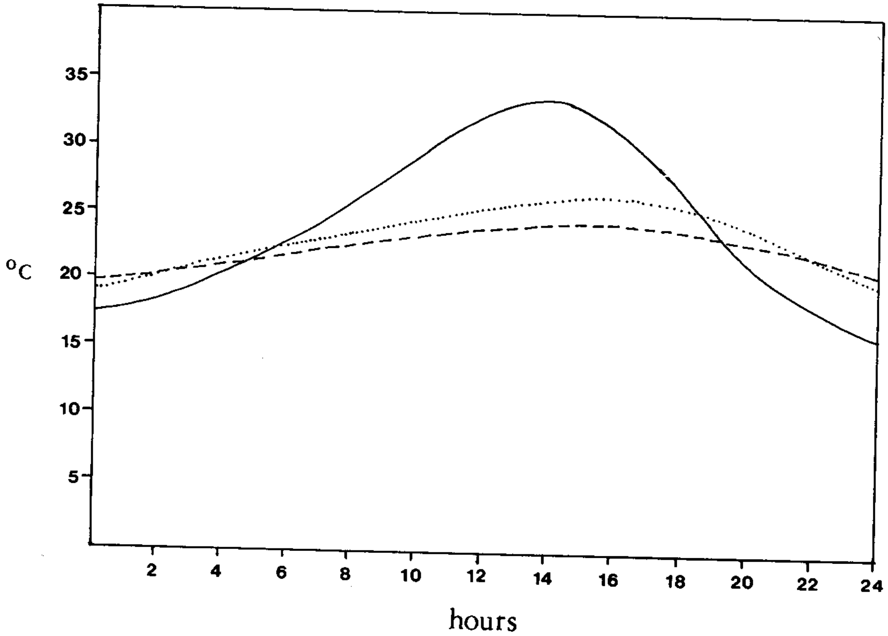

Fig. 10. Temperature changes over 24 hours in midsummer at Blouberg. ——— surface temperature. . . . . . . temperature at 300 mm. – – – temperature at 450 mm.

humidity of more than 90% at 75 mm below the surface. The upper 75 mm of sand is frequently dried out during the day by sun and wind, but as no animals are in this layer during the daylight hours, this presents no danger. At night with the drop in temperature, spray from the sea together with any dew deposition keeps the air close to the sand almost saturated with water vapour, thereby preventing desiccation.

LIGHT

Tylos capensis and *T. granulatus*

It is not possible for sunlight to penetrate more than 25 mm below the surface of the sand; sunlight would thus have very little direct influence on the animals. When exposed to sunlight, the animals rapidly burrow into the sand, and can be said to be strongly negatively photosensitive. When not feeding, both species react to both white and coloured light by becoming immobile, but bright white light has little immediate effect on feeding animals.

EXTRANEOUS FACTORS

During week-ends, both areas studied form part of a popular beach, and are often continuously trampled. This does not seem to have any effect on the nightly emergence of the animals.

Oil pollution

This was noted at the Blouberg population studied, when several observations were made. Crude oil from the ballast tanks of a tanker washed ashore on 7 February 1970. The following day was a spring tide, the result being that the beach was covered with oil from the water line to the HWS mark (Fig. 11a). At the lower levels wave action tended to froth the oil, which was therefore not very thick. Higher up the beach the oil formed a thick solid deposit. Low tide on the night of the 7th was at 2225 hours, when not many animals emerged. Almost all the animals which did emerge were killed, death probably being caused by clogging of the pleopods and a consequent arrest of respiration. About

Fig. 11. a. Oil pollution at Blouberg. b. Exit holes through thick oil.

30 dead animals and about the same number of exit holes were found. On the night of the 8th, low tide was at 2303 hours, when numerous animals emerged (Fig. 11b). Where the oil was not very thick, the animals returned at the high water mark (Fig. 12a). Where the oil formed a thick layer at the high water mark, a few animals returned at a lower level. Many moved above the high water mark, into the low sand dunes, and burrowed amongst the vegetation (Fig. 12b), something not seen before. Of the animals which entered the sand through a thin layer of oil, several were dug up. No trace of oil on the bodies other than at the tips of the pereiopods between the bristles could be seen.

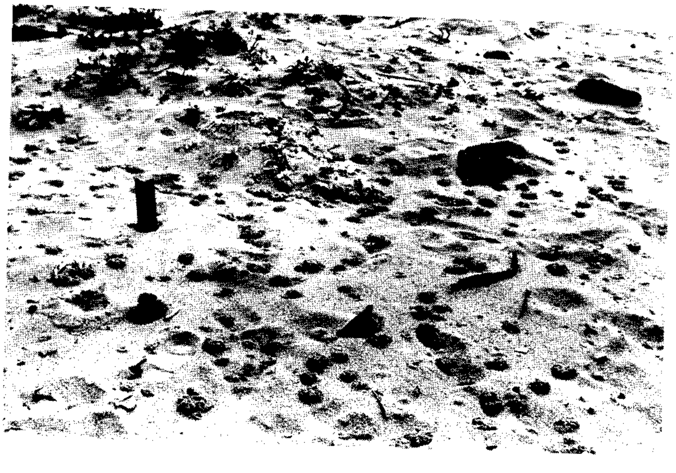

Fig 12. a. Return mounds on thin oil layer. b. Return mounds amongst vegetation in low sand dunes, well above HWS.

Presumably the corkscrew action used in burrowing rubbed off any adhering oil. A food problem was posed as almost all the seaweed was oil-covered. Above the high water mark, very little vegetable matter was present other than the actual dune plants, some of which were eaten. Humidity did not pose any problems, in spite of the fact that the dry surface layer of sand was deeper than at the high water mark. After about three weeks the animals returned to their usual level on the beach, as some of the oil had been removed, while the thinner layers had been covered by wind-blown sand.

LOCAL DISTRIBUTION AND BURROWING

The local distribution of *Tylos* may be discussed under three headings, viz. distribution along the beach, i.e. parallel with the sea; distribution on the beach at right angles to the sea; vertical distribution in the sand. The actual distribution of *Tylos* on any section of beach can be judged by the spread of either the exit holes or the return mounds. This judging of the population spread is easy at the time of spring tides, when the animals emerge and return on clean-swept sand. At the time of neap tides, however, the sea does not remove each day's mounds and holes. An overlapping then occurs, obscuring the distribution. Strong winds also flatten mounds and fill holes, obscuring the spread. A more definite check can be made by digging a trench up the beach, or by actually observing the animals emerging at night.

DISTRIBUTION ALONG THE BEACH

Tylos granulatus

The most important fact to emerge from prolonged observation of a population, is that it is, as a whole, clustered mainly around the high water mark. An explanation for this is that food is deposited at the high tide mark. During spring tides, algae which have been torn loose are left far up the beach. The *Tylos* population at high water of springs is thus far up the beach. At the same time, if a long stretch of beach is observed (about 500 metres) it can be seen that the population is split up into separate clusters along the HWS mark (Fig. 13a). As the height of each tide decreases after the spring tide, the population spreads out, some individuals following the high tide mark as it progresses down the beach, others remaining higher up. The result is that whereas at spring tide the population is split into clusters, at neaps it is outspread and forms a continuous band along the beach (Fig. 13b).

Tylos capensis

Although never as abundant as *T. granulatus*, this species shows a similar distribution along the beach, being clustered high up the beach at springs, and very spread out at neaps.

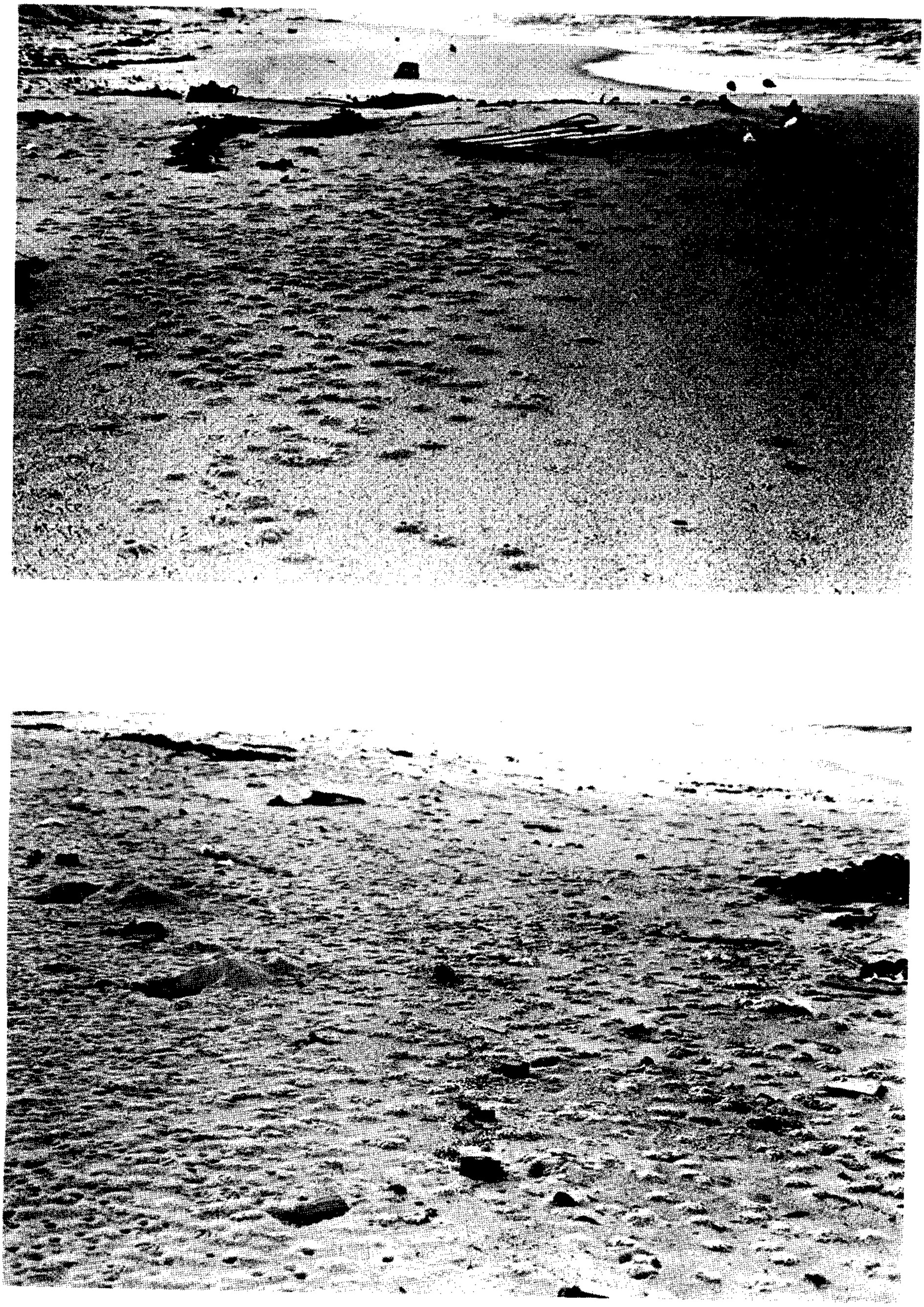

Fig. 13. a. A cluster of return mounds of *T. granulatus* at HWS, Blouberg. b. Blouberg at neaps. Exit holes at left. High tide line at centre marked by blocks of wood, etc. Return mounds at right.

DISTRIBUTION ON THE BEACH AT RIGHT ANGLES TO THE SEA

Tylos granulatus

The term 'at right angles to the sea' is used in preference to 'vertical zonation' as in this case the situation is complicated by the additional distribution vertically in the sand, and by the change in spread with the change in the height of the high water mark. The spread of the population up the beach appears to be related to the range of the high tide. On a beach which has a very flat high water area, such as Groenriviermond or Stormvogelbucht, the population is spread over an area about 100 metres in width. At Blouberg where the beach has a slope of about 1/8, the population inhabits an area about 20 metres in width. Figure 14 indicates the concentration of animals in two half square metres. Set (a), 10 metres above HWN, contained five animals; set (b) at HWN, contained 60 animals. Ten metres below HWN no animals were present.

The Orange River population is unusual in that it is situated on the landward side of a sand ridge which slopes towards the river pools. Here the area occupied is about 30 metres in extent.

Tylos capensis

A similar situation prevails with this species. At Strandfontein, with a slope of about 1/20, the population is spread over about 40 metres. The Breë River population on a much steeper slope occupies an area with a width of about 10 metres.

VERTICAL DISTRIBUTION IN THE SAND

This was obtained by excavating random half square metres. (This area was preferred to that of a full square metre, due to the time needed to complete an excavation.) The volume of sand under this half square metre was divided into layers each 80 mm deep. The distribution of animals in each 80 mm layer was then plotted on rectangles. This excavation was done in each case until no further animals were encountered. The time of day at which the excavation was done was recorded. These results may be seen in Figures 14 to 16.

Tylos granulatus

In Figure 14a–c it can be seen that in the late afternoon the majority of animals are between 80 and 240 mm below the surface. At sunset, the majority are distributed from just below the surface to about 160 mm down. At Ysterfontein (Fig. 14), a beach similar to Blouberg, at about midday the majority are from 240 to 320 mm below the surface. Figure 15a–c of the Orange River mouth shows the distribution of the animals over a length of about 30 metres of beach. The positions of the half square metres may be seen on Figure 17a. The juveniles appear to be concentrated in the upper layers of the sand. As at Ysterfontein and Blouberg at midday, the adults are concentrated at a depth of 160 to 320 mm below the surface. This is again seen in Figure 16d of Agate

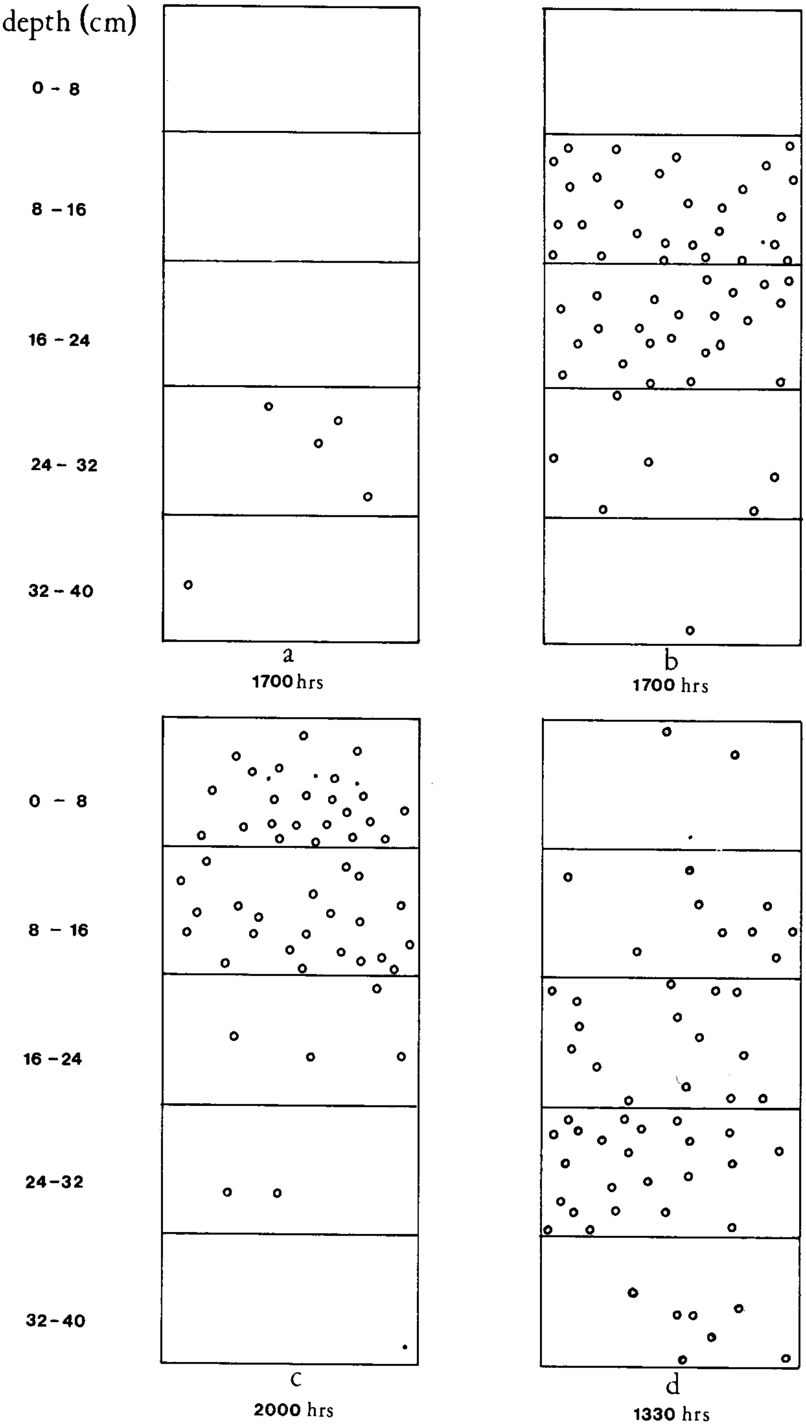

Fig. 14. Vertical distributoin of *Tylos granulatus*. a–c. Blouberg. d. Ysterfontein.

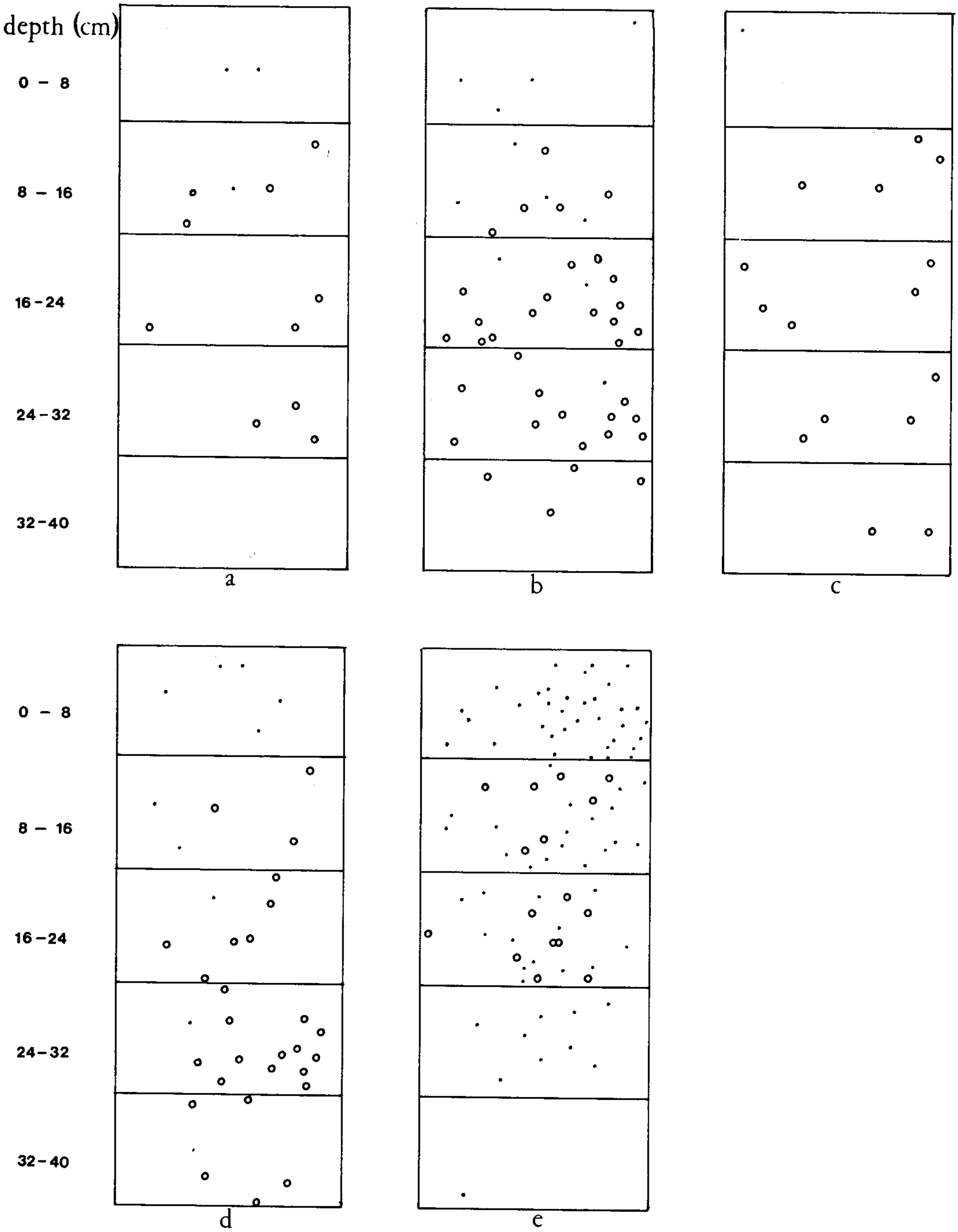

Fig. 15. Vertical distribution of *Tylos granulatus*. a–c. Orange River mouth sand bar. d. Agate Beach, Lüderitzbucht. e. Griffith's Bay, Lüderitzbucht.

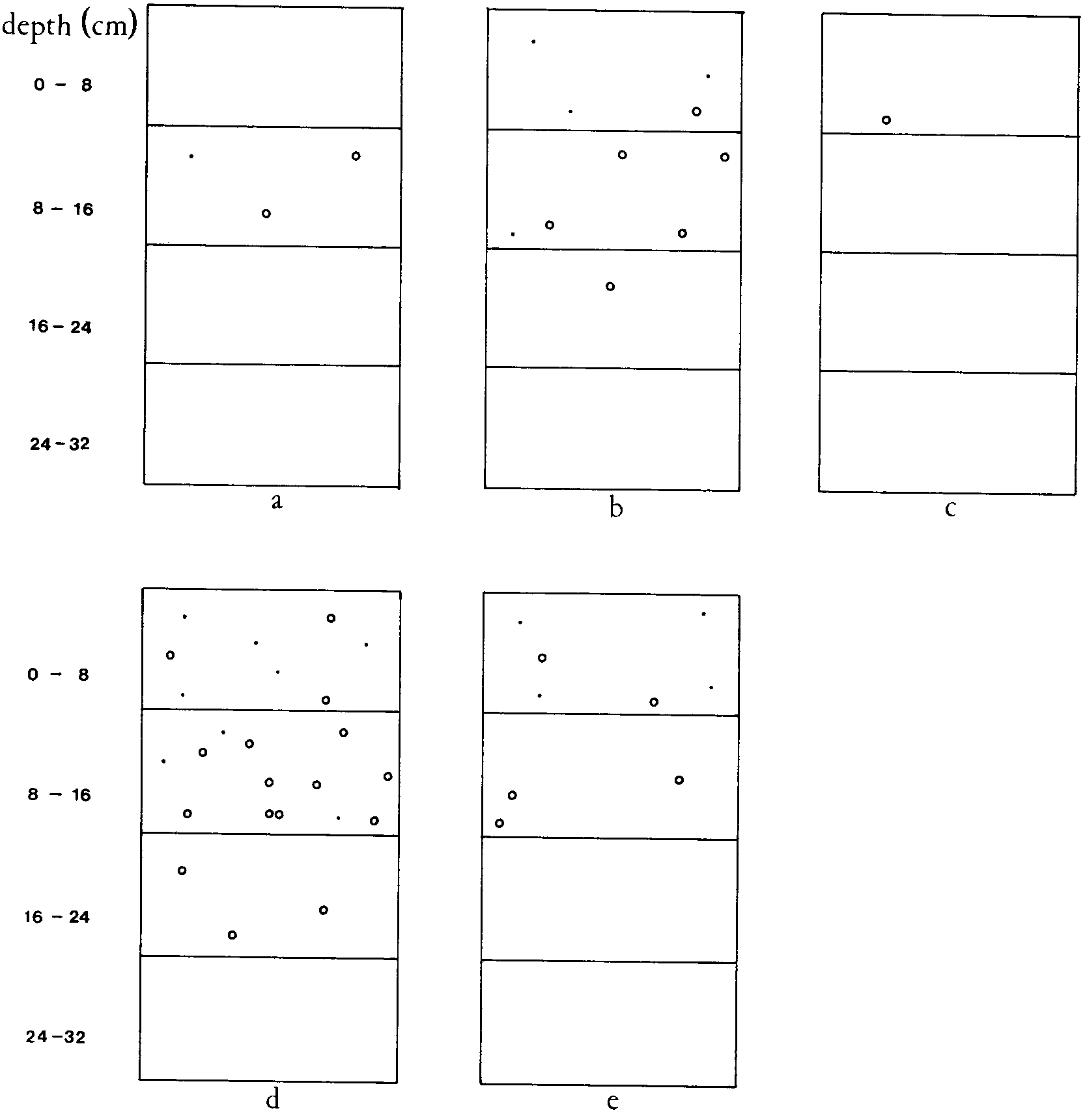

Fig. 16. Vertical distribution of *Tylos capensis*. a–c. Strandfontein. d–e. Breë River.

Beach, Lüderitzbucht, where the juveniles are found in the upper layers. Figure 15e of Griffith's Bay, Lüderitzbucht, represents an unusual vertical distribution which can only be satisfactorily explained by reference to the substrate in which the isopods were found. From the figure it can be seen that whereas the adults are limited to the depths of 80 to 240 mm, the juveniles, although concentrated in the upper 80 mm, are spread throughout the sand to a depth of 320 mm.

For midday the adults are unusually close to the surface, but they could not have burrowed deeper. The fine sand penetrated to a depth of 120 mm but gradually gave way to grit and small pebbles to about 200 mm. This layer was replaced by a deeper layer of large stones and shells. The juveniles could move between these large objects, but not the adults.

Tylos capensis

The vertical distribution of this species was also investigated by means of half square metre excavations, at both Strandfontein and the Breë River (Fig. 16a–e). Beach profiles may be seen in Figure 17c–d, on which the positions of half square metres are indicated by the letters 'a, b, c.' While at no time abundant, it would seem that this species seldom burrows to a depth of more than about 200 mm.

METHOD OF BURROWING

Burrowing was observed on the beach as well as in the laboratory. Captive animals were observed in large perspex/glassfibre containers, as well as in limoria. These latter being 30 mm wide, just allow an adult *Tylos* space to turn a complete circle when digging almost vertically downwards. This meant that the animals were always visible from either of the glass sides at any one point. All observations were done in the dark, using a torch at brief intervals, so as to disturb the animals as little as possible. The sequence of actions used in burrowing is as follows: the animal scoops out a hollow in the sand, using the anterior three pairs of pereiopods. These pass the sand on to the posterior four pairs of pereiopods, which push the sand backwards, to form a little heap behind the animal. The animal then moves sideways, through an angle of about 45°, digs out more sand with the first three pairs of pereiopods, pushes it back with the posterior legs, and forms another heap of sand next to the previous one. This sequence continues, usually five to seven pushes of sand, followed by a pause of about a minute. Each short burst of digging takes the animal a little deeper into the sand, as it moves laterally (usually anti-clockwise) after each push. The overall movement is a helix-shaped path passing vertically through the sand. One complete turn of the helix represents eight or nine backward pushes of sand, and takes the animal about 30 mm into the sand. On the surface this complete turn can be seen as an irregular cone of sand, having eight or nine small peaks if the sand is moist and the grains clinging. When the animal starts digging, the antero-posterior plane is horizontal, but as it progresses, this plane tilts upwards, so that once the animal is in the sand, this plane is vertical. Once below the surface, the backward pushing of the posterior pereiopods closes the hole. As the sand is usually moist below the surface the backward pushing tamps the sand, preventing it from falling back and hindering progress. The actual speed of digging varies, depending on the number of rests. Timing of six animals shows that the usual speed is about 200 mm/12–15 minutes. Once the animal has reached the 'desired' level, it moves around, flexing the pereiopods. This

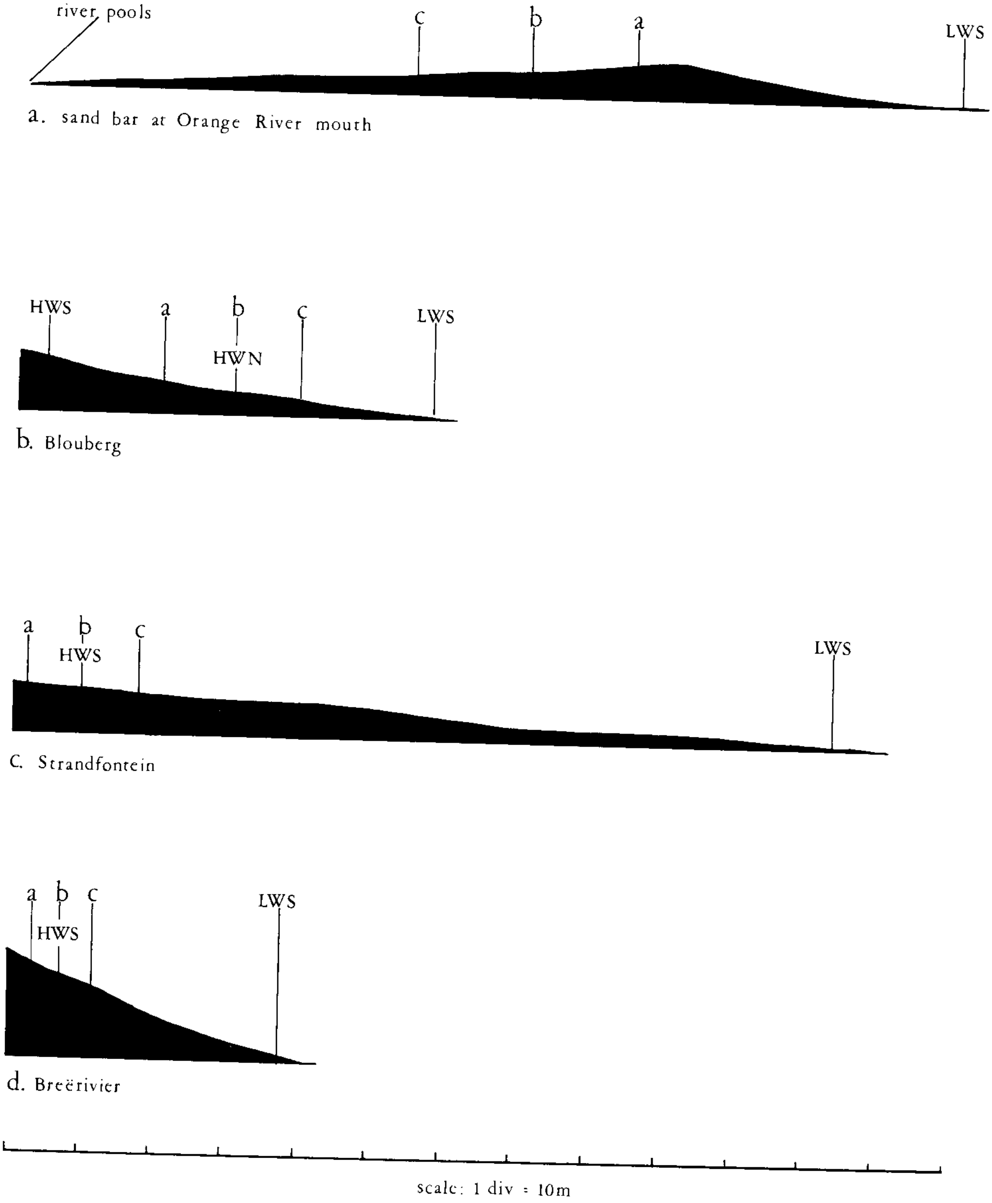

Fig. 17. Beach profiles. LWS—Low water of springs. HWN—High water of neaps. HWS—High water of springs. a. Orange River mouth sand bar. b. Blouberg. c. Strandfontein. d. Breë River.

causes its rounded dorsal surface to press against the sand, thus forming a chamber only slightly larger than itself. Once this is done, the animal curls up and remains in this position. Usually with the eyes ventral, until the time of emerging approaches.

It was sometimes seen that an animal will start digging on a mound, i.e. where another animal has gone down. The surface counts of mounds thus need not give an accurate indication of the number of animals below the surface. For example, at Lambert's Bay the surface count for a random half square metre was 55 mounds, but excavation yielded about 120 adults. Although several animals may enter the sand at the same point, once in the sand they separate and emerge from separate holes.

The actual time taken to emerge, once the animal becomes active, is not known, but is probably much longer than the return digging. This is inferred from observations made at different times of the day. For example, at 1700 hours most of the adults are 80 to 240 mm below the surface. At 2000 hours at the same locality, most of the adults are from just below the surface to 160 mm below. The animals may dig upward either following the path made by their entry or may follow a fresh path. Once the animal reaches the surface and the eyes are exposed, it pauses (Fig. 18a). This pause was observed in all emerging animals, varied in duration, but was usually between 2–15 minutes. Once the animal has left the burrow, its point of exit is marked by a circular hole up to 30 mm deep (Fig. 18b). The animal then immediately starts a rapid apparently random perambulation, stopping only when food is encountered.

From this study of the local distribution and burrowing of both species of *Tylos* the following facts emerge:

1. *Tylos* usually burrows close to the high water mark.
2. At HWS the population is high on the beach and clustered.
3. At HWN the population is lower on the beach and outspread.
4. The animals are distributed in the sand up to a depth of 500 mm in the case of *T. granulatus*, 200 mm in *T. capensis*.
5. The animals burrow with a spiral movement.
6. Re-entry into the sand leaves a cone-shaped mound on the surface.
7. The speed of return to the surface is slower than the speed of re-entry into the sand.
8. Exit points are marked by a shallow circular hole.
9. The animals sometimes return via a path made by another animal.
10. All digging is approximately vertical.

FOOD AND FEEDING

The section dealing with feeding and related topics in *Tylos* has been divided into several sections, viz. actual feeding, i.e. the obtaining of the food, the food preferences, the structure of the alimentary canal, and the actual process of digestion.

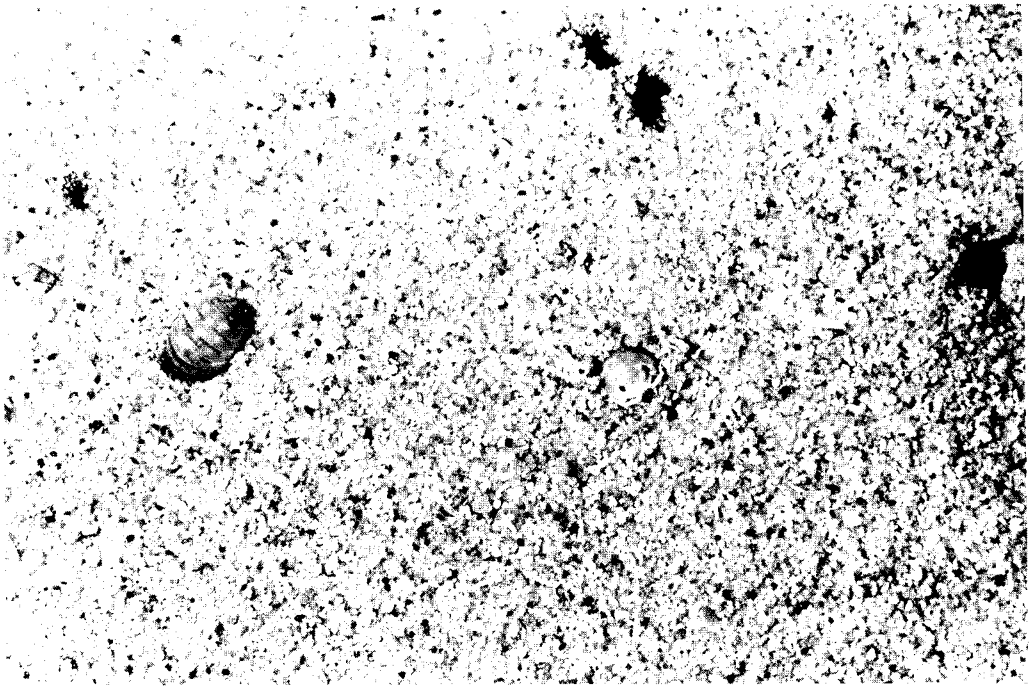

Fig. 18. a. *T. granulatus*. Animal at left starting to burrow, animal at right just emerging. Exit holes at upper right. b. Numerous exit holes of *T. granulatus*.

ACTUAL FEEDING

The feeding of both *T. capensis* and *T. granulatus* is confined to the brief period (two to three hours) that the animals are emerged. It was found that *Tylos* tends to burrow around the high tide mark, moving down the beach as the height of successive tides drops, or up the beach as the level approaches that of spring tide. This is a behavioural adaptation connected with food supply, as any floating debris including sea weeds and dead animals will be left on or near the high tide mark. The mouthparts are adapted for rapidly cutting pieces of food. The gut, particularly the midgut portion, is very capacious. Both these factors allow the animal to eat a maximum amount in the time available. A very rough measure of the amount eaten in the period emerged may be obtained from the following data (see Table 3). Ten specimens of *T. granulatus* were captured as they emerged to feed, weighed, marked, and allowed to feed. These animals were again captured at the end of the feeding period, reweighed and their length measured. They were then killed and the volume of the food in the gut measured by displacement. From this it was found that the animals ate up to 25% of their body weight in the two-hour period involved. A similar situation was found to apply in *T. capensis*.

From observations of animals feeding, a list of foodstuffs was compiled, which is summarized in Table 4. From a survey of the food consumed by the isopods it can be seen that both species are omnivorous, but with a bias towards an herbivorous diet. In this, *T. granulatus* and *T. capensis* resemble the European *T. latreillei* which Arcangeli (1953) describes as feeding on 'decomposed matter'.

From observation it was seen that the majority of adults feed almost exclusively on algae, while the juveniles (less than 15 mm in length) feed mainly on animal matter. The adults which are found around the high water mark feed mainly on the larger brown algae thrown ashore, along with the epiphytes on these algae. It would seem from the table of food matter, that the red algae form the major portion of the food, but relative sizes must be borne in mind. Whereas most of the red algae are small flattened plants, seldom more than 100 mm in length, the brown algae are often several metres in length, with massive stipes. All three brown algae recorded are large plants.

When feeding on *Macrocystis* it was noted that the animals eat only the flattened strap-like portions of the thallus. This results in large piles of stipe being left on the beach, along with the inflated basal portions of the fronds (Fig. 19a). When feeding on *Laminaria* or *Ecklonia* it was noted that the animals congregate on the flattened blades which are eaten from the edges (Figs 19, 20). This preference for the flattened portions results in a typical grazing pattern, i.e. many stipes denuded of fronds (Fig. 20a). Should food be scarce, however, the animals can be seen feeding on the stipes of these two algae. An examination of the mouthparts makes it obvious that feeding on a broad solid surface with no edge on which to start is more difficult than feeding on flattened straps. Animals feed apparently indiscriminately on both moist and dry algae. Feeding

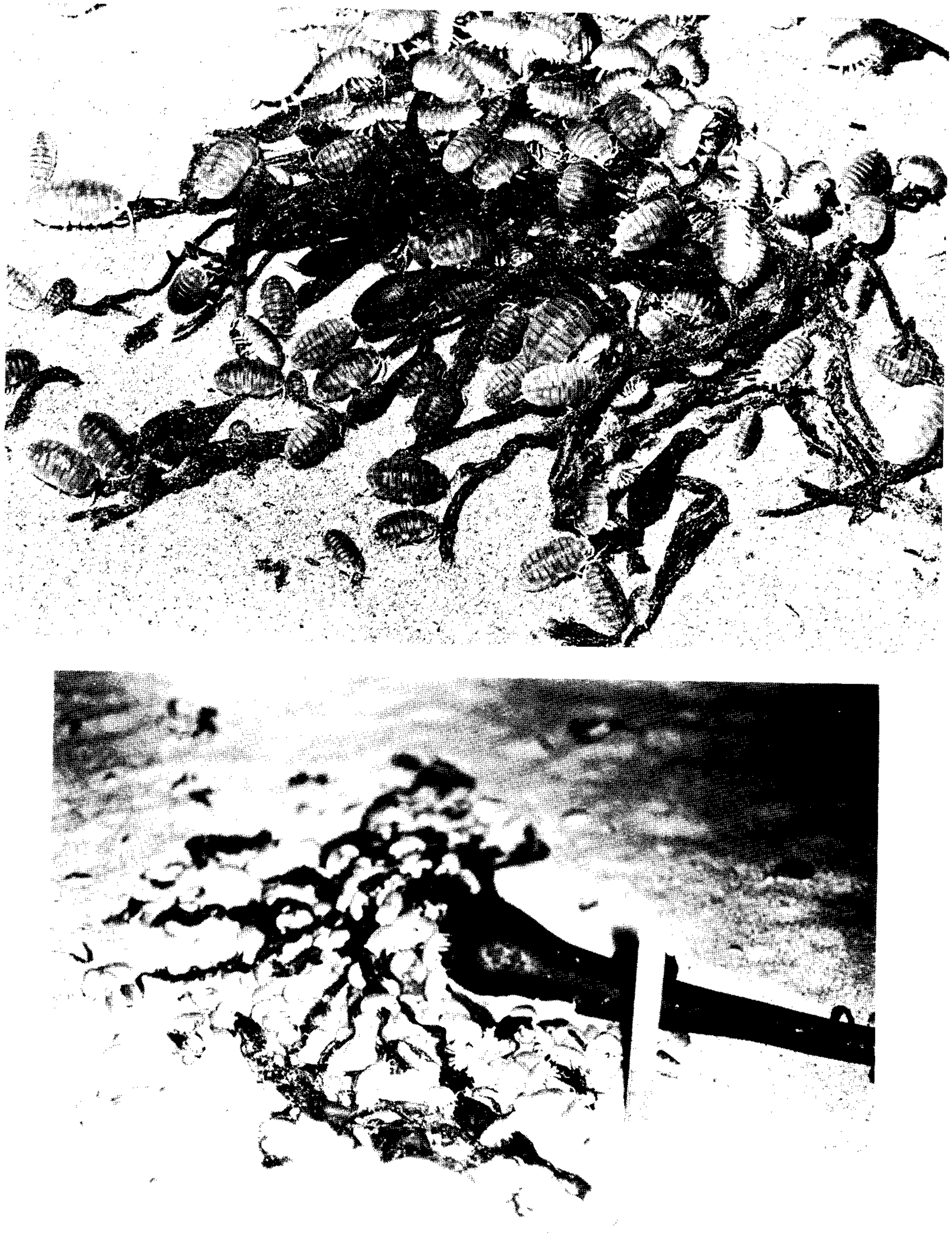

Fig. 19. a. *T. granulatus* feeding on blades of *Macrocystis*. b. *T. granulatus* concentrated around the blades of *Ecklonia*.

Fig. 20 a. Grazing pattern of *T. granulatus*. Denuded stipes in foreground, ungrazed stipes in background. b. *T. granulatus* feeding on the edges of *Laminaria* blades.

on dry algae, although seemingly difficult, can be explained. During the day the kelp is tough and leathery, but at night with no heat for evaporation and with moisture being deposited by dew and sea mists, the fronds soften slightly.

Although the juveniles are occasionally found feeding with the adults on the larger brown algae, the majority are found on the debris lines. Their presence here is to some extent due to a behavioural trait. The juveniles are usually found lower down on the beach than the adults, and often are caught in the waves. Unlike the adults which flatten out to let the water flow over them, the juveniles roll up into a ball, thereby capturing a bubble of air between the pereiopods, making them buoyant. They are carried up the beach by the wave and are left behind on the debris line along with their food. This latter in the juveniles seems to consist mainly of animal matter. If on any one night the number of juveniles feeding on different material is observed, the following sort of numbers may be obtained: jellyfish fragments 17, *Ulva* 5, other substances 5. Should any fish or *Physalia* be washed ashore, larger numbers of juveniles are found feeding on them.

FOOD PREFERENCES

To indicate very approximately the food preferences of *T. granulatus* (presumed to be similar to *T. capensis*) the following procedure was followed: Six containers measuring 400 × 200 mm and 100 mm deep were filled with damp beach sand to a depth of 80 mm. Ten adult *Tylos* were placed in each container. Shallow containers were used to allow for a minimum of time to be spent by the animals in burrowing, and for their easy removal. The containers were kept under normal external light and temperature conditions, sheltered from rain. The containers were left undisturbed for three days, during which time no food was provided. Thereafter food of various types, having been weighed, was placed randomly on the sand in the containers at 1730 hours. A container without animals was used as a control. At 0800 hours the following morning, those pieces of food which had been eaten on were reweighed, the percentage water loss also calculated. The percentage water lost from the remaining piece of food was added to the weight of the remaining piece of food. This total was then subtracted from the original weight of the food. In the first set of tests, the animals were taken from a beach almost devoid of food. The animals were then starved for a further three days. When food was then provided on two consecutive days, those animals which emerged ate large amounts. After this, less food was eaten at any one 'sitting'; the food was then provided at intervals of two to three days.

First choice

Roughly equal amounts (between 0,8 and 2,5 g) of the following six substances were provided: two brown algae—*Macrocystis* and *Laminaria*, one green alga—*Ulva*, one red alga—*Gigartina* sp., cabbage, and fresh fish. All these substances have been observed to have been eaten by *Tylos* at the Blouberg population studied. From Tables 5 to 9 it can be seen that the total amounts of food eaten in descending order are: fish 19,032 g, *Ulva* 5,664 g, *Laminaria* 2,161 g, cabbage 1,889 g, *Macrocystis* 1,481 g, *Gigartina* 0,298 g. If the number of times a particular food was chosen out of the 30 times the food was provided is considered, the following emerges: fish 19, *Ulva* 16, cabbage 10, *Laminaria* 2, *Gigartina* and *Macrocystis* one each. The three foods most preferred are thus fish, *Ulva*, and cabbage, none of which appears regularly in the natural habitat. The three which do appear frequently on the beaches were eaten only on the first night, i.e. when the animals were starved.

It may be assumed that the location of food by *Tylos* is partly by olfactory means, as fish, *Ulva*, and cabbage all have some odour, whereas the red and brown algae are practically odourless when fresh. The second pair of antennae are extremely well developed, and it has been demonstrated in *Ligia* (Hewitt 1907), that these antennae have an olfactory function.

Second choice

As was frequently observed, *Tylos* will feed on dry brown algae even when fresh were available. This aspect was investigated by means of a preference test, done in the same way as the previous test, but using only two containers of 10 animals each. In each was placed a piece of fresh and dry alga (*Ecklonia*) of approximately equal weight. The dry alga was weighed at midday in all cases, so that the water factor would be of minimal importance. The controls show that if weighed at midday, any water taken up during the previous night was again lost by the time of weighing. The dry controls remained at almost constant weight. The percentage water loss for the fresh alga was not calculated, as the fresh alga was never eaten. From Table 10, it can be seen that after six separate feeding sessions, only the dry alga was eaten. An explanation for this preference is probably that the mucilaginous exudation of the fresh alga is too sticky for the mouthparts to cope with, and is thus avoided.

Food preferences of juvenile Tylos

As the juveniles are usually found on the debris lines, where the smaller pieces of plant and animal matter wash up, it was decided to investigate the food preferences of these forms. Two containers of 10 animals each (ranging from 8 to 20 mm) were used. The choice of food given was fish, *Ulva*, *Macrocystis*, cabbage, and *Plocamium* (a small finely divided red alga). The results of this test may be seen in Tables 11 to 14. From this it would seem that as in the adults, the juveniles have a preference for animal matter (0,650 g fish eaten) but that almost similar amounts of *Ulva* and *Plocamium* were eaten (0,305 g and 0,376 g resp.). Cabbage was seldom touched, and *Macrocystis* not at all.

STRUCTURE OF THE ALIMENTARY CANAL (See Fig. 22)

The two main references dealing with the alimentary canal of isopods are Murlin (1902) and Nicholls (1930), both of which deal with forms such as

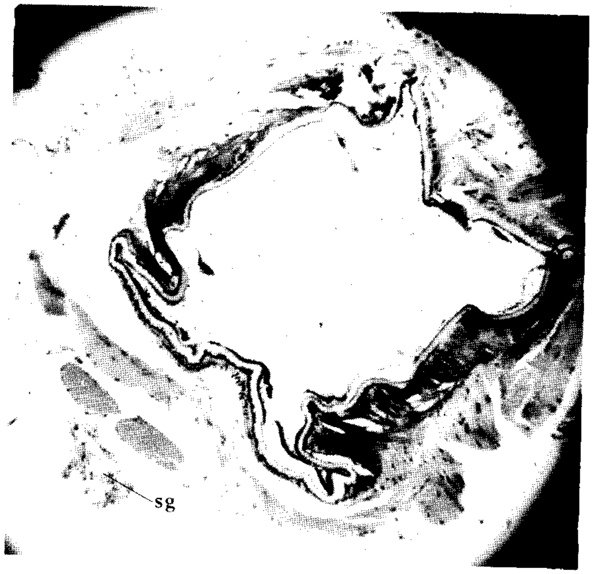

Fig. 21a.

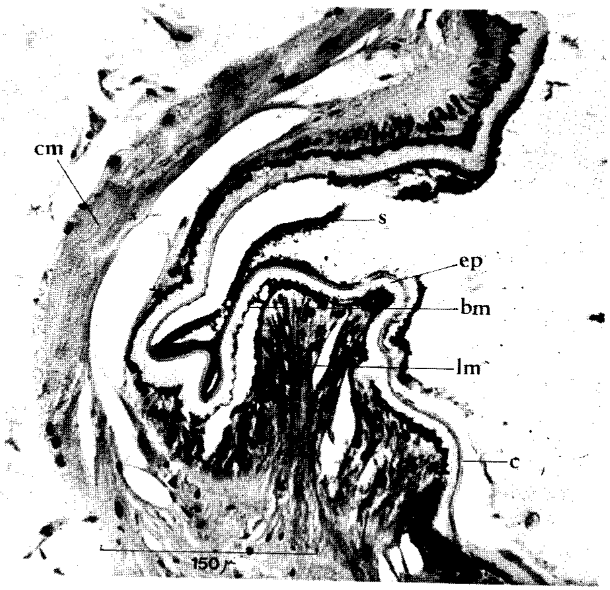

Fig. 21b.

Fig. 21. *Tylos granulatus*. a. Cross-section of oesophagus. b. Portion of wall of oesophagus; b.m.—basal membrane; c.—cuticle; c.m.—circular muscle; ep.—epithelium; l.m.—longitudinal muscle; s.—setae; s.g.—salivary gland

Ligia, Porcellio, Oniscus, and *Philoscia.* The only work dealing with *Tylos* is that of Barnard (1925) which contains a superficial description of the 'stomach' of the animal.

In general terms *Tylos* conforms with the overall isopod pattern, but has several differences, which are mentioned below in the relevant sections. The mouth is situated dorsal to the oral appendages, and just below the frontal lamina of the head. The mouthparts consist of one pair of mandibles, two pairs of maxillae, and a pair of maxillipeds. There is no obvious buccal cavity, the mouth leading directly into the short oesophagus, which together with the gastric mill constitutes the foregut. The walls of the oesophagus are strongly convoluted and are covered with very fine backwardly directed setae. Externally the oesophagus is surrounded by glandular material of the rather ill-defined salivary glands. These latter open into the oesophagus near the mouth. In cross-section (Fig. 21a, b) the oesophagus is roughly square, with the main masses of longitudinal muscles concentrated at the centres of the sides of the square. The chitinous cuticle has outgrowths in the form of numerous setae, and is secreted by a single layer of epithelial cells just beneath it. The entire oesophagus is surrounded by circular muscle fibres which tend to be arranged in large bundles. Bands of muscles stretch from the oesophagus wall to the exoskeleton of the head region, the salivary gland tissue being situated between these bands.

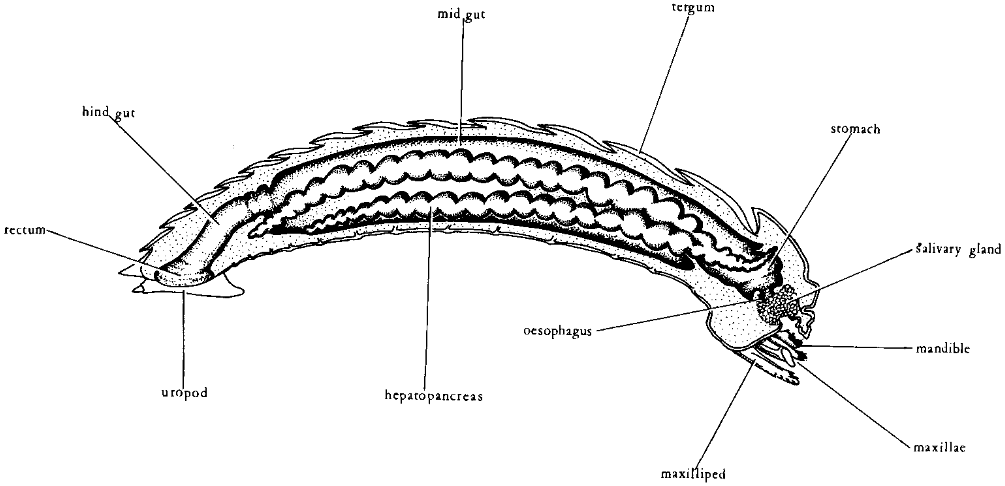

Fig. 22. *Tylos granulatus.* Lateral dissection, showing position of alimentary canal.

The oesophagus opens into the 'stomach' which contains a very efficient gastric mill (Fig. 23), made up of the following structures:

1. The lateral ampullae. These are projecting structures, the median faces of which meet above the opening of the oesophagus. These median faces have a

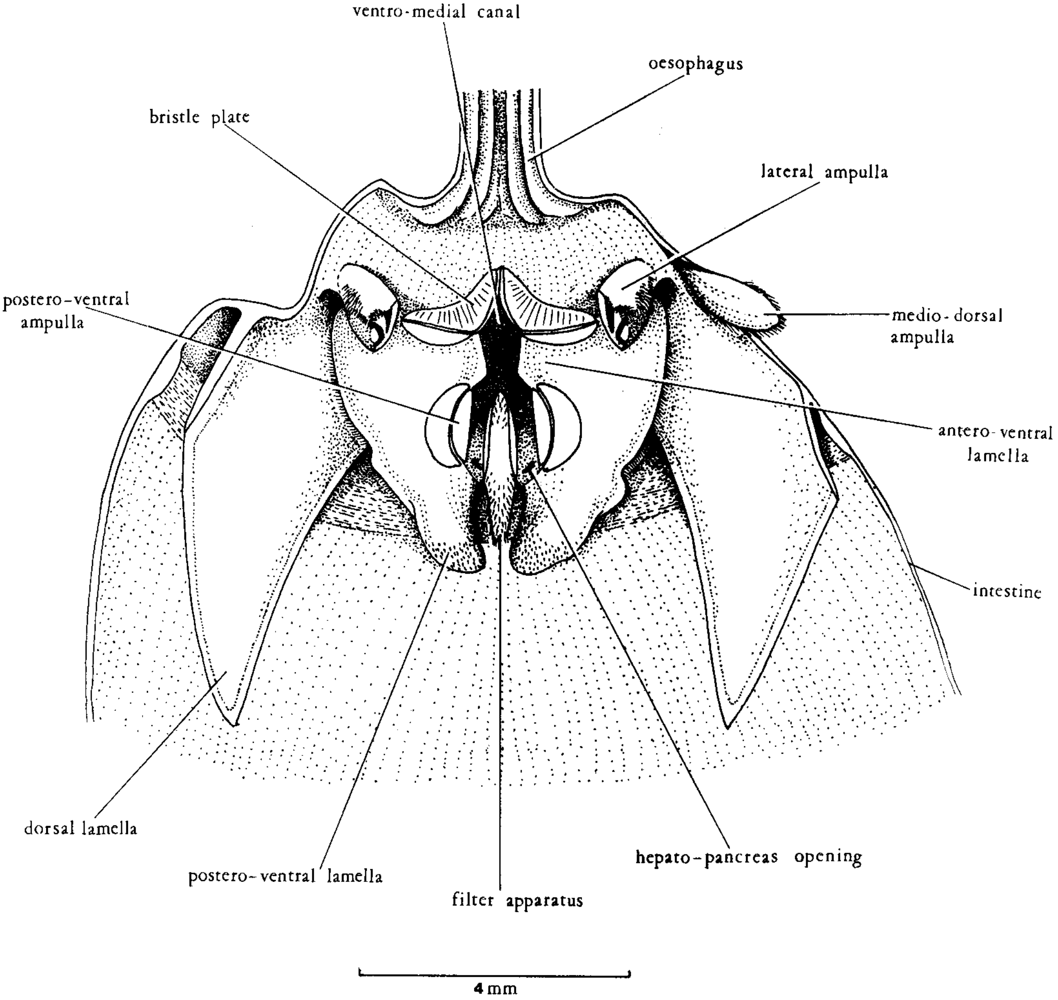

Fig. 23. *Tylos granulatus*. Structure of the 'stomach'.

trilobed chitinous structure possibly used for grinding. *Tylos* lacks the small antero-lateral ampullae found in *Ligia* and related isopods.

2. The median anterior ampulla, situated on the ascending anterior wall. This is a lobed structure fringed with setae.
3. In the floor of the foregut, below the lateral ampullae, is a pair of crescentic bristle plates, formed by the fusion of many bristles. The anterior portion of these plates meet in the midline but diverge posteriorly. Posterior to these plates are the ventral lamellae, while between them is the ventro-median channel.

4. The ventral lamellae may be divided into an anterior and a posterior region. The anterior region, the margin of which is fringed with setae, bears on each side a pair of plates, not mentioned in the description of *Ligia* or any other isopod. These may be termed the postero-ventral ampullae. The latter have a horizontal crescentic plate, as well as a medio-vertical plate, which forms part of the wall of the ventro-medial. The posterior ventral lamellae project into the midgut in the form of two rounded lobes armed with short bristles.
5. In the ventro-medial region, just opposite the medio-vertical plates of the postero-ventral ampullae, is an elongate spindle-shaped structure, the filter apparatus. The anterior portion has a pair of lateral plates which work against the medio-vertical plates of the postero-ventral ampullae. The posterior portion projects between the lobes of the ventral lamellae, and is equipped with numerous setae. This filter apparatus divides the ventro-medial channel into two portions, each of which ends posteriorly at the opening of the hepatopancreas.
6. Situated dorso-laterally and joined along the midline are the two lobes of the dorsal lamina. These are acutely triangular in shape, consist of two layers of chitin, and project into the midgut.

The hepatopancreas

As already mentioned, the gland on each side opens into the posterior portion of the ventro-medial channel. Each gland consists of three tubular moniliform portions, two postero-lateral and one antero-lateral (Fig. 22). The postero-lateral portions stretch back along the mid- and hindgut, almost to the last segment. The short antero-lateral portion stretches obliquely upwards on either side of the 'stomach'. In section (Fig. 24) the hepatopancreas can be seen to consist of a single layer of glandular epithelial cells, around the central lumen of the gland. In places the wall of the gland appears to be more than one layer thick but this is merely due to the convolutions of the gland. The cells are elongate with a highly granular cytoplasm and large deep-staining nuclei. In the distal portion of many of the cells, large vesicles may be seen. These are probably droplets of the secretion of the cells. In addition, many of the cells have large clear central vacuoles. The outer surface of the hepatopancreas has a very thin layer of connective tissue, between which and the glandular cells, very thin circular muscle fibres may be seen. This muscle layer may be continuous but is difficult to assess, being very thin.

The midgut

The gastric mill ends at about the level of the first thoracic segment and opens into the capacious midgut, which stretches back to meet the hindgut at the level of the tenth segment. There is no trace of a typhlosole, as found in *Ligia*. In cross-section (Fig. 25) it can be seen that the midgut is lined with a very fine chitinous intima, in which there is no sign of holes or ostia. Murlin

Fig. 24. *Tylos granulatus.* Cross-section of hepatopancreas; c.—connective tissue; n.—nucleus; va.—vacuole; ve.—vesicle

(1902) mentions the presence of very fine pores in the intima of the midgut of several terrestrial isopods, including *Oniscus* and *Asellota.* Nicholls (1930) could not find these holes in *Ligia,* neither were they present in *Armidillidium, Porcellio,* or *Idotea* (McMurrich 1896). Beneath the intima is a single layer of elongate epithelial cells. These are large cells, about 150 μ in length, and have large deep-staining nuclei. These epithelial cells are remarkable for their large vacuoles surrounded by a thin granular cytoplasm. Numerous granules are visible in this cytoplasm, as well as minute droplets. These may be absorbed digestive products. The outer bases of the epithelial cells are surrounded by a very fine basal membrane. The outermost layer consists of a sheath of connective tissue, with separate bundles of oblique muscle fibres.

The hindgut

The midgut opens into the hindgut at a constriction. The hindgut which forms about one-quarter of the total gut length, occupies the last four segments and opens at the anus, which is covered by the valve-like uropods. The innermost layer of the hindgut is a very fine chitinous intima, beneath which is found a single layer of elongate epithelial cells, similar to those of the midgut (Fig. 26). These cells contain large vacuoles, but not as obvious as those of the midgut. The cytoplasm does not have many inclusions. The epithelial layer is very convoluted, with connective tissue between it and the next muscle layer. The muscu-

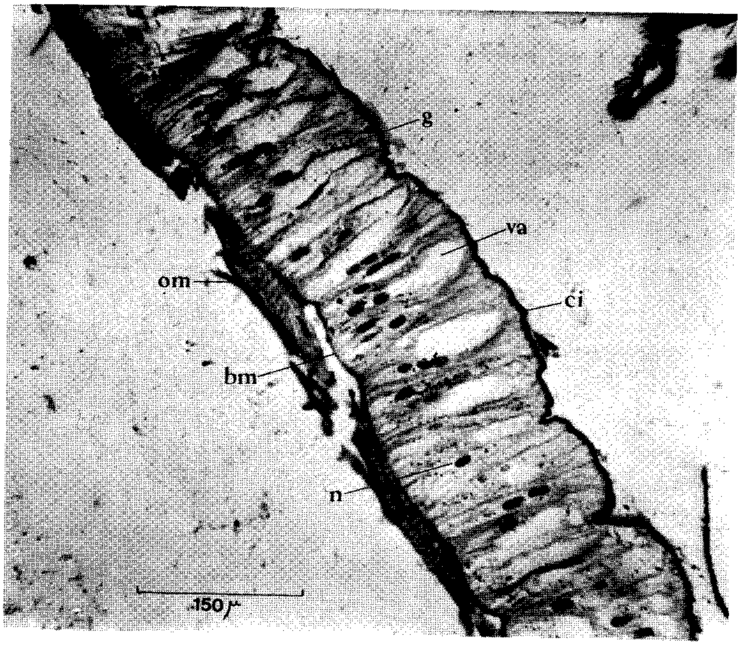

Fig. 25. *Tylos granulatus*. Cross-section of midgut; b.m. – basal membrane; c.i. – chitinous intima; g. – granules; n. – nucleus; o.m. – oblique muscles; va. – vacuole

lar sheath surrounding the hindgut consists as circular as well as longitudinal fibres. The circular fibres form a continuous band around the gut, while the longitudinal fibres are arranged in separate bundles on the circular muscle band.

THE PROCESS OF DIGESTION

The progress of food through the gut involves several stages, some being not particularly clear. The food is manipulated and eventually cut up by the mandibles, then passes into the oesophagus in the form of fairly uniform pieces. The posteriorly directed setae of the oral region all assist the food in moving into the oesophagus, and prevent it from slipping out. The fine hairs of the oesophagus have a similar function. While passing into the oesophagus the food is mixed with the secretion of the salivary glands. (The exact nature of these secretions is uncertain, as very refined techniques are needed to collect and test them. A certain amount of mucilaginous fluid is secreted.) Contraction of the muscles of the oesophagus walls passes the food on to the gastric mill. As none of the structures of this complex is particularly hard, it would seem unlikely that any trituration occurs. Rather it would seem that the lateral ampullae by muscular action force the food against the bristle plates. Similarly the postero-ventral ampullae would work against the filter apparatus, again squeezing the food. Both these actions would result in food plus tiny pieces in suspension, to pass

Fig. 26. *Tylos granulatus*. Cross-section of hindgut; c.i.—chitinous intima; c.m.—circular muscles; l.m.—longitudinal muscles

into the ventro-medial channel. Contraction of the hepatopancreas would force its contents into this channel, to be mixed with the food-fluid, and allow the enzymes present in the secretion to act. Large food particles would be prevented from entering the channel by the posteriorly directed setae and allow the food to pass only backwards into the midgut.

The site of absorption has been the subject of much controversy. It has been shown that in *Nephrops* (Vonk 1960), absorption can and does take place in the midgut. Several decapod crustaceans, including *Astacus* (Jordan 1929), *Nephrops* (Yonge 1924) and *Atya* (Van Weel 1955), have been shown to absorb substances through the hepatopancreas. Nicholls (1930) showed that in *Ligia* absorption took place through the midgut (even though lined with chitin) and also through the hepatopancreas. It is likely that a similar set-up occurs in *Tylos*. With contraction of the hepatopancreas the secretions are forced into the ventro-medial channel, and mixed with the fluid part of the food. Any excess secretion is forced into the upper portion of the gastric mill and mixed with the solid food. With relaxation of the hepatopancreas, the mixture of foods in the channel is drawn into the lumen of the gland. Dissolved food in the form of monosaccharides and amino acids may then be absorbed by the glandular epithelium. Oil droplets are probably also taken up, as is known to occur in *Atya* (Van Weel 1955). Contraction of the muscles of the gastric mill then forces the solid food particles and hepatopancreas fluid into the midgut where a longer process of digestion takes place, and the released substances absorbed through the chitinous intima of the gut (Vonk 1960). Food is probably kept in the midgut for a period of up to 48 hours, depending on the type of food. Observation shows that an adult *Tylos* having fed on *Ecklonia* does not feed on the following night, and probably will not feed on the second night either. The 'storing' of the food probably accounts for the sporadic emergence of the adults. If the midgut is full of digesting food, there would be no need to emerge and feed.

The secretion of the hepatopancreas

From a perusal of the food list, it will be seen that *Tylos* is omnivorous, with a bias towards algae. Omnivorous invertebrates almost invariably possess all three major types of digestive enzymes, viz. carbohydrases, proteases, and lipases. With this in mind, simple qualitative tests were performed to establish the presence of these enzyme types in *Tylos*.

A homogenate of hepatopancreas gland was prepared in the following way. The glands of 40 animals were removed, weighed, and homogenized with a phosphate buffer of pH 7,0. The homogenate was then centrifuged and the supernatant further diluted with buffer to give a 10% homogenate solution.

Carbohydrases: tests were performed for three carbohydrases, cellulase, amylase, and sucrase. In the case of cellulase, a positive control in the form of homogenate of *Helix* midgut was used, as well as a negative control in the form of boiled hepatopancreas homogenate. No cellulolytic activity could be detected in the active *Tylos* homogenate and it was concluded that no cellulase was present. Amylase was tested for by means of starch solutions and Fehling's test for reducing sugar. The latter test was positive, indicating the presence of some amylase-type enzyme. Sucrase was tested for, a positive control in the form of invertase solution being used. A positive Fehling's test indicated the presence of a sucrase-type enzyme.

Lipase was tested for by means of the action of the homogenate on milk, phenolphthalein and NaOH being used as indicators. Fatty acids were released indicating the action of a lipase.

Protease was tested for by the use of congo red fibrin at pH 7,0. Only after 48 hours did any red coloration appear in the experimental tube, indicating that some fibrin has been digested to release the red particles. The test was repeated using a phosphate buffer of pH 8,0. After two hours the experimental tube contents became red. In both tests, a dilute solution of trypsin was used for comparative purposes. It was concluded that some protease was present which operated in the alkaline range.

The results of the test for protease seemed to suggest that the pH of the gut must vary if all the enzymes are to function close to their optimal pH. Several animals were opened and the pH of the gut tested directly. The results of this showed that whereas the pH of the hepatopancreas was 6,3, that of the gastric mill and anterior part of the midgut is 6,9, while the posterior midgut has a pH of 7,4, and the hindgut 6,8. It would seem that the carbohydrases have maximum activity in the foregut and anterior midgut, while the posterior midgut with its higher pH would be the centre of protease activity. The acid pH of the hindgut is probably due to the start of decomposition. The results are similar to those obtained by Nicholls (1930) for *Ligia oceanica*. He found the pH of the hepatopancreas to be in the region of 6,1–6,3, with the pH of the gut usually higher than that of the gland. The pH of the intestine varied from 6,2 to 7,2, while the rectum had an acid pH of 6,0.

RHYTHMICITY

In an attempt to gain more precise information regarding the rhythmic activity of *Tylos*, uninterrupted nightly observations were done on *T. granulatus* for 36 consecutive days. Consecutive observations over a long period were not carried out for *T. capensis*; interrupted observations over several weeks were nevertheless made. So as to get an overall view of the situation, and to see trends in the rhythm, all the information for *T. granulatus* was presented graphically, together with other relevant factors. With reference to Figure 27, the following should be noted.

1. The horizontal axis denotes the 24 hours of the solar day.
2. The vertical axis denotes consecutive days, the actual dates being given.
3. Solid black horizontal lines represent the time emerged by the animals.
4. Stippled areas denote dark of the sun, i.e. night.
5. Curved solid lines indicate low tide, the actual time of low tide being where the line intersects the horizontal day line.
6. Curved broken lines represent high tide, the actual time of high tide being where the line intersects the horizontal day line.
7. As the animals emerge and return over a period of up to 30 minutes, actual time of emergence was taken when at least ten animals could be seen emerging simultaneously. Similarly, time of return was taken when at least ten animals could be seen returning.

Discussion of Table 15 and Figure 27

From the above data several facts emerge, some of which can be explained and others which can only be speculated about. The most obvious fact is that *T. granulatus* is purely nocturnal and usually emerged at least one hour after sunset. (*T. latreillei* by contrast is a diurnal animal, preferring damp shady crevices of rocks. Pardi (1955) made use of this fact when investigating the orientation mechanism of this animal.) The shortest time observed between sunset and emergence was one hour. The shortest time observed between return into the sand and sunrise was 2½ hours. The mean time emerged for the 36 consecutive days of observation was 2,1 hours, the mode 2,0 hours. The longest time out was about 2½ hours while the shortest time out (apart from the exceptional

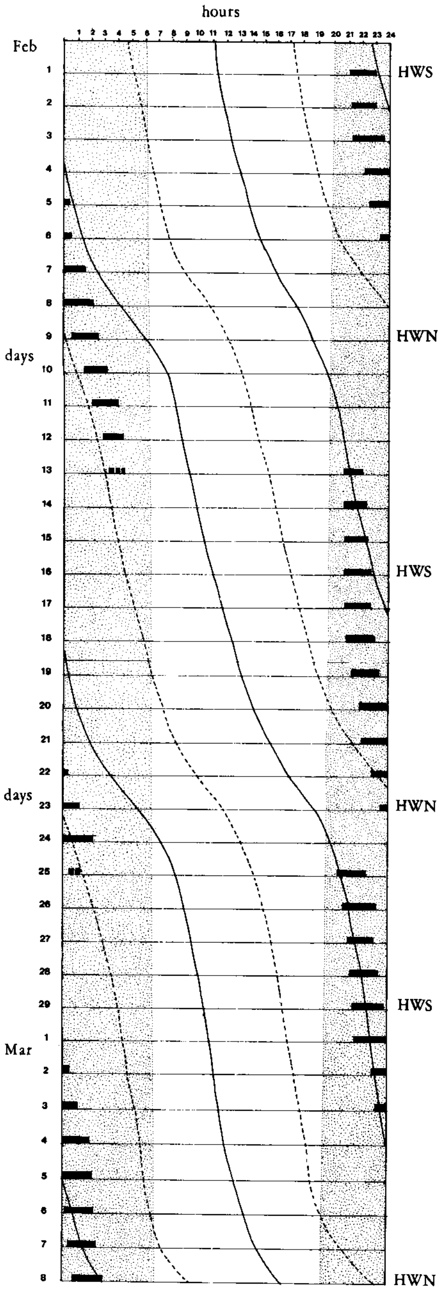

Fig. 27. Rhythmic activity of *Tylos granulatus*.

13th and 25th) was 1½ hours. The time the animals have to feed is thus very short, and appears to be strictly controlled.

It can be seen that there is an overall trend to emerge later each night; this gap between the time of emerging for successive days may be anything from 0 to 1½ hours. Occasionally the animals emerge at about the same time for several consecutive nights, e.g. from the 14th to the 18th inclusive. If the time for re-entry for these days is noted, however, it can be seen that this becomes later each day. If the time between re-entry is plotted against successive days, it can be seen that a line may be drawn through these points at the 24,5 level. This is the mean of the times between re-entry. The mode of this time gap, however, is 24,7 hours. Excepting the unusual days of the 13th and the 25th, the time between re-entry on successive days is always more than 24 hours. If the cycle is one of 24,8 hours which is not unusual for littoral animals, there should be a correlation between the time of emergence of the animals and the time of low tide (or the time of high tide). With this in view, Spearman's Rank Correlation Test was done, using the three sets of consecutive 12-day observations and ignoring the days in between. This test gave positive correlations of 1,0, 0,84, and 0,9. The significance of this correlation was tested, using the 't' test, which showed that the probability of this correlation occurring by chance was less than 0,01, i.e. there is a positive correlation between the time of low tide and the time of emergence. It must be noted that although this test shows positive correlation between tides and the cycles of activity, this does not imply a causative connection between these phenomena. It can be stated with considerable certainty that *T. granulatus* possesses a 24,8 hour (lunar day) rhythm.

An explanation for the consecutive days on which the animals emerge at the same time, may be that not all the same animals emerge, thus each day some animals emerge later than others, and return to the sand later each day. Brown (personal communication) states that in some sandy beach animals which burrow, only part of the population emerges each day. Thus in the mollusc *Bullia digitalis* it has been estimated that only 12% of the population emerges at any one tidal cycle.

If the times for re-entry and emergence are examined against the times of high and low tide, it is seen that on five days out of the 36 the animals emerged near the time of high tide, but only during neap tides. On all the other days they emerge either at low tide, or during ebb tide. It is obviously advantageous to the animals to emerge during a receding tide. If they emerged close to the time of high tide, there exists the possibility of being swept to sea.

As has been shown, *Tylos* has under natural conditions a lunar day rhythm. It thus emerges a little later each night. If this system were invariable, eventually it would not emerge until dawn. Being purely nocturnal, as already stated, this would be most unsuitable. The animals correct for this effect of the lunar day rhythm by a 'switch back' once a certain stage of the cycle is reached. This switch back takes it to the early evening hours after sunset which then allows many days of uninterrupted lunar rhythm. This switch back was seen to operate on the 13th and on the 25th. On the former day a few animals were seen to emerge at about 0300 hours, just on high tide. A vast number emerged at 2045 hours, whereas on the previous day the majority emerged at 0250 hours. It was obviously important not to emerge at 0300 hours on the 13th, i.e. at high tide, as the tides were approaching springs. The animals would be low down on the beach, and the increasing height of the high tide would certainly endanger them. Emerging at 2045 hours brought them out at low tide when it was quite safe for feeding.

Twelve days later, the animals again switched back. A few emerged at 0015 on the 25th, but a great number came out at 2030 hours. Again the tide was approaching springs and although on the 23rd and 24th they had emerged at high tide, the tide was getting higher each day, rendering their late emergence more dangerous. To cause this switch back, there must be some rhythm imposed on the lunar day rhythm. In all probability this is a semi-lunar or 14-day rhythm. This would keep the animals in phase with the spring tides, the period between successive springs being 14–15 days. The fact that the switch back of the 25th occurred only 12 days after the previous one does not disprove this, but may represent an abnormality in the rhythm due to external factors. It is interesting to note that in both the observed switch backs, these occurred four days before the spring tide. That the rhythm is a 15-day one may be inferred if Figure 27 is examined. Twelve days elapsed between the start of observations on 1 February, and the switch back of the 13th. The HWS occurred on the 1st. Three or four days before this the animals would have switched back, i.e. on 28 January. Further evidence for this is that on 28 January the animals were observed to emerge at 2100 hours at Lambert's Bay, 288 km up the coast. (As there are only three 15-day cycles available, statistical verification is not possible. With a minimum of six cycles, 90 days of observations would need to be done.)

As it has been shown that *Tylos* possesses a 24,8 hour rhythm as well as possibly a 15-day rhythm, it remains to investigate whether these are inherent or whether they are triggered by external factors. With this in view, a rather unrefined experiment was performed. A population of 25 animals of *T. granulatus* was placed in a perspex/glassfibre container, having an area of 250 cm^2 and a depth of one metre. This container was placed in a completely dark room, having a temperature of 17°C, and a range of about 3°C. This room was kept in constant darkness for 18 days. The only light was that of a torch used for brief intervals for observation. Food in the form of moist *Macrocystis* and *Ecklonia* was regularly provided so as not to be a limiting factor. The sand used at the start was damp, and at irregular intervals small amounts of sea water were added to prevent drying out.

The animals were left for two days to acclimatize before observations were started. The animals in the darkroom were thus separated from the effects of the tides, temperature fluctuations, and illumination affecting the animals on the beach, which were used as controls. The emergence of the animals from both the beach and the darkroom was plotted against a time axis (Fig. 28). At the

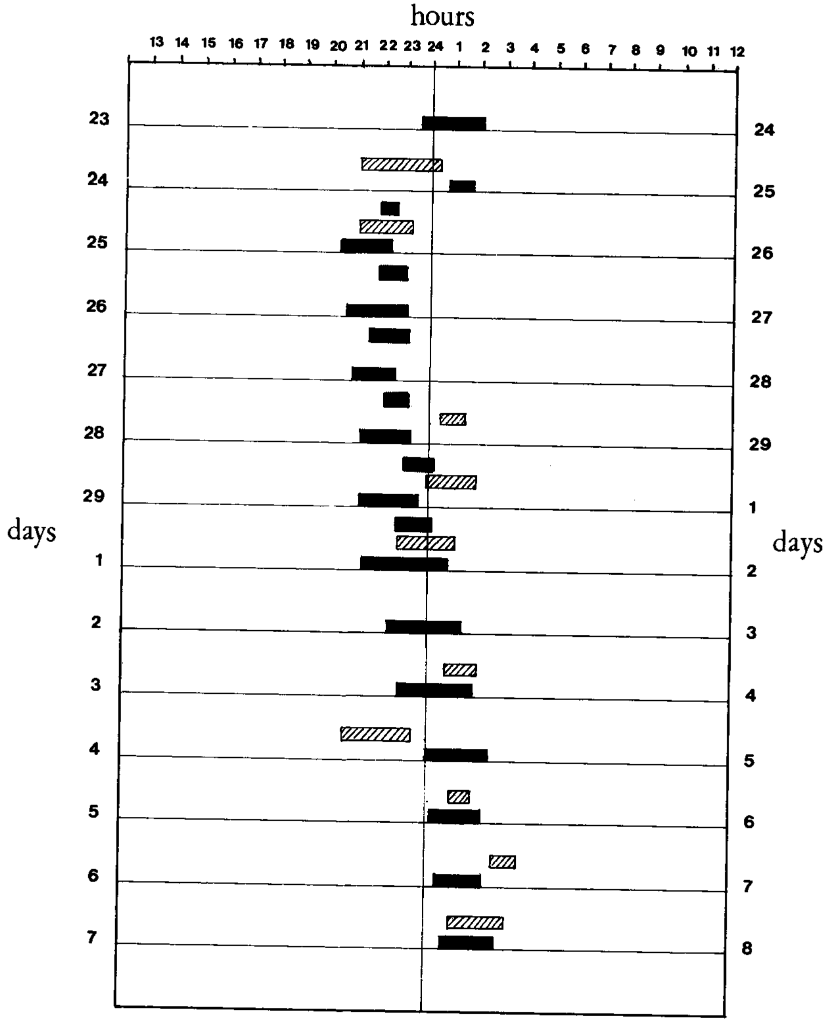

Fig. 28. Rhythmic activity of *Tylos granulatus*.

same time, ten animals were kept in a container of sand, away from the beach but under normal light and temperature conditions. These latter could unfortunately only be observed for six days. These results are also plotted on Figure 28. On the 29th, after it was suspected that not all the same animals emerge each night, the darkroom animals were marked with numbers painted on their dorsal surfaces so as to record in greater detail the exact animals which were emerging. (Marking animals on the beach is not practicable; the number feeding on 0,2 m^2 of kelp was often found to be over 300. A very rough estimate of the number of animals in the study area at Blouberg is between 3 000 and 4 000.)

The results of these observations may be seen in Table 16. From the latter and from Figure 28, the following observations were made:

1. For the period of observation, the experimental animals emerged only during night hours, even though they were subjected to constant darkness.
2. The same animals do not necessarily emerge every night, and on some nights none emerge.

It was found that on 22 March, 29 days after the experimental animals had been placed in the darkroom, nine emerged at 1700 hours, i.e. two hours before sunset. The rhythm which kept the animals nocturnal appeared to be breaking down. The container with the animals was then placed in the open where they received normal light and temperature conditions. The following day the animals emerged at about 2100 hours, almost two hours after sunset. They had thus corrected the time of emergence, once normal light conditions were restored. It is interesting to note that the Blouberg population emerged at 2015 hours on the same day.

Discussion of Table 17 (*Tylos capensis*)

Even from the limited data available for observations on *T. capensis*, several facts may be deduced. As in *T. granulatus* the present species is strictly nocturnal and usually emerges at least one hour after sunset. The time of emergence is again usually close to that of low tide, as in *T. granulatus*, while the actual time emerged is from 1¼ to 2½ hours. Thus a lunar day cycle of 24,8 hours may be inferred for this species. As the animals always emerged at or around the low tide of the dark hours, and as the observations cover a period of almost 2½ months, it may also be inferred that the switch back mechanism, controlled by a 15-day cycle is present in this species.

REPRODUCTION AND GROWTH

Reproduction in *Tylos* is geared to the littoral and almost terrestrial mode of life. Spermatozoa must be transferred to the female without the assistance of water. For this, the male is provided with copulatory stylets. These latter are adaptations of the endopods of the second pair of pleopods. The basal portion of each stylet lies parallel with the posterior margin of the last pereion segment. At the midline, each stylet is bent at a right angle posteriorly. In the adult male of *T. granulatus* this portion can be 3–4 mm in length, and is adpressed to its opposite member. Each is concave on the inner face, the two together forming a channel for the passage of the spermatozoa. (The presence of the stylets, which begin to develop in the very small males, is useful in distinguishing the sexes.) The spermatozoa are produced in the testes, three on each side, situated in segments three and four, dorso-lateral to the gut, and are passed into the stout vasa deferentia. In these the needle-like spermatozoa are clustered into spermatophores. The male genital orifice on pereion segment seven is just opposite the bend in the copulatory stylets, and the spermatophores pass along this channel to be transferred to the female. The actual transfer was never witnessed, and could have taken place at the surface or beneath the sand. Many of the males dissected from almost all the localities were found to have spermatozoa in the vasa deferentia. The ovaries during the breeding season are large sac-like organs stretching between segments two and eight and are situated above the hepatopancreas. A short oviduct leads ventrally to the female genital orifice which is situated at the base of the fifth pereiopods. Oostegites which form the brood pouch for the eggs are not present in all the females. These presumably appear after a moult, when the female has ripening eggs in the ovaries. Ovigerous females of *T. granulatus* were found during January and February from several localities. The minimum length of an ovigerous female is 36 mm, the maximum length found, 41 mm. Up to 1969, two ovigerous females of *T. granulatus* were known, from the mouth of the Schuster's River, collected in February 1937. Numerous ovigerous females have now been collected. The eggs are 1,6–1,8 mm in diameter. Barnard (1940), writing about the first two ovigerous females, states that the oostegites remain flat and that the brood pushes the sternum upwards. This was found to be true in all the later specimens. Barnard mentions that this forcing up of the sternum results in a degeneration of the females' internal organs, and he concludes 'In fact it would seem improbable that the mother could recover after the escape of the brood' (1940: 438). With this in mind, ovigerous females were injected with formalin on capture. When dissected, the alimentary canal and heart were found to be normal, only the ovaries being degenerate. It would seem probable that Barnard's conclusions were the result of imperfect preservation.

Of *T. capensis*, this is the first record of ovigerous females; several were collected from Strandfontein from November to January. The minimum length of an ovigerous female is 20 mm.

From the beginning of September (in *T. capensis*) and the beginning of October (in *T. granulatus*) the ovaries start to enlarge and egg formation commences, even before oostegites become apparent. By the end of January (*T. capensis*) or the end of February (*T. granulatus*) ovigerous females are no longer encountered. In both species it was noted that ovigerous females were only found above the high tide zone, up to 20 metres in *T. capensis*. This is probably connected with incubation of the eggs, as the sand above the high tide mark has a fairly constant and slightly higher temperature than the sand lower down the beach which is influenced by the temperature of the incoming tide.

Measurements of many individuals of *T. granulatus* and *T. capensis* from Blouberg and Strandfontein respectively, if plotted in the form of histograms (Figs 29, 30), show that there are at least four moults and possibly more in the life history of the animals. Figure 29 clearly shows four peaks of size, and if the ecdysis for the very small individuals in the brood pouch is added it seems probable that there are five moults, and that only in the final one do oostegites appear in the females.

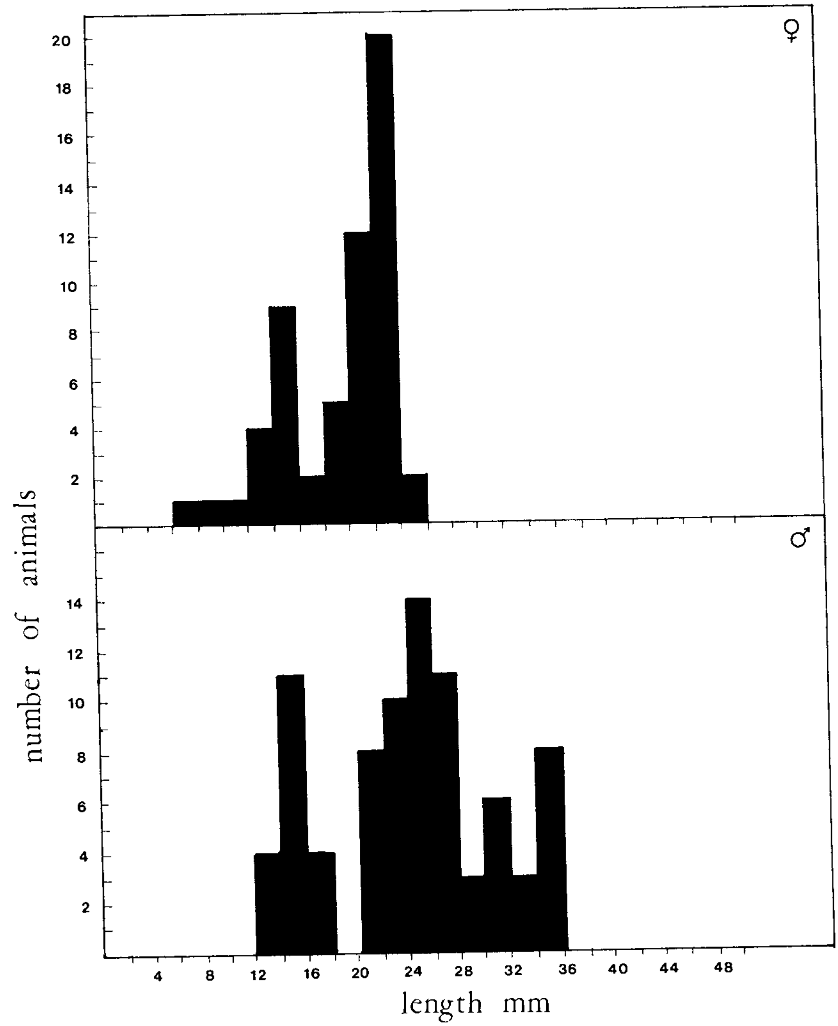

Fig. 29. *Tylos granulatus.* Histogram showing size grouping of males and females.

ASSOCIATION OF *TYLOS* WITH OTHER SPECIES

Tylos granulatus

As a nocturnal inhabitant of sandy beaches, this species would seem at first to have very little contact with other animals. On closer examination a few associations emerge, but one important factor remains unexplained. After more than two years of observation, no predator has been recorded. In the sand itself, the only possible predators could be golden moles (*Chrysochloris capensis*) which occasionally burrow along the upper beaches. Birds such as gulls (*Larus* spp.) and cormorants (*Phalacocorax* sp.) are active during the day when the

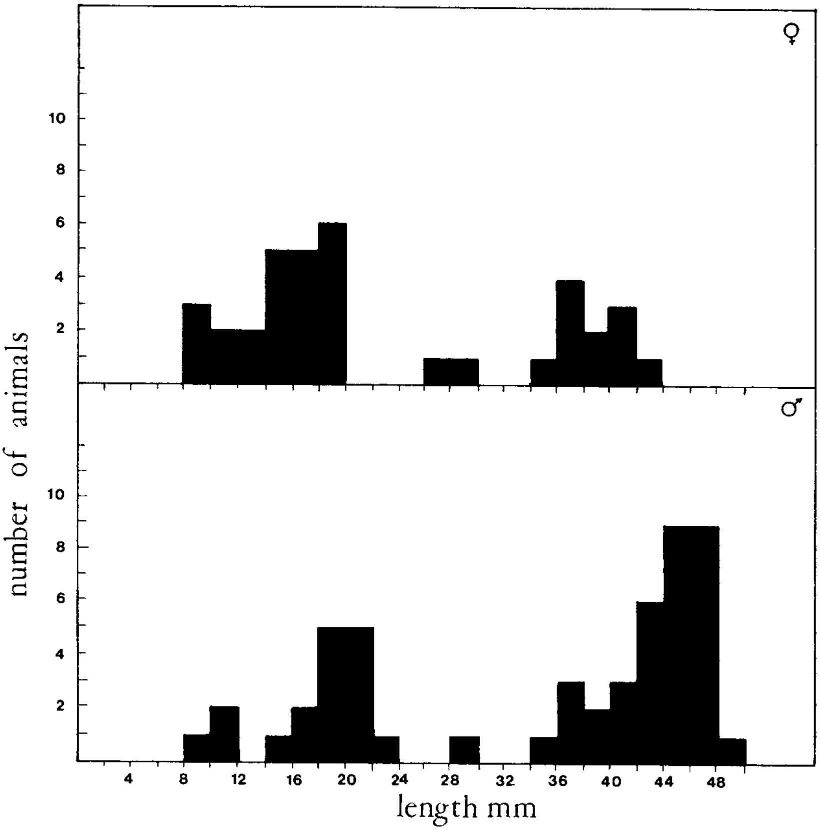

Fig. 30. *Tylos capensis.* Histogram showing size grouping of males and females.

isopods are up to 400 mm beneath the sand. Even probing in the sand is unlikely to expose any animals. It is perhaps possible that genets (*Genetta* sp.) and polecats (*Ictonyx* sp.) from the surrounding bush could prey on the animals at night. This is, however, pure speculation, no proof having been found. Perhaps this species does not have any predators at all.

COMPETITORS

Apart from the competition for space in the sand, and for food amongst the individuals of the species itself, only two food competitors have been observed. These are the amphipod *Talorchestia quadrispinosa* and the carabid beetle *Platychila pallida. Talorchestia* is often seen in great numbers around decomposing kelp, but even in great numbers these animals represent a rather unimportant competitive element, when compared with the amount of algae eaten by the isopods. *Platychila* is a well known member of the sandy beach community, and has a distribution very similar to that of *T. granulatus.* This pale beetle is about 20 mm in length, and is also nocturnal. These insects were often encountered about 150 mm below the surface of the sand when digging for *Tylos*. At night they were often seen scampering over the sand. Possessing relatively large mandibles, they are predacious, and although never seen actually eating *Tylos*, they were often seen feeding alongside the juvenile isopods on the debris lines. They were seen to feed on *Physalia* and other animal matter, and thus represent a fairly important competitive element low down on the beach where only the juvenile *Tylos* feed. Another carabid beetle often found in the sand with *Tylos* is *Acanthoscelis ruficornis*. Also a predator, fewer of these were found than of the previous beetle. *Pachyphalaria capensis*, a tenebrionid beetle, is often found with *Tylos*, scavenging mainly on algae, but does not occur in sufficient numbers to constitute an important competitor.

COMMENSALS

Barnard (1932: 218) noted the following, when dealing with *T. granulatus*: 'A minute oligochaete lives among the pleopods. It is 2,5–3,0 mm in length, whitish, with 4 bundles of straight and apically simple spines in each segment usually 3 spines in each bundle. It may be termed *Enchytraeus tylidus* n.sp.' Many specimens of this oligochaete were found on animals from all the localities listed. Samples of 10 adults and 10 juveniles (less than 20 mm in length) from Blouberg and Lambert's Bay were examined. The results are given in Table 18. From this it can be seen that almost all the adults carry these commensals, and that the juveniles are 'infected' only after they have reached a length of about 20 mm. The worm may breed beneath the pleopods as structures resembling egg cases have been found. On further investigation it was found that since Barnard's mention of the worm, it has passed unnoticed and has never appeared in the *Zoological Record*. The oligochaete has been found only on *T. granulatus* and is probably an obligative commensal, confined to this single species.

Another commensal was a tiny mite which was sometimes found between the pleopods, but more usually beneath the extensions of the fifth abdominal segment and beneath the uropods in the region of the anus, where the exoskeleton is relatively thin. No visible damage due to the commensal could be seen in any of the animals examined. From one to four mites may be present per isopod; of 25 examined, 9 carried the mites. Dr G. C. Loots (personal communication) states that the mite is an undescribed species of the genus *Veigaia*. He also notes that the members of this family usually play a predatory role in micro-habitats, especially in rich soil. This is the first record of a member of the family having been found commensal on an invertebrate. Dr Loots suggests that the mites may feed on the faeces of the isopod; this would account for their concentration in the pleon region.

Tylos capensis

As with the former species, no predator has been found for this species.

The beetles *Acanthoscelis ruficornis, Platychila pallida* and *Pachyphalaria capensis* have all been found in association with *T. capensis* in False Bay.

COMMENSALS

Mites of the same species of *Veigaia* as were found on the former species of *Tylos* were collected from specimens from Strandfontein, Breë River, and Knysna. 11% of the Knysna isopods, 8% of the Breë River, and 5% of the Strandfontein animals carried the mites.

Also found on *T. capensis* were the third larval stage of some rhabditiform nematode, but only from the Strandfontein population. The minute worms were found in numbers of up to 100 per individual, between the pleopods, and caused no apparent damage. Hyman (1951) notes that many of these nematodes are organic detritus feeders, sometimes epizootic on invertebrates.

COMPARISON OF SPECIES AND DISCUSSION

From the present study it is apparent that the two species are very similar both structurally and with regard to their behaviour. The most obvious difference is that of distribution, *T. granulatus* being strictly west coast, *T. capensis* strictly east coast, with no overlap. The difference in sea temperatures for the east and west coasts undoubtedly has an effect on the temperature of the intertidal area. The higher sea temperature of the east coast may account for the earlier breeding season of *T. capensis*. There are also obvious differences in the size of the adults of the species, ovigerous females of *T. granulatus* being almost twice the length of those of *T. capensis*. Structurally the difference between the species is small, and lies in the degree of granulation of the exoskeleton, and the development of the ventral processes of the fifth pleon segment. Other differences which have been noted are in the choice of beach and in the depth to which the adults burrow. *T. granulatus* is found only on exposed beaches and burrows to a depth of up to 400 mm, whereas *T. capensis* only goes down to about 300 mm, and may be found on both exposed as well as sheltered beaches.

Judging from the numbers especially in *T. granulatus*, this genus is very well adapted to its ecological environment. This latter—the sandy beach, poses several problems to its inhabitants involving wave action, stability of the substrate, food supply, predators, temperature/light/humidity fluctuations, tidal rhythms. By being nocturnal and by burrowing into the sand, the animals have simultaneously solved several of these problems. There are no predators on the beach at night, whereas if the animals emerged during the day they would be vulnerable (particularly the juveniles) to being preyed on by sea birds. In spite of the relatively large surface-temperature and humidity fluctuations, beneath the sand these factors remain relatively constant. Emergence at night ensures that the temperature of the surface has dropped, thereby reducing the danger of desiccation. This latter factor is also reduced as the relative humidity increases at night. Burrowing also reduces the risk of exposure to wave action.

The most important adaptation of *Tylos* is its possession of lunar rhythms. By manifesting a lunar-day rhythm closely correlated with the time of low tide, and by being nocturnal, the animals emerge during the nocturnal low tide. This gives protection from wave action. Food in the form of organic debris is washed ashore with the high tide and left stranded at the ebb. The animals can thus feed quite safely. By restricting the time of feeding to two hours, a limit is placed on the amount capable of being eaten. This is compensated for in several ways. As the animals burrow at or near the high tide mark, the time spent in searching for food is reduced. Being omnivorous and possessing all the major types of digestive enzymes, there is no great need to be very selective with regard to the type of food. The mouthparts are very efficient and the gut capacious, thus a maximum amount of food may be eaten in the time available.

The possession of a semi-lunar rhythm ensures that the animals are kept in phase with the spring tides. In this way animals may emerge on a rising tide during neaps, but never during springs. Once again the danger of being swept to sea is eliminated. To what extent the external environmental factors influence the rhythms, and to what degree they are endogenous, is difficult to assess. That the rhythms are to some extent endogenous, is demonstrated by the fact that they continue to function under constant darkness, away from the sea. Temperature would appear to have little if any influence on the rhythm. This is necessary, for, to quote Brown (1959: 1539): 'To possess adaptive significance for the organism, a considerable degree of temperature independence is needed to permit the cycles to retain their normal lengths when exposed to the natural temperature fluctuations.' It has been shown that *Uca* and *Cambarus* retain their rhythm under constant temperatures ranging from 6 to 26°C. Temperatures within two or three degrees of freezing point, however, are capable of inhibiting the rhythm, through a slowing down of the metabolic rate. Brown (1961) introduces another factor which has bearing on the maintenance of rhythm. In *Uca*, animals which are kept together in the laboratory under constant conditions exhibit rhythms with precision, but if kept separately in individual containers, they show a gradually decreasing amplitude in their rhythms. Once a separated individual is joined by another, the rhythm is restored. This social factor has not been further investigated, and remains largely unexplained. It is likely that this has some bearing on the problem of *Tylos* where, on the beach under natural conditions, the rhythms are fairly precise and are exhibited by the population as a whole rather than by the individuals, but in the laboratory where only a small portion of the population is studied, the rhythms are subject to greater variation. External light must have some controlling and supplementing effect on the rhythms involved. Thus if low tide is close to sunset, the animals would come to the surface, and only if the light intensity is low enough will they emerge. This testing of the light intensity is probably the function of the pause observed in all emerging animals. In this connection it was noted that the animals seldom emerged at the time of full moon.

The possibility also exists that the rhythms are not endogenous, and that under so-called 'constant' conditions, animals such as *Uca* are still responding to some less obvious external factor. It would seem from preliminary work carried out by Brown and his co-workers that this external factor may be correlated with barometric pressure, but is not this pressure itself.

SUMMARY

1. An introductory ecological/biological study of *Tylos granulatus* and *Tylos capensis* has been carried out.
2. Complete descriptions and synonymies for both species have been given.
3. The geographical distribution of *T. granulatus* was established as being from Cape Point to northern South West Africa, while that of *T. capensis* was from False Bay to southern Natal.
4. It was found that both species inhabit sandy beaches of varying slope, and sand of varying grain size.
5. Both species burrow in the sand around the high tide mark, moving up or down the beach as the height of the high tide moves.
6. *T. granulatus* was found to burrow to a depth of about 400 mm, *T. capensis* to a depth of about 300 mm.
7. Both species execute a helix-shaped path through the sand.
8. Entry point into the sand is marked by a low mound of sand, exit by a shallow hole.
9. Both species were found to be omnivorous, with a leaning towards an algal diet in the adult stage.
10. Food preference tests indicated that the adults and juveniles preferred animal matter to vegetable matter, and that the adults preferred dry algae to fresh.
11. The structure of the alimentary canal and associated structures were investigated, as well as the process of digestion.
12. Both species were found to be strictly nocturnal.
13. The rhythmic activity of both species was investigated. Both were found to possess a lunar-day rhythm, bringing them out of the sand at or close to low tide.
14. A semi-lunar rhythm is postulated. This would account for a switch back observed in the times of emergence. This mechanism militates against the animals' emerging at the time of high water of spring tide.
15. Oviposition and release of young was found to take place in midsummer, i.e. December to February.
16. Five moults are thought to occur during the animals' life span.
17. No predators were found for either species.
18. No important food competitors were found.
19. Both species were found to carry up to five specimens of a commensal mite per isopod.
20. *T. granulatus* adults were often found to have several specimens of a commensal oligochaete amongst the pleopods.

21. *T. capensis* from Strandfontein was found to carry rhabditiform nematode larvae amongst the pleopods.

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REFERENCES

Arcangeli, A. 1953. Precisazioni ecologiche sui generi *Ligia* Fabr. e *Tylos* Latr. (Crostacei. Isopodi terrestri). *Atti Accad. Sci., Torino* **87**: 200–212.

Barnard, K. H. 1924. Contributions to a knowledge of the fauna of South West Africa. III. Crustacea, Isopoda Terrestria. *Ann. S. Afr. Mus.* **20**: 231–236.

Barnard, K. H. 1925. The digestive canal of isopod crustaceans. *Trans R. Soc. S. Afr.* **12**: 27–36.

Barnard, K. H. 1932. Contributions to the crustacean fauna of South Africa. 11. Terrestrial Isopoda. *Ann. S. Afr. Mus.* **30**: 179–388.

Barnard, K. H. 1940. Contributions to the crustacean fauna of South Africa. XII. Further additions to the Tanaidacea, Isopoda, and Amphipoda, together with keys for the identification of the hitherto recorded marine and fresh-water species. *Ann. S. Afr. Mus.* **32**: 381–543.

Brown, A. C. 1959. The ecology of South African estuaries. Part IX: Notes on the estuary of the Orange River. *Trans R. Soc. S. Afr.* **35**: 463–473.

Brown, F. A. 1961. Physiological rhythms. *In:* Waterman, T. H. *ed. The physiology of Crustacea.* **2**: 401–430. New York, London: Academic Press.

Budde-Lund, G. 1885. *Crustacea Isopoda terrestria, per familias et genera et species.* Hauniae: Nielsen & Lydiche.

Budde-Lund, G. 1906. Die Landisopoden. *Dt. Südpol.-Exped.* **9**: 69–92.

Budde-Lund, G. 1909. Isopoda I: Land-Isopoden. *In:* Schultze, L. *Zoologische und anthropologische Ergebnisse einer Forschungsreise in westlichen und zentralen Südafrika.* **2**: 53–70. Fischer: Jena. *Denkschr. med.-naturw. Ges. Jena* **14**: 53–70.

Collinge, W. E. 1945. Note on some South African terrestrial Isopoda. *Ann. Mag. nat. Hist.* (11) **12**: 344–347.

Dollfus, A. 1895. Voyage de M. E. Simon dans l'Afrique australe. Crustacés isopodes terrestres. *Mém. Soc. zool. Fr.* **8**: 345–352.

Haughton, S. H. 1931. The late Tertiary and recent deposits of the west coast of South Africa. *Trans. geol. Soc. S. Afr.* **34**: 19–58.

HEWITT, C. G. 1907. *Ligia. L.M.B.C. Mem. typ. Br. mar. Pl. Anim.* **16**: 1–37.

HYMAN, L. H. 1951. *The Invertebrates* **3**. Acanthocephala, Aschelminthes, and Entoprocta. New York, Toronto, London: McGraw-Hill.

JACKSON, H. G. 1928. The morphology of the isopod head. Part II. The terrestrial isopods. *Proc. zool. Soc. Lond.* **1928**: 561–595.

*JORDAN, H. J. 1929. Vergleichend Physiologisches über Resorption. *In: Handbuch der normalen und pathologischen Physiologie.* **4**: 167–180. Berlin: Springer.

KRAUSS, F. 1843. *Die südafrikanischen Crustacea.* Stuttgart: Schweizerbart.

*McMURRICH, J. P. 1896. The epithelium of the so-called midgut of the terrestrial isopods. *L. Morph.* **14**: 83–108.

MATZAKIS, J. 1956. Observations éthologiques sur les *Tylos* (Isopodes Onicoides) du Rousillon. *Vie Milieu* **7**: 107–109.

MEAD, F. 1968. Observations sur l'ecologie de *Tylos latreillei* Audouin (Isopode Tylidae) et sur son comportement en milieu natural. *Vie Milieu* **19**: 345–362.

MENZIES, R. J. 1952. The occurrence of a terrestrial isopod in plankton. *Ecology* **33**: 303.

MURLIN, J. R. 1902. Absorption and secretion in the digestive system of land isopods. *Proc. Acad. nat. Sci. Philad.* **54**: 284–359.

NICHOLLS, A. G. 1930. Studies on *Ligia oceanica.* II. The processes of feeding, digestion and absorption, with a description of the foregut. *J. mar. biol. Ass. U.K.* **17**: 675–705.

PANNING, A. 1924. Isopoda. *Beitr. Kennt. Land.-u. Süsswasserfauna Dt.-SüdwAfr.* **2**: 171–201.

PARDI, L. 1955. L'orientamento diuno di *Tylos latreillei* (Aud. & Sav.). *Boll. Ist. Mus. Univ. Torino* **4**: 167–196.

SOIKA, A. G. 1954. Ecologia, sistematica, biogeographica ed evoluzione del *Tylos latreillei* Aud. (Isop. Tylidae). *Boll. Mus. civ. Stor. nat. Venezia* **7**: 63–84.

STEBBING, T. R. R. 1910. Report on the marine biology of the Sudanese Red Sea. 14. The Crustacea, Isopoda, and Tanaidacea. *J. Linn. Soc.* (Zool.) **31**: 215–230.

VANDEL, A. 1943. Essai sur l'origine, l'évolution et la classification des Oniscoidea (isopodes terrestres). *Bull. biol. Fr. Belg.* suppl. **30**: 1–136.

VANDEL, A. 1945. La répartition géographique des Oniscoidea (crustacés isopodes terrestres). *Bull. biol. Fr. Belg.* **79**: 221–272.

VANDEL, A. 1952. Le genre 'Porcellio' (crustacés, isopodes, Oniscoidea) évolution et systématique. *Mém. Mus. natn. Hist. nat., Paris* (n.s. zool.) **3**: 81–192.

VANDEL, A. 1960. Isopodes terrestres. *Faune Fr.* **64**: 1–416.

*VAN WEEL, P. B. 1955. Processes of secretion, restitution and resorption in gland of midgut of *Atya spinipes* Newport. *Physiol. Zool.* **28**: 40–54.

VONK, H. J. 1960. Digestion and metabolism. *In:* WATERMAN, T. H., *ed. Physiology of Crustacea* **1**: 291–316. New York, London: Academic Press.

*YONGE, C. M. 1924. Studies on the comparative physiology of digestion. 11. The mechanism of feeding, digestion and assimilation in *Nephrops norvegicus. Br. J. exp. Biol.* **1**: 343–389.

(* – original not seen)

TABLE 1

Collecting localities for *Tylos granulatus*

B.K. = present author U.C.T. = University of Cape Town

Locality	*Collector*
Ventura wreck site, S.W.A.	B.K.
Möwe Point, S.W.A.	B.K.
Anichab, S.W.A.	Panning, B.K.
Lüderitzbucht, S.W.A.	Budde-Lund, Panning, U.C.T., B.K.
Orange River mouth	U.C.T., B.K.
Hondeklip Bay	Barnard, U.C.T.
Groenriviermond	B.K., U.C.T.
Lambert's Bay	B.K., U.C.T.
Paternoster	B.K.
Saldanha Bay, Langebaan	Barnard, B.K., U.C.T.
Ysterfontein	B.K.
Melkboschstrand	Barnard, B.K.
Blouberg, Milnerton	Barnard, B.K.
Hout Bay	B.K., U.C.T.
Noordhoek	B.K., U.C.T.
Olifantsbosch	B.K.
Witsands Bay	B.K.

TABLE 2

Collecting localities for *Tylos capensis*

Locality	*Collector*
Simonstown	Budde-Lund
Muizenberg	Barnard, B.K.
Strandfontein	B.K.
Macassar Beach	B.K.
Somerset Strand	Barnard, Stebbing
Gordon's Bay	Stebbing
Pringle Bay	B.K.
Kleinmond	Barnard
Wilderness	Barnard
Breede River estuary	B.K.
Keurbooms River mouth	Barnard
Knysna	B.K., U.C.T.
Plettenberg Bay	Barnard, B.K.
Whitney	S.A. Museum
Port Elizabeth	B.K.
East London	S.A. Museum
Natal	Natal Museum

TABLE 3

Weight of food eaten by adult *Tylos* at single feeding session

Length (mm)	Prefeeding weight (g)	Postfeeding weight (g)	Weight eaten (g)	Volume (cc)	$\frac{\text{Wt eaten}}{\text{Body wt}} \times 100$
47	7,622	8,785	1,163	1,2	15,26
44	5,523	6,667	1,144	1,3	20,71
43	5,175	6,357	1,182	1,2	22,83
42	5,291	6,163	0,872	0,9	16,47
41	4,154	5,181	1,027	1,0	24,73
41	5,276	6,297	1,021	1,1	19,35
39	4,112	5,004	0,892	0,8	21,70
38	4,097	5,144	1,047	1,0	25,55
38	4,037	4,918	0,881	0,9	21,82
37	3,912	4,614	0,702	0,6	17,95

TABLE 4

Food list of *Tylos granulatus*

(Only substances observed to be eaten included)

Vegetable matter

Phaeophyta
Ecklonia maxima
Laminaria pallida
Macrocystis pyrifera

Chlorophyta
Bryopsis sp.
Codium fragilae capense
Enteromorpha sp.
Ulva sp.
Rhodophyta
Aristothamnion purpuriferum
Botryoglossum platycarpus
Carrodaria virgata
Carpoblepharis flaccida
Ceramium planum
Champia lumbricalis
Gigartina stiriata
Gymnogongrus dilatatus
Gymnogongrus vermicularis
Phyllemenia hieroglyphica
Plocamium cornutum
Porphyra capensis
Pterosiphonia cloiophylla
Suhria vittata

Cabbage
Onion
Orange
Watermelon
Bread

Animal matter
Haarder
Joseph shark
Nudibranchs
Gastropod egg cases
Horny branchiopod shells
Jellyfish
Portuguese Man-of-War
Red bait tests
Cormorant
Tern

Food list of *Tylos capensis*

Phaeophyta
Ecklonia maxima
Laminaria sp.
Sargassum heterophyllum
Chlorophyta
Caulerpa sp.
Codium fragilae capense
Ulva sp.
Rhodophyta
Champia compressa
Pterosiphonia cloiophylla
Suhria vittata

Sour fig leaves
Ruppia maritima
Watermelon

Cormorant
Haarder
Hydroid perisarc

TABLE 5

Food preferences of *Tylos granulatus*

31/7/68 Box	1	2	3	4	5	6	Total	Control	% Water loss
Macrocystis	—	—	1,481	—	—	—	1,481	—	—
			0,000						
			1,481						
Laminaria	1,670	—	—	—	—	1,515	2,161	1,471	
	0,000					1,024		1,433	2,6
	1,670					0,491		0,038	
Gigartina	—	—	—	—	—	1,869	0,298	1,653	
						1,571		1,494	9,6
						0,298		0,159	
Cabbage	1,096	—	—	1,129	—	—	0,111	0,908	
	1,075			1,039				0,823	9,1
	0,021			0,090				0,085	
Ulva	—	1,985	2,100	2,159	—	1,778	0,502	1,447	
		1,974	1,934	1,930		1,682		1,233	
		0,011	0,166	0,229		0,096		0,214	
Fish	2,071	2,100	1,956	2,520	2,221	2,814	12,055	3,745	
	0,000	0,880	0,000	0,000	0,000	0,747		3,677	1,8
	2,071	1,220	1,956	2,520	2,221	2,067		0,068	

Table 6

Food preferences of *Tylos granulatus*

1/8/68 Box	1	2	3	4	5	6	Total	Control	% Water loss
Macrocystis	—	—	—	—	—	—	—	—	—
Laminaria	—	—	—	—	—	—	—	—	—
Gigartina	—	—	—	—	—	—	—	—	—
Cabbage	0,895	1,198	—	—	0,640	—		1,841	1,4
	0,797	1,028			0,587		0,321	1,815	
	0,098	0,170			0,053			0,026	
Ulva	1,729	1,668	—	—	1,169	1,403		1,011	3,6
	1,619	1,460			1,005	1,265	0,510	0,964	
	0,110	0,208			0,164	0,138		0,037	
Fish	1,933	2,100	2,085	2,520	1,849	1,748		1,708	4,0
	0,793	0,897	0,436	1,414	1,520	1,237	5,938	1,639	
	1,140	1,203	1,649	1,106	0,329	0,511		0,069	

TABLE 7

Food preferences of *Tylos granulatus*

2/8/68 Box	1	2	3	4	5	6	Total	Control	% Water loss
Macrocystis	—	—	—	—	—	—	—	—	—
Laminaria	—	—	—	—	—	—	—	—	—
Gigartina	—	—	—	—	—	—	—	—	—
Cabbage	0,840	—	—	—	—	—	0,019	1,231	
	0,821							1,178	4,3
	0,019							0,053	
Ulva	—	—	—	—	—	0,834	0,123	1,230	
						0,711		1,061	
						0,123		0,169	
Fish	2,633	1,689	1,878	—	2,020	—	0,906	1,793	
	2,485	1,426	1,607		1,796			1,696	5,4
	0,148	0,263	0,271		0,224			0,097	

TABLE 8

Food preferences of *Tylos granulatus*

5/8/68 Box	1	2	3	4	5	5	Total	Control	% Water loss
Macrocystis	—	—	—	—	—	—	—	—	—
Laminaria	—	—	—	—	—	—	—	—	—
Gigartina	—	—	—	—	—	—	—	—	—
Cabbage	—	—	0,737 0,676 0,061	—	—	—	0,061	1,097 1,016 0,081	7,4
Ulva	—	—	1,883 1,698 0,185	—	—	—	0,185	1,682 1,492 0,190	11,3
Fish	1,612 1,593 0,099	—	2,230 2,215 0,015	— —	— —	— —	0,114	2,262 2,173 0,089	3,9

TABLE 9

Food preferences of *Tylos granulatus*

8/8/68 Box	1	2	3	4	5	6	Total	Control	% Water loss
Macrocystis	—	—	—	—	—	—	—	—	—
Laminaria	—	—	—	—	—	—	—	—	—
Gigartina	—	—	—	—	—	—	—	—	—
Cabbage	1,965	1,771	—	—	1,888	—	1,377	2,130	
	1,670	1,455			1,122			1,833	1,5
	0,295	0,316			0,766			0,297	
Ulva	2,067	2,339	1,534	1,900	2,252	1,625		2,254	
	1,657	1,410	1,334	0,788	0,847	1,337	4,344	2,220	13,9
	0,410	0,929	0,200	1,112	1,405	0,288		0,034	
Fish	—	—	1,810	—	—	—		2,085	
			1,791				0,019	1,944	6,7
			0,019					0,141	

TABLE 10

Dry/fresh brown alga (*Ecklonia*) preference test

Date		Box 1	Box 2	Control	Total eaten (g)
16/9/68	Dry	1,413	1,455	1,754	
		1,263	1,268	—	
		0,150	0,187	—	0,337
	Fresh	2,445	2,647	2,611	
		—	—	—	—
18/9/68	Dry	1,475	1,377	1,580	
		1,398	—	—	
		0,077	—	—	0,077
	Fresh	2,424	1,956	2,192	
		—	—	—	—
20/9/68	Dry	1,586	1,611	1,863	
		1,381	1,453	—	
		0,205	0,158	—	0,363
	Fresh	1,932	2,289	1,849	
		—	—	—	—
22/9/68	Dry	1,711	1,623	1,695	
		—	1,358	—	
		—	0,265	—	0,265
	Fresh	1,981	2,035	2,107	
		—	—	—	—
25/9/68	Dry	1,349	1,392	1,512	
		1,219	—	—	
		0,130	—	—	0,130
	Fresh	2,193	2,401	2,385	
		—	—	—	—
28/9/68	Dry	1,604	1,449	1,449	
		—	1,385		
			0,064	—	0,064
	Fresh	2,035	1,991	1,941	
		—	—	—	

TABLE 11

Food preferences of juvenile *Tylos*

15/9/68	Box 1	Box 2	Control (g)	Total eaten (g)	% Water loss (g)
Fish	0,539	0,616	0,602		
	0,495	0,488	0,599		
	0,044	0,128	0,003	0,172	4,2
Ulva	0,441	0,429	0,460		
	0,368	—	0,419		
	0,073		0,041	0,073	9,1
Plocamium	0,504	0,481	0,490		
	0,464	0,449	0,464		
	0,040	0,032	0,026	0,072	5,4
Macrocystis	0,771	0,754	0,798		
	—	—	—	—	—
Cabbage	0,681	0,703	0,665		
	—	0,642	0,611		
		0,061	0,053	0,061	8,0

TABLE 12

Food preferences of juvenile *Tylos*

17/9/68	Box 1	Box 2	Control (g)	Total eaten (g)	% Water loss (g)
Ulva	0,388	0,413	0,409		
	0,327	0,363	0,367		
	0,061	0,050	0,042	0,111	10,3
Plocamium	0,453	0,420	0,484		
	—	0,381	0,463		
		0,039	0,021	0,039	4,4
Macrocystis	0,683	0,703	0,698		
	—	—	—	—	—
Cabbage	0,535	0,613	0,550		
	—	—	—	—	—
Fish	0,477	0,522	0,492		
	0,369	0,496	0,474		
	0,108	0,026	0,018	0,134	3,8

TABLE 13

Food preferences of Juvenile *Tylos*

19/9/68	Box 1	Box 2	Control (g)	Total eaten (g)	% Water loss (g)
Ulva	0,325	0,369	0,410		
		0,309	0,388		
		0,060	0,032	0,060	8,0
Plocamium	0,503	0,486	0,471		
	0,420	0,445	0,449		
	0,083	0,041	0,022	0,124	4,8
Macrocystis	0,705	0,720	0,684		
Cabbage	0,489	0,532	0,516		
	0,471	—	0,477		
	0,018		0,039	0,018	7,5
Fish	0,613	0,586	0,590		
	0,526	0,484	0,570		
	0,087	0,102	0,020	0,189	3,4

TABLE 14

Food preferences of juvenile *Tylos*

22/9/68	Box 1	Box 2	Control (g)	Total eaten (g)	% Water loss (g)
Ulva	0,440	0,419	0,398		
	0,397	0,401	0,360		
	0,043	0,018	0,038	0,061	9,6
Plocamium	0,621	0,570	0,597		
	—	0,529	0,574		
		0,041	0,023	0,041	3,9
Macrocystis	0,580	0,694	0,689		
Cabbage	0,388	0,412	0,370		
	—	0,389	0,340		
		0,023	0,030	0,023	8,3
Fish	0,664	0,580	0,683		
	0,570	0,529	0,652		
	0,094	0,061	0,031	0,155	4,5

Table 15

Data for 36 consecutive days observation of *Tylos granulatus*

Date	Time emerged	Time returned	Hours out	Hours between returns
1/2/68	2050	2230	2,50	
2	2100	2300	2,00	24,67
3	2115	2330	2,50	24,50
4	2210	0015	2,25	24,83
5	2230	0030	2,00	24,16
6	2315	0130	2,25	24,83
8	0005	0210	2,00	24,67
9	0040	0230	2,00	24,33
10	0125	0305	1,50	24,58
11	0200	0330	1,50	24,41
12	0245	0420	1,50	24,83
13	0300	0330	0,50	23,16
	2045	2220	1,50	18,50
14	2045	2215	1,50	23,91
15	2045	2230	2,00	24,25
16	2045	2240	2,00	24,16
17	2045	2240	2,00	24,00
18	2045	2250	2,00	24,16
19	2030	2310	2,50	24,33
20	2150	2350	2,00	24,67
21	2200	0015	2,25	24,41
22	2245	0110	2,50	24,91
23	2340	0210	2,25	25,00
25	0020	0040	0,34	22,50
	2030	2230	2,00	21,83
26	2040	2310	2,50	24,67
27	2100	2240	1,75	23,50
28	2120	2315	2,00	24,58
29	2120	2345	2,25	24,50
1/3/68	2130	0020	2,70	24,58
2	2230	0100	2,50	24,67
3	2300	0130	2,50	24,50
5	0010	0210	2,00	24,67
6	0015	0215	2,00	24,08
7	0030	0220	2,00	24,08
8	0045	0250	2,00	24,50

TABLE 16

Data for observations on darkroom animals of *T. granulatus*

Date	Time emerged	Time returned	Individuals
24/2/68	2120–2145	0030	8 animals
25	2115–2215	2320	3 animals
26	—	—	
27	—	—	
28	0030	?	3 animals
29	0005	0150–2000	1, 2, 3, 6, 7, 11, 15, 16, 18, 21, 20
1/3/68	2250–2330	0040–0115	2, 3, 6, 8, 9, 7, 10, 11, 13, 15, 18, 19
2	—	—	
3	0045–1000	0156–0210	4, 6, 8, 10, 11, 13, 15, 18, 20
4	2040–2200	2230–2330	2, 4, 5, 6, 7, 10, 11, 12, 13, 14, 15, 17, 18, 19, 20
5	—	—	
6	0100	?	
7	0250	0315	2
8	0105	0125–0130	2, 3, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 17, 18, 20, 21, 22

TABLE 17

Data for observations on *Tylos capensis*

Date	Time emerged	Time returned	Hours out	Low tide
15/1/70	0210	0335	1,40	0247
16/1/70	0315	0430	1,25	0416
19/1/70	2040	2255	2,25	2011
25/1/70	2245	0115	2,50	2304
28/1/70	2320	0150	2,50	0002
31/1/70	0140	0340	2,00	0222
4/2/70	2040	2325	2,75	2029
9/2/70	2305	0120	2,25	2343
11/2/70	2340	0210	2,50	0018
19/2/70	2025	2255	2,50	2055
27/2/70	2340	0215	2,25	0004
5/3/70	2005	2240	2,60	2012
6/3/70	2025	2310	2,75	2051
9/3/70	2220	0035	2,25	2238

TABLE 18

Numbers of oligochaete *Enchytraeus tylidus* present on adult and juvenile *Tylos granulatus*

Locality	Number of oligochaetes per individual *Tylos*							
		0	1	2	3	4	5	6
Blouberg	No. adults	—	2	5	—	1	1	1
	No. juveniles	9	1	—	—	—	—	—
Lambert's Bay	No. adults	—	2	2	3	2	1	—
	No. juveniles	7	2	—	1	—	—	—

INSTRUCTIONS TO AUTHORS

Based on

CONFERENCE OF BIOLOGICAL EDITORS, COMMITTEE ON FORM AND STYLE. 1960.
Style manual for biological journals. Washington: American Institute of Biological Sciences.

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Examples (note capitalization and punctuation)

BULLOUGH, W. S. 1960. *Practical invertebrate anatomy.* 2nd ed. London: Macmillan.

FISCHER, P.-H. 1948. Données sur la résistance et de le vitalité des mollusques. *J. Conch., Paris* **88**: 100–140.

FISCHER, P.-H., DUVAL, M. & RAFFY, A. 1933. Etudes sur les échanges respiratoires des littorines. *Archs Zool. exp. gén.* **74**: 627–634.

KOHN, A. J. 1960*a*. Ecological notes on *Conus* (Mollusca: Gastropoda) in the Trincomalee region of Ceylon. *Ann. Mag. nat. Hist.* (13) **2**: 309–320.

KOHN, A. J. 1960*b*. Spawning behaviour, egg masses and larval development in *Conus* from the Indian Ocean. *Bull. Bingham oceanogr. Coll.* **17** (4): 1–51.

THIELE, J. 1910. Mollusca: B. Polyplacophora, Gastropoda marina, Bivalvia. *In:* SCHULTZE, L. *Zoologische und anthropologische Ergebnisse einer Forschungsreise im westlichen und zentralen Süd-Afrika.* **4**: 269–270. Jena: Fischer. *Denkschr. med.-naturw. Ges. Jena* **16**: 269–270.

ZOOLOGICAL NOMENCLATURE

To be governed by the rulings of the latest *International code of zoological nomenclature* issued by the International Trust for Zoological Nomenclature (particularly articles 22 and 51). The Harvard system of reference to be used in the synonymy lists, with the full references incorporated in the list at the end of the article, and not given in contracted form in the synonymy list.

Example

Scalaria coronata Lamarck, 1816: pl. 451, figs 5 *a, b*; Liste: 11. Turton, 1932: 80.