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The Grapsidae and Ocypodidae (Decapoda: Brachyura) of Tanzania

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(With 8 figures in the text)

Twenty-nine species of the Grapsidae and 15 species of the Ocypodidae were collected from the littoral zone in the area around Dar es Salaam. Nine species of Grapsidae and three of Ocypodidae were new records for the East African area, bringing the total of recorded species for the region to 35 and 26 respectively. The distribution of these crabs indicates a very limited endemism in the western Indian Ocean, with the majority of species forming an attenuated extension of the abundant Indo/West Pacific brachyuran fauna.

The habitat preference of each species is described. Within each subfamily there is a relative uniformity in general habitat preference, mode of life and manner of feeding. The species of each subfamily are then separated by substrate choice and preferred level on the shore. The greatest numbers of species occur in the most diverse habitats—the creek mangrove, the coastal mangrove and the reef flat.

Contents

Introduction

A collection of littoral crabs of the families Grapsidae and Ocypodidae was made in Tanzania between November 1970 and May 1972, predominantly from a series of locations near to Dar es Salaam. Over 2500 crabs were collected from 182 stations, which embraced the full range of accessible habitats. This collection was subsequently deposited in the British Museum (Natural History), under the Register Numbers 1973: 22–99 and 1973: 574–656.

This paper reports upon the above collection, in the first part on the taxonomy and zoogeography of the species collected, and in the second part on their ecology. The nomenclature used by Guinot (1967) in her survey of the Brachyura of the Western Indian Ocean has largely been followed, but the subgeneric divisions proposed for *Macrophthalmus* (Barnes, 1967) and *Uca* (Bott, 1954) have been included, and the genera of the Sesarminae follow the extensive revisions by Serène & Soh (1970) and Serène (personal communication).

I have not followed the recent and exhaustive subdivision of *Uca* by Bott (1973), as it is too early to judge whether this will be generally accepted.

I am grateful to the various specialists who assisted me with the identification of material, and who so freely advised me on the taxonomic complexities—Dr R. S. K. Barnes, Dr A. Crosnier, Dr D. Guinot and Dr R. Serène. I owe great thanks to the Director and Trustees of the British Museum (Natural History) who defrayed the cost of shipping the collection from Dar es Salaam, and who permitted me to examine the material in their care. The staff of the Crustacean Section were, as always, of invaluable help during my studies there.

Taxonomy and distribution

An area comprising the mainland coast of Kenya and Tanzania and the inshore islands such as Pemba and Zanzibar was selected for the purpose of comparing the present collection with earlier records, and this region will be referred to as the East African area. It is not suggested that this area, which extends from 1°N to 11°S, is a faunistic unit, but in fact no additional species are recorded until Hafun (11°N) and Inhambane (24°S) are reached. This may well be in part due to the vagaries of collecting, but it indicates that the East African area lies in the middle of a relatively uniform tropical zone extending from the entrance to the Gulf of Aden to the tropic of Capricorn. At Hafun, in northern Somalia near the entrance to the Gulf of Aden, species characteristic of the Red Sea and Persian Gulf are encountered such as *Ocypode saratan* (Forskål, 1775). South of Inhambane elements of the south African fauna appear, such as *Paracleistostoma fossulum* Barnard, 1955 and *Parasesarma catenata* (Ortman, 1897). Previous records of the Grapsidae and Ocypodidae from the East African area are widely scattered in the early literature, the more important of which include A. Milne Edwards (1868), Hilgendorf (1869), Pfeffer (1889), Ortmann (1893), Doflein (1904) and Lenz (1905, 1910, 1912). These records are conveniently summarized in the recent reviews by Banerjee (1960), Barnard (1950), Barnes (1970), Crosnier (1965) and Guinot (1967): they are all included in Table I, as Ban, Bar, Bs, C and G respectively, which also gives details of the species found in the present collection. Ignoring synonyms, the previous records list 30 species of Grapsidae and 15 species of Ocypodidae from the East African area. Twenty and 12 of these species respectively featured in the current collection, together with nine grapsids and three ocypodids new to the area.

Consideration will first be given to the 13 species which have been previously recorded from the area, but which were not encountered during this investigation, in order to judge what credence should be given to these earlier records. Some of them are unsupported by specimens, and have not subsequently been confirmed.

Species 1–2. *Geograpsus grayi* and *Geograpsus crinipes*. These are large crabs of essentially terrestrial habits, and if present they should certainly have featured in the collection. *Geograpsus grayi* is reliably recorded from Madagascar (Crosnier, 1965), Aldabra (Grubb, 1971), and from Zanzibar and various small Indian Ocean islands (Banerjee, 1960): I have confirmed the identity of the specimen from Zanzibar in the British Museum (Nat. Hist.). *Geograpsus crinipes* occurs on the Amirantes, Aldabra, Cosmoledo and Chagos, based on material in the British Museum (Nat. Hist.) where the samples from the last three locations were all misidentified as *Geograpsus stormi*: it seems certain that the *Geograpsus stormi* which Grubb (1971) recorded as common on Aldabra was in fact *Geograpsus crinipes*. There are no confirmed records of *G. crinipes* from

TABLE I

The Grapsidae and Ocypodidae of the East African area, including those recorded by previous workers and those newly found in the present collection. The reviews which summarise earlier records are abbreviated thus: Barnerjee, 1960 (Ban), Barnard, 1950 (Bar), Barnes, 1970 (Bs), Crosnier, 1965 (C), Guinot, 1967 (G). Some of the synonyms which have been used previously are given in parentheses beneath the currently accepted name

	Source	Whether found in present collection
Family Grapsidae		
Subfamily Grapsinae		
Geograpsus Stimpson, 1858		
G. crinipes Dana, 1851	Ban, G	
G. grayi (H. Milne Edwards, 1835)	Ban, C, G	
G. stormi de Man, 1895	Ban, G, Bar	yes
Grapsus Lamarck, 1801		
G. albolineatus Lamarck, 1818	Ban, G	
(*G. strigosus* Herbst, 1799)	Bar	
G. fourmanoiri Crosnier, 1965	C, G	yes
G. intermedius de Man, 1888	Ban, G	
G. longitarsus Dana, 1851	Ban, G	
G. tenuicrustatus (Herbst, 1783)	Ban, C. G.	yes
(*G. maculatus* Hoffman, 1874)	Bar	
Metopograpsus H. Milne Edwards, 1853		
M. messor (Forskål, 1775)	Ban, C, G, Bar	yes
M. oceanicus (Jacquinot, 1852)	Ban, G	yes
M. thukuhar (Owen, 1839)	Ban, C	yes
Pachygrapsus Randall, 1839		
P. minutus A. Milne Edwards, 1837	C, G	yes
?*P. planifrons* de Man, 1888	new record	yes
Ilyograpsus Barnard, 1955		
I. paludicola (Rathbun, 1909)	C, G	yes
Subfamily Varuninae		
Thalassograpsus Tweedie, 1950		
T. harpax (Hilgendorf, 1893)	new record	yes
Pseudograpsus H. Milne Edwards, 1837		
P. elongatus (A. Milne Edwards, 1873)	G	yes
Ptychognathus Stimpson, 1858		
P. onyx Alcock, 1900	G	
Varuna H. Milne Edwards, 1830		
V. litterata (Fabricius, 1798)	Bar, C, G	
V. tomentosa Pfeffer, 1889	G	
Subfamily Sesarminae		
Helice de Haan, 1833		
H. leachi Hess, 1865	C, G	yes
Metasesarma H. Milne Edwards, 1853		
M. rousseauxi H. Milne Edwards, 1853	C, G	
Nanosesarma Tweedie, 1950		
N. (*Nanosesarma*) *minutum* (de Man, 1887)	new record	yes

TABLE I *cont.*

	Source	Whether found in present collection
Selatium Serène & Soh, 1970		
S. brocki (de Man, 1887)	new record	yes
S. elongatum (A. Milne Edwards, 1869)	C, G	yes
Sarmatium Dana, 1851		
S. crassum Dana, 1851	new record	yes
Neosarmatium Serène & Soh, 1970		
N. smithi (H. Milne Edwards, 1853)	Bar, C, G	yes
N. meinerti (de Man, 1887)	Bar, C, G	yes
Sesarmops Serène & Soh, 1970		
S. impressum (H. Milne Edwards, 1837)	C, G	yes
Chiromanthes Gistel, 1848		
C. guttatum (A. Milne Edwards, 1869)	Bar, C, G	yes
(*Sesarma bidens* (de Haan, 1835))	G	
Holometopus H. Milne Edwards, 1865		
H. eulimine (de Man, 1898)	new record	yes
?*H. obesus* (Dana, 1851)	new record	yes
H. ortmanni (Crosnier, 1965)	C	yes
(*Sesarma erythrodactylum africanum* Ortmann, 1894)	C, G	
Parasesarma de Man, 1890		
P. leptosomum (Hilgendorf, 1896)	G	yes
P. plicatum (Latreille, 1806)	Bar, C, G	
Subfamily Plagusiinae		
Plagusia Latreille, 1804		
P. immaculata Lamarck, 1818	new record	yes
P. tuberculata Lamarck, 1818	Bar, C, G	yes
Percnon Gistel, 1848		
P. abbreviatum (Dana, 1851)	new record	yes
P. guinotae Crosnier, 1965	C, G	yes
P. planissimum (Herbst, 1804)	C, G	yes
Family Ocypodidae		
Subfamily Ocypodinae		
Ocypode Weber, 1795		
O. ceratophthalmus (Pallas, 1872)	Bar, C, G	yes
O. cordimanus Desmarest, 1825	Bar, C, G	
O. kuhli de Haan, 1835	Bar, G	yes
Uca Leach, 1814		
U. (*Uca*) *dussumieri* (H. Milne Edwards, 1852)	G	
U. (*Uca*) *tetragonon* (Herbst, 1790)	C, G	yes
U. (*Uca*) *urvillei* (H. Milne Edwards, 1852)	Bar, C, G	yes
U. (*Uca*) *vocans vocans* (Linnaeus, 1758)		yes
(*U.* (*Uca*) *marionis marionis* (Desmarest, 1823))	C, G	
U. (*Uca*) *vocans excisa* (Nobili, 1906)		yes
(*U.* (*Uca*) *marionis excisa* Nobili, 1906)	C, G	
U. (*Minuca*) *annulipes* (H. Milne Edwards, 1852)	Bar, C, G	yes
U. (*Minuca*) *gaimardi* (H. Milne Edwards, 1852)	C	yes
U. (*Minuca*) *inversa* (Hoffman, 1877)	Bar, C, G	yes

TABLE I *cont.*

	Source	Whether found in present collection
Subfamily Scopimerinae		
Dotilla Stimpson, 1858		
D. fenestrata Hilgendorf, 1869	Bar, C, G	yes
Subfamily Macrophthalminae		
Macrophthalmus Desmarest, 1823		
M. (Macrophthalmus) grandidieri A. Milne Edwards, 1867	Bar, C, G	yes
(*M. hilgendorfi* Tesch, 1915)	Bar, G	
M. (Macrophthalmus) milloti Crosnier, 1965	new record	yes
M. (Macrophthalmus) parvimanus Guerin, 1834	new record	yes
M. (Macrophthalmus) telescopicus (Owen, 1839)	Bs	
M. (Macrophthalmus) cf. verreauxi H. Milne Edwards, 1848	new record	yes
M. (Mareotis) depressus Ruppel, 1830	C	yes
M. (Mopsocarcinus) bosci Audouin & Savigny, 1825	Bar, Bs, C, G	yes

the East African area. Thus both species are common on the various small islands of the western Indian Ocean, where as semi-terrestrial species they are favoured by the less competitive insular environment. Neither are regular inhabitants of the more rigorous mainland habitat though, and the only confirmed report from the East African area is the single specimen of *Geograpsus grayi* from Zanzibar.

Species 3–5. *Grapsus* spp. Five species of this genus have previously been recorded from East Africa, but taxonomically this is a very difficult group. Since there is the added complication that the commonest species—*Grapsus fourmanoiri*—has only recently been described (Crosnier, 1965) it is inadvisable to accept any of the earlier records without subsequent confirmation. Banerjee (1960) was unable to locate any material of *Grapsus longitarsus* or *Grapsus intermedius* emanating from East Africa, or indeed even from the western Indian Ocean, and their presence in this area is most unlikely. He did identify material as *Grapsus albolineatus*, but Crosnier (1965) subsequently redetermined all such material from East and South Africa as *Grapsus fourmanoiri*. It is fairly certain that only the two species of this prominent genus collected in the present study do occur in East Africa.

Species 6–7. *Varuna* spp. *Varuna litterata* is a common and widespread species, and there is a specimen from Pemba in the British Museum (Nat. Hist.). *Varuna tomentosa* was initially described from Zanzibar (Pfeffer, 1889). Both species obviously occur in the East African area, and the reason neither featured in the present collection is that they are typical of estuarine areas, an environment which it was not possible to examine.

Species 8–10. These are small species from the mangrove, an environment which is notoriously difficult to sample comprehensively, and it is scarcely surprising that a few such crabs escaped collection. *Metasesarma rousseauxi* was initially described from Zanzibar, conclusively proving its presence, and there is no reason to doubt the records of *Parasesarma plicatum* and *Ptychognathus onyx*.

Species 11. *Ocypode cordimanus*. This is a large readily identified species, but I did not find it, and neither did Jones (1972) in the course of a detailed study of *Ocypode* at Watamu, Kenya. Crosnier (1965) has confirmed that *Ocypode cordimanus* occurs in Madagascar, and there is material in the British Museum (Nat. Hist.) from Aldabra and the Seychelles. In the same collection is material from Dar es Salaam and Mombasa assigned to *O. cordimanus*, but this proved to consist of only very small specimens which were not capable of positive determination, and in any case seemed more correctly referrable to *O. kuhli*. Thus like *Geograpsus crinipes* this species is common on the smaller Indian Ocean islands, but its presence in East Africa is not confirmed.

Species 12. *Uca dussumieri*. This was recorded by Pfeffer (1889), but has not been found since in East Africa, and I can locate no material from the area. It is very similar to *Uca urvillei*, which is common throughout the area, but which was not recorded by Pfeffer. The likely explanation is that he misidentified *U. urvillei* as *U. dussumieri*.

Species 13. *Macrophthalmus telescopicus*. The taxonomy of the group of species with very long eyestalks, to which *M. telescopicus* belongs, has only recently been clarified by Serène (1973*c*). Nevertheless this record is correct, for the specimen from Zanzibar on which it is based (B.M. Reg. No. 1964.7.1.109) is clearly still *M. telescopicus* under its new and more restrictive definition.

A few other points concerning the taxonomy of earlier records can be mentioned here. The present collections of *Uca vocans* reinforce the views of Crosnier (1965) and Serène (1973*a*) that there is no validity in the formal taxonomic separation of *Uca vocans* forma *vocans* and *Uca vocans* forma *excisa*. The only difference between them is in the shape of the male major chela, and both forms were found together in each population sampled. They are merely dimorphic males of a single species, a phenomenon already known in other crabs (Hartnoll, 1963; Vernet-Cornubert, 1958). *Uca annulipes* has sometimes been regarded as a form of *Uca lactea* (de Haan, 1835), with the typical *Uca lactea* in Australia, *Uca lactea* forma *annulipes* in East Africa, and intermediate forms between (Macnae, 1968). Generally *Uca annulipes* has been regarded as a distinct species (Serène, 1973*b*, *d*).

Following from the above discussions, it emerges that of the 30 grapsids and 15 ocypodids previously recorded from East Africa only 26 and 13 respectively can be considered reliable. To these must be added those species first recorded from the area as a result of the present collection, to give a total for the area of 35 species of Grapsidae and 16 species of Ocypodidae (Table II). The 12 newly found species are listed below, together with the nearest locations from which they have previously been recorded.

Pachygrapsus planifrons	Coetivy Island
Thalassograpsus harpax	Red Sea
Holometopus eulimine	Madagascar, South Africa
Holometopus obesus	Molucca Islands
Selatium brocki	Andaman Islands
Sarmatium crassum	Madagascar, South Africa
Nanosesarma minutum	Madagascar
Plagusia immaculata	Madagascar
Percnon abbreviatum	Madagascar, Iles Glorieuses
Macrophthalmus milloti	Madagascar
Macrophthalmus cf. verreauxi	Madagascar, Red Sea
Macrophthalmus parvimanus	Seychelles, Madagascar

TABLE II

Species list of the Grapsidae and Ocypodidae in the East African area

Grapsidae	
Geograpsus grayi	*Selatium brocki*
Geograpsus stormi	*Selatium elongatum*
Grapsus tenuicrustatus	*Sarmatium crassum*
Grapsus fourmanoiri	*Neosarmatium smithi*
Metopograpsus messor	*Neosarmatium meinerti*
Metopograpsus oceanicus	*Sesarmops impressum*
Metopograpsus thukuhar	*Chiromanthes guttatum*
Pachygrapsus minutus	*Holometopus eulimine*
?*Pachygrapsus planifrons*	?*Holometopus obesus*
Ilyograpsus paludicola	*Holometopus ortmanni*
Thalassograpsus harpax	*Parasesarma leptosomum*
Pseudograpsus elongatus	*Parasesarma plicatum*
Ptychognathus onyx	*Plagusia immaculata*
Varuna litterata	*Plagusia tuberculata*
Varuna tomentosa	*Percnon abbreviatum*
Helice leachi	*Percnon guinotae*
Metasesarma rousseauxi	*Percnon planissimum*
Nanosesarma minutum	
Ocypodidae	
Ocypode ceratophthalmus	*Dotilla fenestrata*
Ocypode kuhli	*Macrophthalmus grandidieri*
Uca annulipes	*Macrophthalmus milloti*
Uca gaimardi	*Macrophthalmus telescopicus*
Uca inversa	*Macrophthalmus cf. verreauxi*
Uca vocans	*Macrophthalmus parvimanus*
Uca tetragonon	*Macrophthalmus depressus*
Uca urvillei	*Macrophthalmus bosci*

In most cases their discovery in East Africa involves a relatively small extension to their known range, for nine of them were already known from the islands of the western Indian Ocean or the mainland of South Africa, and one from the Red Sea. The only major extensions are for *Holometopus obesus* and *Selatium brocki*, not previously known westwards of the Molucca and Andaman Islands respectively. The identifications of *Pachygrapsus planifrons* and *Holometopus obesus* must be regarded as provisional. *Holometopus eulimine* has only recently been separated from the much more abundant *Holometopus ortmanni* by Crosnier (1965). All the earlier records from East Africa were attributed to *Holometopus eulimine sensu lato*, and it has not been possible to substantiate any of them as being the genuine *H. eulimine*, although they may in part have been based upon material of that species. The taxonomy of the species of *Macrophthalmus* with long eyestalks has been confused, and previously all material from the western Indian Ocean has been assigned to the single species *M. telescopicus*. Crosnier (1965) described a second species—*M. milloti*—and more recently Serène (1973*c*) has shown that in fact there are three closely allied species in the group, *M. telescopicus*, *M. milloti* and a third species, which he then

designated *M. verreauxi*. It now transpires that this third species will need further revision (Serène, pers. comm.), but for convenience I will refer to it here as *Macrophthalmus cf. verreauxi*. All three species are now known to occur in the East African area, *M. telescopicus* by virtue of the specimen in the British Museum (Nat. Hist.) already mentioned, and the other two by their representation in the present collection. These taxonomic problems probably explain why some of the 12 species were not previously recorded in East Africa, and others are small and uncommon, but there remain several large species in readily accessible habitats which have not been collected until now—*Macrophthalmus parvimanus*, *Percnon abbreviatum*, *Plagusia immaculata* and *Selatium brocki*.

It is neither appropriate nor possible to enter into a full discussion of the zoogeographic affinities of the East African grapsids and ocypodids, but a few points merit consideration. Out of the 51 species from the area only three, *Macrophthalmus telescopicus*, *Metasesarma rousseauxi* and *Varuna tomentosa*, have been recorded only from Zanzibar. Thus for these families there is no major difference between the faunas of Zanzibar and the mainland, which is only to be expected when they are separated by a mere 40 km of shallow water. The three species are rare, and their discovery on Zanzibar reflects only the more intensive collecting on that small island. In contrast Madagascar is separated from East Africa by 400 km of deep water, and there are appreciable faunal differences as shown below.

	E. African species	Common spp.	Madagascan spp.
Grapsidae	35	27	41
Ocypodidae	16	14	20

There are ten species found in East Africa but absent from Madagascar: only one of these is endemic to the east coast of Africa, the other nine also occurring in the central or eastern Indian Ocean or having an Indo-Pacific distribution. Of the 20 species in Madagascar but not in East Africa five are endemic, but the other 15 are found also in the eastern Indian Ocean or are Indo-Pacific. The general pattern is of a spread from regions to the east, most species reaching both East Africa and Madagascar, a few East Africa only, and rather more reaching Madagascar only. This westward spread is made clear when the general distribution of the 51 East African species is analysed.

East Africa only	1 sp	9 spp restricted to western Indian Ocean
East Africa and Madagascar	5 spp	
East Africa, Madagascar & Red Sea	3 spp	
East Africa to east Indian Ocean	4 spp	42 spp extending to the east
East Africa to Indonesia	4 spp	
East Africa to west Pacific	34 spp	

There is only a limited endemism in the extreme west of the Indian Ocean, most of the Grapsidae and Ocypodidae being an attenuated extension of the abundant Indo/west Pacific fauna. The fact that the mainland fauna is more attenuated than that of Madagascar suggests that the majority of species have reached the area as larvae carried by the South Equatorial current (Fig. 1), rather than by spreading along the coasts of India and the Persian Gulf. The South Equatorial current flows westwards from Indonesia and meets the African

coast just north of Madagascar at about 10°S, where it divides to flow northwards as the East African coastal current and southwards as the Mozambique current between Madagascar and the mainland. It thus washes the shores of both Madagascar and the African mainland.

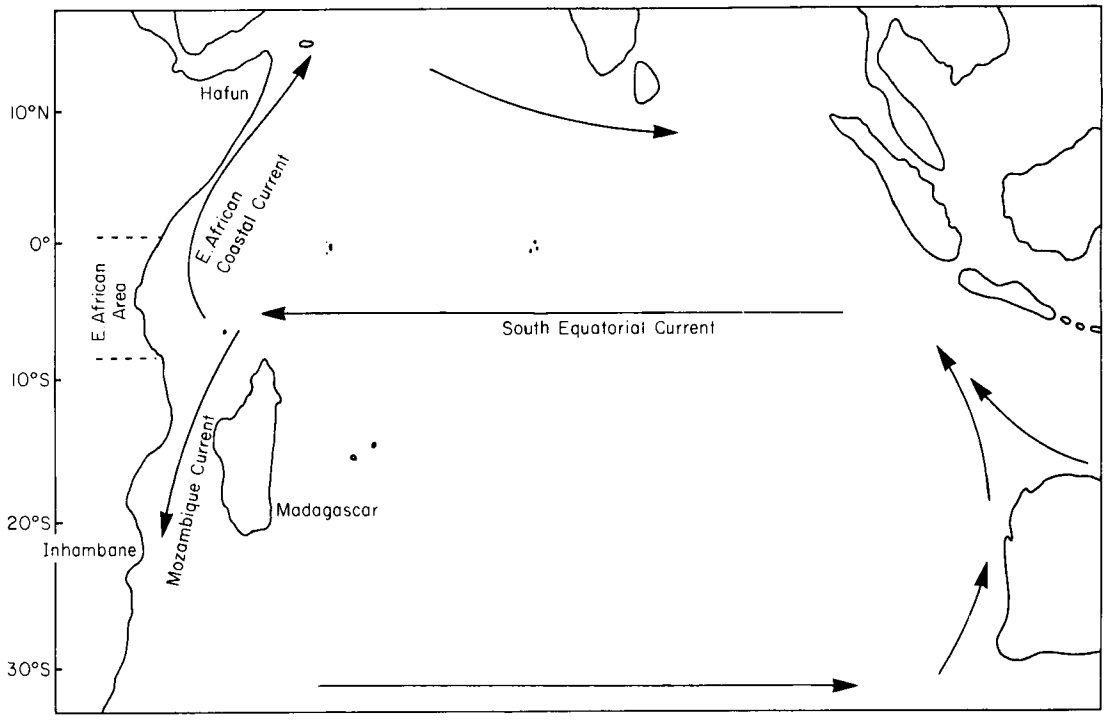

FIG. 1. The Indian Ocean to show the surface currents during the southern winter (after Newell, 1957).

Ecology

The literature dealing with the taxonomy of the East African grapsids and ocypodids has already been reviewed above, but these papers provide little information on the ecology of the crabs. The ecological studies from the area deal only with the genera *Ocypode* (Jones, 1972) and *Dotilla* (Hartnoll, 1973), but for comparative purposes there are several valuable reports from adjacent regions of the western Indian Ocean. These cover muddy substrates in Madagascar (Derijard, 1966), terrestrial habitats on Aldabra Island (Grubb, 1971), rocky shores on Inhaca Island (Kalk, 1958), sandy shores on Inhaca (Macnae & Kalk, 1962*a*), mangrove shores on Inhaca (Macnae & Kalk, 1962*b*) and the general Indo-Pacific mangrove environment (Macnae, 1968).

The environment

A brief description of the various habitats will form a useful preface to the accounts of the environmental preferences and relative abundance of the crabs. There is an extensive intertidal zone, as is to be expected when the tides have a mean spring range of 3·3 m and a mean neap range of 1·1 m. The tides are basically semi-diurnal, but with a diurnal inequality which becomes increasingly marked at periods of neap tides. The shores in the

Dar es Salaam area can be divided into four basic categories—rocky, exposed to semi-exposed sand, sheltered muddy-sand or mud with coastal mangrove, and very sheltered with creek mangrove. A typical shore of each type is described below, but intermediates occur, as do atypical areas with components from two or more types.

Rocky shore (Fig. 2).

This is almost universally comprised of raised coral limestone in the Dar es Salaam area, with a rather stereotyped shore profile which perhaps limits the abundance of certain species. Generally a vertical or heavily undercut cliff extends from mean low water neaps to above extreme high water, with the rock surface greatly eroded. Below mean low water

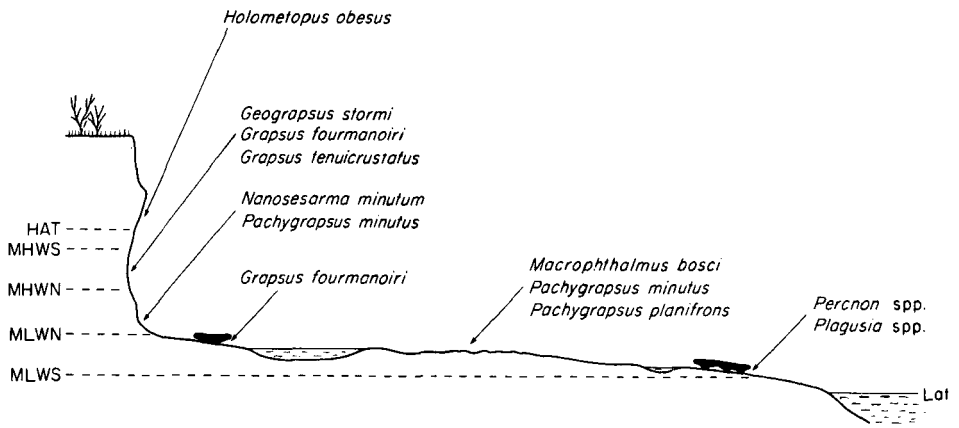

FIG. 2. A diagrammatic section of a typical rocky shore in the Dar es Salaam area with the vertical scale greatly exaggerated. The habitats of the Grapsidae and Ocypodidae are indicated.

neaps a gently sloping reef flat, often several hundred metres wide, extends to extreme low water. This flat provides a complex mosaic of habitats, with an expanse of mainly dead coral interspersed with patches of sand, algae and sea grass, and a scattering of pools and coral boulders. Less common are shores of beachrock, which usually present a more regular profile and provide rather different conditions, especially on the lower shore.

Sandy shore (Fig. 3)

There is a steep slope from the top of the shore down to about mean tide level, with a substrate of coarse well drained sand. At the foot of the slope there is commonly a water-logged area with a growth of sea grass, and seaward of this a broad expanse of gently sloping sand. This sand is of a finer grade than on the steep slope, but it still drains well at low tide, and on this drained sand the sea grass re-appears just below mean low water neaps.

Coastal mangrove shore (Fig. 4)

There is a relatively steep slope of well drained sand from the top of the shore down to mean tide level, but of a finer grade than in the corresponding area on an exposed sandy shore. The coastal mangrove covers a relatively limited zone from just above mean tide level down to slightly above mean low water neaps. The landward half of this zone is

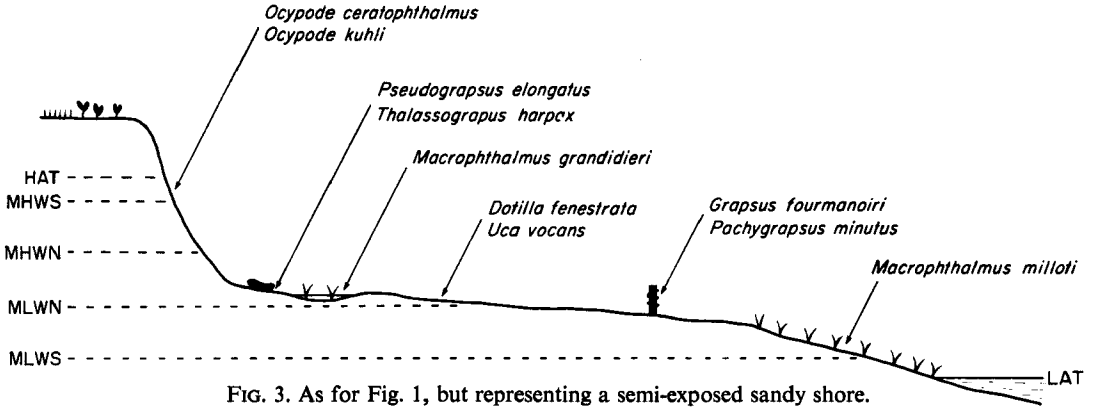

FIG. 3. As for Fig. 1, but representing a semi-exposed sandy shore.

dominated by *Avicennia marina*, the seaward side by *Sonneratia alba*, and the substrate becomes increasingly muddy towards the sea. Beyond the mangrove an expanse of gently sloping muddy-sand or mud stretches to low water, well drained in some parts but water-logged and with pools of standing water in others.

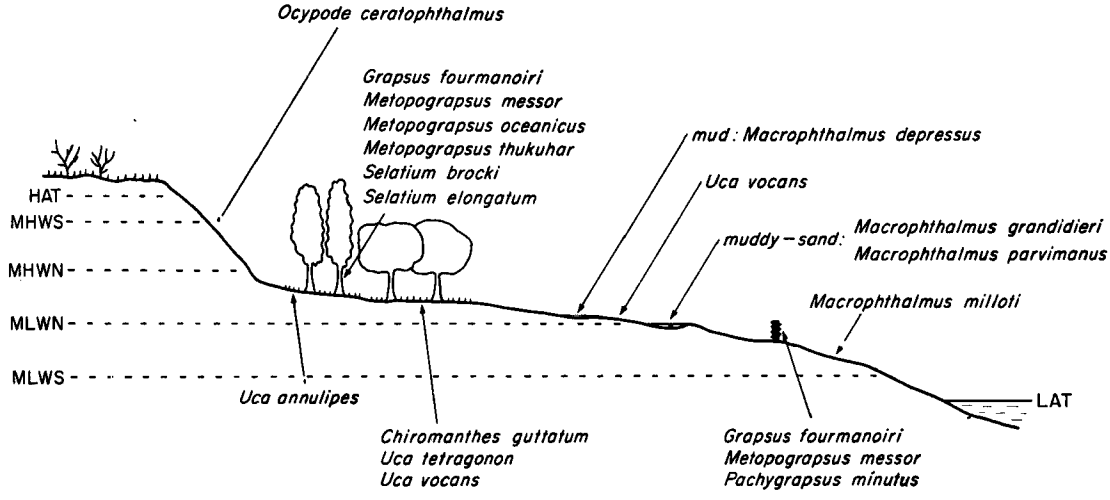

FIG. 4. As for Fig. 1, but to show a sheltered shore of mud and muddy-sand with a belt of coastal mangrove.

Creek mangrove (Fig. 5)

Very sheltered inlets develop a complex creek mangrove community. It is difficult to subdivide this and to relate it to precise tidal levels, but a series of zones have been defined grading from those at higher levels with firmer and drier conditions to those at lower levels with wetter and muddier substrates.

(a) The fringe of terrestrial scrub and grassland, at about highest tide level.

(b) A firm dry sand flat from the level of highest tides down to mean high water springs. This is bare except for the succulents *Arthrocnemum indicum* and *Salicornia pachystachia*, and stunted bushes of *Avicennia marina* on the lower side.

(c) Just below mean high water springs an *Avicennia* zone with open stands of pure *Avicennia marina* and a substrate which is firm when drained at low water.

(d) *Ceriops* dominated zone, occupying most of the interior of the mangrove seaward of the *Avicennia*. A muddy but moderately well drained substrate, with dense *Ceriops tagal* and some *Bruguiera gymnorhiza* and *Xylocarpus granatum*.

(e) *Rhizophora* dominated zone with nearly pure *Rhizophora mucronata*, forming a mosaic with the *Ceriops* zone and occupying the poorly drained muddy areas.

(f) The "mixed mangrove" community, extending from the *Ceriops*/*Rhizophora* mosaic down to the edges of the creeks at about mean low water neaps. All six mangrove species occur here, and *Sonneratia alba* is limited to this zone. The substrate is soft and muddy, but is locally firmer on the banks of the creeks.

(g) The creeks, with standing water and muddy bottoms. *Rhizophora* and some other mangroves grow in the creeks.

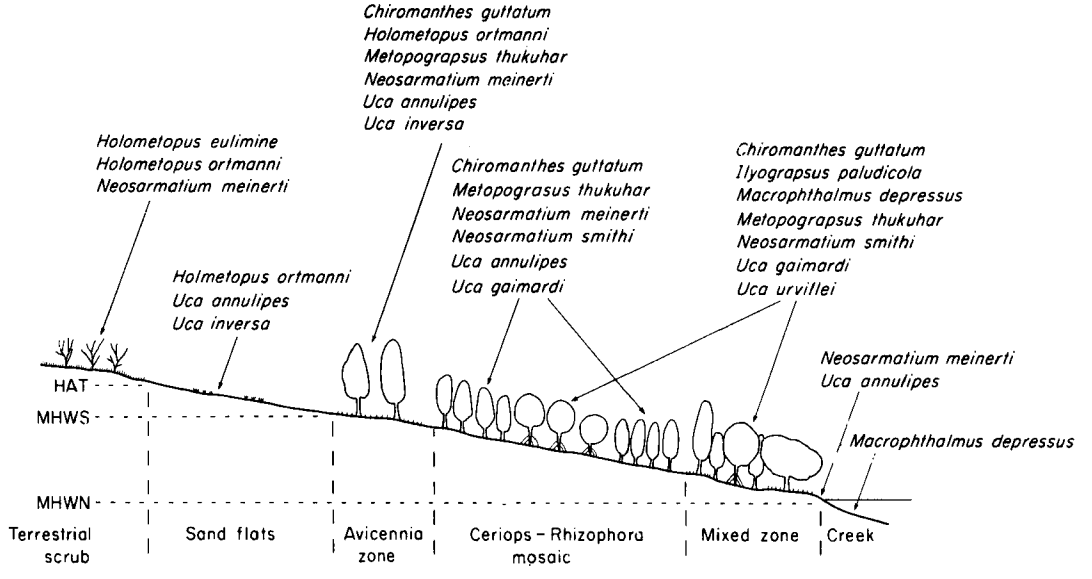

FIG. 5. As for Fig. 1, but a very sheltered shore with creek mangrove.

In addition collections were made from a miscellany of pilings, pipe lines and fish traps, which constituted outposts of hard substrate on otherwise soft shores. They had a characteristic fauna quite different from that of their surroundings. Areas under fresh water influence were also examined, including the mouths of small permanent streams and of larger seasonal watercourses. Unfortunately no large permanent river estuaries were accessible.

Habitat preference

Details are given below of the habitat preferences observed for each species in the Dar es Salaam area. Relevant observations from studies in other areas are discussed where appropriate.

Grapsus tenuicrustatus. On steep cliffs, usually between mean low water neaps and mean high water springs, but extending beyond this range in favourable conditions. Active by day, but very agile and retreats quickly into crevices if disturbed. On Aldabra it was seen running around among the *Casuarina* needles inland from the top of the cliff (Grubb, 1971).

Grapsus fourmanoiri. It is found on cliffs together with *G. tenuicrustatus*, but in addition it occurs on boulders on the reef flat, on pilings, and on trees and stones in the coastal mangrove belt. At Inhaca it was observed to be characteristic of quieter water than *G. tenuicrustatus* (Kalk, 1958).

Geograpsus stormi. On cliffs, but always well concealed under overhangs or in caves or crevices, and probably foraging nocturnally. Of similar habits in Madagascar (Fourmanoir, 1954), and also in Mauritius where Baissac, Lubet & Michel (1962) record it (as *G. lividus*) from damp crevices in the upper part of exposed rocky shores. In contrast a number of reports ascribe a much more terrestrial habit to this species on Aldabra Island (Grubb, 1971; Macnae, 1971; Taylor, 1971), but it is probable that all of these reports refer to *Geograpsus crinipes* (see section on taxonomy), a species which is elsewhere (Banerjee, 1960) seen to be of markedly terrestrial habits.

Metopograpsus messor. A scarce species, occurring in the coastal mangrove where it climbs trees or shelters beneath roots and stones. Kalk (1958) records it from quite exposed rocky shores on Inhaca, but there may be some confusion with *M. oceanicus*.

Metopograpsus oceanicus. Of similar habits to *M. messor*, but common in the coastal mangrove, especially in the seaward *Sonneratia* zone. Some occasional specimens extend onto semi-exposed rocky shores.

Metopograpsus thukuhar. In the landward side of the coastal mangrove belt, and generally distributed through the creek mangrove, where it is found on or under roots and logs. Also frequents pilings, etc. in sheltered locations.

Pachygrapsus minutus. A small and abundant species, with a widespread distribution on hard substrates where the surface is such as to provide adequate shelter, either by erosion or by the epibiota. The empty shells of dead barnacles are particularly favoured.

Pachygrapsus planifrons. Rare, the only two specimens found coming from slabs of eroded dead coral on one of the outer reefs (Maziwe Island).

Ilyograpsus paludicola. From soft mud in creek mangrove. Probably not as rare as its scarcity in the collection suggests, for it is a very small species.

Thalassograpsus harpax and *Pseudograpsus elongatus*. These species were found together in a single station. This was beneath stones on poorly drained coarse sand at mean tide level.

Helice leachi. The single specimen was found amongst *Salicornia* at the landward side of an area of creek mangrove.

Nanosesarma minutum. A small cryptic species found from MLWN downwards. In crevices on cliffs or from algal covered stones, always in sheltered areas with thin muddy deposits on the rock.

Selatium brocki. A large active crab in the coastal mangrove, either climbing the trees or sheltering beneath stones.

Selatium elongatum. Occurs in the coastal mangrove with the same habits as *S. brocki*, and one specimen was recovered from a *Sonneratia* tree in the creek mangrove. Fourmanoir

(1954) records it from pools at HWS in Madagascar, but I did not observe it in such a situation.

Sarmatium crassum. An uncommon species in creek mangrove, where specimens were collected from the *Ceriops* and mixed zones.

Neosarmatium meinerti. A large burrowing species. Common in the *Avicennia* and *Ceriops* zones of creek mangrove, and extending into the Rhizophora zone. Also common in areas of strong freshwater influence.

Neosarmatium smithi. Similar to *N. meinerti*, but even more shy in its habits, and with a preference for the muddier regions of the creek mangrove. Occurs in the *Ceriops* zone, but commonest in the *Rhizophora* zone. At Inhaca both *N. meinerti* and *N. smithi* are apparently restricted to a narrow zone on the landward side of the *Avicennia* (Macnae, 1968).

Sesarmops impressum. Two specimens only, from the *Ceriops* and mixed zones of the creek mangrove.

Chiromanthes guttatum. Occasionally found in coastal mangrove, but very abundant in the creek mangrove. Here it is rare in the landward fringe, but common from the *Avicennia* through to the mixed zone. It is a particularly bold species, quickly emerging from its burrows after disturbance and wandering freely over the substrate.

Holometopus eulimine. A rare species which burrows in mud and sand near high water. It occurs in creek mangrove, but is most common where there is a marked freshwater influence. It displays a similar preference for estuarine conditions in Mozambique (Macnae, 1968).

Holometopus ortmanni. Another burrower, very common in creek mangrove from the landward fringe into the *Avicennia* zone. It also extends into areas of freshwater influence.

Holometopus obesus. The single specimen occurred in a crevice above HAT on an exposed cliff.

Parasesarma leptosomum. One specimen from coastal mangrove, and a few from the *Ceriops* and mixed zones of creek mangrove.

Plagusia spp. In crevices or under overhangs on the middle and lower levels of rocky shores. They are strong swimmers (cf. Hartnoll, 1971) and one specimen was found on the outboard motor of a moored boat. Kalk (1958) recorded *Plagusia depressa* in Inhaca on exposed rocky shores from MHWN upwards.

Percnon spp. The three species occupy similar habitats on the reef flat, either below stones or slabs of dead coral or in pools. On Inhaca *Percnon planissimum* occurs on exposed rocky shores from MLWS down (Kalk, 1958). In the Seychelles *Percnon* is found on cast up coral boulders on the algal ridge area of the reef (Taylor, 1968), and in Madagascar near low water on very exposed reefs or rocky shores (Plante, 1965).

Ocypode ceratophthalmus. Burrows in the steep sandy slope on the upper shore in conditions ranging from exposed shores to sheltered beaches with coastal mangrove. Occasional specimens even occur on the bare sand flat on the landward side of the creek mangrove.

Ocypode kuhli. Burrows in the steep sandy slope at the top of exposed shores. On Kenyan shores *O. kuhli* prefers more exposed shores than *O. ceratophthalmus*, and also inhabits a higher level on the shore (Jones, 1972). They show similar habitat preferences at Inhaca (Macnae & Kalk, 1962*a*). *O. kuhli* is absent on Aldabra, but *O. cordimanus* is present at a

higher level than *O. ceratophthalmus* (Grubb, 1971). Perhaps *O. kuhli* and *O. cordimanus* are ecologically very similar species which are not found sympatrically.

Uca annulipes. In coastal mangrove it occurs in the drier landward part of the mangrove proper, and along the base of the sand slope on the landward side. In creek mangrove it is abundant in the *Avicennia* and *Ceriops* zones, and also occurs in the landward sand flat and the deeper zones of the mangrove. It extends into areas with strong freshwater influence.

Uca gaimardi. Confined to the wetter parts of the creek mangrove, being common in the *Ceriops*, *Rhizophora* and mixed zones where it replaces *U. annulipes.*

Uca inversa. Abundant on the bare sand flat forming the landward part of the creek mangrove, with a few specimens extending into the *Avicennia* zone.

Uca vocans. This species of *Uca* is the most tolerant of wave action. It occurs mainly between MTL and MLWN: small numbers occur on sheltered sandy shores, and their abundance increases as the substrate becomes muddier. In coastal mangrove it occurs on the flats to the seaward of the mangrove, and within the mangrove itself, but becomes very scarce towards the landward edge. *Uca vocans vocans* and *Uca vocans excisa* show no ecological distinction, reinforcing the view that they are dimorphic males of a single species.

Uca tetragonon. Found in coastal mangrove, slightly higher on the shore than *U. vocans*, and with a preference for very stony areas.

Uca urvillei. Restricted to the wetter areas of the creek mangrove. It occurs in the *Ceriops* zone, but becomes abundant only in the *Rhizophora* and mixed zones, especially beside the creeks.

Dotilla fenestrata. On exposed sandy shores, with a few specimens extending onto muddy sand: occurs between MLWN and MHWN where the surface is well drained. Full details of its distribution have been given elsewhere (Hartnoll, 1973).

Macrophthalmus grandidieri. From about MTL down to MLWN, on muddy sand and mud where the surface does not drain completely.

Macrophthalmus parvimanus. A similar distribution to *M. grandidieri*, but less abundant and favouring slightly muddier conditions.

Macrophthalmus milloti. Restricted to the lower shore from ELWS to MLWN. Prefers muddy sand, but a few specimens are found on sand and mud.

Macrophthalmus cf. verreauxi. This was only separated from the more abundant *M. milloti* long after the collections were made. It occurs within the same general distribution as *M. milloti*, but its precise limits are not known.

Macrophthalmus depressus. On muddy shores to the seaward side of coastal mangrove. In soft mud in the *Rhizophora* and mixed areas of creek mangrove, and in the beds of the drainage channels. At Inhaca it occurs in similar situations, but also on the bare sand to the landward of the *Avicennia*: there it feeds at high tide, but remains buried at low tide (Macnae & Kalk, 1962*b*).

Macrophthalmus bosci. Usually on hard substrates, either eroded surfaces on the reef flat or on pieces of stone or coral lying on soft shores. It either shelters in eroded hollows

or hides beneath the stones. Occasionally specimens found burrowing in well drained areas of sand or muddy sand.

By and large each of the subfamilies of the Grapsidae and Ocypodidae shows a relative uniformity in its general habitat preference, mode of life and manner of feeding, although there are insufficient data to permit such generalization in the case of the Varuninae. These characteristics tend to differentiate the subfamilies ecologically, and within the subfamilies there is a finer ecological distinction of the species by detailed habitat preference and preferred shore level.

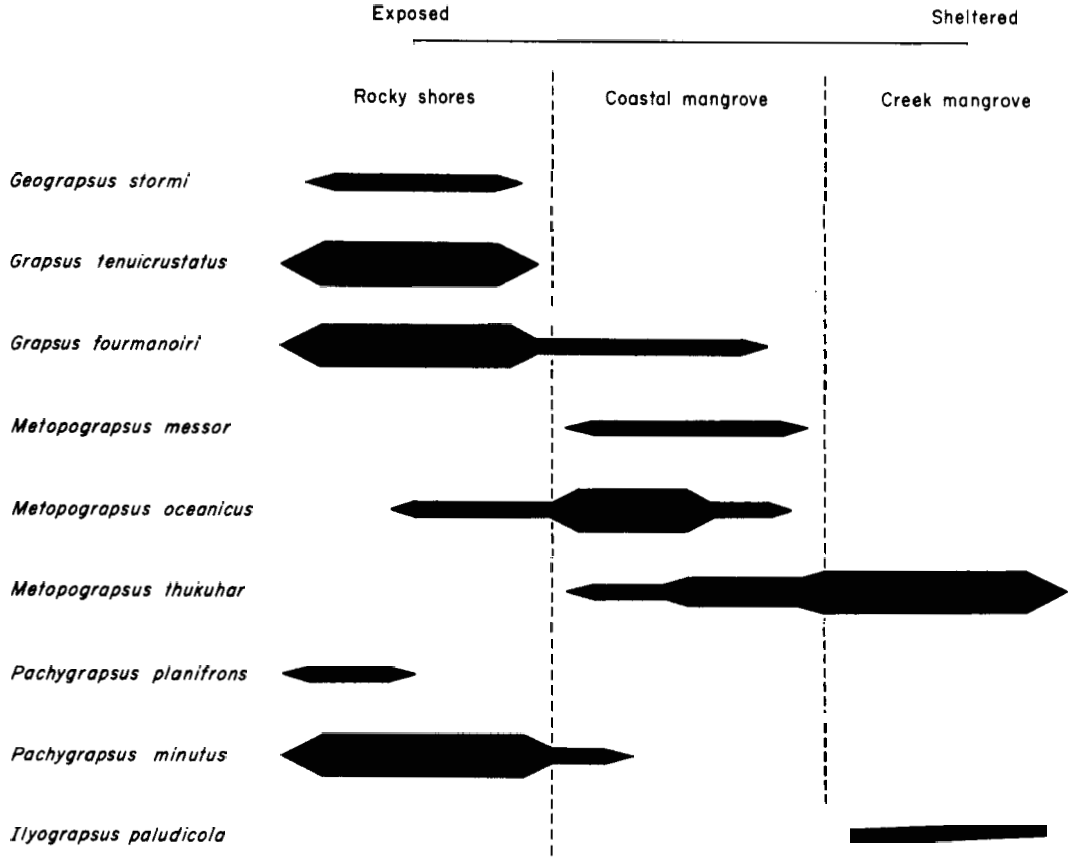

FIG. 6. A diagrammatic representation of the distribution of the Tanzanian Grapsinae in relation to wave exposure. The thickness of the line indicates the relative abundance.

The Grapsinae are essentially active crabs associated with hard substrates, rapid movers and good climbers. They do not burrow, but take shelter in crevices, under stones or amongst roots. The habits of *Ilyograpsus* are not known in any detail, but within the remaining genera *Pachygrapsus* is separated ecologically from the others by its very small size. This enables it to use shelter unsuited to the larger crabs, and it is additionally restricted to lower levels on the shore. The main distinction between the larger *Grapsus* and *Metopograpsus* is by their tolerance of wave action, the former being characteristic of exposed and the latter of sheltered shores. Figure 6 illustrates the distribution of the species of

this subfamily in relation to the exposure/shelter gradient. From this *Metopograpsus oceanicus* and *M. messor* appear to be close competitors, with the former distinctly dominant in East Africa. In Madagascar *M. oceanicus* is absent, and *M. messor* is abundant and fills the vacant niche. *M. messor* similarly has a wide and common distribution in the Seychelles (Taylor, 1968).

The Sesarminae are basically burrowers in soft substrates with omnivorous feeding habits, although some species are partially microphagous deposit feeders. There are several deviants from this general pattern. *Selatium* is a climbing genus, found either in mangrove trees or beneath stones near their bases, and is ecologically closer to the Grapsinae than the rest of the Sesarminae. *Nanosesarma* is a small cryptic form found on hard substrates in sheltered areas, where it replaces *Pachygrapsus* which is found in similar situations in more exposed areas. *Holometopus obesus*, if the habitat of the single specimen is typical, is anomalous for the genus by inhabiting rocky cliffs. The remainder of the subfamily are typical burrowers, or at least ground dwellers on soft substrates, and all inhabit the sheltered mangrove environment. The common species are separated on the one hand by size and on the other by tidal level. *Neosarmatium* is a large burrowing genus of relatively shy habits and strong territorial behaviour: *N. meinerti* is dominant in the upper part of the mangrove, *N. smithi* in the lower portion. A second group is made up of smaller crabs of bolder freely wandering habits with a loose attachment to their burrows. This is represented by *Holometopus ortmanni* in the landward section and by *Chiromanthes guttatum* through the body of the mangrove.

The Plagusiinae are active crabs inhabiting exposed rocky shores. They are restricted to the middle and lower parts of the shore, and are thus complementary to the large Grapsinae which occupy the upper parts. *Plagusia* prefers crevices and overhangs on the middle shore, *Percnon* to shelter beneath boulders on the lower shore.

The Ocypodidae are all burrowers in soft substrates, with the exception of *Macrophthalmus bosci* which is a cryptic resident on hard surfaces. The Ocypodidae are differentiated from the Sesarminae by their feeding method, for the latter are basically omnivorous scavengers while the former are selective deposit feeders, although *Ocypode* is in part macrophagous. Within the Ocypodidae the main ecological division again depends basically on feeding habits. *Ocypode*, *Uca* and *Dotilla* feed upon drained surface deposits by forming pseudofaecal pellets and so usually inhabit the drier areas. *Macrophthalmus* feeds where there is standing water, and so burrows in the wetter parts of the shore. Within each of these divisions the species are further discriminated by their preference for grade of deposit and tidal level (Fig. 7).

Relative abundance

Over 2500 crabs were collected from 182 stations. In each case the habitat was noted and the number of each species recorded, and this has enabled a rough analysis of the relative abundance of the various species in the different habitats. To facilitate this the stations were partitioned amongst ten major habitats, which represent the major facies of the various shores described earlier. These ten are:

1. Steep cliffs, extending from about MLWN to above HAT.
2. Reef flats, a broad gently sloping area from MLWN downwards.
3. Steeply sloping sand from MTL upwards.

TABLE

The numbers of each species collected in each of

	Rocky cliffs			Reef flats			Sandy slope			Sand flat			Muddy sand		
	A	B	C	A	B	C	A	B	C	A	B	C	A	B	C
Geograpsus stormi	7	100	6												
Grapsus fourmanoiri	58	52	52	23	21	15									
Grapsus tenuicrustatus	38	100	34												
Metopograpsus messor															
Metopograpsus oceanicus				2	4	1									
Metopograpsus thukuhar															
Pachygrapsus minutus	1	1	1	90	86	57				1*	1	<1			
?Pachygrapsus planifrons				2	100	1									
Ilyograpsus paludicola															
Thalassograpsus harpax										2*	100	<1			
Pseudograpsus elongatus										10*	100	2			
Helice leachi															
Nanosesarma minutum	6	55	5										1*	9	<1
Selatium brocki															
Selatium elongatum															
Sarmatium crassum															
Neosarmatium meinerti															
Neosarmatium smithi															
Sesarmops impressum															
Chiromanthes guttatum															
Holometopus eulimine															
?Holometopus obesus	1	100	1												
Holometopus ortmanni															
Parasesarma leptosomum															
Plagusia immaculata				1	100	1									
Plagusia tuberculata				3	100	2									
Percnon abbreviatum				1	100	1									
Percnon guinotae				6	100	4									
Percnon planissimum				6	100	4									
Ocypode ceratophthalmus							78	97	56						
Ocypode kuhli				1	2	1	50	98	36						
Uca annulipes															
Uca gaimardi															
Uca inversa															
Uca vocans										6	3	2	80	38	29
Uca tetragonon															
Uca urvillei															
Dotilla fenestrata							12	3	9	314	89	92	26	7	9
Macrophthalmus grandidieri										1	1	<1	106	92	38
Macrophthalmus parvimanus													14	58	5
Macrophthalmus milloti										1	2	<1	43	93	16
Macrophthalmus depressus													1	3	<1
Macrophthalmus bosci	1	3	1	24	60	15				9	23	3	5	13	2
Total crabs in habitat	112			159			140			344			276		

* Specimens associated with hard material lying on the soft substrate.

III

ten major habitats. For further details see text

Mud			Coastal mangrove			Creek mangrove			Pilings etc.			F.W. influence			Total no. of specimens
A	B	C	A	B	C	A	B	C	A	B	C	A	B	C	
															7
			6	5	2				25	22	50				112
															38
			7	100	3										7
			53	96	22										55
			9	24	4	16	43	2	12	32	24				37
									13	12	26				105
															2
						1	100	<1							1
															2
															10
						1	100	<1							1
4*	36	6													11
			6	100	2										6
			14	93	6	1	7	<1							15
						2	100	<1							2
						20	27	2				54	73	62	74
						5	100	<1							5
						2	100	<1							2
			7	2	3	294	98	28							301
						2	40	<1				3	60	3	5
															1
						240	91	23				25	9	29	265
			1	12	<1	7	88	1							8
															1
															3
															1
															6
															6
						2	2	<1				1	1	1	81
															51
			26	9	11	251	90	24				3	1	3	280
						30	100	3							30
						49	100	5							49
32	15	46	90	43	37										208
			21	100	9										21
						104	100	10							104
															352
9	5	13	1	1	<1										117
8	33	12	2	8	1										24
2	4	3													46
14	38	20	1	3	<1	21	57	2							37
			1	3	<1										40
69			245			1048			50			86			2529

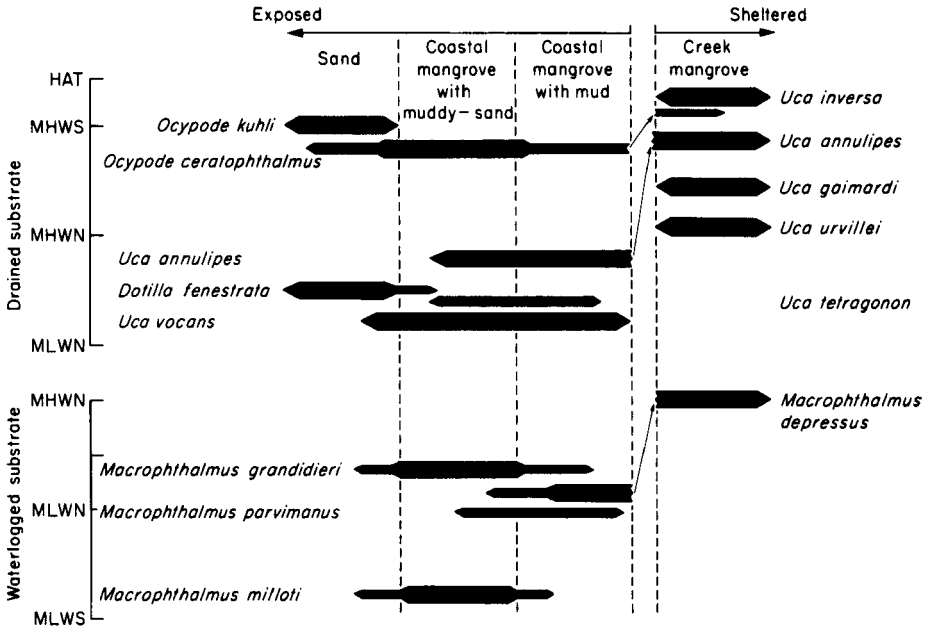

FIG. 7. Diagrammatic representation of the distribution of the Tanzanian Ocypodidae. Species characteristic of drained and waterlogged surfaces are separated, and the distribution of each is shown in relation to wave exposure and tidal level. The thickness of the line indicates relative abundance.

4. Sand flats, from MTL downwards.
5. Muddy-sand flats.
6. Mud flats.
7. Coastal mangrove, limited to the part of the shore occupied by the mangrove itself.
8. Creek mangrove.
9. Pilings, pipe lines, fish trap poles, etc.
10. Areas with marked freshwater influence.

The 182 samples were partitioned amongst these ten habitats, and the results are expressed in Table III so as to show the following for each species: in column A, the number of specimens collected in each habitat. In column B, this number expressed as a percentage of the total specimens of that species collected from all habitats. In column C, this same number expressed as a percentage of the total specimens of all species collected from that habitat. This gives a general survey of the distribution and abundance of each species, but it must be accepted with several reservations. Not all the habitats were sampled with equal effort, and some are in any case much easier to sample efficiently than others—the interior of the mangrove is particularly difficult. Nor was the sampling always random, for special efforts were often made to collect the rarer species. There were also great differences in the ease with which different species were collected. Thus *Dotilla fenestrata* was easily collected in large numbers from its shallow burrows in well drained sand, whereas *Neosarmatium smithi*, although common, was seldom extracted from its burrows in the muddy interior of the mangrove. There are wide differences between the number of

species in the different habitats, with the creek mangrove (18 species), coastal mangrove (15 species) and reef flat (11 species) having the greatest diversity. This is in keeping with their ecological complexity, for they offer a much wider range of niches than other more uniform environments such as the flats of sand and mud. The various species also differ in the range of habitats in which they were found. Most are fairly restricted, for 32 species occurred in only one or two of the ten habitats, but seven occurred in three, four (*Grapsus fourmanoiri*, *Uca vocans*, *Macrophthalmus grandidieri* and *Macrophthalmus depressus*) in four, and *Macrophthalmus bosci* in five. The particular versatility of *Macrophthalmus bosci* is because it can not only inhabit eroded hard substrates, but is also able to burrow into sand and muddy sand.

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Appendix

A key to the females of **Uca** *in East Africa*

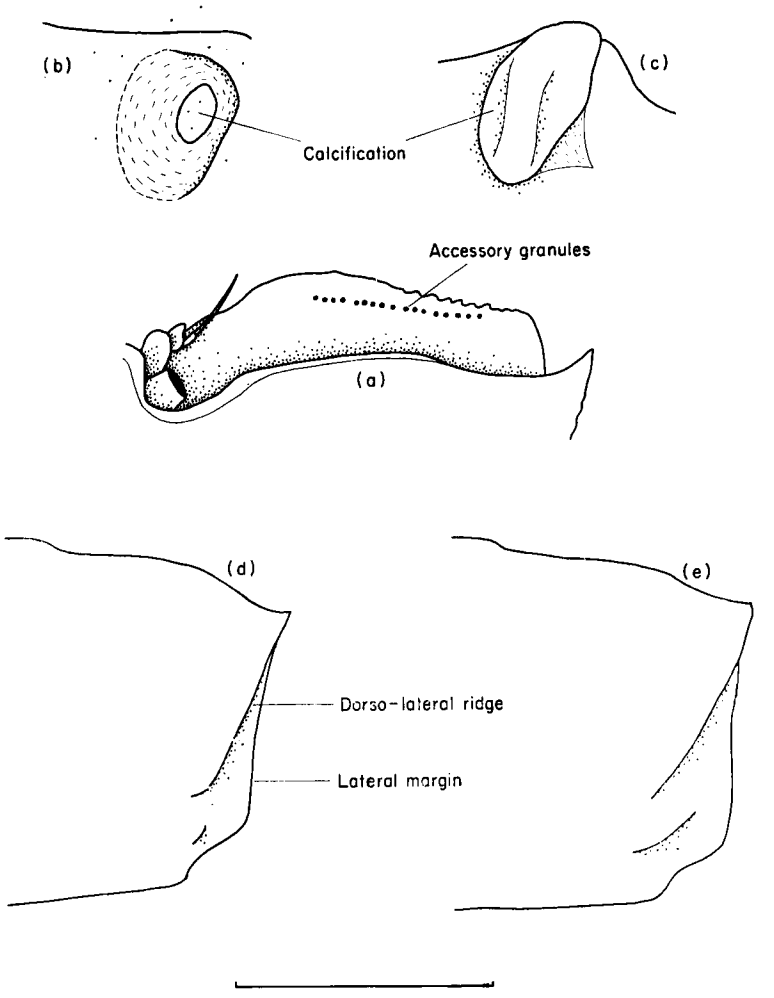

FIG. 8. (a) *Uca urvillei*, dorsal view of right orbit of female with eyestalk cut at base. (b) *Uca tetragonon*, vulva of right side. (c) *Uca vocans*, vulva of right side. (d) *Uca annulipes*, right side of carapace of female. (e) *Uca inversa*, right side of carapace of female. Scale line represents 5 mm for (a), (d) and (e), 1 mm for (b) and (c).

The males of *Uca* are for the most part easily distinguished from each other, and most keys to the genus rely upon features of the major cheliped of the male. Thus the males of East African *Uca* are readily identified by the excellent keys in Crosnier (1956) and Serène (1973*b*), but these keys are not applicable to females. The following key enables the females to be easily identified, except in the case of *U. annulipes* and *U. inversa* where only very minor differences could be found.

1. Front narrow (Subgenus *Uca*) 2
– Front broad (Subgenus *Minuca*) 4
2. Lower border of orbit with a prominent row of accessory granules (Fig. 8(a)) .. .. *Uca urvillei*
– No row of accessory granules 3

3. Post-orbital width less than 15 times width of narrowest region of front. Vulva closed by a flexible membrane bearing a small calcification (Fig. 8(b)) .. .. *Uca tetragonon*
– Post-orbital width more than 18 times width of narrowest region of front. Vulva closed by a large projecting calcified operculum which is normally immovable (Fig. 8(c)) .. .. .. *Uca vocans*
4. Merus of third walking leg less than twice as long as broad .. .. *Uca gaimardi*
– Merus of third walking leg more than twice as long as broad 5
5. Post orbital tooth acute. From this tooth the dorso-lateral ridge runs back in a straight line, or with a slight but even curvature (Fig. 8(d)) .. .. *Uca annulipes*
– Post orbital tooth obtuse. From this tooth the dorso-lateral ridge initially runs back postero-laterally for a short distance, but then postero-medially, with a marked inflection at the point where it separates from the keeled lateral margin (Fig. 8(e)) .. .. *Uca inversa*