the

TAXONOMY, ECOLOGY AND SOCIAL BEHAVIOUR
of the
TASMANIAN SHORE CRABS
(crustacea, brachyura)
of the families
GRAPSIDAE AND OCYPODIDAE
Leptograpsus variegatus (Fabricius)

Male, carapace length 53.0 mm (WAM 240.62),
Dorre I., Shark Bay, Western Australia.

(Photograph: Athol Beswick)

*L. variegatus* belongs to the subfamily Grapsinae (family Grapsidae). Species of this subfamily are common throughout the world on intertidal, wave-beaten, rock platforms. This species is one of the geographically most widespread of Tasmanian shore crabs. The body and legs are flattened, enabling the animal to crawl into narrow crevices and the legs are provided with spines which allow it to hold on to the wave-beaten surfaces of the platforms. Although the number of gills is relatively large, their volume is reduced; the animal is able to spend long periods out of water feeding on encrusting algae in the upper part of the shore. The specimen figured here, an adult male, possesses the enlarged chelipeds typical of adult male grapsid crabs.
THE TAXONOMY, ECOLOGY AND SOCIAL BEHAVIOUR
OF THE TASMANIAN SHORE CRABS (CRUSTACEA, BRACHYURA)
OF THE FAMILIES GRAPSIDAE AND OCYPODIDAE

by

DESMOND JOHN GERALD GRIFFIN, M.Sc. (N.Z.)

submitted in fulfillment of the requirements for
the degree of
Doctor of Philosophy

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April, 1966
Except as stated in the text of this thesis, no material is incorporated heretofore which has been submitted for the award of any other degree or diploma in any University and to the best of my knowledge and belief no material is included which has previously been written or published by any other person except where due acknowledgement is made in the usual form: Smith (personal communication), Brown (unpublished) or Green (1952).

A small part of this work has been carried out in collaboration with B. M. Campbell (Queensland Museum) and due acknowledgement of this is made in the appropriate place in the text. The joint paper (Campbell & Griffin, 1966) appears in Appendix II.

(D.J.G. Griffin)
Hobart, 29 April, 1966.
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THE TAXONOMY, ECOLOGY AND SOCIAL BEHAVIOUR
OF THE TASMANIAN SHORE CRABS (CRUSTACEA, BRACHYURA)
OF THE FAMILIES GRAPSIDAE AND OCYPODIDAE

Abstract

Tasmania, which lies within the cool temperate Maugean marine province of Australia, possesses nine species of grapсид crabs and two ocypodids. Like related species in other parts of the world they are almost entirely confined to the littoral zone where they are the dominant brachyurans.

The report is divided into three main parts. Throughout, the results of these studies are compared with similar investigations on other Brachyura and, where applicable, other animals in general.

In dealing with the taxonomy of the species, particular attention is paid to the geographically widespread groups of species: Lepasgrapsus variatus (Fabricius), Cyclocoeloma granulosus H. Milne Edwards and the congeneric species in the southern Indo-Pacific, Plagusia capensis de Haan and its close relative, P. cantipes de Haan. There are marked changes with growth in most of these species and in several, some characters vary clinally. C. granulosus and the warm temperate Australian C. nudominii show marked character divergence towards their region of sympatry. The grapsid and ocypodid fauna of Tasmania is zoogeographically most closely related to that of the Australian mainland; there are some similarities to, and some important differences from, those of other temperate regions outside Australia, particularly New Zealand.

The ecological distributions of the eleven Tasmanian species are described, from field observations, in relation to substrate,
wave action, salinity, cover and major tidal levels on the shore and compared with those of the dominant intertidal organisms and other Tasmanian Brachyura. Breeding and moulting cycles in two species are described briefly and compared with those of the other species. The numbers and relative volumes of the gills are considered in relation to the habitat and behaviour of the species. The arrangement of different types of hairs on the mouthparts are described in relation to feeding and the species' habitat. Finally, the behaviour of the species in the laboratory is examined and compared with species' distributions in nature. Each species sometimes occurs together with others but is most abundant in a particular type of habitat, in which other species do not occur in maximum abundances. There are the usual morphological, physiological and behavioural adaptations in each species to the characteristic habitat. The laboratory behaviour of the species shows a close parallel with the species' distributions in nature. Over all, most of the species differ widely in their fundamental niche requirements and competition for space appears to be of little or no importance in determining their distributional limits.

The patterns of social and maintenance behaviour of the two cyzopodid species, Holoccius cordiformis (H. Milne Edwards) and Hemiplex latifrons (Haswell), are described from observations in the field and of marked individuals in a terrarium. The two species are most active when their burrows are uncovered by the tide. The feeding, burrowing, fighting and sexual behaviour of each comprise rather stereotyped postures. The behaviour of H. cordiformis resembles that of some species of fiddler crabs (Uca) and in other ways that of the sand or soldier crabs (Dotilla species).

The major supporting paper deals with a review of the Australian spider crabs of the family Majidae and includes an annotated key to all described species.
1. INTRODUCTION

1.1 THE BRACHYURA AS CRUSTACEA

The true crabs or Brachyura form, within the suborder Reptantia, a section of the crustacean order Decapoda. This order, containing almost one third of all known species of Crustacea (Waterman & Chace, 1960), otherwise comprises the nectonic shrimps and prawns (suborder Natantia), the benthonic lobsters and crayfish (section Macrura) and diverse squat lobsters, hermit crabs and half crabs (section Anomura). As in other decapods and many higher Crustacea, the cephalic and thoracic segments are fused into a cephalothorax covered dorsally by a carapace which overhangs laterally to enclose the fleshy gills arising from the proximal parts of the thoracic appendages and the wall of the thorax. The Brachyura are universally distinguished from other decapods by the great symmetrical reduction in size of the seven-segmented abdomen which is flattened and reflexed under the thorax. Anteriorly, the eyes are borne on stalks and, like the ventrally placed antennules and antennae, generally arise from sockets. Characteristically, the first three thoracic appendages, the maxillipeds, are modified to assist the three posterior pairs of cephalic appendages which are
specialised for feeding. Of the remaining five pairs of thoracic appendages, the first (chelipeds) are typically chelate and used in a variety of activities, particularly in grasping food. The chelipeds are usually grossly enlarged in adult males and are used in fighting and in sexual display. The posterior four pairs are used in locomotion, the last being modified in various ways in some families.

The abdomen in the adult female is usually wide and subovate and four well-developed, biramous pairs of appendages or pleopods are present, their edges fringed by numerous long setae. Prior to hatching, the extruded eggs are held under the body of the female by the abdomen and pleopods. In the male the abdomen is narrow and only the pleopods of the first segment are typically well-developed and uniramous. They serve as intromittent organs and are generally aided by the variously developed second pair.

The postembryonic life history of brachyurans typically includes a number of temporarily planktonic larval stages - up to four zoeal and one megalopa stage. Like other arthropods, growth proceeds by means of a number of ecdyses, or molts, and metamorphosis. Such a growth pattern has profound influence on the organism throughout life, the period
of intermoult being one of recovery from the previous moult and preparation for the next. As in other crustaceans and in insects, this stadal growth in brachyurans is regulated hormonally by the release from storage organs of secretions of special parts of the central nervous system. Secondary sexual dimorphism (through unequal development of the chelipeds and abdomen) is also regulated hormonally in brachyurans (Hélène Charniaux-Cotton, R. Dennell, L.M. Passano, G. Tessier, Dorothy E. Bliss and J.H. Welsh in Waterman, 1960, 1961).

The Brachyura are amongst the most phylogenetically advanced crustaceans, with well developed nervous systems and in many cases, complex patterns of behaviour.

1.2 THE SYSTEMATIC POSITION OF THE GRAPSIDAE AND OCYPODIDAE

The crabs belonging to the families Grapsidae and Ocypodidae are characterized most readily, albeit rather loosely, by their pronouncedly rectangular, straight-sided carapace, with a wide anterior edge to the outer angles of which reach the prominent eyestalks. Along with a number of other families such as the Goneplacidae, the Pinnotheridae (pea crabs), the Palicidae (in which the
last pair of ambulatories are reduced in size), and the Cecarcinidae (land crabs), the Grapsidae and Ocypodidae were long grouped together as the "square fronted" crabs, termed the Catometopa by H. Milne Edwards in 1837 and the Grapsidea by Dana in 1851. As such, they were separated from the "round fronted" crabs, the Cyclometopa or Cancroidea, which included families such as the Xanthidae and Portunidae (swimming crabs) in which the carapace is typically wider than long and broadly subovate instead of square.

However, such terms as Grapsidea and Cancroidea have little phylogenetical significance and palaeontological evidence suggests only distant connection between the Cancridae and the other families mentioned above (Glaessner, 1960). Fossil grapsids and ocypodids are doubtfully known earlier than the Tertiary by which time they are already distinct groups. Ocypodids (and the morphologically and ecologically similar Mictyridae) are possibly most closely related to the deep water Conoplacidae whilst the Grapsidae share several features with the Cecarcinidae. Evidence from study of fossils also suggests a closer affinity of the Oxyrhyncha (spider crabs) with the Oxystomata (pebble crabs and box crabs) rather than with the "grapsoids" and "cancroids".
As the Brachyrhyncha, these latter two diverse groups have been contrasted by Alcock, Rathbun and latter day workers on recent genera, with the narrow fronted, generally triangular Oxyrhyncha, the other superfamily of the subsection Brachynatha. They contain, according to recent estimates (Waterman & Chace, 1960), nearly 76% of the species included in the Brachynatha and almost 64% of the 1,428 or more species of Brachyura.

1.3 THE ECOLOGICAL RELATIONS OF THE GRAPSIDAE AND OCYPODIDAE

Ecologically, grapsids and ocypodids are typical inhabitants of the sea shore where they live in the crevices of cliffs and platforms, under stones (Grapsidae) or in burrows on the sand or mudflats (Ocypodidae) whilst some species are found in shallow parts of the continental shelf and others inhabit estuaries or the banks of freshwater streams. Many species are active during the day and roam over cliff, sandy beach or mudflat. Hence, they have widely attracted the attention of naturalists during the last two centuries or more. Many species were, in 1758, foundation members of the Linnaean genus Cancer and others were first described much earlier.
In tropical regions where rocky outcrops occur, the relatively large grapsines (species of *Grapsus* and *Pachygrapsus*) are conspicuous members of the intertidal biota. Thus, Crane (1947) noted that on the west coast of central America, individuals of *Grapsus grapsus* (Linnaeus) are commonly seen sunning themselves on the top of large rocks in areas exposed to surf. This species is similarly common in Jamaica (Hartnoll, 1965a). In the Indo-West-Pacific the closely related *G. tenuicrustatus* (Herbst) is equally prominent in the same kind of habitat. On the beach rock areas of the coral cays seaward of the Great Barrier Reef this species is present in thousands, sometimes with a second species, *G. albolineatus* Lamarck (McMichael & Yaldwyn, 1965). Under stones on tropical shores species such as the small *Pachygrapsus transversus* (Gibbes) and large species of *Geograpsus* are common; species of *Pagurus* and *Porcellon* are found at low tide level on rocky shores and reefs. Species of *Goniopsis* and *Sesarma* are extremely abundant in muddy banks of streams, and fiddler crabs (*Uca* species) are the dominant macro-organisms of mangrove swamps throughout the world (Altevogt, 1955; Crane, 1941a, 1947; MacNae and Kalk, 1962a; Verway, 1930). The closely related ghost crabs (*Ocypode* species) are likewise conspicuous on sandy beaches, both sheltered and surf beaten (Crane, 1947; MacNae & Kalk, 1962b). In eastern Australia
the soldier crabs (Mictyridae) are extremely abundant on sandy beaches.

But in many tropical and subtropical regions numerous species of other families of crabs are present intertidally. Xanthids are particularly numerous and diverse, especially on coral reefs and under stones (Crane, 1947; Gillett & McNeill, 1962; Knudsen, 1960) and some portunids such as *Scylla serrata* (Forskål) and species of *Thalamita* are also prominent intertidal organisms both on coral reefs and mudflats (Gillett & McNeill, 1962; Miss Elizabeth C. Pope, personal communication).

In temperate regions these non grapsid-ocypodid crabs become less common and the grapsids far outnumber any of the other brachyurans (Garth, 1957; McNeill, 1962; see also Smelling, 1959).

1.4 THE TASMANIAN BRACHYURA AND THE GRAPSIDAE AND OCYPODIDAE AS IntERTIDAL ANIMALS

Slightly more than 60 species of Brachyura are known from Tasmania (Guiler, 1952a, 1956). The majority of these are found on the shallower parts of the shelf and deeper. Among the commoner species are dromiids of the genera
Petalomera and Dromidiopsis, majids such as Leptomithrax gaimardii (H. Milne Edwards), Notomithrax minor (Filhol) and Naxia aurita (Latreille), the portunids Nectocarcinus integrifrons (Latreille) and N. tuberculosus A. Milne Edwards, xanthids such as Pilumnus tomentosus Latreille and Actaeas peronii (H. Milne Edwards) and the giant Pseudocarcinus gigas (Lamarck) and some leucoisiids such as Ebalia tuberculosa (A. Milne Edwards) and E. intermedia Miers (Griffin, unpublished).

Intertidally, the xanthids Pilumnus rufopunctatus Stimpson and Heteropanope serratifrons (Kinahan), the cancrid Cancer novaezealandiae (Jacquinot) and the gone-placid Litocheira bispinosa (Kinahan) are sometimes found intertidally under stones whilst the majid Notomithrax ursus (Herbst) and the crab-like lithodid anomuran Lomis hirta (Lamarck) are locally quite abundant near low tide mark on open rocky shores. The porcellanid anomuran Petrolisthes elongatus H. Milne Edwards is extremely common near low tide under stones on many beaches, sheltered and open alike, the leucoosiid Philyra laevis Bell can be seen moving up with the incoming tide on almost any sandy estuary or embayment. Soldier crabs, Mictyris platycheles (H. Milne Edwards), are present in thousands on intertidal sandy beaches and the little flat backed hymenosomid,
Halocarcinus australis (Haswell), is present on many muddy estuaries amongst weeds.

In this context the Tasmanian grapsids and acylopsids are undoubtedly the dominant intertidal crabs. They are present on all beaches, except open sandy ones, in crevices, under stones and in burrows.

1.5 THE PHYSICAL ENVIRONMENT OF THE INTERTIDAL REGION
AND SOME PHYSIOLOGICAL ADAPTATIONS OF INTERTIDAL CRUSTACEA

Crabs, like other animals, are faced with problems such as coping with the presence of other animals of the same kind and of other kinds (including predators and parasites), the extremes of the weather and of exploiting the environmental components, food and a place in which to live (H.C. Andzawartha & L.C. Birch quoted by Hodgkin, 1960: 38). But within these components, intertidal organisms, and to no less an extent, intertidal crabs, are subject to certain unique environmental factors. These include the results of extreme pressure from breaking waves, the dessicating effects of exposure to air alternating with wetting by the sea as the tide alternately rises and falls and, rather more than the inhabitants of other ecological regions of the sea, they are subject to fresh water dilution of the seawater medium,
especially in estuaries and near the mouths of rivers.

Physiological adaptations to such an environment concern mainly ionic regulation, excretion and respiration (Robertson, 1960; Parry, 1960; Edney, 1960).

Crustaceans universally maintain an ionic concentration in the blood plasma different from that of the environment. The gills are the site of continuous absorption of ions which replace those lost through urine secretion via the antennal glands. This urine is in virtually all cases isosmotic with the blood, even in species subject to an external medium of lowered salinity.

Respiratory adaptation to terrestrialness, at least in brachyurans, has involved a reduction in relative volume of the gills. But overall there are remarkably few modifications in the most terrestrial of crustaceans. Even the best adapted land decapods must return to the sea to spawn.

1.6 THE PHYSICAL ENVIRONMENT OF TASMANIA

Tasmania is a triangular island lying but a few hundred miles off the south east corner of the continent of Australia, apex southward, the broad base facing the Victorian coast. From north-eastern and north-western corners extend more or less longitudinal, shallow, undersea
ridges, scarcely more than 30 fathoms deep, topped by many relatively small islands (Bennett & Pope, 1960). Off the west and east coasts the continental shelf drops rather sharply to the slope less than 50 miles offshore. Low, geologically old mountains 4,000-5,000 ft. high lie along the west coast and towards the centre of the island giving rise to streams and rivers which flow into the sea mainly along the west, central north and south east coasts, whilst a block of similarly low mountains in the north east gives rise to rivers flowing into the north eastern region. (Banks, 1965; Davies, 1965).

The coastal rocks comprise gently sloping outcrops of granite along the north east coast and along localized west coast areas, basalt and dolerite outcrops and promontories along parts of the north coast and elsewhere, Precambrian and Cambrian quartzites and Permian shales and sandstones (Bennett & Pope, 1960; Banks, 1965).

Almost the whole of the western and northern east coasts are open to the full effect of the wind driven sea but the north coast is somewhat sheltered by the islands to the east and west, and the south east coast by the prominent Freycinet and Tasman Peninsulas and Bruny Island lying north-south. However, the basic pattern of exposure to wave action is modified by differences in wind patterns on the different coasts (Bennett & Pope, 1960).
Air temperatures range from -2°C to 42°C although these are rare (Bennett & Pope, 1960). Mean ranges in south-eastern Tasmania are from about 11°C to 22°C in January and February and from 4°C to 13°C in June-July (Guiler, 1950; Langford, 1965). The warmest coastal regions are around the north and northern east coasts.

Sea temperatures range from about 9°C in winter to 18°C in summer in south-eastern Tasmania, but higher temperatures obtain along the northern east and north coasts (Guiler, 1950; Bennett & Pope, 1960), and are universally higher in shallow, inshore waters.

Tasmania lies just north of the subtropical convergence on the edge of the West Wind Drift which washes the west coast particularly. The east coast is subject to the south-east swinging warm East Australian current.

The tides in Tasmania are of the semi-daily type and are of low amplitude (see section 4.1) and barometric pressure is thus of greater significance than in areas where the tidal range is large. Mean monthly barometric pressures fluctuate rather irregularly but tend to be higher around the early part of the year (Guiler, 1950). Lowest tides occur in the morning in winter and in the afternoon in summer so that intertidal organisms are subject to the extremes of temperature during maximum exposure to air. The effects of such extremes are, however, mitigated to some
extent by the tendency of warmer offshore winds to blow during the morning and of cooler onshore winds during the afternoon.

Lastly, the marine organisms of Tasmania belong biogeographically to the Maugan cool temperate region which also includes Victoria and eastern South Australia (Bennett & Pope, 1960); Tasmania is particularly characterized by the presence of the large fucoid-like strap weeds *Durvillea* (= *Sarcophycus*).

### 1.7 SCOPE OF THE PRESENT STUDY

The emphasis throughout this study of Tasmanian shore crabs is on species as natural units, their morphological, ecological and ethological characteristics, the ways in which they are isolated from each other and the results of such isolation.

In the first part, dealing with taxonomy, attention is paid to intraspecific variation, hardly to the content of generic groupings. Some particularly widespread species are treated in detail and the results compared with those for other animals.

The second part deals with the ecological distribution of the Tasmanian species, their degree of overlap and the
reflection of these distributions in certain adaptations, morphological, physiological and behavioural. Little attention is paid to temporal fluctuations in abundance.

In the third part, the ethology of two species is particularly examined and the phylogenetic relations based on such species' attributes are discussed.

2. ACKNOWLEDGEMENTS

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3. T A X O N O M Y

3.1 INTRODUCTION, MATERIALS AND METHODS

At the commencement of this study, eight species belonging to the family Grapsidae and two belonging to the Ocypodidae were considered to be present in Tasmania. Two of these had been described by the end of the eighteenth century, six were described by the French carcinologist, H. Milne Edwards (1837, 1853) in the middle of the nineteenth century and two by workers in Australia, W.A. Haswell and T. Whitelegge, towards the end of the nineteenth century. Previous Australian monographs on Crustacea (Haswell, 1882b; Hale, 1927a) had dealt briefly with most of these and M.W.F. Tweedie (1942) had treated the Tasmanian species in more detail. Guiler (1952a, 1956) had listed the species and given further distributional data. The ten species were:

- Leptograpsus variegatus (Fabricius)
- Brachynotus octodentatus (H. Milne Edwards)
- Brachynotus spinosus (H. Milne Edwards)
- Cyclograpsus audouinii (H. Milne Edwards)
- Helice haswellianus (Whitelegge)
- Paragrapsus quadridentatus (A. Milne Edwards)
- Paragrapsus gaimardii (H. Milne Edwards)
- Plagusia capensis de Haan
- Heloccius cordiformis (H. Milne Edwards)
- Hemiplax latifrons (Haswell)
Australian workers all appeared to miss the description in Jacquinot & Lucas (1853) of a further species based on material collected in 'Hobart'. This species was *Cyclovarpus tasmanicus* Jacquinot. Although well illustrated, *C. tasmanicus* was very briefly described. It has been found impossible to identify this species with any known from Tasmania or with any known species of *Cyclovarpus* and its status and relationships must unfortunately remain in doubt for the present time.

During the conduct of the present studies, *B. octodontatus* was investigated throughout its range by Dr. R.W. George (Western Australian Museum) who concluded that the species should be placed in the genus *Leptograptes*. This decision is followed here.

Soon after the initiation of the present studies it was learned, through the kindness of Professor W. Stephenson (University of Queensland Department of Zoology) that Bruce M. Campbell (now at the Queensland Museum) was completing taxonomic studies on the eastern Australian grapsids of the subfamily Sesarminae, with special reference to the genus *Sesarma*. It was considered most suitable to co-operate with Campbell in a comprehensive treatment of the Australian representatives of this subfamily. So far, four genera, *Helice*, *Holograpus*, *Cyclovarpus* and *Paragrapus*, have been dealt with (Campbell & Griffin, 1966). The genera *Helice*,...
Holograpsus and Paragrapsus, together with Cyclograpsus insularum (a new non-Australian species), were dealt with by Campbell and the remaining species of Cyclograpsus became part of the present study. The results of this investigation of the Australian and other southern temperate species of Cyclograpsus are given here in detail and it is shown that the Tasmanian (and south-eastern Australian) populations of this genus should be known as Cyclograpsus granulosus H. Milne Edwards, 1853. This species, originally described from Tasmania, was previously considered synonymous with C. audouini. The other sesarmines included in the joint work are dealt with only briefly. Campbell has considered that Helico hasuellianus should be placed in a new genus, for which the name Holograpsus has been proposed. Current investigations of the Tasmanian grapsids has shown the presence, in eastern Tasmania, of a third species of Paragrapsus, P. laevis (Dana), previously known from eastern mainland Australia.

De Haan’s name Plagusia capensis is here used for the species generally known as Plagusia chabrus because of some past confusion about the identity of Linnaeus’s Cancer chabrus.

The names of the two ocypodids remain unchanged.
In this section then, the taxonomy of the Tasmanian representatives of the Grapsidae and Ocypodidae is dealt with; in the case of the genera *Cyclograpsus* and *Plagusia*, some closely related species are also dealt with. The emphasis is at the species level and detailed discussions of genera are not included.

The treatment of each species includes synonymies, descriptions (where necessary) and, where appropriate, detailed discussion of variation and the distinctness and taxonomic status of the Tasmanian, or at least Australian, populations. The synonymies include all references to previous studies on Australian material; only basic references are given to treatments of Tasmanian species in regions outside Australia.

In "Material examined" is listed the number of specimens and their size range and the localities from which they were collected. Australian localities are usually listed from west to east, north to south on the west coast and south to north on the east coast. Tasmanian localities (see text-figure 1) are arranged in order from north west eastwards and southwards, west coast localities appearing last. The localities from which Tasmanian material was examined include some at which species were identified in the field and material not collected for detailed examination. Selected material from these collections is deposited in the Tasmanian Museum.
Museums, material from which is given special mention in the text or is figured, are designated by the following abbreviations: AM, Australian Museum, Sydney; DM, Dominion Museum, Wellington; NM, Muséum National d'Histoire Naturelle, Paris; QM, Queensland Museum, Brisbane; QVM, Queen Victoria Museum, Launceston; SAM, South African Museum, Cape Town; SM, South Australian Museum, Adelaide; TM, Tasmanian Museum, Hobart; USNM, United States National Museum, Washington; VM, National Museum of Victoria, Melbourne; and WAM, Western Australian Museum, Perth.

The section "Localities previously reported" includes data from earlier literature arranged in summary form for each major area: Australia, New Zealand, Pacific Ocean, South America and South Africa, references to papers giving detailed locality lists for these areas being included in parentheses.

The terminology used in dealing with morphology is mainly that employed by Calman (1909) and by Rathbun (1918a: figs. 1, 2).

The system of measurements also for the most part follows that explained by Rathbun (1918a: 8) and is as follows:

Carapace length: measured on median line from anterior to posterior margin.
Carapace width: measured at widest part unless otherwise stated.

Frontal width: measured anteriorly between the inner margins of the orbits (except in the Plagusiinae where it is measured between the postero-dorsal terminations of the antennular fossae).

Interorbital width: measured between the exorbital spines.

Anterolateral margin length: shortest distance between the tip of the exorbital spine and the widest part of the carapace.

Cheliped or ambulatory leg length: measured along the ventral edge of the fully extended appendage from the articulation of the coxa with the sternum to the tip of the dactyl. The length of individual segments or portions of the cheliped or leg is measured along the dorsal (anterior) edge. The width of any segment is measured at its widest part.

In several cases, the discussions of variations employ statistical analysis. The methods used mainly follow Bailey (1959) and are briefly outlined in appendix I.

The two families and six subfamilies dealt with here, along with the eleven Tasmanian species (twice underlined) considered valid and the closely related ones also treated,
TEXT-FIG. 1  Map of Tasmania and outlying islands showing localities mentioned in the text. (For more detailed map of the River Derwent see text-figure 35.)

Adventure B. .... 55
Arthur R. .......... 63
Bellerive.......... 45
Bicheno.......... 24
Binalong B. ....... 20
Blackman B. ....... 34
Blackman's B. ..... 50
Boggy Ck. .......... 21
Bridgewater....... 47
Brown's R. .......... 50
Carlton........... 40
Coal R. .......... 41
Coles B. .......... 26
Crayfish Ck. ...... 4
Currie Harb. ...... 1a
Dentention R....... 5
Devonport......... 12
Direction, C........ 44
Don............... 11
Double Ck. ......... 30
Dunalley B. ....... 35
Eaglehawk B. .... 36
Eddystone Pt. .... 19
Egg I. .......... 57
Elwick B. .......... 48
Emu B. .......... 8
Falmouth......... 23
Forestier, C. .... 27
Forth R. .......... 10
Fossil I. .......... 37
Franklin.......... 57
Frazer B. .......... 1b
George B. .......... 21
Goose I. .......... 1c
Gordon............ 53
Grant Pt. .......... 20
Gravelly Beach... 14
Green Pt.......... 64
Green's Beach.... 13
Howden........... 51
Hunter I. .......... 65
Inglis R. ........... 7
Interview R. ...... 62
Isthmus E. ......... 54
Kelso............... 13
Kingston.......... 50
Low Hd. .......... 15
Lune R. .......... 58
Lymington......... 56
MacLaine's Ck. .. 29
Margate.......... 51
Maria I. .......... 33
Montagu R. ....... 2
Ninepin Pt. ...... 53
Norfolk B. ........ 36
North Pt. .......... 3
North-west B. .... 51
Orford........... 31
Oyster Cove ...... 52
Fieman R. .......... 61
Pipe Clay L. .... 42
Firates B. ....... 37
Pittwater......... 41
Ralph's B. .......... 43
Remarkable C. ... 38
Restdown Pt. ...... 46
Rheban........... 32
Risdon Cove...... 46
Rocky C. .......... 6
Sandy B. .......... 49
Scamander......... 22
Sleepy B. .......... 25
Snug B. .......... 52
Sorell, C. ....... 60
Southport........ 58
Stanley.......... 3
Strahan.......... 59
Swan B. .......... 16
Swan I. .......... 18
Swansea.......... 28
Taroona.......... 50
Tasman I. ....... 3
Triabunna...... 29
Ulverstone...... 9
Waterhouse I. .... 17
Wivenhoe......... 8
Wynyard......... 7
can be separated as follows.  (Families and subfamilies after Rathbun 1918a; genera of Sesarminae partly after Campbell & Griffin.)

1 Third maxillipeds incompletely closing mouthfield, leaving between them a rhomboidal gape exposing mandibles. Front of carapace occupying at least half distance between external orbital angles. Carapace usually square..................

..........................Family GRAPSIDAE...................... 2

--- Third maxillipeds closing mouthfield or, at most, leaving a narrow oval gape, mandibles not visible. Front of carapace usually less than one-third distance between external orbital angles, often a narrow, more or less deflexed, lobe. Carapace usually transversely elongate..................

..........................Family CYCPODIDAE..................14

2(1) Antennules folding almost transversely out of sight beneath front.......................... 3

--- Antennules folding vertically, antennular fossae deep clefts in front of carapace medial to orbits and visible in dorsal view..........................

..........................Subfamily Plagusiinae..............13
(3) Outer surface of third maxillipeds lacking an oblique hairy ridge.............. 4

Outer surface of third maxillipeds crossed obliquely by a hairy ridge. Subfamily Sesarminae...... 6

(4) Suborbital border running downwards towards mouthfield........ Subfamily Grapsinae........ 5

Suborbital border not running downwards towards mouthfield but supplemented by a rather distant suborbital crest in line with anterior border of epistome....... Subfamily Varuninae

A single Tasmanian species, Brachynotus spinosus (H. Milne Edwards), further distinguished by three sharp anterolateral spines on carapace behind external orbital angles, straight and strongly de- flexed front and acute distal dorsal spine on ambulatory meri.

(4) Branchial regions crossed by 8-9 obliquely transverse ridges. Merus of cheliped ventromedially expanded as a prominent, toothed crest. Merus of first ambulatory leg with about three spines on distal edge posteroventrally; merus of fourth leg with distal edge rounded posteroventrally........

.......................... Leptograpsus variegatus (Fabricius)
Branchial regions with a few short oblique ridges posteriorly close to edge of carapace. Merus of cheliped subcylindrical, nowhere expanded as a crest. Meri of ambulatory legs lacking distal spines posterovertrally.................................

Leptograpsodes octodentatus (H.Milne Edwards)

6(3) Carapace deep, vaulted, anterolateral margin with a distinct notch. Ambulatory legs slender. Terminal segment of female abdomen one and one-half times as broad as long...........<br>Halograpsus haswellianus (Whitelegge)

Carapace strongly depressed, anterolateral margins either entire or else distinctly toothed. Ambulatory legs sturdy. Terminal segment of female abdomen twice as broad as long......................... 7

7(6) Anterolateral margins of carapace entire; postfrontal lobes indistinct; front curving smoothly downwards..............<br>Cyclograpsus H.Milne Edwards.. 6

Anterolateral margins of carapace distinctly toothed; postfrontal lobes distinct; front forwardly projecting, rather shelf-like................

Paragrapsus H.Milne Edwards....11

3(7) Long tufts of hair arising from between bases of ambulatory legs......................... 9
A few short hairs arising from between bases of ambulatory legs, not projecting as tufts........10

9(3) Carpus of first ambulatory leg with felt on dorsal and anterior surfaces distally and also extending along whole length of propodus on anterior surface...........C. audouinii H. Milne Edwards

Carpus of first ambulatory leg naked, propodus with felt distally only.........................

........................C. lavauxi H. Milne Edwards.

10(3) Inner surface of palm of chela in male distinctly and densely granular medially. Frontal and anterolateral parts of carapace and legs moderately to strongly granular. C. granulosus H. Milne Edwards

Inner surface of palm weakly granular. Carapace and legs smooth, or only weakly granular........


11(7) Anterolateral margins with one tooth behind external orbital angle..............................


Anterolateral margins with two teeth behind external orbital angle.............................12
12(11) First ambulatory leg with felt on anterior surface of carpus and propodus; propodus of fourth leg dorsally and ventrally felted.

\[ \text{P. laevis (Dana)} \]

First ambulatory leg with felt on ventral surface of propodus only; propodus of fourth leg with a distal ventral tuft of felt only.

\[ \text{P. gaimardii (H. Milne Edwards)} \]

13(2) Surface of carapace everywhere pubescent except for more or less prominent tubercle behind each orbit on dorsal surface and about three short oblique ridges posterolaterally on branchial regions. Distal edge of merus of third ambulatory leg posterovertrally rounded.

\[ \text{Plagusaia capensis de Haan} \]

Surface of carapace with prominent naked tubercles anterolaterally, posterolaterally and behind each orbit. Distal edge of merus of third ambulatory leg bearing a sharp spine posterovertrally.

\[ \text{Plagusaia dentipes de Haan} \]

14(1) An orifice or recess, edge of which is thickly fringed with hair, between bases of second and third ambulatory legs. Antennular flagella
or rudimentary, folding obliquely or almost vertically, interantennular septum broad.......... Subfamily Ocypodinae.

A single Tasmanian species, *Heloecius cordiformis* (H. Milne Edwards), further distinguished by abdomen in male being almost as broad as sternum at base, subequal chelipeds in both sexes, inflated epibranchial regions and high, arched, laterally unnotched carapace.

No special recess between bases of any legs, antennular flagella well developed, folding transversely, interantennular septum very narrow.......... Subfamily Macrophthalminae

A single Tasmanian species, *Hemiplus latifrons* (Haswell), further distinguished by deflexed, broad front occupying more than one-third total interorbital width, merus of external maxillipeds bearing a deep diagonal sulcus and low, flattened carapace with margins bearing two rounded teeth behind external orbital angle.

Diagnoses of the two families precede the detailed treatment of the included species.
3.2 Family GRAPSIDAE

Carapace usually quadrate, usually little wider than long, lateral borders either straight or very slightly arched. Orbits at or very near anterolateral angles. Front very broad, mouthfield square. A generally large and rhomboidal gape between third maxillipeds; palp articulating at anterolateral angle, or at summit, or at middle of anterior border of merus. Interantennular septum very broad. Male openings sternal. (Alcock, 1900, modified).

Littoral, among rocks; pelagic, in drift weed and timber; inhabiting estuaries and marshes or rivers, rarely on land (Rathbun, 1918a).

3.21 Subfamily GRAPSINAE

Genus Leptograpsus H. Milne Edwards, 1853

Leptograpsus variegatus (Fabricius)

Text-fig. 2-6, 7a-c. Pl. 1, 6A

Synonymy:

Cancer variegatus Fabricius, 1793; 450 (type locality: "In Americae meridionalis Insulis"; type not extant - fide Rathbun, 1918a)

Leptograapsus variegatus; H. Milne Edwards, 1853: 172.


Grapsus strigilatus White, 1842: 78 (type locality: New Zealand; type in British Museum (Natural History), London).

Grapsus planifrons Dana, 1852a: 249 (type locality: Valparaíso, Chile; type in U.S. National Museum, Washington (USNM 2343) - fide Rathbun, 1918a); 1852b: 333; 1855: pl. 21, fig. 3a-e. Cunningham, 1871: 493.

Leptograapsus planifrons; Cano, 1889: 92, 99, 238.

de Man, 1890: 84.


Sesarma pentagona Hutton, 1875a: 41 (type locality: New Zealand; location of types unknown); 1875b: 279.

Miers, 1876: 44. Filhol, 1886: 393. Thomson, 1912: 238.

The following names listed by Kingsley (1880) under L. variegatus are not to be included in the synonymy of this species:

Grapsus pictus Quoy & Gaimard, 1824: 523, pl. LXXVI, fig.2 (type locality: "Isle Guam"). (=Grapsus rudis H. Milne Edwards, 1853 = Grapsus tenuicrustatus Herbst, 1783 — fide Banerjee, 1960; not Grapsus pictus Latreille, 1803 = Grapsus grapsus (Linnaeus, 1758) — fide Rathbun, 1918a).

Leptograpsus Bertheloti H. Milne Edwards, 1853: 172 (type locality: "Iles Canaries") (=? Pachygrapsus marmoratus (Fabricius, 1787) — fide Rathbun, 1918a).
Grapsus marginatus Kingsley, 1880: 196. (nomen nudum).

MATERIAL EXAMINED: A total of 127 specimens (65 males, 62 females, carapace length 9.3 - 67.3 mm).

*Australia:* Western Australia: Dorre I. and Berniet I., Shark B.; North I., W. Wallabi I. and Southern Group, Abrolhos Islands; Pt. Gregory Reef, N. of Geraldton;

Rat I.; Lancelin I.; Garden I.; Clifton St. Beach, Bunbury; 1 mile E. of Frenchman B., near Albany; N.E. Mondrain I. and N. Wilson I., Recherche Archipelago.

*Bass Strait:* Citadel I., Glennie Group; Currie Harb., King Island; Deal I. *Tasmania:* Swan I. Eddystone Pt.; Binalong B.; Bicheno; Sleepy B.; Coles B.; C. Forestier;

Marina I.; Fossil I., Pirates B.; Remarkable Cave.


LOCALITIES PREVIOUSLY RECORDED:

*Australia:* Fourteen localities from Shark B. (Western Australia) in the north west, through South Australia and Bass Strait, to Rockhampton (Queensland) in the north east.
(Balss, 1935); not Victoria (Bennett & Pope, 1953).

New Zealand: Fifteen localities from C. Maria van Dijmen in the north to Dunedin in the south (Chilton & Bennett, 1929; Bennett, 1964).

Pacific Ocean: Middleton Reef, Tasman S. (McNeill, 1937); Norfolk I. (Grant & McCulloch, 1907); Sunday I., Komadoos (Chilton, 1911); Easter I. (Rathbun, 1913a; Porter, 1937).

South America: Twenty-seven localities from Paita, Peru in the north to Valparaiso, Chile in the south; Juan Fernandez I. (Garth, 1957).

DISTRIBUTION:

Southern warm temperate Indo-Pacific Oceans from Western Australia to western South America. The records of this species from Shanghai (Heller, 1862) and Pernambuco, Brazil (Kingsley, 1880) were refuted by Balss (1935: 142) but are repeated by Garth (1957). As Dr. L.B. Holthuis (personal communication, January, 1966), says, Dr. Wilson, who donated the material from Pernambuco on which Kingsley's record was based, was a rich citizen of Philadelphia who often bought natural history objects and presented those to the Philadelphia Academy of Sciences. It is therefore well possible that mislabelled specimens were obtained by him. Since the species has not been recorded from Brazil since 1880 Kingsley's record is best regarded as highly dubious at least.
TEXT-FIG. 2 I epiocaris eus (Lamarck). Male, c. 1.5 mm (W W: 210.62). b, Shark II, B. A.: a, front of carapace, ventral aspect; b, right half of carapace, dorsal aspect; c, right first ambulatory leg, merus and carpus, posterior aspect; d, right fourth ambulatory leg, merus and carpus, posterior aspect; e, left third maxilliped, outer aspect; f, right first ambulatory leg, propodus and dactyl, posterior aspect; g, right fourth ambulatory leg, propodus and dactyl, posterior aspect.
In the tropical Pacific, western Indian and Atlantic oceans species of the genus *Grapus* Lamarck occupy a habitat similar to that occupied by *L. variegatus* in southern temperate latitudes. (Rathbun, 1913a; Edmondson, 1959; Banerjee, 1960; Forest & Guinot, 1961; Crosnier, 1965; Sakai, 1965).

**DESCRIPTION:**

**Carapace:** Slightly broader than long, strongly depressed; lateral margins strongly and uniformly convex, two teeth behind external orbital angle, first tooth the larger, distance between teeth slightly less than length of exorbital tooth along its outer border. Regions of dorsal surface moderately well defined, especially posteriorly mid-dorsally, cervical and branchiocardiac grooves evident. Branchial regions with seven to nine prominent, equidistant, weakly curved, obliquely transverse ridges tending posteriorly towards midline, sixth and eighth ridges sometimes interrupted or short; intermediate ridges sometimes present between sixth and seventh or seventh and eighth major ridges, arising at or not far from lateral edge. Hepatic regions with four or five short, unequal ridges parallel to those of branchial regions.

Postfrontal lobes strong, lateral two (above inner border of orbits) narrower and further advanced than medial two (epigastrics). Frontal and protogastric regions
covered by tubercles which are prominent except close to frontal border, those on postfrontal lobes larger and broader; a few short transverse ridges posteriorly. Meso-gastric region with a few weak transverse ridges anteriorly, smooth posteriorly. Other mid-dorsal regions smooth.

Front broad projecting almost horizontally, edged by numerous small tubercles.

Orbits with posterior edge inwardly notched, sloping posterolaterally towards stout, sharp exorbital tooth which is not as far advanced as front.

Suborbital border with several small spinules. Ventral edge of exorbital tooth with a few small spines at base.

Antennular fossae small, transversely oval. Basal antennal article small, broadly triangular, set obliquely, antennae small. Suborbital tooth immediately outside basal antennal article narrow, acute and ventrally keeled.

Anterior border of mouthfield prominently concave, minutely tuberculate. Palate with three longitudinal ridges.

Epistome moderately broad. A tuberculate lateral ridge extending obliquely forwards from anterior border of mouthfield to opening of 'green gland'.

Pterygostomian regions smooth. Subhepatic regions with interrupted transverse ridges.
Sternum.— Smooth or very weakly punctate; weakly hirsute anteriorly.

Third maxillipeds.— Mostly smooth. Merus with a few interrupted, oblique to transverse ridges and a sharp, low ridge close to medial edge, lateral edge straight or very weakly and irregularly curved, anterolateral angle obtusely rounded.

Chelifeds.— Massive in adult male.

Ischium with inner border distally with a few blunt tubercles.

Merus subtrigonal, ventromedial edge a strong, flattened crest dorsally crossed by strong, transverse, interrupted ridges extending on to crest to give its edge a strongly tuberculate appearance, crest distally expanded and terminating in about four very strong blunt spines or tubercles; ventrolateral edge also strongly tuberculate; ventral surface smooth and concave.

Carpus with weak, short, transverse ridges on dorsal surface and some blunt tubercles towards medial edge; dorsomedial edge bearing midway along a short, broad, blunt spine; dorsolateral edge weakly tuberculate.

Chela extremely stout; palm compressed, as high as long, dorsal surface with numerous strong tubercles which extend part way down outer surface; ventral edge with slightly smaller tubercles or interrupted transverse ridges
TEXT-FIG. 3 *Leptograpsus virens* W. A. (Fabricius). Right cheliped: a, male, c.l. 51 mm (WAM 210.62), Duns L. Shark B. W. A.; b - d, chela only; b, female, c.l. 35.7 mm (WAM 11255), Fiddyment Pt. Torr.; c, male, c.l. 16.7 mm (WAM 236.62), Matilda Is., W. A.; d, male, c.l. 67.3 mm (WAM 279.62), Alabilla Is.
especially dense around base of fixed finger; outer surface otherwise with a line of tubercles or a single uninterrupted ridge extending obliquely from middle of outer surface proximally to tip of fixed finger. Fingers stout and very strongly toothed on inner edges, especially at base of dactyl; widely gaping proximally in adults, fixed finger with inner edge more or less strongly angled midway along, basal portion sometimes weakly toothed or smooth in adults. Dactyl almost twice as long as palm, strongly curved, inner edge concave, dorsal surface tuberculate proximally.

**Ambulatory legs.** Long and strongly compressed, third leg the longest (slightly more than 1½ times carapace length), second leg only slightly shorter.

Coxa of second and third legs with an erect, flattened, distally acute lobe.

Merus in all legs with posterior surfaces bearing interrupted transverse ridges which extend around ventral edge and over crested dorsal edge giving the latter a tuberculate appearance and on to dorsal part of anterior surface; ridges weakly developed in last leg; dorsal crest terminating in a small, sharp spine; distal edge of all except last leg with three or four blunt spines postero-ventrally, last leg sometimes weakly tuberculate, or, more often, smooth posteroventrally.
Carpi with a single dorsal ridge terminating in a broad sharp spine, another ridge, with a line of short hairs just below it, on posterior surface.

Propodi of almost uniform width throughout their length, distal edge with a few short, slender spines posterodorsally; dorsal and ventral surfaces with short, spine-like hairs; a row of short simple hairs posterodorsally on first to third legs, posterodorsally on last leg and sometimes sparse or even absent.

Dactyli terminating in a sharp spine and armed on both dorsal and ventral edges with a double row of long, stout, spine-like hairs.

**Male abdomen.**—Elongate triangular, of seven distinct segments, widest at middle of laterally convex third segment, edges of following segments weakly sinuous, fifth and sixth segments laterally convex, seventh segment laterally weakly concave and distally rounded; sixth and seventh segments of equal length, 1.3 times length of fifth segment. Surfaces generally smooth.

**Male first pleopod.**—Stout, narrowing slightly distally, densely setose distally, setae especially dense on abdominal portion of tip, in a slightly sparser clump around edge of flap at end of short lateral groove, also extending part way down lateral surface.
along lateral margin from the tip of the exorbital spine to the widest part of the carapace); number of tubercles along the frontal border between the lateral grooves running up from close to the basal antennal article, the number on the anterior border of the mouthfield and on the suborbital border; and number of major branchial ridges behind the second anterolateral tooth.

2. Chalipods: length and height of the chela and length of the dactyl; number of spines or tubercles on the ventromedial edge and distal crest of the merus, number of tubercles on the dorsal and dorsolateral surfaces of the palm and number of teeth on the basal half of the inner edge of the fixed finger.

3. Ambulatory legs: length and greatest width of the ambulatory meri of all legs; number of spines on the posterior ventrodistal border of all meri.

The results show no differences between the samples in any of these characters significant enough to warrant specific or subspecific separation. This is especially true for dimensions of the carapace where analysis of first order relationships (carapace width/carapace length etc.) give almost identical values for each of the samples. Changes in some of these dimensions do occur with growth. Thus, while the ratio carapace width/length remains fairly constant (1.08-1.18), there are very slight changes in
other ratios, interorbital width and frontal width decreasing in relation to carapace width and the length of the anterolateral margin increasing.

Text-figure 4 shows these changes in the shape of the carapace. In juveniles (a) the carapace is almost straight-sided and the front is relatively narrow in relation to the interorbital width but wide in relation to total width. In large adults (e,f) the sides of the carapace are strongly convex and the front is wide in relation to interorbital width but narrow in relation to total width. Throughout growth there appears to be little difference between the frontal width and the anterolateral margin length. In text-figure 5A the growth of three dimensions of the carapace are shown in relation to carapace length (see also appendix 1).

In the case of the ambulatory meri, the relative dimensions of which show only slight changes with increased overall size, these appear to be small but consistent inter-population differences in the ranges and means of the length/width ratio (table 1 and text-figure 6 C,D).

The greatest difference is between samples from north-western (1) and eastern Australia (3); south-western specimens (2) are similar to north-western ones and those from New Zealand (4) resemble eastern Australian ones. Consistent, but very slight, north-south trends in these
TABLE 1  Geographical variation in the ratio length/width of the abductory hood of *L. variegatus*. The upper row of each set gives the mean (together with its standard error) and the lower, the range.

<table>
<thead>
<tr>
<th>Number</th>
<th>N.W.A. 1 (33)</th>
<th>S.W.A. 2 (23)</th>
<th>E.A. 3 (29)</th>
<th>N.Z. 4 (9)</th>
<th>Chile (2)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>1.95 (0.016)</td>
<td>2.01 (0.026)</td>
<td>2.12 (0.018)</td>
<td>2.07 (0.030)</td>
<td>1.95 -</td>
</tr>
<tr>
<td></td>
<td>1.7 - 2.2</td>
<td>1.7 - 2.1</td>
<td>1.9 - 2.3</td>
<td>1.9 - 2.2</td>
<td>1.6 - 2.0</td>
</tr>
<tr>
<td>2</td>
<td>1.92 (0.020)</td>
<td>2.00 (0.028)</td>
<td>2.08 (0.044)</td>
<td>2.06 (0.032)</td>
<td>2.0 -</td>
</tr>
<tr>
<td></td>
<td>1.7 - 2.2</td>
<td>1.7 - 2.3</td>
<td>1.9 - 2.3</td>
<td>1.9 - 2.2</td>
<td>2.0</td>
</tr>
<tr>
<td>3</td>
<td>1.90 (0.020)</td>
<td>1.91 (0.021)</td>
<td>2.02 (0.017)</td>
<td>2.03 (0.036)</td>
<td>1.9 -</td>
</tr>
<tr>
<td></td>
<td>1.7 - 2.2</td>
<td>1.7 - 2.2</td>
<td>1.8 - 2.2</td>
<td>1.9 - 2.2</td>
<td>1.9</td>
</tr>
<tr>
<td>4</td>
<td>1.77 (0.019)</td>
<td>1.79 (0.020)</td>
<td>1.90 (0.016)</td>
<td>1.66 (0.041)</td>
<td>1.80 -</td>
</tr>
<tr>
<td></td>
<td>1.5 - 2.0</td>
<td>1.6 - 3.0</td>
<td>1.7 - 2.1</td>
<td>1.6 - 2.0</td>
<td>1.7 - 1.9</td>
</tr>
</tbody>
</table>

1 Shark B. and Abrolhos Is; 2 remainder of Western Australia; 3 Queensland, New South Wales and Tasmania; 4 New Zealand.
TEXT-FIG. 5 *Leptograpsus variegatus* (Fabricius). A, relative growth of three dimensions of the carapace: a, carapace width; b, intermaxillary width; c, anterolateral margin length. Regressions from calculating free data for all material examined grouped into 5 mm classes; data shown is from 32 specimens from N.W. Australia (Mullakh 1, and Shark 1). B, relative growth of the chela in males (closed circles) and females (open circles) plotted logarithmically. Regressions calculated as in A: a and c, c.d. up to 27 mm, b, and d, 20 mm or more.
The following numerical (meristic) characters exhibit relative constancy with growth and little geographical variation; number of major branchial ridges (6 or 9), number of spines on the distal posteroventral edge of the ambulatory meri (merus 1: 2-5; merus 2: 2-4; merus 3: 1-4; merus 4: 0-1) and number of spines on the distal medial crest of the merus of the cheliped (4-6, seldom 3, 7 or 8). However, the number of tubercles on the frontal border, on the anterior border of the mouthfield and on the suborbital border show wider variation within populations and very slight interpopulation differences. (Table 2 and text-figures 6A, B). The trends in these characters are much the same as those shown by the ambulatory meri. The number of tubercles on the ventromedial edge of the merus of the cheliped shows similarly wide variation.

Lastly, the number of tubercles on the dorsal surface of the palm of the cheliped and the number of teeth on the proximal part of the inner edge of the fixed finger of the chela show small changes with growth, the former increasing (from 3-10, in individuals of carapace width less than 20 mm, to around 20 in individuals of more than 50 mm carapace length) and the latter decreasing (generally 3 teeth but individuals of carapace length around 40 mm or above sometimes lack teeth and so have this proximal portion smooth).
TABLE 2 Geographical variation in meristic characters in *L. variegatus*. Arrangement of data as in Table 1.

<table>
<thead>
<tr>
<th>Character</th>
<th>Locality (number of specimens)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>N.W.A. (33)</td>
</tr>
<tr>
<td>Number of frontal tubercles</td>
<td>28.7 (0.78)</td>
</tr>
<tr>
<td></td>
<td>22 - 38</td>
</tr>
<tr>
<td>Number of tubercles on anterior border of mouth-field</td>
<td>14.4 (0.43)</td>
</tr>
<tr>
<td></td>
<td>11 - 22</td>
</tr>
<tr>
<td>Number of spines on suborbital border</td>
<td>15.4 (0.42)</td>
</tr>
<tr>
<td></td>
<td>12 - 20</td>
</tr>
</tbody>
</table>
TEXT-FIG. 6  *Lepiograpbus variogatus* (Fabricius). Frequency polygons showing geographic variation in four characters. Vertical scale represents number of specimens. 1, North west Australia; 2, south west Australia; 3, eastern Australia; 4, New Zealand.
Milne Edwards that *Grapsus planifrons* Dana and *L. gavi* may be synonymous.

Bennett (1964: 80) recently included, without comment, *Sesarma pentagona* Hutton in the synonymy of *L. variegatus*. According to Hutton's original description (repeated by Miers, 1876: 44) *S. pentagona* was based on a small specimen ("0.67 inches long"), carapace 1.37 times as broad as long, subquadrate and smooth. It agrees with *L. variegatus* in the almost vertically deflected front with four raised "projections", obliquely striated branchial regions, anterolateral margin with two "teeth", pterygostomial regions ("area on each side of mouthfield") with moniliform transverse striae, trigonal, striated mesus of the cheliped ("arms"), very broad and compressed ambulatory nori ("third joint of legs"), and distal segments of the ambulatories ("outer joints and claws") tomentose. There are no important differences from small specimens of *L. variegatus* and the subquadrate shape of the carapace is characteristic of the latter. It seems quite probable, therefore, that Hutton's species is to be included in *L. variegatus*.

Amongst the synonyms of this species listed by Kingsley appeared the name, *Grapsus marginatus*, attributed by Kingsley to Latreille (1803). Dr. L.B. Holthuis (personal communication) has kindly informed me that this name was not used by Latreille nor can he find any use of
it by an author prior to Kingsley. It is therefore apparent that the name is a nomen nudum since no description was given of it. I can find no record of the name being used by more recent authors. As a nomen nudum the name has no nomenclatorial standing.

The illustrations of *L. variegatus* given here are designed to parallel those given for species of *Grapsus* by Banerjee (1960).

Genus *Leptograpsodes* Montgomery, 1931

*Leptograpsodes octodentatus* (H. Milne Edwards)

Text-fig. 7d-e, 8, 9a. Pl. 2A, 6a.

Synonymy:

*Cyclograpsus octodentatus* H. Milne Edwards, 1837: 80

(type locality: King I., Bass Strait; type in Muséum National d'Histoire Naturelle, Paris - fide Montgomery, 1931)

*Heterograpsus octodentatus*; Tesch, 1918: 106 (in key).

Male, 1924: 69; 1927a: 182, fig. 183; 1927b: 312.


Guiler, 1952a: 40.

*Exechynotus octodentatus*; Tesch, 1918: 106 (in key). Male,

1924: 69; 1927a: 182, fig. 183; 1927b: 312. Sals, 1935:


TEXT-FIG. 7 Male left first pleopods of Tasmanian Grapsinae: a - c, *Leptograpsus variegatus* (Fabricius), c.l. 53 mm (NM 240.62), Darre L., Shark B.; d - f, *Leptograpsus acutidentatus* (H.M. Edw.), c.l. 26.1 mm, (Tm.), Pirates B., Tas.: tip in abdominal aspect to the left and in sternal aspect to the right, whole pleopod in abdominal aspect in the centre.
Leptocharpsodes webbaysi Montgomery, 1931: 452, pl. 25, fig. 5; pl. 26, fig. 1, 1a, 1b (type locality: Long Island, Abrolhos Islands; types not extant).

Leptocharpsodes octodontatus; George, 1962: 71.

MATERIAL EXAMINED: A total of 55 specimens (28 males, 27 females, carapace width 11.2 - 33.0 mm).

Strait: King I.; Hunter I.; Goose I.

Tasmania: Just W. of Crayfish Ck.; Rocky C.; Hawley Beach, Devonport; Low Head; Waterhouse I.; Pirates B.; C. Direction; Blackman's B.; Adventure B., Bruny I.; Conical Harb. (S. of Picman R.); just S. of Interview R.; just N. of Arthur R.

LOCALITIES PREVIOUSLY REPORTED: Twenty seven localities from the Abrolhos Islands, Western Australia to the north coast of Tasmania (George, 1962).

DISTRIBUTION:

Restricted to Australia, from the Abrolhos Islands in the west, through South Australia, Victoria, to north-western northern and eastern coasts of Tasmania; not found on the east coast of the mainland north of Victoria (F.A. McNeill, personal communication to R.W. George).

DESCRIPTION:

A detailed description of this species was given by Montgomery (1931) and a shorter one by Tweedia (1942); the synonymous Grapsus inornatus Hess was redescribed by de Man (1887).
Amongst the distinguishing features are the very strongly convex lateral borders of the carapace, the anterior half bearing three teeth behind the external orbital angle (not two as stated by Tweedie), the last very small; the long, outwardly smooth and inwardly sparsely tuberculate chelae with the fixed finger moderately bent from the palm and the absence of spines from the posterior ventrodorsal border of the ambulatory meri.

The carapace bears on the branchial regions, close to the lateral edge, a few weak ridges and the suborbital spine is three-sided and only moderately large. The fingers of the chela are strongly toothed, those of the fixed finger near the base generally grouped into a strong lobe. The propodi and dactyli of the ambulatory legs bear short, stiff, black, spino-like hairs.

Male abdomen.—Seven-segmented, widest at the middle of the laterally convex third segment, following segments narrowing uniformly, edges weakly concave, to distal edge of sixth; seventh segment laterally strongly concave basally.

Male first pleopod.—Long, quite slender, weakly curved outwards distally, sternal surface with a moderately long groove towards medial surface ending in distal flap; lateral surface sparsely setose, medial surface with numerous setae extending from base to tip; a moderately dense tuft of setae at the tip almost concealing short, blunt,
TEXT-FIG. 1  *Legimpagopus occidentalis* (M. Edw.). Valencia, c. 26.1 mm (FMNH). Texas II, Texas: a, right chela, outer aspect; b, same, inner aspect; c, right first ambulatory leg, propodus and dactyl, anterior aspect; d, right fourth ambulatory leg, propodus and dactyl, posterior aspect; e, left third maxilliped, outer aspect.
homy tip and flap on sternal surface.

Colour. - Olivaceous, mottled or spotted with dark brown (Tweedie). Carapace mottled with purple and yellow (George). The underside of the body, the chelipeds and legs are usually much paler than the carapace and the mottling, which occurs on the dorsal surface of the chelipeds and legs, is sometimes bright red.

REMARKS:

Montgomery, following views expressed to him by de Man, placed Leptograpscodes in the subfamily Grapsinae. This placing was accepted by George and is followed here. However, it should be noted that there are reasonably strong similarities to the Australian varunine Brachynotus spinosus (Milne Edwards) in the shape of the maxus of the third maxillipeds, the appearance of the front in ventral view, especially the straight suborbital border, and in the form of the male first pleopods. The two species are quite different in the shape of the carapace and of the male chela. The presence in L. octodentatus of two pairs of postfrontal lobes, the strong tuberculation of the anterior part of the dorsal surface of the carapace and the presence of transverse striations on the ambulatory maxi are all reminiscent of species of Grapsus and allied grapsines.

Montgomery realised that his Leptograpscodes webhaysi was very close to the species then known as Brachynotus
octodentatus but listed some differences between the two. Balse (1935) considered the two species almost certainly identical and in this view was followed by George (1962), whose acceptance of Montgomery's view on the subfamilial placing led to the at present unfamiliar combination, Leptograpsodes octodentatus. Hess's Grapsus inornatus has been considered a synonym of the present species since the time of Tesch (1913) although the type locality of the former (Sydney) is almost certainly outside the geographical range of the species (see above).

In a study of this species throughout its geographical range Dr. R.W. George (1962 and personal communication December, 1962) examined a total of 84 specimens (50 males, 34 females, carapace width 10 - 70 mm). Eight characters were studied in detail including all those mentioned as delineating L. webhaysi and G. inornatus by Montgomery and de Man respectively. The characters concerning ridges around the orbits appear difficult to evaluate and the differences (cited by Montgomery) too slight to warrant specific separation. All other characters, including the prominence of the pits on the dorsal surface of the carapace, the dentition and shape of the fingers and ornamentation of the carpus of the cheliped are subject to significant variation with either age or sex, sometimes both. Montgomery's material (adult females), according to that author's description, agrees entirely with the typical
adult females examined by George; Hess's material, according to the latter's description, does not support any taxonomic separation of eastern and western populations.

Examination of the Tasmanian material to hand fully supports George's conclusions; in addition to the characters already found to vary with age and sex it appears that the ridges on the branchial region also become less prominent with increasing overall size.

3.22 Subfamily VARUNINAE

Genus Brachynotus de Haan, 1835

**Brachynotus spinosus** (H. Milne Edwards)

Text-fig. 9b-g, 10. Pl. 2B.

**Synonymy:**


**Brachynotus spinosus:** Tesch, 1918: 106 (in key)

Tweedie, 1942: 16, fig. 3. Guiler, 1952a: 40.

**Eriocheir spinosus:** Hale, 1927a: 184, fig. 185; 1927b: 312, fig. 2.

**TYPE LOCALITY:** Vanikoro, Santa Cruz, Pacific O.; types in Muséum National d'Histoire Naturelle, Paris.
zido de Man.

MATERIAL EXAMINED: A total of 62 specimens (27 males, 35 females, carapace width 6.4 - 16.5 mm).

**Tasmania:** Detention R.; just W. of Crayfish Ck.;
Triabunna; Double Ck.; Proser R. at Orford; Carlton R.;
Dunalley B.; Fort Direction; Pittwater; Bellerive Beach;
Sandy B.; Howden; Margate; Oyster Cove; Huon R. at Lymington.

LOCALITIES PREVIOUSLY REPORTED:

**Australia:** "Australia" (A. Milne Edwards); "eastern Australia" (Ortmann). South Australia: common (in South Australia) (Hale, 1927a); Bay of Shoals and Busby I., Kangaroo I. (Hale, 1927b). Victoria: Pt. Phillip (Fulton & Grant). **Tasmania:** Brown's R. and Carlton (Tweedie); N. of Piesen R. (Guiler).

**Pacific Ocean:** Upolu, Samoa (de Man).

**DISTRIBUTION:**

South-eastern Australia, South-west Pacific Ocean.

**DESCRIPTION:**

Good descriptions of this species were given by de Man (1891) and Tweedie (1942).

The distinguishing features are the presence of three spines on the anterolateral margin, behind the prominent external orbital spine, the second of these smaller than the others and rounded instead of sharp, the concave front and
Text-fig. 9  a, Lepiograpsodes octodensus (H.M. Edw.). Male, c.l. 26.1 mm (TM), Pirates B. Tas.: front of carapace and orbit (LIIS), ventral aspect.
b-g, Brachynotus spinosus (H.M. Edw.). Male, c.l. 16.5 mm, Pittwater: b, front of carapace and orbit (LIIS), ventral aspect; c, left third maxilliped, outer aspect; d, right first ambulatory leg, propodus and dactyl, anterior aspect; e, right fourth ambulatory leg, propodus and dactyl, posterior aspect; f, right chela, outer aspect; g, same, inner aspect.
weak postfrontal lobes, the oblique ridge from the third anterolateral spine to the posterior edge of the carapace, the large, pyramidal, 3 edged, suborbital spine, the outwardly smooth and inwardly granular chelae with a strong tuft of hairs at the end of the palm between the fixed fingers on both inner and outer surfaces in males only, the presence of a strong distal dorsal spine on the ambulatory meri and stout, black, spine-like hairs distributed sparsely on the ambulatory propodi and dactyli, males also having prominent tufts of hair on the ventral surfaces of these two segments of the first ambulatories.

**Abdomen.**—Seven segmented, in the male widest towards distal edge of laterally convex third segment, following segments smoothly tapering to close to distal edge of sixth which narrows abruptly, seventh segment much narrower than sixth. Fifth segment markedly concave laterally.

**Male first pleopod.**—Moderately stout and hardly tapering; short groove on sternal surface towards lateral surface ending in definite flap; strong tufts of hairs, confined to distal part of the pleopod, borne towards tip of flap and surrounding horny tip of pleopod; a few short hairs extending a little way down abdominal surface somewhat medially.

**Colour.**—Dull green or brown with or without white markings, which may be so extensive as largely or wholly to replace the colour (Tweedie). Innumerable colour variations occur; some examples are green, others different shades of brown. Some are very dark brown, with large or small white markings,
while others have the whole upper surface of the carapace milk-white (Hale, 1927a). Hale’s remarks apply quite satisfactorily to Tasmanian populations. Banding of the legs is quite common.

REMARKS:

Tweedie (1942: 17) considered that records of this species from the tropical Pacific required confirmation. Comparison of Tasmanian material, Tweedie’s and Hale’s descriptions and figures with de Man’s description and figure of specimens from Samoa does not reveal to me any differences which might be regarded as warranting specific separation of Australian material from Samoan. De Man also compared his specimens with material from Australia.
Since the time of Dana (1852a), various authors have united the previously described species here considered valid - *C. punctatus*, *C. audouinii*, *C. granulosus* and *C. lavauxi* (= *C. whitei*) - under the first name and accorded this a southern temperate circum polar distribution (see Tesch, 1918; Balss, 1935; and Barnard, 1950). Since that time also, each species has been misidentified from time to time, resulting in incorrect distributions. *C. granulosus* has never been positively identified since the time of Milne Edwards; *C. lavauxi* was recorded from Australia by Haswell (1882b) and from the Kermadec Islands by Chilton (1911) who at first, following Miers (1876), considered it conspecific with *C. whitei* but later (Chilton & Bennett, 1929) as distinct. Rathbun (1918a) gave good reasons for separating *C. audouinii* from *C. punctatus* and Tesch (1918) inferred that both *C. punctatus* and *C. audouinii* occurred in Australia; Balss (1935), however, allowed the former only subspecific status, and Barnard (1950) considered the two to form a single species. The present study supports a partial return to the multiplicity of species originally envisaged by Milne Edwards (1837, 1853).
Of the characters which can be used to separate the species dealt with here, two, the pattern of felting of the ambulatory legs and the shape of the abdomen in the male (particularly of the third and sixth segments) stand out as universally applicable because of their distinctiveness. Other reasonably reliable characters include the shape of the chela in the male, the shape of the carapace and the degree of granulation; the shape of the merus of the third maxillipeds differs little in the five species whilst in all except C. punctatus the male first pleopod is so similar as to be virtually useless as a taxonomic character.

3.23.1 The Australian species of Cyclograpsus

Cyclograpsus granulosus H. Milne Edwards

Text-fig. 11 a-e, 13 a-c, 15. Pl. 3A, 7A.

Synonymy:

Cyclograpsus granulosus H. Milne Edwards, 1853: 197.

Haswell, 1882b: 104. Guiler, 1952a: 40. Campbell & Griffin, 1966: 141, 152, text-fig. 4B, 6B; pl. 21, fig. 3; pl. 23, fig. 7.


Cyclograpsus audouinii; Tweedie, 1942: 12, fig. 4. (Not Cyclograpsus audouinii H. Milne Edwards, 1837: 78.)
TYPE: Lectotype (selected on the advice of J. Forest), a female, carapace width c. 22 mm, Tasmania, Mm. Quoy & Gaimard; Muséum National d'Histoire Naturelle, Paris. Specimen complete and in good condition.

MATERIAL EXAMINED:
A total of 145 specimens (36 males, 59 females, carapace width 7 - 35 mm).
South Australia: Kingscote and Shoal B., Kangaroo I.
Victoria: Beaumaris; Apollo B.; Lady B. Bass Strait:
Fraser B. and south of Currie Harb., King Island; Gooch Island. Tasmania: Stanley; Detention R.; Ulverstone; Hawley Beach, Devonport; Green's Beach, Kelso; Falmouth; Bicheno; Cola's B.; Meredith R. at Swansea; Rheaian;
Pirates B.; Cellerivo; Sandy B.; North West B.; Oyster Cove; Gordon; Ninepin Pt.; ½ n. north of Arthur R.

LOCALITIES PREVIOUSLY REPORTED:
Tasmania: North coast of Tasmania (Haswell; Guiler, 1952a); shore near Brown's R. (Twodde); Eaglehawk Neck, Blackman's B. and Gordon (Guiler, 1952a); Swansea and all exposed coasts of Tasmania (Guiler, 1956).

DISTRIBUTION:
Tasmania and Victoria, extending westward to Kangaroo Island, South Australia.
It appears highly probable that the range of this species coincides with the Maugean cool temperate province of Bennett & Pope (1953).

DESCRIPTION:

Carapace.—Broader than long, lateral margins anteriorly strongly divergent, widest about 1/3 carapace length from front, posteriorly weakly convergent. Surface very strongly granular anteriorly around anterolateral margins and front. A finely beaded, elevated ridge extending around frontal and unbroken lateral margins.

Regions generally poorly defined. Gastrocardiac groove prominent, cervical groove weak, cardiac and intestinal regions weakly demarcated. Several punctuations or shallow depressions anteriorly at posterior part of hepatic region, centrally at each end of gastrocardiac groove, and posteriorly lateral to intestinal regions.

Front moderately deflexed, clearly visible from above, strongly bilobate or sometimes quadrilobate, median frontal furrow extending posteriorly almost to opposite widest part of carapace. Orbits with posterior edge almost uniformly concave, junction with front almost a right angle, lateral angle raised as a sharp triangular tooth, posterior border transverse to oblique and sloping posterolaterally.

Suborbital ridge composed of about 16 strong, distinct granules.
TEXT-FIG. 11  Australian Cyclograpsus species:  a–e, C. granulosus H. Milne Edwards, male, c.w. 29 mm (TM G1076), Rheban, Tasmania (a,b,e); male, c.w. 35 mm (AM P12450), Goose I., Bass Strait (c,d).  f–j, C. ausouinii H. Milne Edwards, male, c.w. 26.5 mm (WAM 203,62), Woodman's Pt., W.A. (f,g); male, c.w. 22 mm (AM P1840), Mosman B., N.S.W. (h,i); male, c.w. 18.5 mm (QM), Noosa, Queensland (j).

a and f, right chela, outer aspect; b,g, same, inner aspect; c,h, right first ambulatory leg, propodus and dactyl, anterior aspect; d,i, right fourth ambulatory leg, propodus and dactyl, posterior aspect; e,j, right third maxilliped.
TEXT-FIG. 12  *Cyclograpsus lavauxi* H. Milne Edwards (a-e), male, carapace width 20 mm (DM), Island B., New Zealand and *C. punctatus* H. Milne Edwards (f-j), male, c.w. 37.8 mm (SAM), "South Africa". Arrangement as in text-figure 11.
Chelipeds. - Carpus smooth, except for narrow minutely granular areas dorsomedially.

Chela of male longer than high, palm enlarged distally, compressed, surface smooth except for a prominently granular raised swelling almost centrally on inner surface, larger granules tending to form a longitudinal ridge; ventral edge generally strongly concave at junction of fixed finger. Fingers weakly gaping proximally except in very large males which have fingers gaping for their entire length, gape linear. Dentition strong in both fingers, toothed inner edge of fixed finger straight.

Ambulatory legs. - Moderately robust, long (second leg almost 1 \(\frac{1}{2}\) times carapace width), compressed, surfaces weakly pitted and finely granular dorsally.

First leg with carpus naked, propodus distally felted on anterior surface, a dorsal triangle of felt widening distally extending half length of segment, a narrow row of felt medially and two smaller rows ventrally, 1 anteroventral and 1 posterovenital; dactyl with 6 longitudinal rows of felt, 3 dorsal ones wider than ventral but usually distinct.

Second and third legs naked except for fine rows of felt on dactyli.

Last leg with carpus naked; propodus naked except for short distal triangular area of felt dorsally as on first leg;
dactyl with 6 rows of felt, dorsal 3 broad but usually distinct, others slender.

Bases of ambulatories bearing very short hairs which do not protrude between legs as tufts.

Sternum.—Anterior segments generally naked, sometimes weakly hirsute.

Male abdomen.—Third segment laterally convex or narrowing from base, widest part of abdomen, following segments tapering to base of sixth. Sixth segment subpentagonal, lateral borders subparallel for proximal half or weakly convergent, distally strongly convergent to just short of distal margin; seventh segment slightly longer than wide with subparallel to weakly convergent margins, distally rounded.

Colour.—Carapace deep red or purple to brownish red, sometimes with paler yellowish mottling, especially posteriorly; legs with similar colouring, chelae pale yellow to white on both outer and inner faces,

*Cyclograpsus audouinii* H. Milne Edwards,

Text-fig. 11 f-j, 13 d-f, 15. Pl. 3B, 7B

Synonymy:


*Cyclograpsus audouinii*; Stimpson, 1907: 132. Tesch, 1918: 126. Male, 1924: 70; 1927a: 176, fig. 176; 1927b: 312
Montgomery, 1931, p. 456. Campbell & Griffin, 1936: 141, 150, text-fig. 4A, 6A; pl. 21. fig. 1, 2; pl. 23, fig. 5, 6. (Not Cyclooramnus audouinii; Edmondson, 1925: 56 (= C. integer; H. Milne Edwards)).


Cycloaramnus lavauxi; Haswell, 1882b: 103 (Not Cycloaramnus lavauxi H. Milne Edwards, 1853: 197)

Cycloaramnus punctatus; Ortman, 1894: 729 (part: Sydney specimens only). (Not Cycloaramnus punctatus H. Milne Edwards, 1837: 78)

Cycloaramnus punctatus audouinii; Balss, 1935: 142

TYPE: Lectotype (selected on the advice of J. Forest), a male, carapace width c 27 mm, New Guinea, MM. Quoy & Gaimard; Muséum National d'Histoire Naturelle, Paris. The dorsal surface of the carapace is badly damaged and the right fourth ambulatory leg has the propodus and dactyl missing while the left third ambulatory has the carpus and following segments missing; the specimen is otherwise intact.

MATERIAL EXAMINED: A total of 234 specimens (142 males, 92 females, carapace width 4.8 - 40.5 mm)

Western Australia: Salmon B., Rottnest I.; Freshwater B.; Pt. Peron; Cottesloe Beach; Cowaramp B.; Koombana
Bunbury; Duke of New Orleans B.; Oyster Harbour, Albany; Woodmans Pt.; Pallinup Estuary; Christmas I. & Middle I.; Recherche Archipelago. South Australia: Flinders I.; St. Vincent's Gulf. New South Wales: Shell Harbour; Wollongong; WInday I., Lake Illawarra; Botany B.; Coogee; Little Sirius Cove and Mosman B., Port Jackson; North Harbour, Manly; Broken B.; Pittwater; 2 m. S. of Tuggerah Lakes; Port Macquarie. Queensland: mouth of Elliott R.; Hervey B.; Noosa.

LOCALITIES PREVIOUSLY REPORTED:

Western Australia: Brown's Sta. and Dirk Hartog I., Shark B.; North Fremantle Beach; Princess Royal Harb., Albany district (Balss, 1935); North beach, Fremantle (Montgomery). South Australia: Nuyts Archipelago (Hale, 1924); Kangaroo I. (Hale, 1927b). New South Wales: East Australia (Tesch); Sydney (Ortmann); Pt. Jackson or Sydney (Stimpson).

DISTRIBUTION:

Australia, from Shark B. (Western Australia) in the north west, through South Australia, to Hervey B. (Queensland) in the north east, but excluding Victoria and Tasmania. The type locality, "New Guinea", appears to be outside the geographical range of this species.
DESCRIPTION:

Carapace.—Broader than long, lateral margins almost uniformly convex, widest close to half carapace length from front. Surface smooth or very finely granular around anterolateral margins and front only. A minutely granulate, elevated ridge extending around frontal and unbroken lateral margins.

Regions poorly demarcated, gastro-cardiac groove prominent. Several punctulations anterolaterally and posteromedially.

Front moderately deflected, clearly visible from above, transverse to uniformly convex or bilobate, median frontal furrow extending to just behind orbits.

Orbito with posterior edge almost uniformly concave, junction with front almost a right angle, laterally raised and sharply pointed, posterior border transverse.

Suborbital ridge composed of about 17 strong, distinct granules.

Chelipeds.—Carpus smooth except for minutely granular narrow portion dorso-medially.

Chela of male longer than deep, compressed, palm enlarged distally, surface smooth except for a medial longitudinal ridge of strong granules on raised swelling on inner surface. Ventral edge straight or very weakly concave at junction of fixed finger. Fingers widely gaping
TEXT-FIG. 13  Male left first pleopods of Australian *Cyclopterus* species: a-c, *C. granulosus* H. Milne Edwards, male, c.w. 27 mm (TM G1077), Sandy Bay, Tasmania and *C. audouinii* H. Milne Edwards, male, c.w. 25 mm (WAM 203.62), Woodman's Pt., W.A.  

Tip in abdominal aspect to the left (a,d) and in sternal aspect to the right (c,f), whole pleopod in abdominal aspect in the centre (b,e).
TEXT-FIG. 14  Male left first pleopods of *Cyclograpsus lavauxi* H. Milne Edwards (a-c), male, c.w. 20 mm (DM), Island B., New Zealand and *C. punctatus* H. Milne Edwards (d-f), male, c.w. 37.8 mm (SAM), "South Africa". Arrangement as in text-figure 13.
proximally, dentition strong in both fingers, toothed inner edge of fixed finger strongly convex midway along, weakly concave distally.

**Ambulatory legs.** Long, second leg almost 1 ½ times carapace width, moderately robust, compressed, surfaces generally smooth.

First leg with carpus and following segments felted, especially on anterior surfaces; carpus with broad band of felt along distal edge usually extending proximally as two very short rows, 1 dorsal and 1 medial; propodus with two dense longitudinal rows, 1 dorsal and 1 medial, extending for almost entire length and joined by fine lines, in addition 2 short rows of felt, 1 anteroventral and 1 posteroventral; dactyl with 6 longitudinal rows, 3 dorsal ones wider than others and usually almost coalesced.

Second and third legs naked except for a single fine mid-dorsal row of felt on propodus and 6 rows on dactyli as in first leg.

Last leg with carpus often bearing a slender mid-dorsal row of felt, propodus with a strong row of felt mid-dorsally which widens distally, dactyl with 6 rows of felt, dorsal 3 extremely wide, hardly separated.

Long tufts of hair between bases of ambulatory legs arising from anteroventral and posteroventral surfaces of bases, tufts equally long between first and second and second and third legs.
Stemum.—Anterior 2 segments generally strongly hirsute, hairs clumped anteromedially anterior to, and around anterior margin of, abdominal fossa.

Male abdomen.—Third segment convex laterally or widening slightly from base to just short of distal edge, widest part of abdomen, following segments tapering to base of laterally strongly convex sixth, sides of which are proximally subparallel or narrowing slightly, distally straight, junction of proximal and distal portions sharply angled or smoothly rounded. Seventh segment with sides concave basally, tip rounded.

Colour.—Carapace dorsally brownish purple, very often darker anteriorly than posteriorly; legs similar in colour with paler markings, chelae pale on outer and inner surfaces; lower surfaces pale. Specimens from mud-flats and reefs often mottled with purple, dark grey or brownish-grey (Male, 1927a, modified).

REMARKS:

Through the kindness of Edwin H. Bryan Jr. of the Bernice P. Bishop Museum, Honolulu, it has been possible to examine four specimens (two males and two females) included in the material recorded from Wake Island in the central west Pacific Ocean by Edmondson (1925: 56) as C. audouinii. These specimens are correctly referable to C. integer: H. Milne Edwards.
In the Australian Museum collections, which undoubtedly belong in *C. audouinii*, bear the locality label "Tasmania, Dec. 1896, old collection". No other collections from Tasmania contain this species; the label is very probably erroneous.

Several New South Wales specimens referable to *C. audouinii* are very similar to some specimens of *C. lavoelli* in some characters. For instance, the sixth segment of the abdomen in the male widens slightly from the base instead of tapering, the third segment in some *C. lavoelli* also widens from the base as is typical in *C. audouinii*; the shape of the coxa in the male is likewise similar. However, the pattern of felting of the ambulatory legs is strikingly different in all specimens of the two species.

Intraspecific variation in *C. granulosus* and *C. audouinii*.

The cool temperate *Cyclocarsus granulosus* can be easily separated from *C. audouinii*, which is distributed throughout warm temperate Australian shores, on the basis of a few characters such as the much stronger granulation of the carapace and ambulatory in *C. granulosus*, the absence in that species of large tufts of hairs between the bases of the ambulatory legs and of felting on the carpus.
TEXT-FIG. 15 Relative growth in Australian *Cyclograpsus* species. A, scatter diagram showing relationship between frontal width and length of the anterolateral margin, size of each circle, square, etc. proportional to number of specimens (from 1 - 4). *C. audouinii*: ○ Western Australia, ▲ South Australia, △ New South Wales and Queensland. *C. granulosus*: ● Tasmania, △ Bass Strait and Victoria. Regression lines calculated from all specimens of each species grouped into 2 mm size classes. B, relative growth of the chela in males (filled circles) and females (open circles) of *C. granulosus* from S.E. Tasmania. Regressions calculated for 2 mm size classes; a and c, c.w. up to 14 mm; b, d, c.w. 16 mm or more.
of the first ambulatory leg, all of which show almost no interspecific overlap. There are, however, numerous other characters which show more or less wide variation but nevertheless distinguish most specimens of either species.

In the early part of the study of these two species, specimens were examined from adjacent geographic areas, viz., Victoria and South Australia. The most interesting features of this material were, in each species, the striking differences in some characters, from specimens from other parts of the range and the greater dissimilarity of specimens of the two species. Thus, the Victorian C. granulosus were very strongly granular and the South Australian C. audouinii completely smooth; there also appeared to be intraspecific differences in the shape of the male chela, male abdomen and to a slightly lesser extent in the felting of the ambulatory areas.

In order to determine the amount of variation in the two species, as many characters as were reasonably amenable to analysis were selected for special study. These were of two kinds, those which could easily be measured (quantitative) or counted (meristic), e.g. length, width, etc., of the carapace, number of granules on the suborbital border; and those in which some degree of subjective grouping was required to permit analysis (qualitative). Of these
TABLE 3. Comparison of the typical appearance of 18 characters in *Cyclograpsus granulosus* and *C. audouinii*.

<table>
<thead>
<tr>
<th>Designation</th>
<th>Character</th>
<th><em>C. granulosus</em></th>
<th><em>C. audouinii</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>a</td>
<td>Greatest width of carapace</td>
<td>close to $1/3$ carapace length from front</td>
<td>almost $1/2$ carapace length from front</td>
</tr>
<tr>
<td>b</td>
<td>Lateral margins</td>
<td>widely divergent anteriorly</td>
<td>uniformly convex</td>
</tr>
<tr>
<td>c</td>
<td>Frontal margin</td>
<td>quadrilobate</td>
<td>straight or convex</td>
</tr>
<tr>
<td>d</td>
<td>Surface of carapace</td>
<td>strongly granular close to front and anterolateral edge</td>
<td>smooth</td>
</tr>
<tr>
<td>e</td>
<td>Anterior sternal segment</td>
<td>naked</td>
<td>hirsute</td>
</tr>
<tr>
<td>f</td>
<td>Carpus of first ambulatory leg</td>
<td>naked</td>
<td>terminal tuft of felt dorsally</td>
</tr>
<tr>
<td>g</td>
<td>Propodus of first ambulatory leg</td>
<td>terminal tuft of felt dorsally</td>
<td>anterior surface with 3–4 rows of felt</td>
</tr>
<tr>
<td>h</td>
<td>Dactyl of first ambulatory leg</td>
<td>3 distinct rows of felt dorsally</td>
<td>3 coalesced rows of felt dorsally</td>
</tr>
<tr>
<td>i</td>
<td>Propodus of fourth ambulatory leg</td>
<td>terminal tuft of felt dorsally</td>
<td>dorsally felted for distal $2/3$</td>
</tr>
<tr>
<td>j</td>
<td>Dactyl of fourth ambulatory leg</td>
<td>3 distinct rows of felt dorsally</td>
<td>3 coalesced rows of felt dorsally</td>
</tr>
<tr>
<td>k</td>
<td>Ventral edge of male chela</td>
<td>strongly concave at base of fixed finger</td>
<td>straight</td>
</tr>
<tr>
<td>l</td>
<td>Inner face of male chela</td>
<td>prominent central group of granules</td>
<td>single, longitudinal row of granules</td>
</tr>
<tr>
<td>m</td>
<td>Inner edge of fixed finger of male chela</td>
<td>weakly convex</td>
<td>strongly angled midway along</td>
</tr>
<tr>
<td>n</td>
<td>Gape between fingers of male chela</td>
<td>linear throughout</td>
<td>wide for basal half, linear distally</td>
</tr>
<tr>
<td>o</td>
<td>Third segment of male abdomen</td>
<td>widest basally and straight sided</td>
<td>widest distally and straight sided</td>
</tr>
<tr>
<td>p</td>
<td>Sixth segment of male abdomen (basal half)</td>
<td>edges narrowing</td>
<td>edges subparallel</td>
</tr>
<tr>
<td>q</td>
<td>Sixth segment of male abdomen (distal half)</td>
<td>concave or notched distally</td>
<td>straight</td>
</tr>
<tr>
<td>r</td>
<td>Seventh segment of male abdomen</td>
<td>straight</td>
<td>concave basally</td>
</tr>
</tbody>
</table>

Note: Intermediate characters shared by both species (where not apparent from inspection):
- c: front bilobate and medially concave
- d: surface of carapace weakly granular anterolaterally
- o: edges of segment 3 uniformly convex.
the first can be quickly dealt with.

Significant differences between the two species are hardly apparent in rigorous statistical analysis of relative growth of the carapace. Although at first glance there are apparent differences in the shape of the carapace, this is masked by very large variation. Only in the relationship between the width of the front and the length of the anterolateral margin are there significant differences (text-figure 15A). Here, the test for significance of the difference between the regressions for the two species gives the highly significant value for \( t \) of 4.50 (method as in Simpson & Roe, 1939: 277-9, see appendix 1). 

\( C. \text{ granulosus} \) has a slightly broader and shorter anterolateral margin. The values of \( b \) (in the equation \( y = a + bx \)) are very similar for the two species (\( C. \text{ granulosus} \), 0.310; \( C. \text{ audouinii} \), 0.315) but the \( a \) values show a much greater difference (−0.39 and +0.20 respectively).

There is very close similarity in the number of suborbital granules in the two species, the average number in \( C. \text{ granulosus} \) being just less than 16 (range in 90 specimens, 12-19) and in \( C. \text{ audouinii} \) just less than 17 (13-20 in 73 specimens).

Relative growth of the chela shows little interspecific difference. Text-figure 15B shows the data for
TEXT-Fig. 16 Geographic variation in Australian Cyclograpsus species. A - C, variation in individual characters and D, mean of summated values for 17 characters. The lines connect percentage of the sample (plotted vertically) showing the character typical for each of the two species from nine areas. For further explanation see text.
the typical characters of the species; low values also suggest feature 1 but the opposite of 2.

Scrutiny of table 4 and text-figure 16 indicates, as suggested by the examination of the samples from South Australia and Victoria mentioned initially, that in several characters the adjacent peripheral populations (and presumably sympatric ones as well) of each of the two species are the more strongly differentiated. Examples of such characters are the degree of hairyness of the sternum (character e), presence of felt on the fourth ambulatory propodus (i) and the shape of the sixth abdominal segment in the male (p) (text-figure 16A) which show this trend in both species; and the shape of the lateral margin of the carapace (a), the form of the frontal margin (c) and the shape of the third abdominal segment in the male (o) (16C) in which this trend is apparent in C. granulosus but hardly evident in C. audouinii. Most of the other characters show a mixture of trends, populations of C. audouinii in the western part of its range (Western and South Australia) showing stronger development towards the region of sympathy and those in the east, weaker development. In some characters in both species there appears to be a tendency towards greater similarity at the adjacent peripheries of their range (16B). A similar trend is apparent in the frontal width/anterolateral margin length relationship.
TABLE 4. Percentage occurrence, in pooled samples from nine regions, of typical appearance of 17 characters in Australian *Cyclograpsus* species. The number after each region is the number of specimens in the sample (and the number of males). For meaning of characters see Table 3.

<table>
<thead>
<tr>
<th>Character</th>
<th>C. audouinii</th>
<th>C. granulosus</th>
<th>C. audouinii</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Geographical Regions</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>CWA¹</td>
<td>SWA²</td>
<td>SA³</td>
</tr>
<tr>
<td>a</td>
<td>83(10)</td>
<td>90(17)</td>
<td>77(12)</td>
</tr>
<tr>
<td>b</td>
<td>83(6)</td>
<td>98(12)</td>
<td>83(6)</td>
</tr>
<tr>
<td>c</td>
<td>42(6)</td>
<td>55(12)</td>
<td>54(6)</td>
</tr>
<tr>
<td>d</td>
<td>100(12)</td>
<td>79(12)</td>
<td>92(12)</td>
</tr>
<tr>
<td>e</td>
<td>100(12)</td>
<td>88(12)</td>
<td>100(12)</td>
</tr>
<tr>
<td>f</td>
<td>100(12)</td>
<td>95(12)</td>
<td>100(12)</td>
</tr>
<tr>
<td>g</td>
<td>0(6)</td>
<td>2(6)</td>
<td>30(6)</td>
</tr>
<tr>
<td>h</td>
<td>25(6)</td>
<td>64(6)</td>
<td>69(6)</td>
</tr>
<tr>
<td>i</td>
<td>92(6)</td>
<td>74(6)</td>
<td>62(6)</td>
</tr>
<tr>
<td>j</td>
<td>90(6)</td>
<td>100(6)</td>
<td>50(6)</td>
</tr>
<tr>
<td>k</td>
<td>90(6)</td>
<td>88(6)</td>
<td>50(6)</td>
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<tr>
<td>l</td>
<td>70(6)</td>
<td>76(6)</td>
<td>92(6)</td>
</tr>
<tr>
<td>m</td>
<td>80(6)</td>
<td>47(6)</td>
<td>92(6)</td>
</tr>
<tr>
<td>n</td>
<td>70(6)</td>
<td>41(6)</td>
<td>100(6)</td>
</tr>
<tr>
<td>o</td>
<td>70(6)</td>
<td>71(6)</td>
<td>83(6)</td>
</tr>
<tr>
<td>p</td>
<td>90(6)</td>
<td>94(6)</td>
<td>92(6)</td>
</tr>
<tr>
<td>q</td>
<td>40(6)</td>
<td>88(6)</td>
<td>92(6)</td>
</tr>
</tbody>
</table>

¹Western Australia from Rottnest I. to Bunbury, ²Western Australia from Albany to Recherche Archipelago, ³South Australia, ⁴Victoria, ⁵Bass strait, ⁶North Coast of Tasmania, ⁷South-eastern Tasmania, ⁸New South Wales, ⁹Queensland.
Then all the characters are considered together (10 b), the concept of greater dissimilarity around the region of sympathy is still supported, despite the mixture of trends.

3.23.2 The non-Australian southern temperate species of *Cyclograpsus*

*Cyclograpsus lavauxi* H. Milne Edwards

Text-fig. 12 a-e, 14 a-c. Pl. 3C, 7C

*Cyclograpsus audouinii* Dana, 1853b: 359; 1855: pl. 23 fig. 2 (Not *Cyclograpsus audouinii* H. Milne Edwards, 1837: 72.)

*Cyclograpsus lavauxi* H. Milne Edwards, 1853: 197.

*Cyclograpsus lavauxi* Miers, 1876: 41. Filhol, 1886: 390, pl. 41, fig. 4-6. Thomson, 1913: 238. Chilton & Bennett, 1923: 770. Richardson, 1949a: 34. Bennett, 1956: p. 64, fig. 98-100. Campbell & Griffin, 1966: 141, 143, text-fig. 3B, 5B; pl. 20, fig. 4; pl. 23, fig. 4.


**TYPES:**

*C. lavauxi*. - Lectotype (selected on the advice of J. Forest), a male, carapace width c 23 mm, New Zealand,
G. Lavaux; Museum National d'Histoire Naturelle, Paris. This specimen lacks the right second and left first ambulatory legs but is otherwise in excellent condition.

C. whiteli. - Holotype, a female, carapace width 27 mm, New Zealand; Museum National d'Histoire Naturelle, Paris. The carapace of this specimen is slightly cracked close to the midline posteriorly, but otherwise in excellent condition.

MATERIAL EXAMINED: A total of 22 specimens (11 males, 11 females, carapace width 8.5 - 20 mm).
New Zealand: Sandy Beach, Bay of Islands; Waiheke I., Auckland; Waihou B., eastern Bay of Plenty; Waitere Beach, Levin; Kau Ft. and Island Bay, Wellington; Pulling Ft., Otago Harbour.

DISTRIBUTION:
Throughout New Zealand, from Bay of Islands in the north to Otago Harbour in the south; not extending outside New Zealand.

DESCRIPTION:
Carapace. - Broader than long, widest about 1/4 carapace length from front, postero-lateral margins subparallel. Surface smooth or very weakly granular antero-laterally and close to frontal margin. A microscopically granular,
Elevated ridge extending around unbroken margins.

Regions poorly defined, gastrocardiac groove prominent. Punctulations absent except for a shallow one antero-laterally, midway between external orbital angle and gastrocardiac groove.

Front wall deflexed, barely visible in dorsal view, convex to weakly bilobate, median frontal furrow prominent, extending to opposite widest part of carapace.

Orbits with posterior edge uniformly concave to sub-quadrato, sometimes sloping obliquely posterolaterally, junction with front sharp, outer angle a sharp point, not advanced as far as level of front.

Suborbital ridge composed of about 14 strong, irregular granules.

Chelipeds: Carpus smooth except for a minutely granular area at dorso medial angle.

Chela of male longer than deep, compressed, dorsal and ventral edges of palm subparallel, surface smooth except for a strongly granular longitudinal ridge medially on inner face. Ventral edge of chela straight or very weakly concave at base of fixed finger. Fingers gaping as an almost right angled triangle for about proximal third, narrow and linear beyond this, dentication weak, uniform; fixed finger weakly convex midway along inner edge, weakly concave distally.
Ambulatory legs. - Long (second leg about 1.4 times
carapace width), surfaces generally smooth; dactyli long
and slender.

First leg with carpus naked. Propodus moderately
flected on dorsal surface for distal half, anterior surface
with slender median line of felt for about the distal half
of the segment, shorter and even more slender indistinct
rows anteroventrally and posteroventrally. Dactyli with
6 distinct, slender longitudinal rows of felt extending
entire length, three dorsal ones wider than others.

Second and third legs with propodi bearing a distal
transverse row of felt on dorsal surface extending for
distal two-thirds, narrowing proximally. Dactyli with
6 rows of felt, 3 dorsal ones very wide, hardly distinct,
others very sparse.

Moderately long tufts of hair arising from between
bases of first and second, and second and third ambulato-
ries, absent from between third and fourth.

Sternum. - Anterior 2 segments very sparsely pubescent,
second segment almost naked.

Male abdomen. - Third segment convex laterally or with
edges almost straight and widening slightly distally to
just short of distal edge, following segments tapering to
base of sixth segment, sides of which are strongly convex,
subparallel for proximal half, distally narrowing,
junction of proximal and distal portions smoothly rounded, seventh segment such narrower than sixth, wide proximally, distally rounded.

Colour: Carapace pale yellow, notched red anterically; legs similar with irregular red mottling dorsally; lower surface of body and ambulatores and both outer and inner surfaces of chelae pale.

Remarks:

Examination of photographs, kindly forwarded by Dr. J. Forest, of the lectotype of C. lavauni and of the holotype of C. whitei, strongly suggests that the two are in fact conspecific, as Chilton (1911) and students of the New Zealand Crustacea before him had considered. Certainly, the descriptions given of the two species by Milne Edwards (1853) were too inadequate to allow ready discrimination between the two. However, when confronted by a large series of specimens, Chilton & Bennett (1933) recognised two species and must naturally have assumed that one was C. whitei. The characters attributed to the latter species by Chilton & Bennett do not exist in the holotype of C. whitei but for the most part typify the recently described C. insularum Campbell & Griffin, 1966. The specific name lavauni is used for this species to avoid confusion with C. insularum which has been characterized
TYPES:

C. punctatus. - Holotype, a male, carapace width c 31 mm, Indian Ocean, M. Reynaud; Musée National d'Histoire Naturelle, Paris. The right cheliped and carpus and following segments of the left third ambulatory leg are missing, but the specimen is otherwise in perfect condition.

C. reynaudi. - Holotype, a male, carapace width c 22 mm, False Bay, M. Reynaud; Musée National d'Histoire Naturelle, Paris. This specimen is intact. Details of the types and type localities of the other synonymous species are given by Rathbun (1918a) and by Garth (1957).

MATERIAL EXAMINED: A total of 13 specimens (9 males, 4 females, carapace width 10.0 - 37.8 mm), South Africa.

DISTRIBUTION:

South Africa, from Port Nolloth on the west coast to Natal on the east coast (Barnard). Chile, from Los Vilos to San Vicente; Juan Fernandez I. (Garth).

DESCRIPTION:

Good descriptions of this species were given by Rathbun (1918a) and by Barnard (1950).
REMARKS:

The form of the male first pleopod of this species (text-figure 14 a-c) immediately sets it apart from any of the other species of _lograp_ discussed here. Other differences are to be found in the shape of the abdomen in the male, the sixth segment in _C. punctatus_ being more sharply angled midway along its lateral edge, in the chela of the male, the ventral edge being more convex basally, the gape wider and the inner surface of the palm less tuberculate, and in the pattern of felting on the first and fourth ambulatory legs. The shape of the abdomen in _C. cinereus_ Dana, the other Chilean Cyclograapsus, immediately sets it apart from _C. punctatus_ (see Rathbun, 1918a, pl. 98).

The conspecific unity of South African and Chilean specimens is attested to by Rathbun (1918a) who examined specimens from both areas; attempts by me to obtain Chilean material have been unsuccessful. This species was recorded by Stimpson (1907) from Hong Kong; that locality is quoted by Rathbun (1918a) without comment but its existence there seems doubtful.
3.23.3 Remaining Tasmanian Sesarmidae

Genus Holograpaena Campbell & Griffin, 1966

Holograpaena haswellianus (Whitelegge)

Pl. 2C

Restricted synonymy:

Chasmagnathus conversus Haswell, 1882a: 550. Not

Chasmagnathus conversus de Haan, 1835.

Chasmagnathus haswellianus Whitelegge, 1889: 229.

Holograpaena haswellianus; Campbell & Griffin, 1966: 135,
text-fig. 1B, 2B; pl. 20, fig. 2; pl. 23, fig. 2
(synon.).

MATERIAL EXAMINED: A total of 135 specimens (75 males,
60 females, carapace width 5 - 21 mm).

Tasmania: Montague R.; Detention R.; Don R. at Don;
Gravelly Beach, Tamar R.; Boggy Ck.; Double Ck.;
Blackman B. at mouth of Bream Ck.; Jordan R. near
Bridgewater; near Restdown Pt.; Risdon Cove; Elwick B.;
Bellerive; Brown's R.; Howden; Margate; Lower Egg I.;
Huon R. at Franklin;

LOCALITIES PREVIOUSLY REPORTED:

South Australia: Port R.; Murray R. (Hale, 1927a).
Tasmania: Brown's R. (Tweedie, 1942). New South Wales:
Shoalhaven (Haswell, 1882); Port Jackson (Whitelegge).


21 localities from Port Adelaide R. (South Australia) to Pioneer R. (Queensland), doubtfully Darnley I.

(Campbell & Griffin, 1966).

DISTRIBUTION:

Confined to Australia, from Pioneer R. (Queensland) in the north east to Port Adelaide R. (South Australia) in the south east and throughout Tasmania.

REMARKS:

A full description of this species is given in Campbell & Griffin (1966). The carapace is slate clive to dark chocolate or reddish in colour, with variable paler mottling. The upper surfaces of the legs are similar in colour to the carapace but with increased mottling. The dorsal surfaces of the carpus of the cheliped and chela are raw umber fading to cream ventrally. The lower surfaces are pale cream (Campbell & Griffin).

The species was shifted from its place in Helice de Haan to a new genus because the inner margin of the orbit is not oblique but forms a distinct angle with the front of the carapace, the front is broad, the male abdomen tapers regularly and the epistome does not project beyond the front in dorsal view. In these four characters H. haswellianus differs strongly from species of Helice.
Genus *Paragrapbus* H. Milne Edwards, 1853

*Paragrapbus quadridentatus* (H. Milne Edwards)

Pl. 2D

Restricted synonymy:

*Cyclograpbus quadridentatus* H. Milne Edwards, 1837: 79.

*Paragrapbus quadridentatus*; Campbell & Griffin, 1966: 160, text-fig. 8A, 1OA; pl. 22, fig. 1; pl. 23, fig. 9

(synon.).

MATERIAL EXAMINED: A total of 78 specimens (45 males, 33 females, carapace width 6-26 mm).

**Tasmania:** North Pt.; Wynyard; Ulverstone; Green's Beach, Kelso; Low Head; Pirate's Bay; Pittwater; C. Direction; Bellerive; Sandy B.; Kingston; Houtden; Ninepin Pt.; Adventure B., Bruny I.; Huon R. at Lymington.

LOCALITIES PREVIOUSLY REPORTED:

**Tasmania:** North coast (of Tasmania) (Haswell, 1882b);

Brown's R. (Tweedie, 1942); Southport & Eaglehawk Neck (Guiler, 1952a); Swansea; Recherche L. (Guiler, 1956). Three localities from Lady B. (Victoria) to King I., Bass Strait (Campbell & Griffin, 1966).

**DISTRIBUTION:**

Restricted to south-eastern Australia (Victoria and Tasmania).
REMARKS:

A full description of this species is given by Campbell (in Campbell & Griffin, 1966). \textit{P. quadridens} is easily distinguished from the two other species of \textit{Paragrapbus} by its possession of only one tooth behind the external orbital angle.

The dorsal surface of the carapace is greenish grey or pale brown in colour. The legs are similar but tinged with pink or purple. The carapace is spotted dorsally with irregular, very dark spots sparsely distributed, at least posteriorly, with more numerous microscopic spots scattered amongst them. The legs and dorsal surfaces of the chelae possess only scattered microscopic spots. The under surfaces are pale cream (Campbell & Griffin).

\textit{Paragrapbus gaimardii} (H. Milne Edwards)

Pl. 4A, 7E.

Restricted synonymy:


\textit{Paragrapbus gaimardii;} Campbell & Griffin, 1966: 160, 164, text-fig. 9A, 10B; pl. 22, fig. 3; pl. 23, fig. 11 (synon.).
MATERIAL EXAMINED: A total of 100 specimens (55 males, 45 females, carapace width 5 - 37 mm).

**Tasmania:** Detention R.; Crayfish Ck.; Inglis R.; Wynyard; Forth R.; Emu B.; Swan B., Tamar R.; George B.; Boggy Ck.; Triabunna; MacLaine's Ck.; Double Ck.; Prosser R. at Orford; Blackman B. at mouth of Bream Ck.; Dunalley B.; Eaglehawk B.; Pittwater; Coal R.; Pipe Clay Lagoon; Ralph's B.; R. Derwent at Bridgewater; Elwick B.; Sandy B.; Brown's R.; Howden; Oyster Cove; Isthmus B., Bruny I.; Huon R. at Franklin and Lymington; Southport; Lune R. estuary; Strahan.

LOCALITIES PREVIOUSLY REPORTED:

South Australia: common (Hale, 1927a). Victoria:

Pt. Phillip (Haswell, 1862b). **Tasmania:** North coast (Haswell, 1862b); Brown's R.; Sandy B. (Tweedie, 1942); George's B.; Ralph's B.; Pipe Clay Lagoon; Dodges Ferry (Guiler, 1952a); all sheltered (Tasmanian) coasts (Guiler, 1956).

3 localities from Coorong (South Australia) to Queenscliff (Victoria) (Campbell & Griffin, 1966).

DISTRIBUTION:

Restricted to south-eastern Australia, from Adelaide in the west through Victoria and throughout Tasmania.
REMARKS:

A full description of this species is given by Campbell (in Campbell & Griffin, 1966). The dorsal surface of the carapace is yellowish brown in colour with dark spots on all surfaces visible in dorsal view. On the anterior half of the carapace the spots are smaller but more tightly packed, sometimes running together to form large blotches. The spots extend on to the undersurfaces anteriorly, on the anterior surfaces of the ambulatory legs and on all surfaces of the distal three segments. The lower surfaces are otherwise grey or cream. The outer surfaces of the chelae are orange, especially dorsally (Campbell & Griffin, 1966).

Paragrapus laevis (Dana)

Pl. 4B, 7F.

Restricted synonymy:

Chasmagnathus laevis Dana, 1853a: 252.

Paragrapus laevis; Campbell & Griffin, 1966: 160, 162, text-fig. 8B, 10C; pl. 22, fig. 2; pl. 23, fig. 10 (synon.).

MATERIAL EXAMINED: A total of 66 specimens (49 males, 17 females, carapace width 5.5 - 37.4 mm).

Tasmania: MacLaine's Ck.; Double Ck.; Prosser R. at Oxford; Blackman B. at mouth of Dream Ck.
LOCALITIES PREVIOUSLY REPORTED:

Victoria: Pt. Phillip; Western Port; Lake's Entrance
(Fulton & Grant). New South Wales: Sydney (Haswell, 1882b); Pt. Jackson (Miers, 1884). Queensland: Pt. Mollo
(Haswell, 1882b); Brisbane R. (Snelling, 1959 - as Paraerapsus gaimardii; Campbell, personal communication)

16 localities from Port Phillip (Victoria) to
Brisbane R. (Queensland) (Campbell & Griffin, 1966)

DISTRIBUTION:

Restricted to eastern Australia, from Moreton B.
(Queensland) in the north, through Victoria to south-eastern
Tasmania. Its presence in Tasmania is now fully confirmed;
previously its existence here had been supported by only
one specimen in the Australian Museum collections (AM P7418).

REMARKS:

A full description of this species is given by
Campbell (in Campbell & Griffin, 1966). The carapace and
legs are covered dorsally with small dark red spots which
run together but leave irregular bare spots. These bare
areas are most common posteriorly on the carapace and on
the legs. Anteriorly, the red spots are much denser,
usually running together completely to form a solid red
area with few pale spots. The carpus of the cheliped and
chela are red dorsally, fading to cream ventrally
(Campbell & Griffin, 1966).
Campbell has dealt briefly with the differences between *P. gaimardii* and *P. lacvis* and has commented upon one specimen from Victoria which appears to be intermediate between the two species in at least nine characters. Figures provided there show the rather different appearance of this specimen, a large male, from either *P. gaimardii* or *P. lacvis*.

Examination of 30 specimens (mainly adult males) from eastern Tasmania similarly reveals rather striking differences, in some characters, from the mainland specimens of this species (according to the descriptions and illustrations by Campbell). This is particularly true of four characters:

1. The felting of the propodus of the first ambulatory leg;
2. the felting of the propodus of the fourth ambulatory leg;
3. the raising of the second sternite above the first in the males; and
4. the shape of the sixth segment of the abdomen in the male.

Thus, in the 30 specimens examined, the felt on the anterior surface of the first ambulatory propodus is rather clearly divided by a thin longitudinal naked strip, instead of covering the whole surface except for a naked distal strip centrally, in 9 specimens (32%); the felt on the dorsal surface of the fourth ambulatory propodus is confined to the distal third, instead of extending for
two-thirds of the length, in 12 specimens (43%); the second sternite is raised above the first, instead of the junction between the sternites being smooth, in 13 (53%) of the 24 males; and lastly, 7 males (35%) have the sixth segment almost twice as broad as long rather than only $1\frac{1}{2}$ times as broad as long.

There also appear to be intraspecific differences in the width between the external orbital angles compared to the greatest width of the carapace, the depth of the division between the two frontal lobes, the prominence of the postfrontal lobes and the granulation of the inner surface of the chela in the male. All Tasmanian specimens are mostly dark red in colour as is typical in $P.$ laevis. In most characters, particularly granulation of the inner surface of the chela, felting of the ambulatory appendages and form of the junction between the first and second sternites, there are marked changes with growth.

Although there would thus appear to be some consistent differences between these Tasmanian specimens and the mainland ones it must be emphasized that in all cases the former are still easily separated from specimens of $P.$ gainardii, in which the front is very weakly concave or straight and forwardly projecting as a shelf, the felt on the first ambulatory propodus is confined to the ventral surface where it occupies the distal two-thirds, and the fourth ambulatory propodus bears only a ventral tuft of felt distally.
These changes in appearance parallel the situation described above for the Australian *Cyclograpsus* species, although the tendency appears to be towards slightly greater similarity of *P. laevis* to *P. gaimardii*. Geographical intraspecific differences also exist in *P. gaimardii*. For instance, Campbell mentions that the distal patch on the fourth ambulatory propodus is better developed in Victorian than in Tasmanian specimens of *P. gaimardii*.

3.24 Subfamily PLACUSIINAE

**Genus Plagusia de Haan, 1835**

*Plagusia capensis* de Haan

Text-fig. 17-24 Pl. 5A, 6C

**Synonymy:**

*Cancer chabrus* Linnaeus, 1758: 628; 1764: 438.


Placusia guinosa Macleay, 1835: 66 (type locality: South Africa)


The following species, all based on the megalopa stage, are also generally included in the synonymy of this species:

Haeastia nutica Krauss, 1843: 54

Haeastia elegans Dana, 1852b: 448, pl. 31 fig. 2a-i.

Haeastia paederus Stebbing, 1910: 348

Haeastia mawsoni Rathbun, 1916b: 1

TYPES AND TYPE LOCALITIES OF Cancer chabrus AND Placusia capensis:

Cancer chabrus Linnaeus: type locality: "In Mari Indico"; type not extant.

Placusia capensis de Haan: lectotype (selected on the advice of L.B. Holthuis), a female, carapace length 40 mm, carapace width 44 mm, labelled "Kaap de Goede Hoop" (Cape of Good Hope), leg H.B. van Noortok, 1826-1834 and bearing registered number Crust.
TEXT-FIG. 17. Morphological variation in some features of Plagusia species: a, P. capensis de Lann, male, carapace length 39.9 mm (USNM 219.62), Castlepoint, New Zealand; b, male, c.l. 36.2 mm (USNM 1986), Lottin Pt., New Zealand; c, dentipes de Lann, male, c.l. 36.8 mm (USNM 221.62), Lottin Pt., New Zealand; d, female, c.l. 15.6 mm (USNM 9013), Garden L., Western Australia; e, female, c.l. 14.5 mm (USNM 212.62), Western Australia; f, male, c.l. 19.2 mm (USNM 238.62), Lottin Pt., New Zealand; g, male, c.l. 26.7 mm (USNM 9013), Garden L., Western Australia; h, female, c.l. 43.2 mm (USNM 33234), Easter I., suborbital border (L.D.): i, male, c.l. 33.2 mm (USNM 214.62), Lottin Pt., New Zealand; j, female, c.l. 38.1 mm (USNM 214.62), Lottin Pt., New Zealand; k, male, c.l. 41.8 mm (USNM 214.62), Lottin Pt., New Zealand; l, male, c.l. 44.0 mm (USNM 33234), Easter I., suborbital border (L.D.).

Abbreviations: a, antennule; a', antenna; a.m., anterior border of mouthfield; b.a., basal antennal article; c, eye; e.o., external orbital spine; f, front; s.o., suborbital border. 1–g, P. capensis, variation in ornamentation of inner lobe of left basal antennal article: h, male, c.l. 37.9 mm (USNM 221.62), South Africa; i, male, c.l. 38.9 mm (USNM 1986), Castlepoint, New Zealand; j, male, c.l. 44.0 mm (USNM 219.62), 1 m., of Frenchman L., Western Australia; k, female, c.l. 44.9 mm (USNM 221.62), Kadar Head, Lottin Pt., Western Australia; l, male, c.l. 50.5 mm (USNM 9013), Garden L., Western Australia; m, male, c.l. 43.3 mm (USNM 1986), Castlepoint, New Zealand; n, P. dentipes de Lann, male, c.l. 45.2 mm (USNM 33234), Easter I., inner lobe of left basal antennal article.

1–a, P. capensis, anterior border of mouthfield: b–d, female, c.l. 14.5 mm (USNM 212.62), Western Australia; e, male, c.l. 15.6 mm (USNM 9013), Garden L., Western Australia; f, male, c.l. 26.7 mm (USNM 9013), Garden L., Western Australia; g, male, c.l. 36.8 mm (USNM 9013), Garden L., Western Australia; h, male, c.l. 36.2 mm (USNM 22034), Easter I., western Australia; i, male, c.l. 36.2 mm (USNM 22034), Easter I., western Australia; j, female, c.l. 36.2 mm (USNM 22034), Easter I., western Australia; k, male, c.l. 36.2 mm (USNM 22034), Easter I., western Australia; l, female, c.l. 36.2 mm (USNM 22034), Easter I., western Australia; m, male, c.l. 36.2 mm (USNM 22034), Easter I., western Australia; n, male, c.l. 36.2 mm (USNM 22034), Easter I., western Australia; o, male, c.l. 36.2 mm (USNM 22034), Easter I., western Australia; p, female, c.l. 36.2 mm (USNM 22034), Easter I., western Australia; q, male, c.l. 36.2 mm (USNM 22034), Easter I., western Australia; r, female, c.l. 36.2 mm (USNM 22034), Easter I., western Australia; s, female, c.l. 36.2 mm (USNM 22034), Easter I., western Australia; t, male, c.l. 36.2 mm (USNM 22034), Easter I., western Australia; u, female, c.l. 36.2 mm (USNM 22034), Easter I., western Australia; v, male, c.l. 36.2 mm (USNM 22034), Easter I., western Australia.
TEXT-FIG. 17. MORPHOLOGICAL VARIATION IN SOME FEATURES OF \textit{PLAGUSIA} SPECIES (FOR EXPLANATION SEE OPPOSITE).
D. 2216. Rijksmuseum van Natuurlijke Historie,
Leiden. The specimen is intact.

STATUS OF THE NAME Cancer chabrus Linnaeus, 1758.

The original description of Cancer chabrus was extremely short and hardly diagnostic but it was followed by a slightly longer one in Mus. Ludov. Ulr. 1764, p. 438. Study of this latter appears to confirm that the specific name chabrus was correctly applied by later authors following White’s transference of it to Planusia. In this combination the name chabrus has been used at least twenty nine times. Several workers (at least nine), notably Stolling (1903), have preferred to use de Haan’s name canensin for the species and Dr. Isabella Gordon (quoted by Richardson, 1949b: 130) considers that this name is better used. The types of species chabrus are not extant but those of canensin are in good condition in the Rijksmuseum van Natuurlijke Historie, Leiden (see above). According to Dr. L.B. Holthuis (personal communication, January, 1966), the following possibilities are available for fixing the name of this species.

1, selection of a neotype for Cancer chabrus;
2, petitioning of the International Commission of Zoological Nomenclature for use of their plenary powers to invalidate Linnaeus’s name.

The first procedure has the advantage of conforming to the most often used name, the second has the disadvantage
of leaving a specific name unused.

In the present report, the name *capensis* is retained pending implementation of the first of the above procedures. It is intended that the lectotype selected above for *P. capensis* will be also designated the neotype of *Cancer chabrus* Linnaeus.

**MATERIAL EXAMINED:** A total of 31 specimens (41 males, 39 females, carapace length 8.2 - 71.2 mm).

**Australia:** Western Australia: Lancelin I.; reef flat at Yanchep; West End Reef and Radar Reef, Rottnest I.; Fremantle; Garden I.; Clifton St. Beach, Bunbury; Russellton; Chatham I., near Nozmalup; Albany; 1 m. E. of Frenchman B., Albany; Cheyne Beach; Hopetoun; Esperance; South Australia: "South Australia".

**Victoria:** Pt. Phillip. Bass Strait: Currie Harb., King I. Tasmania: "Tasmania"; off Stanley; Eddystone Pt.; Grant Pt.; Eichano; Sleepy B.; C. Forestier; Maria I.; Fossil I., Pirates B.; Tasman I.; Adventure B., Bruny I. New South Wales: Shell Harbour; S.W. Rocks, Trial Harb.; Hungry Pt., Port Hacking; Port Jackson; Coogee; Long Reef, Collaroy; Bondi Beach; Fort Denison; Fairy Bower, Manly.

**New Zealand:** Goat I. Beach, Leigh; Otatau I., Auckland; Lottin Pt., C. Runaway; Castlepoint.

**South America:** Juan Fernandez I.

**South Africa:** "South Africa".
LOCALITIES PREVIOUSLY REPORTED:


New Zealand: Eighteen localities from Doubtless E. in the north to Otago in the south (Chilton & Bennett, 1929; Bennett, 1964); "rare in the south, common in the north" (Bennett, 1964).


South America: Five localities from Bay of Taltal in the north to Los Vilos in the south; Juan Fernandez (Garth, 1957).


DISTRIBUTION:

A circumpolar southern hemisphere cool temperate species confined to the Indo-Pacific.
DESCRIPTION:

Carapace.—As wide as long, greatest width about \( \frac{1}{2} \) carapace length from front, lateral margins convex, bearing anterolaterally three equidistant, strong, forwardly directed, sharp, subtriangular spines, the last at widest part of carapace. Surface mostly smooth, covered nearly everywhere by a mat of short curled hairs. A shallow, semicircular groove centrally. Three short, oblique, weakly tuberculate ridges on branchial regions posterolaterally close to edge; a naked, blunt tubercle just behind, and slightly medial to, each orbit; a pair of sharp spines situated transversely immediately behind front.

Front weakly concave and deflexed, bearing 10-14 broad spines or blunt tubercles around edge. A shallow medial groove extending from weak central notch on edge of front back to opposite posterior border of orbit.

Orbits deep, U- or V-shaped, margins smooth, weakly notched medially, inwardly bearing a strong, blunt spine anteriorly, outer margin formed by a broad, strong, weakly curved spine. Suborbital border a ridge of 6-15 flattened spines variously grouped into lobes.

Antennular fossae deeply incised into front, narrow, U-shaped, bounded laterally by a vertically bilobate ridge. Antennules folding longitudinally and almost vertically.
Basal antennal article L-shaped, consisting of a slender vertical lobe medially, and broad, short, horizontal portion laterally, the former terminating in about three spinules or tubercles, medial edge minutely spinulose. Antennae short.

Anterior border of mouthfield with a narrow incision medially and bearing on each side a single submedial spine and, separated from this by a broad U-shaped hiatus, three broad flattened lobes variously incised into smaller lobes or spines.

Third maxillipede.- Merus subquadrate, lateral edge bearing midway along a lobe with several low tubercles in a transverse row, surface basomedially raised and very weakly tuberculate, at least more distally.

Chelipede.- Moderately long and enlarged in the adult male, ischium, merus and carpus subtrigonal, chela strongly compressed.

Ischium with two ventral ridges each of 4-7 blunt spines.

Merus with three strongly spinous or tuberculate ridges, spines of ventromedial and dorsal ridges long, those of ventrolateral ridge short.

Carpus with blunt spines in six rows dorsally and laterally, spines in mid-dorsal rows sharper, medial 3 rows short, others extending full length of carpus,
TEXT-FIG. 19. Right third ambulatory leg, posterior aspect, of Plagusia capensis de Llana (a - e) and of P. denisei de Llana (g) and left third maxilliped, outer aspect (f), of P. capensis: c, e and f, male, c.l. 62.8 mm (DM Cr 1223), Castlepoint, N.Z.; g, male, c.l. 45.2 mm (USNM 33231), Easter l. a - d, merus only: a, male, c.l. 18.1 mm (SAM), South Africa; b, male, c.l. 56.4 mm (WAM 5013), Garden l., W.A.; d, male, c.l. 71.2 mm (TM), Tasmania.
lateral 3 rows proximally convergent.

Chela in adult male massive, deep, enlarged towards distal part of palm. Palm with 3 lobate ridges extending longitudinally along outer surface, each ridge divided longitudinally into two parts, a narrow dorsal row of close-set, large, rounded tubercles and a broad ventral part comprising smaller scattered tubercles. Ventral surface with a single ridge, outwardly distinctly lobate, inwardly comprising small scattered tubercles. Dorsal surface bearing three single rows of laterally compressed tubercles, those towards inner surface spinous. All ridges separated by broad areas covered by a dense mat of curled hairs. Inner surface with scattered tubercles, in rows which are sometimes ill-defined, more dense ventrally and in a group distally towards dorsal surface, otherwise smooth. Fingers short, widely gaping throughout their length, inner edges bearing a few large blunt teeth, fixed finger inwardly excavate and spooned distally. Dactyl with a single lobate ridge on outer surface and a mid-dorsal and mid-ventral ridge leaving a single medial smooth area on inner surface; all ridges bearing numerous large tubercles basally, tubercles decreasing in number and size distally; distal half of dactyl smooth. Fixed finger weakly bent from palm, with a mid-ventral ridge only and smooth distally.
Chela in juvenile and adult female small, palm tapering slightly distally, fingers as long as palm, inner edges adjacent throughout their length.

Ambulatory legs.—Long, third the longest (about twice length of carapace), second slightly shorter, strongly compressed, bases and ischia subcylindrical, meri subtrigonal. Long hairs in a dense fringe on posterior surfaces arising from ventral ridge on meri, from both dorsal and ventral ridges of carpi and propodi and from dorsal ridge of dactyli.

Coxae with an erect, truncate or spinate flattened lobe arising posteriorly.

Meri rather deep, dorsal edge convex, bearing numerous short, compressed, distally curved, sharp spines, the most distal the largest; surface covered by a dense mat of curled hairs in three narrow rows on anterior surface and in three very broad rows on posterior surface separated by two narrow longitudinal ridges, the more dorsal finely serrate along its upper edge, the more ventral one smooth. A narrow mid-ventral area of hairs bounded by two ridges extending whole length of meri.

Carpi and propodi with five narrow, elevated, smooth ridges, one dorsal, two ventral, one on anterior surface and one on posterior surface; a dense mat of curled hairs between ridges.
TEXT-FIG. 20. Male right first pleopods of *Pegasus* species: a–c, *P. capensis* de Haan. Male, c.1. 62.8 mm (USNM 1221), Castle Point, New Zealand. d–f, *P. dentipes* de Haan. Male, c.1. 32.2 mm (USNM 45534), Mitasaki, Japan. Tip in abdominal aspect to the left and in sternal aspect to the right, whole pleopod in abdominal aspect in the centre.
Dactyli ventrally bearing two rows of stout, spine-like hairs.

**Sternum.** - In male covered by short curled hairs, surface close to edge of each sternite usually naked and smooth; tuberculate lobules sometimes projecting in from edge.

**Male abdomen.** - Of seven segments, all wider than long, first two segments very short, narrowing distally; widest at base of third segment; following segments tapering, laterally very weakly concave, sixth segment weakly convex laterally, seventh segment subtriangular, proximal width slightly exceeding length, edge laterally weakly concave, tip rounded. Surface covered by a fine mat of hairs leaving naked only a broad transverse line across each segment not far from base and another close to distal edge, the two joined by a central longitudinal naked ridge, a naked area also around lateral edge; central ridge of sixth segment extending from base of segment to transverse ridge, in seventh segment only central longitudinal ridge and marginal ridges present.

**Male first pleopod.** - Stout, trigonal, medially strongly concave, distally slightly expanded, tip truncate; groove on sternal surface close to medial edge terminating in a large sternal flap. Tip bearing short, stout hairs completely encircling a short, broad, concave, horny apical process, surface of pleopod elsewhere naked.
Colour.- Carapace, chelipeds and ambulatory legs various shades of red, naked ridges on dorsal surfaces darker, hairs yellowish. Undersides pale or creamy.

REMARKS:

3.24.1 Variation in Plagusia capensis

In assessing the variation within and between populations of _P. capensis_ particular attention was paid to the following characters:

1. Carapace: total length, width at the third, second and first lateral spines, interorbital width and frontal width; number of tubercles on the front, anterior border of the mouthfield and suborbital border and number of spinules or tubercles around the tip of the inner lobe of the basal antennal article; degree of tuberculation of the carapace behind the orbits and close to the posterolateral edge and of the sternum and abdomen of the male.

2. Chelipeds: length and height of the chela; arrangement of tubercles on carpus and chela.

3. Ambulatory legs: length of the merus of the third leg; number of spines on the dorsal edge of the third merus.

Analysis of the samples shows no differences between samples which would warrant specific or even subspecific separation of the widespread populations. A large number
TEXT-FIG. 21  Relative growth of five dimensions of the carapace in *Plagurus capensis* de Haan: a, carapace width at third anterolateral spine; b, carapace width at second spine; c, carapace width at first spine; d, interorbital width; e, frontal width. Regression lines calculated from data for all specimens examined grouped into 5 mm classes. Data shown is from 26 specimens from eastern Australia.
of characters show significant changes with growth.

In the growth of the carapace there is a very slight relative increase in the width of the carapace from the front to the widest part of the carapace, at the third lateral spine. This is reflected in a gradual decrease in the ratios frontal width/carapace width, interorbital width/carapace width etc., most marked in those for the anterior dimensions (see text-figure 21). The regressions for the dimensions carapace width/carapace length calculated from the data from all specimens grouped into 5 mm classes, give the following values of $a$ and $b$ (in equation $y = a + bx$): width of carapace at third spine, $a = 0.63$, $b = 1.06$; width of carapace at second spine, $a = 0.59$, $b = 0.97$; width of carapace at first spine, $a = 2.99$, $b = 0.79$; interorbital width, $a = 4.46$, $b = 0.54$; frontal width, $a = 1.25$, $b = 0.20$.

There appear to be small interpopulation differences in the ranges and means of the ratios carapace width/length, frontal width/carapace width, etc. In Australasian samples the maximum differences between sample means increases towards the anterior part of the carapace, being less than 20% of the total sample range in the case of ratios concerning second and third anterolateral spines and about 30% for interorbital width and frontal width. Sample means are virtually identical for New South Wales and Tasmanian material and there is a slight difference
between south-western and central western Australian samples, values for those from the former being higher. New Zealand specimens generally resemble eastern Australian ones. Material from Juan Fernandez and South Africa present sample means differing by about 20% of the range but there are no clear trends in relationships of these small samples. Clines in these characters are hardly well defined, in contrast to the situation in *L. variegatus*.

Relative growth of the chela proceeds in the usual brachyuran fashion with a very marked difference in the relative size and relative height of the chela between juveniles and females on the one hand and adult males on the other (text-figure 18 c-f). The dactyl in adult males is typically weakly curved; text-figure 18f shows an unusual but not unique specimen with the dactyl very strongly hooked and curved proximally.

Of the wide variations in meristic characters, nearly all are due to growth. They are of two kinds: those in which the rate of change in juveniles is markedly greater than in adults (e.g., number of tubercles or spines around the frontal margin, number of tubercles along the suborbital border - text-figure 23B) and those in which the growth rate appears to be constant from juveniles to adults (number of tubercles on the anterior border of the mouthfield - text-figure 23A, number of spinules or tubercles on the tip of the inner lobe of the basal antennal article,
TEXT-FIG. 22  Morphological variation in two characters of *Plagius* species. A: frequency polygon showing difference between *P. dentipes* de Haan and *P. capensis* de Haan in number of frontal tubercles. Data taken from adults only (carapace length more than 20 mm). B. variation with growth in spinulation of basal antennal article in *P. capensis*. Size of circle proportional to number of specimens (1 - 4); regression line calculated from all data grouped into 5 mm size classes.
number of spines on dorsal border of the ambulatory maxa).

The changes in the number of tubercles on the sub-
orbital border and number of spines on the dorsal edge of
the ambulatory maxa are the most marked. In the former
(text-figure 17p-u; 238) there is a decrease which is very
rapid in juveniles (b, in equation \( y = a + bx \), being
-1.55), very small specimens (text-figure 17p) possessing
a very large number of spinules (20-30) which are particu-
larly minute laterally. In adults (carapace length more
than about 27 mm) the decrease is still significant
(b = -0.073) but the rate much less, the border comprising
8-12 more or less broad lobes.

There is a constant rate of increase (b = 0.18) with
growth in the number of spines on the dorsal edge of the
third ambulatory maxa (text-figures 18a-d; 24), small
specimens having a few large spines whilst in adults there
are a very large number of small spines.

There is a sharp increase in juveniles in the number
of spines on the front. In very small specimens there
are less than 10 spines around the front. In adults, in
which there is no significant change with growth, the aver-
age number is 13.27 (\( \bar{x} 1.848 \) in 52 specimens) (text-figure
22a).

In the spinulation of the apex of the inner lobe of
the basal antennal article (text-figure 17b-g; 225) there
is with increasing size a significant, though small,
increase in the number of spinules or lobes - from 1-3 in juveniles to 6 in some large adults ($b = 0.040$).

There is no significant increase in the number of tubercles on the anterior border of the mouthfield (text-figures 17i-n ; 23A), the basic arrangement, of one lobe medially on each side of the midline separated from three lateral lobes, being the same throughout growth, although the tips of the lobes in some small specimens (text-figure 17) are in turn divided into a number of smaller lobes. In this character there is very wide variation.

Other variable characters include the form of the erect lobe on the coxae of the ambulatory legs (sometimes distally divided into two to four small spines and sometimes concave or truncate); the number of distal spines on the dorso-medial surface of the carpus of the cheliped (usually two or three in adults but sometimes absent in juveniles); and the degree of separation of the most ventral of the ridges on the outer surface of the palm from the midventral ridge, the two ridges tending to be incompletely separated close to the origin of the fixed finger in adults.

The arrangement of tubercles on the dorsal surface of the carpus of the cheliped is fairly constant. In all, there are five longitudinal rows, the outer two convergent basally and comprising a larger number of tubercles.
In all the characters so far mentioned there appears to be only very small interpupulation differences.

Lastly, the presence of a strong tubercle behind each orbit, the degree of tuberculation of the three ridges on the posterolateral part of the dorsal surface of the carapace and the extent and degree of tuberculation of the naked areas on the male sternum are subject to considerable change with age. In all cases there is an increase, with overall size, in the prominence of tubercles. In small specimens the small area behind each orbit is naked, or weakly hirsute, the posterolateral ridges are faint and the naked areas of the sternum are smooth. In large adults there is a strong, sometimes spinous, tubercle behind each orbit, the posterolateral ridges are well developed and sometimes tuberculate and the naked areas on the sternum are moderately extensive and sometimes tuberculate (pl. 6A, 7C). Miers (1886: 273 - footnote) stated that the posterolateral areas of the carapace were smooth, or almost so, in two South African specimens but bearing well developed ridges in some New Zealand specimens. Barnard (1950: 156) stated that South African specimens examined by him, except in the case of a large specimen, lacked a prominent tubercle behind the orbit. Specimens examined during the present study hardly support taxonomic separation of South African populations on the basis of these characters; the absence of tubercles or
TEXT-FIG. 23  Variation with growth in two characters of *Plagiosa copensis* de Haan (open circles) and *P. dentipes* de Haan (closed circles). Regression lines calculated from all data for *P. copensis* only, grouped into 5 mm size classes. In B, *a* refers to specimens with carapace length less than 22 mm; *b*, carapace length more than 25 mm. Size of circles proportional to number of specimens (from 1–4).
ridges in South African specimens is understandable since in Australian and New Zealand material such a tuberculate appearance is only found in rather large specimens (carapace length greater than 55 mm). Miers and Barnard both apparently had access only to specimens smaller than this. However, these characters do appear to vary clinically, being weakly expressed in South African specimens and strongly in Australian and New Zealand ones but this is certainly masked by variations due to age.

Milne Edwards's two species, \( P. \) tomentosa from the Cape of Good Hope and \( P. \) gaimardii from Tongatabou were only briefly diagnosed originally. It appears that their description as distinct species from \( P. \) capensis was based mainly on the appearance and number of the spines or tubercles on the frontal border. As has been pointed out already above, there is wide variation in this character; South African specimens are well within the range of the material from other areas.

Stebbing (1905: 48) quoted Krauss as considering \( Plagusia \) tomentosa to be "extraordinarily near to \( P. \) dentipes". This is not supported by the present study. It is possible that \( P. \) gaimardii is synonymous with \( P. \) dentipes since the type locality of the former, Tonga, is tropical and well within the range of the latter but well outside the known cool temperate range of \( P. \) capensis.
3.24.2 The relationships of *P. capensis* to *P. dentipes* and its place within the genus *Plagusia*

Amongst the several other species of the genus *Plagusia*, *P. capensis* is undoubtedly most closely related to the pan-tropical Indo-West-Pacific species, *P. dentipes* de Haan (type locality: Japan). Amongst the features in which the two species both differ from other species of the genus are the presence of several spines on the dorsal border of the ambulatory meri in addition to a terminal spine and the almost smooth, rather than strongly tuberculate, carapace (Tesch, 1918: 128; Rathbun 1918a: 332). There would appear to be other differences in the shape of the male abdomen and first pleopod.

Grant & McCulloch (1907: 153) enumerated five differences separating *P. capensis* and *P. dentipes*; these concerned 1, the presence of a spine on the lower distal border of the ambulatory meri; 2, the size of spines on the dorsal border of the ambulatory meri; 3, the number of spines on the front; 4, the presence of tubercles on the hepatic (anterolateral) and branchial (posterolateral) regions of the carapace; and 5, the presence of hairs around these latter prominences. Chilton (1911: 558) considered only the first and fourth of Grant & McCulloch's differences to be valid. Tesch (1918: 129 - in key) mentioned one additional difference, the tuberculation of
the grooves between the main ridges of large tubercles on the outer surface of the chela in the male.

Considering the doubts expressed already of the validity of some characters in separating the two species and the possibility that there might be a gradation of characters between the two which would warrant subspecific unification, a moderately large series of specimens were examined. The specimens (15 males, 16 females, carapace length 5.7 - 53.5 mm; Australia: C. Moreton (Breman Shoals), Pt. Cartwright, Caloundra and Coolangatta (Queensland); Pacific Ocean: Norfolk I., Lord Howe I., Easter I.; Japan: Misaki (Sagami B.), Enoshima.) identified as \( P. \) dentipes were obtained from the collections of the Australian Museum, the U.S. National Museum and the Western Australian Museum. (see text-figures 17h, c, v; 12b, h; 19g; 20d-f; 22A; 23; 24; pl. 5B, 6D).

Study of these specimens shows the two species to be easily separable on the basis of the following characters (those typical of \( P. \) dentipes given first).

1. **Front:** The number of tubercles or spines around the margin is less (mean 7.70 ± 1.302 in 20 specimens - text-figure 22A).

2. **Supraorbital margin:** strongly tuberculatate, not smooth.

3. **Surface of the carapace:** very strongly tuberculatate
TEXT-FIG. 24  Geographical and age variation in spination of third ambulatory merus of Plagusia capensis de Haan (open circles, etc.) and P. dentipes de Haan (filled circles, etc.). Regression line calculated for data from all specimens of P. capensis grouped into 5 mm size classes. ○ eastern Australia, △ Western Australia, ▽ South Africa, □ New Zealand, × Chile, ● Queensland and Lord Howe I., ◀ Japan, ▼ Easter I. Size of circles, squares, etc., proportional to number of specimens (from 1–3).
and naked behind the orbits and o. Both the hepatic and branchial regions (i.e. antero- and postero-laterally) (pl. 68).

4. The inner (vertical) lobe of the basal antennal article bears at its tip only one spine (text-figure 17h).

5. Ambulatory maxil: a few very strong spines on the dorsal border (5-7, average 6) and a strong terminal spine present on the ventral edge posteriorly (text-figures 19g; 24;).

6. Thoracic sternum of male: naked areas very extensive and strongly tuberculate (pl. 7D).

7. Male abdomen: naked areas very extensive (pl. 7D).

The two species can be less easily separated on the basis of the better defined longitudinal arrangement of the tubercles on the inner surface of the palm and the slightly greater tuberculation of the grooves between the principal ridges on the outer surface of the male chela in P. dentipes. The most ventral of the outer ridges and the mid ventral ridge are not separated at the origin of the fixed finger (text-figure 18b, h) and the dorsal tubercles of the carpus of the cheliped are in groups rather than rows (text-figure 18h). The male first pleopod in P. dentipes bears longer hairs distally (text-figure 20d-f).

The two species show no apparent differences in relative growth of the various dimensions of the carapace
or in the number and arrangement of tubercles and/or spines on the anterior border of the mouthfield and sub-orbital border (text-figure 23A, B).

_P. dentipes_ thus appears quite definitely to be a valid species. It shows much less variation than does _P. capensis_ and its resemblance in some characters (e.g. spinulation of the front and spination of the dorsal border of the ambulatory meri) to juveniles of _P. capensis_ is striking. A very good coloured illustration of _P. dentipes_ has recently been given by Sakai (1965: pl.99).

### 3.3 Family OCCYPODIDAE

Carapace usually quadrata, usually much wider than long. Front usually of no great breadth, often a narrow, more or less deflexed lobe. Orbits occupying all of anterior border of carapace outside front, outer wall (between far ends of upper and lower borders) often defective.

Mouthfield usually large and a little narrower anteriorly. Third maxillipeds foliaceous and usually completely covering mouthfield but never leaving between them a wide, rhomboidal gap; palp of external maxillipeds coarse, articulating at or near antero-external angle of merus; exognath generally slender and often more or less concealed.

Amphibious, littoral and estuarine crabs, burrowing and commonly gregarious (Alcock, 1900, modified).
3.31 Subfamily CYCLOIDINAE

Genus Holoecius Dana, 1851

Holoecius cordiformis (H. Milne Edwards)

Text-fig. 25a-g, 26a-c, 27a-c. Pl. 4C

Synonymy:

Galasinus cordiformis H. Milne Edwards, 1837: 53

Holoecius cordiformis; Dana, 1852a: 248. Hess, 1865: 144.
Heller, 1874: 75. Haswell, 1893b: 91 (synon.).
Chilton & Bennett, 1929: 762 (synon.). Tweedie, 1942: 23, fig. 9. Guinot, 1962: 10, fig. 7a, b.

Holoecius inornatus Dana, 1852a: 248 (type locality: "New South Wales"; type probably not extant).
1852b: 321; 1855: p1. 19 fig. 7.


Holoecius signatus Hess, 1865: 145 (type locality: Sydney; type in Gottingen Museum). (Not Galasinus signatus Hess, 1865: 146, p1. VI fig. 6).
TEXT-FIG. 25  Tasmanian Ocypodidae:  a - g, Heloecius cordiformis (H.M. Edw.), male, c.w. 21.5 mm (Th),
Smug S. (a - c, e, g); female, c.w. 20.0 mm (Th),
Margaree, (d, f); h - l, Hemihex latifrons (Haswell),
male, c.w. 25.5 mm, (Th), near Lynyard (h - j, l);
female, c.w. 20.5 mm, same data as for male (k).
a, h, front of carapace (LHS), ventral aspect;  b, i,
right chela of male, outer aspect;  c, j, tip of same,
inner aspect;  d, k, right chela of female, outer
aspect;  e, f, right cheliped, merus and carpus,
oblique inner aspect (e, male, f, female);  g, l, left
third maxilliped, outer aspect.
MATERIAL EXAMINED: A total of 65 specimens (38 males, 27 females, carapace width 5 - 25 mm).

Tasmania: Crayfish Ck.; Swan B., Tamar R.; Double Ck.; Proser R. at Orford; Eaglehawk B.; Risdon Cove; Elwick B.; North West B.; Mazgate; Snug B.

LOCALITIES PREVIOUSLY REPORTED:
East coast of Australia (Hess, 1865). Tasmania: "Tasmania" (Haswell); Brown's R. and Orford (Tweedie).

DISTRIBUTION:
Confined to eastern Australia, from Brisbane R. in the north to Tasmania in the south.

Hess (1865: 144) recorded this species from "South Australia" under the name Heloecius inornatus Dana. It has not since been recorded west of Western Port, Victoria, so that its presence in South Australia should be regarded as unlikely.

REMARKS:
A reasonably good description and figure of this species were provided by Tweedie (1942: 23, fig. 9).
The suborbital border bears, not far from the base, a small, sharp, slender spine. As Tweedie notes, the first three ambulatory meri are densely hairy dorsally and ventrally. However, this is true only of the males; females have all the ambulatory meri naked, the dorsal, anteroventral and posteroventral edges of the meri being finely tuberculate. The whole of the ventral surface of the merus of the cheliped is also densely felted in the male but naked in females. Sexes can be separated on the basis of this last character down to a carapace width of 5 mm. Females, and juveniles of both sexes have a relatively small chela with the fingers somewhat longer than the palm.

The basal teeth of the dactyl of the cheliped are generally grouped into a prominent lamina.

Supplementary characters include the presence of more or less broad, spooned hairs on the tip of the endopodite of the second maxilliped and of "woolly" hairs on inner edge of the merus.

The male first pleopod has previously been figured by Guinot (1962).

The carapace, legs and proximal segments of the chelifeds of this species are dark greenish blue obscurely mottled with brown, the palm of the chelae dull slate blue, paler distally and fading to white on the fingers (Tweedie, 1942).
3.32 **Subfamily MACROPHTHALMINAE**

**Genus Hemiplax** Heller, 1865

**Hemiplax latifrons** (Haswell)

Text-fig. 25h-1, 26d, e, 27d-f. Pl. 4D

**Synonymy:**

**Macrophthalmus latifrons** Haswell, 1882a: 549; 1882b: 90.

Tesch, 1915: 154-5.

**Microphthalmus latifrons;** Fulton & Grant, 1906: 19

(incorrect subsequent spelling of *Macrophthalmus latifrons* Haswell).

**Hemiplax latifrons;** Etheridge & McCulloch, 1916: 13,

pl. iv, fig. 4-5; pl. vi, fig. 3-4. Male, 1927a: 186, fig. 187. Tweedie, 1942: 25, fig. 10.

**TYPE:** Holotype, a male, carapace width 29.6 mm, a dry specimen fixed on glass with printed label "Type Macrophthalmus latifrons, Hasw. Loc. Port Phillip, Victoria" and registered as P.697. Australian Museum, Sydney. The carapace is slightly fractured, the first right ambulatory leg is missing and all the right ambulatory legs, except the first, are independently fixed to the glass.

**MATERIAL EXAMINED:** A total of 77 specimens (45 males, 32 females, carapace width 8 - 26 mm).

a & d, right first ambulatory leg of male, anterior aspect. b, right first ambulatory leg of female, anterior aspect. c & e, right fourth ambulatory leg of male, posterior aspect.
Tasmania: Wynyard; Swan B., Tamar R.; Prosser R. at Oxford; Carlton R. near Carlton; Eaglehawk B.; Coal R.; Pittwater; Risdon Cove; Brown's R.; North West B.; Margate; Snug B.; Huon R. at Franklin.

LOCALITIES PREVIOUSLY REPORTED:

South Australia: St. Vincents Gulf; Port R. (Hale).

Victoria: Fisherman's Bend, Port Phillip; Western Port; Wilson's Promontory (Fulton & Grant). Tasmania: Oxford; Carlton R. (Tweedie).

DISTRIBUTION:

Confined to south-eastern Australia, from St. Vincents Gulf through Victoria to Tasmania.

REMARKS:

A reasonably good description of this species was provided by Tweedie (1942: 25. fig. 10) and it has also been figured by Hale (1927a: fig. 167).

The second to fourth ambulatory legs are densely felted in both sexes, the first leg being naked with the merus finely tuberculate along the edges.

The male pleopod bears a dense fringe of plumose setae along its lateral surface. The distal flap is almost wholly on the sternal surface and the tip bears quite a dense cluster of simple setae.
Supplementary characters include the presence of poorly expanded, deeply serrate spooned hairs on the tip of the endopodite of the second maxilliped and of simple hairs on the inner edge of the merus.

Individuals of this species are generally dark greenish or greyish brown, the chelae paler (Tweedie, 1942). The underside of the body is also pale and there may be a transverse band of pale pink across the central sternites.

H. latifrons can be distinguished from the New Zealand congener H. hirtipes (Jacquinot) by the slightly narrower front (\( \frac{1}{4} - \frac{1}{5} \)) carapace width (Tweedie) as opposed to \( \frac{1}{3} \) carapace width in the New Zealand species (Richardson, 1949a: 36). Examination of material of H. hirtipes (an adult male and female (AM P700) in the Australian Museum’s collections) show the following other differences between the two species:

1. The eyestalks are slender and reach fully to the tip of the exorbital spine in H. latifrons but are stout in H. hirtipes and shorter, not nearly reaching the exorbital spine;

2. the carapace widens markedly posteriorly in H. latifrons but narrows in H. hirtipes;

3. the anterolateral margin bears two broad rounded lobes behind the orbit in H. latifrons and two sharp flattened spines in H. hirtipes;
TEXT-FIG. 27. Male left first pleopods of Tasmanian Ocypodidae. a - c, *Helicea longipes* (H. Milne Edwards), male, c.w. 21.5 mm (TM), Snug B., Tas. d - f, *Hemiplus latifrons* (Hasswell), male, c.w. 25.5 mm (TM), near Wynyard, Tas. Tip in abdominal aspect to the left and in sternal aspect to the right, whole pleopod in abdominal aspect in the centre.
4. The carpus of the cheliped is long and slender in *H. latifrons* without a spine but short and fairly stout in *H. hirtipes* with a dorsal spine on the inner surface.

The relationship of *H. latifrons* to species of *Macrophthalmus* requires further elucidation in view of these strong differences from *H. hirtipes*.

### 3.4 DISCUSSION

#### 3.41 PATTERNS OF VARIATION AND TAXONOMY OF RELATED GROUPS

Species, "groups of actually or potentially inter-breeding natural populations which are reproductively isolated from other such groups" (Mayr, 1963: 19) are eventually becoming recognized rightly as natural units rather than as arbitrary classes of objects (Mayr, 1963: 21).

Recently, their biological properties have been excellently reviewed in detail by Mayr in his "Animal species and evolution". The fact that separate species do not inter-breed usually leads to the existence of morphological discontinuities although these are sometimes small and limited to one or two characters, as in sibling species. Whilst populations sometimes acquire reproductive isolation without morphological change of an equivalent magnitude nothing is to be gained by assigning the status of species...
to widely separated populations in the absence of genetic or other evidence. Species, and subspecies (defined by Mayr (1963: 248) as "aggregates of local populations of a species inhabiting a geographic subdivision of the range of the species...") must at all times differ taxonomically one from the other, that is, they must be capable of morphological characterization. The degree of taxonomic difference considered to justify subspecific separation is a matter of some dispute but a reasonable set of alternatives has been given by Mayr, Linsley & Usinger (1953), all of which necessitate being able to allocate 75% of any sample to one subspecies or another.

The points outlined above are of particular relevance in discussing the results of the present study. Three taxa have been concentrated on, Leptograpthus variegatus, Cyclocrapsus granulosus and Plagusia capensis. Up till recently, all had at some time been considered widespread species with distributions extending through much of the temperate southern ocean. During last century, all had also been divided by some taxonomists into several species with rather localized distributions. Despite attention to differences in morphological characters which might lead to demarcation of distinct, more localized species or subspecies, the results have been much as expected, except in the case of the restricted Cyclocrapsus granulosus, Tasmania previously being considered to possess a species
shared with at least the rest of Australia. The South African, Australasian and South American populations of *L. variegatus* and *P. capensis*, although widely separated geographically, show about 80% overlap in even the least widely varying characters. It seems significant that these two species, with conspecific populations throughout their range, both belong to genera or groups of genera which characteristically possess species widely distributed latitudinally in the tropics and sub-tropics whilst all but one species of *Cyclograpalus*, namely *C. integer*, have very localized or longitudinal distributions (Rathbun, 1918a; Tesch, 1918; Banerjee, 1960; Forest & Guinot, 1961; Campbell & Griffin, 1966). The South African and Chilean *C. punctatus*, historically grouped with *C. granulosus*, is in fact extremely different from Australian and New Zealand species of the genus, the form of the male first pleopod indicating little affinity between South African and Australasian populations. *P. capensis* appears somewhat similar in the pattern of differences but in *L. variegatus* greatest interpopulation differences are found within Australia, particularly between the populations of eastern and western Australia.

The more or less recent studies on the population structure of species, reviewed by Mayr, have shown that nearly all populations of a species are involved in one (or several) of three structural elements: clines,
geographical isolates and hybrid belts. Of these, the animals studied here appear particularly involved in the first. Thus, of those characters which show an appreciable amount of variation in *L. variegatus*, the number of tubercles on the anterior border of the mouthfield and the length/width ratios of the second and third ambulatory pairs appear to vary clinically (see tables 1 and 2). Similarly, in *P. capensis* there appears to be clinal variation in the prominence of the hepatic and branchial tubercles on the carapace and of the tuberculation and extent of the naked areas on the sternum and abdomen of the males. In these two species the clines are latitudinal rather than longitudinal. In the Australian *Cyclograpsus* species there are very well developed clines in several characters, notably the degree of granulation of the surface of the carapace and legs and the shape of the third and sixth abdominal segments in the male (tables 3 and 4). These clines are not markedly latitudinal.

Among the most evident features of the three groups is the independent nature of the variation in some of the characters, a well known phenomenon in all species. Again, this feature is best shown by the Australian *Cyclograpsus* species. These two show an overall greater dissimilarity towards the adjacent peripheries of their geographical ranges, so that sympatric individuals are much more easily distinguishable from each other than are those from areas
which are widely separated geographically. In some characters however, there is a tendency for greater similarity towards the area of sympatry (text-figure 16). Similar changes in the appearance and relative expression of characters may also exist in the Australian Paragrapus laevis and P. qaimardii. On the other hand, Plagusia capensis and P. dentipes, the geographical ranges of which meet around central eastern Australia, are almost as equally distinct from each other throughout most of their respective ranges.

This phenomenon of intraspecific change associated with sympatry of normally allopatric, closely related species, termed 'character divergence' or 'character displacement', has now become fairly well known (Brown & Wilson, 1956; Hutchinson, 1959; Mayr, 1963). One of the best studied examples has been a group of Asiatic birds, the rock nuthatches of the genus Sitta. There these two species show gradual changes, in overall size and bill length and in width, size and distinctness of the facial stripe, towards the region of sympatry so that they are distinguishable at a glance although rather similar when allopatric (see Brown & Wilson, 1956: 49-50; Mayr, 1963: 33, fig. 4-2). Brown & Wilson (1956: 50-51, fig. 3) cited the Palearctic and Nearctic ants of the genus Lasius in which seven characters exhibit independent trends leading to distinct differences in their region of overlap and
convergence when they are allopatric. Amongst the
Brachyura, a case of character divergence has recently
been elucidated by Tashian & Vernberg (1958) in the well
studied American fiddler crabs, Uca. Originally des-
cribed as separate species, the north eastern Uca pugnax
(Smith) and the south eastern U. zapax (Smith), have been
considered only subspecifically distinct by most workers
since the beginning of this century (Rathbun, 1916a). How-
ever, in northeastern Florida these two forms are still
quite distinct from each other and exhibit intraspecific
differences in size and the shape of the major chela of
the male. The two forms are also readily separable there
on the basis of colour, courtship display and general ecol-
ogy and thus in reality warrant the status of full species.
Crane (according to Brown & Wilson) has found that in
species of Uca the greater degree of differentiation in
colour and courtship display of the male occurs where
species' distributions overlap. Lastly, similar trends
exist in some central eastern Pacific swimming crabs of
the genus Portunus (W. Stephenson, personal communication,
November, 1964). Accentuation of differences between
species in this way may be the result of competition between
a cognate pair of species (Brown & Wilson, 1956). Certainly,
changes in bill shape in birds may so arise. Undoubtedly,
this kind of evidence is as good as any indicating the full
species status of populations.
Among Australian decapods the closest parallel to the above situations for the Grapsidae is undoubtedly to be found in the spiny lobsters (or crayfish) of the genus Jasus which, like species of Plagusia, live in crevices in the infra-littoral. The circum-polar, southern cool temperate populations of this genus have mostly been considered to form a single specific unit and for at least the last 50 years they have been known as Jasus lalandei (H. Milne Edwards). Recently, however, Holthuis (1963) has produced evidence that this 'species' is actually divisible into six good species, one each in South Africa, the southern Indian Ocean at St. Paul and Amsterdam Islands, south-eastern Australia, New Zealand, Juan Fernandezes and Chile and the southern Atlantic Ocean at Tristan da Cunha. These species are, according to Holthuis, separable mainly on the basis of the sculpturing of the abdominal somites, and there are differences also in the details of the spines and tubercles on the dorsal surface of the carapace and in the shape of the male pleopods. Dr. R.W. George (personal communication, July, 1964; 1965, unpublished), on the other hand, considers Australian and New Zealand populations to be conspecific and has shown the existence in them of longitudinal clines, increased abdominal sculpturing being correlated with higher sea temperatures.

The related lobsters of the Panulirus jayakari group, which occur throughout the warm Indo-West-Pacific,
in the case of one species (the very widely distributed
P. longipes (A. Milne Edwards)), also appear to show a
division into eastern and western groups. Thus George &
Holthuis (1965) divide this species, on the basis of
the colour patterns of the abdomen and legs, into two
subspecies, one in the Indian Ocean as far east as the
Malayan Archipelago and one distributed mainly in the
western Pacific east to Fiji; intermediate forms do,
however, exist. Colour patterns are surprisingly distinct
in all other species of the group too which, in contrast
to P. longipes, have more restricted distributions.

There is a need for an examination of more material
of L. variegatus and P. capensis to determine more fully
the extent of clinal variations, and likewise of C. granu-
losus and C. audouinii to find to what extent the changes
in the western region of sympathy are mirrored in the
eastern region around northern Victoria and southern
New South Wales.

Because of the reproductive isolation of species
and the concomitant lack of gene exchange between such
groups, the patterns of variation in even closely related
species tend to be different (Mayr, 1963: 301). However,
it is equally true that the more closely related are the
taxa the greater is the tendency for the same characters
to vary in similar fashions. At least this should be
true of cognate taxa since, like conspecific populations,
they share a common genetic heritage. Indeed, not too different patterns of variation in the same characters are to be found in some groups of species. Thus, several closely related species of the Australian brachyuran genus Chlorinoides, small, shelf inhabiting majid spider crabs with the carapace and legs prominently ornamented by simple or lobate spines, exhibit markedly parallel variation in spinulation of the major spines of the carapace and legs. Amongst the 20 or so species currently placed in the genus, several groups can be distinguished by the kinds of variation in the terminal knobs on some of these spines (Griffin, unpublished). Among the natant decapods, palaemonid prawns characteristically vary in the number of spines along the dorsal and ventral edges of the rostrum, which in this, and other related families, is typically long (Valdyan, 1957, 1960). Mayr (1963: 301-2) briefly mentions the drongos (the Dicruridae), a group of long tailed birds distributed throughout the Old World, the species of which each show similar variation in the same characters. The question whether the search for distinct species in a seemingly uniform group of populations could more fruitfully be conducted by using precisely those characters which clearly separate other congeneric species is thus surely a valid one.

Two of the taxa studied here belong to groups which have shown themselves to be taxonomically difficult. It
is only recently that the status of several species of Gaussia, notably the Atlantic G. azapsus (Linnaeus) and the Indo-Pacific G. hemicentrotus (Herbst) has been put on a firm basis with detailed study of large numbers of specimens (Banerjee, 1960). Species of this genus, like G. varicatus, which they resemble in general appearance and ecology, exhibit constancy in the ridging of the branchial regions and the spinulation of the posterior ventro-distal border of the ambulatory meri but vary fairly widely in the tuberculation of the frontal border, the form of the chela and the proportions of the ambulatory meri.

The status of the widely distributed tropical and subtropical species of Plagusia is still an open question. Rathbun (1918a: 232) considers that there are two full species, P. immaculata Lamarck and P. depressa (Fabricius), the latter in turn divided into an Atlantic nominate subspecies and an Indo-Pacific one, P. depressa tuberculata Lamarck. On the other hand, Tesch (1918: 123), following an earlier opinion by Laurie in 1906, considers all three to be subspecies of P. depressa. The characters separating these taxa are cited by both Rathbun and Tesch as being the relative prominence of the squamiform tubercles of the carapace, the number of fringes of hair on the posterior surfaces of the ambulatory meri and the form of
TEXT FIG. 28. Known geographical distribution within Australia of the 9 species of Tasmanian Grapsidae. That for *L. octodentatus* follows George (1962). In the case of *Plagusia*, *Cyclograpsus* and *Paragrapsus* species the distribution of an Australian congener (*P. dentipes, C. audouinii* and *P. laevis* respectively) is shown by open instead of filled circles. As far as possible, each circle represents a single locality.
the coxal lobe on the ambulatories, *P. depressa depressa* having the coxal lobe dentate distally, *P. d. tuberculata* having an entire lobe. If the results of the present study of *P. capensis* can be at all validly extrapolated to this problem, the last of these characters, at least, should be used with great caution.

Studies of relative growth have proved of disappointingly little value in separating the species and populations dealt with here. Closely related species, at least amongst many Brachyura, certainly exhibit common patterns in this feature. In the species of *Chloinoidea* mentioned above, groups can be defined on the basis of their agreement in these patterns. Analysis of relative growth does, however, provide valuable assistance in the taxonomy of some crabs, notably the small, oceanic species of *Planes* (see Chace, 1951) and the eastern Pacific *Portunus* species mentioned above. Study of relative growth may be helpful in further study of species of *Plagusia* and of *Paragrapsus laevis* and *P. caimardi*. Relative growth of characters subject to sexual dimorphism, for instance the chelipeds, show common patterns amongst closely related species. Since relative dimensions of the carapace and legs, and parts of them, are notorious in the Brachyura for their change with growth, it need hardly be stressed that when attempting to separate species by relative proportions,
one must constantly seek out these changes to which every individual is subject. Indeed, if this part of the study has revealed anything, it is by contrast, the value of studying such growth changes. These studies may reveal the existence of additional characters separating species, characters which would otherwise be discarded as too variable. The ready separation of $P. \text{capensis}$ and $P. \text{dentipes}$, which this study has shown possible, is evidence of this.
3.12 ECOOECOGRAPHY AND RELATIONSHIPS OF THE TASMANIAN 
CRAPSID AND OCYPODID FAUNA

Of the eleven Tasmanian crapsids and ocypodids, all but two are widely distributed throughout Tasmania. These two are *Icnotopus variegatus* and *Paracrapsus laevis* which appear to be confined to the northern part of the east coast (perhaps due to the influence of the warm East Australian current), the latter being known only from a small central area. Up to the time of the commencement of this study *L. octodentatus* had been reported only from the north coast. This species is, however, quite widely distributed throughout Tasmania.

None of the species is confined to Tasmania. However, five species are otherwise known only from Victoria and eastern South Australia. These are *C. granulosus*, *P. quadridentatus*, *P. seimardii* and *H. latifrons* which are endemic to Australia and *H. spinosus* which is known also from 2 localities in the central west Pacific Ocean. The distributional limits of these species are additional evidence for the existence of the south-eastern Australian "Haugean" marine province (Bennett & Pope, 1953, 1960).

Of the remaining six species, three (*H. hagwellianus*, *P. laevis* and *H. cordiformis*) have an eastern distribution in Australia, being known from as far north as Brisbane (Queensland) and throughout Victoria; the distribution of
of those species which occur outside Victoria and South Australia, *Leptograpsus variegatus* is the only one which is not known from central eastern Australia. The distribution of this species is western and extends to the Abrolhos Islands in the north west; it is not known outside Australia.

Two species only, *Leptograpsus variegatus* and *P. capensis*, are widespread outside Australia, the former being known from New Zealand, Middleton Reef, Norfolk I., and the Kermadecs in the south west Pacific and Easter I., Juan Fernandez and Chile in the south east Pacific, whilst *P. capensis* occurs also in South Africa and at Lord Howe I., but not at Middleton Reef or Easter I. Within Australia, both species are widely distributed southern forms, *Leptograpsus variegatus* extending north to Shark Bay in the west and Rockhampton (Queensland) in the east, *P. capensis* to the Abrolhos Islands in the west and to just north of Sydney (New South Wales) in the east.

The distribution patterns of the eleven species are compared in Table 5; text-figure 30 shows the Tasmanian distribution of four species, the two with limited eastern distributions and two with wider distributions. Text-figures 28 and 29 show the Australian distributions of all species.

The eleven Tasmanian species are at present included in nine genera. Four of these, *Leptograpsodes*, *Helograpsus*
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1 South Africa, 2 Western Australia, north of Abrolhos I., 3 remainder of Western Australia, 4 South Australia, 5 Victoria, 6 New South Wales, 7 Queensland, 8 Pacific Ocean west of Tuamotu Archipelago, 9 New Zealand, 10 Pacific Ocean east of Tuamotu Archipelago.
and Haliotis, which are monotypic and Peracra anus, which contains three species, are restricted to Australia and New Zealand, which contains one other species, is represented only in New Zealand and perhaps the south Pacific. The genera Promisus, Cyclocoeionus and Placuna, all containing fairly large numbers of species, are widely represented throughout the Indo-West-Pacific.

Lastly, the monotypic Leptocra anus is a widely distributed southern warm temperate genus. Thus, of the five genera found outside Australia three are widespread Indo-West-Pacific taxa and four are represented in other temperate regions including New Zealand.

Of the grapsid subfamilies, the best represented is the Sesarminae with five species and three genera; the other subfamilies are each represented by one or two species and genera.

The relationships of the Tasmanian (and south eastern Australian in general) grapsid and ocypodid fauna are clearly with the rest of Australia and the Indo-West-Pacific. There, the local species and genera find their closest relatives if they are not actually present themselves. Certainly, there are similarities with other non-Australian cool temperate regions, particularly New Zealand, such as the sharing of the species Leptocra anus and Placuna and the genera Cyclocoeionus and Hemiplax. The relationships of southern temperate marine
TEXT-FIG. 30  Known Tasmanian distribution of four species of Grapsidae. As far as possible each circle represents a single locality.
faunas and floras are a source of great interest to students of intertidal ecology and numerous similarities between the distribution patterns of the species has been reviewed by Guiler (1952d), Knox (1960, 1963) and others. However, New Zealand, which like Tasmania possesses rather few grapsids and acypodids (Bennett, 1964), differs notably from Tasmania in the dominance of many of its shores by varunines of the genus Hemigrapsus Dona, not by sesarmines. The New Zealand species of this genus are markedly different from the Tasmanian var- 
unuine Erachymotus spinosus. It is doubtful too, if the 
Australian Hemiplax latifrons is more closely related to the New Zealand H. hirtipes than to species of the Indo- 
Pacific genus Macrocheiralthus which is well represented on warm temperate to tropical Australian shores.

Chile (Garth, 1957) shares two species with Tasmania (see Table 5) and, apart from this, one genus, Cyclocraeus. The two species of the latter genus are quite different from Australasian species, one, C. punctatus being found also in South Africa which possesses one species in common with Tasmania. Both Chile and South Africa (Barnard, 1950) possess varunines rather different from Tasmanian ones (species of Curtegrapsus, Hemigrapsus and Aratus in Chile and of Varuna in South Africa). The similarities of the grapsid faunas of southern temperate regions due to sharing of L. variegatus and P. cauensis may be accounted for by
the possible existence in these species of relatively long-living larvac, widely travelling by means of the West Wind Drift. Other similarities, particularly between Tasmania and New Zealand, may derive from common origins in present warm or tropical regions at a time when temperatures were much lower than they are now and land configurations also different. The Tasmanian grapside and ocyopodicids appear to show similar patterns in their geographical distributions and relationships to those of other Australian Orachyura (Stephenson, 1962; Griffin, 1966).
4. E C C L O G Y

4.1 INTRODUCTION

One of the features of almost any coastline most obvious to an observer is that the animals and plants which live there are arranged in certain horizontal levels, or zones, on the shore, different kinds of animals typifying each zone from the level of low tide to high tide. When these zones, and the animals in them, are studied at different localities it is also apparent that there are changes in the width and complexity of each zone and that the animals within the same zone are of different kinds according to the type of shore. These features are as obvious as the differences in the nature of the substrate, whether it is rocky or muddy, and the kinds of waves that occur there, whether they are large or small. Other environmental factors, such as the amplitude and rhythm of the tides and the range of salinity and temperature, even though they are less obvious, are of great importance in determining the nature of these faunistic and floristic differences.

A wealth of literature now exists on the nature of intertidal zonation. Much of this has been descriptive rather than analytical (for universal features see reviews by Stephenson & Stephenson, 1949; Doty, 1957; and Southward, 1958; for features of southern hemisphere temperate zones
see Knox, 1960, 1963) It is apparent that each horizontal zone presents similar patterns of zonation throughout the world, at least so far as rocky shores are concerned, although the outwardly similar organisms in different geographical regions may belong to different species, genera or sometimes even families.

The terminology for the various zones has been widely debated (see Hedgepath, 1957; Lewis, 1961) but the Stephenson's scheme has been accepted by numerous workers in this field and is followed here. The area between the extreme limit of spray and salt air and the extreme low level uncovered by tides is divided into an upper supralittoral fringe above the level not washed by all tides, a middle midlittoral zone (in Tasmania subdivided into an upper and lower part) above the level not uncovered by all tides and a lower infralittoral fringe (Southward, 1953: 141). These zones of course suffer different amounts of exposure to air. In Tasmania the percentage of time that each is uncovered is as follows: for the supralittoral fringe, 70-100%, the upper midlittoral 18-80%, the lower midlittoral 0-36% and for the infralittoral fringe 0-28% (Guiler, 1953d: 33).

It is intended that in this section the factors which differentiate the various types of shore and the characteristic Tasmanian organisms will be briefly reviewed. The
ecology of intertidal animals and plants of Tasmania has
been intensively studied over the past 15 years, mainly by
Guiler (1952 et seq.) and lately by Bennett & Pope (1960)
and the following account is based largely on their observa-
tions. The prevailing temperatures and other physical
factors have already been detailed for Tasmania (see
section 1.6). The shores of Tasmania are subject to regu-
lar semidiaily tides with one high every twelve hours,
marked diurnal inequality existing between both highs and
lows (Guiler, 1950; Doty, 1957). Maximum tidal range (at
the time of spring tides) is rather small, even on exposed
coasts - 5.4 feet at Cape Sorell (west coast) and 4.18 feet
at Matsuonyer Island (south coast) (Bennett & Pope, 1960;
see also Doty, 1957). In more sheltered areas the range is
much less (about four feet at Hobart).

Seashores can be roughly divided, according to sub-
strate, into rocky coasts, sandy beaches and muddy estu-
aries. Such a division contrasts the type of substrate
or surfaces available for colonization by organisms: solid
as opposed to soft. Shores can also be classified accord-
ing to the type of prevailing wave action. Thus both rocky
coasts and sandy beaches may be subject to pounding breakers
or they may be sheltered from wave action; estuaries
are completely sheltered, a necessary condition for the
settling out of the fine silt and clay which, together
with the decomposition of dead organisms, gives them their
characteristic muddy appearance.

The following five types of shore are recognised here according to the type of substrate: **rocky cliffs and platforms** where the shelter available is mostly in the form of crevices, which may be horizontal or vertical; **boulder beaches** where the fragments of rock are large, in the order of a foot or more in diameter and often piled on top of one another, to a depth of several feet above the underlying sand; **stony beaches** where the fragments of rock are small, in the order of a few inches in diameter, often smoothly rounded through weathering and piled on top of one another to a depth of only a few inches; and **sandy beaches and estuaries** where fragments of rock are mostly absent. This last category may be subdivided into **stony estuaries** and **open estuaries**. In estuaries the substrate may consist mostly of sand or an appreciable amount of silt or clay may be present.

Classification of shores on the basis of the degree of exposure to wave action has long caused some difficulty as different workers tend to attribute different meanings to terms such as "exposed" and "sheltered". Bennett & Pope (1960: 221) have proposed a division of exposed coasts into four categories ranging from "maximal exposure" through "sheltered open coasts". A rather broader scheme is used here because a narrower one would be superfluous in dealing
with the small numbers of species of crabs which generally range rather widely anyway. In the present account then, shores are divided into three types according to wave action: **fully exposed** - areas where the waves are strong and regular and break over the beach as "white, foamy water" e.g. north-east coast of Tasmania (Bennett & Pope's "maximal and submaximal exposure"); **semi-exposed** - areas subjected to surf "without much force", "small waves" and "choppy seas", e.g. north coast and Pirates Bay on the south-east coast (Bennett & Pope's "moderate exposure" and "sheltered open coasts"; and **sheltered** - areas where even small waves are rare, the sea generally being calm except during storms, e.g. Sandy Bay.

The salinity of the water at these various shores shows little variation and except near river mouths is not subject to any appreciable dilution. The only exception to this concerns lagoons and estuaries. In the former, salinities are sometimes higher than in the sea (Guiler, 1951). In estuaries the salinity is generally lower and shows great variation, particularly in the infralittoral about midway between the head of the estuary and the mouth (Moore, 1958: 191-9).

The majority of the work on intertidal ecology in Tasmania has been devoted to the organisms inhabiting cliffs, shelves and boulder beaches, particularly the exposed ones, where the zonation of the more or less sessile organisms is
most obvious. Thus, the review papers of Guiler (1950, 1952d, 1960) and the survey carried out by Bennett & Pope (1960) have dealt particularly with such shores. The animals and plants on Tasmanian rocky coasts appear to occur in four major zones, the supralittoral fringe, the upper midlittoral, lower midlittoral and the infralittoral fringe.

The supralittoral fringe is variously bounded on the upper side by an orange red lichen, a black sooty growth or it may be altogether devoid of organisms. The fringe itself is dominated by the two small litterinid snails, _Malaepha unifasciata_ (Gray) and _M. praetermissa_ (May) which sometimes occur together, although favouring slightly different conditions with respect to spray, and frequently extend into the midlittoral. The large isopod _Linna australiensis_ (Dana) is commonly found in dense clusters under boulders.

The upper midlittoral is dominated by the small barnacles _Chamaeispho columnus_ (Spengler) and _Chthamalus antennatus_ Darwin (and in sheltered bays, _Elminius modestus_ Darwin), the larger barnacle _Cathaphragma polymerus_ Darwin (particularly on northern coasts), several small false limpets, _Siphonaria_ species, and, some true limpets, notably two small ones, _Patelloidea latistriata_ (Angas) and _Notoacmaea petterdi_ (T. Woods) and the large _Cellana solida_ (Blainville) and in some areas, particularly those less
exposed, the small mussels Brachidontes rostratus (P. Hauer) which sometimes forms extensive sheets, the very small Modiolaria pulcher (Lamarck) and the large Mytilus edulis planulatus (Lamarck).

The snails Entebicium nana (Lamarck) and Astrocochlea species are molluscs of semi-exposed rocky shores. In addition, the red sea anemone, Actinia tenebrosa Parquar may be found on the undersides of stones in this zone.

The ill-defined upper boundary of the lower midlittoral zone is formed on the less exposed coasts by prominent masses of tubes of the tubicolous polychaete, Calcinaria cuspidata Lamarck which occurs just below Brachidontes. On the more exposed coasts, however, the lower midlittoral is dominated by encrusting coralline algae such as species of Lithophyllum and Corallina officinalis L. which, when mixed with the numerous other algae, give to this zone a characteristic patchwork appearance of dull purple and bright green. Other algae, such as species of Caulerpa and Codium also occur in this zone. The dominant animals are molluscs - limpets such as Patellina varoni (Blainville) on exposed coasts and P. albida Tenison Woods and Patelloida alticostata (Angus), on more sheltered ones and the large chiton Patelloplax costata (Blainville) and Sypharochiton pelliserpentis (Auoy & Cainard). The multicoloured asteroid, Patiriella calcar (Lamarck), is common fairly low down on the shore.
or in remnant pools higher up. On rocky coasts not subject to full exposure the lower part of the midlittoral zone is dominated by prominent growths of the widespread brown alga, *Hermosira banksii* (Turn.) Decaisne.

On rocky coasts the crabs *Lomis birta*, *Notomithrax ursus*, and, in sheltered areas, *Petrolisthes elongatus* are not uncommon under stones, the last sometimes being the dominant decapod (see section 1.4).

The infralittoral fringe is dominated on the more exposed coasts by the giant fucoid alga, *Durvillea potatorum* Aresch and on the more sheltered shores by either brown algae such as species of *Cystophora*, *Macrocystis*, *Acrophora* and a variety of others.

Sheltered areas, such as lagoons and estuaries, have received little attention in Tasmania. Guiler (1951) studied Pipe Clay Lagoon, an extensive, shallow, sheltered area of water in south eastern Tasmania and the following account is based on Guiler's (1952d) review.

The upper part of the lagoon shore is bounded by scrub (*Arthrocnemum* sp.), small plants such as species of *Salicornia* and the snail *Salinator solida* (von Martens). Below this are found other small snails such as *Vembicium melanostoma* (Gmelin), the elongate turret shell *Lubitium lawleyanum* (Gmelin), and the wedge-shaped bivalve, *Anapella cycladea* (Lamarck). The soldier crab, *Mictyris platychelis,*
is also found at this level in sandy areas.

The lower part of the shore is dominated by beds of the eel grass, *Zostera marina* with several species of mollusc scattered throughout. The lower boundary of the intertidal area is dominated by the top shell *Austrocochlea constricta* (Lamarck) or a closely related species and below this are found clumps of the ascidian *Pyura praeputialis* (Haller) and several molluscs. The pebble crab, *Philyra laevigata* moves up and down with the tide and is a normal inhabitant of the lower midlittoral and infralittoral.

In comparing the zonation of this estuary with other shores Cuillen (1952d: 33-34) considers the uppermost part of the shore (that dominated by *Salinator*) to be equivalent to the supralittoral fringe, the "supra *Zostera* zone", dominated by molluscs, to the upper mid littoral, the "*Zostera* zone" to the lower midlittoral and the "infra *Zostera* zone" mostly to the infralittoral fringe.

It is within the general framework outlined above that the ecological distribution in Tasmania of the nine grapsid and two ocypodid crabs are considered here. The section essentially deals with the distribution and abundance of these species, and the factors responsible for such species' attributes. Inasmuch as the times at which species breed are related to such features they are briefly described here with special reference to temporal fluctuations in breeding intensity in two species. Fluctuations in moulting
intensity, the occurrence of which is apparently related temporally to breeding, are also described. Apart from morphological adaptations to particular habitats, the factors which appear most likely to influence an intertidal animal species' distribution on a particular type of shore are its ability to survive desiccation when faced with high temperatures whilst uncovered by water and its ability to extract food from its surroundings. Therefore the number and relative volumes of the gills, the regions most affected by desiccation, are discussed in relation to habitat and behaviour. For each species, the mouthparts, particularly the inner ones and the arrangement and types of hairs on them, are detailed. The correlations between the field observations and each species' behaviour under laboratory conditions are then explored in an effort to determine whether there are differences between these features which might be due to competition with other animals for space and food. Such competition is probably important where marked discrepancies exist between distribution of species when associated with other species (as under natural conditions) and behaviour when alone (as under laboratory conditions).

4.2 ECOCOLOGICAL DISTRIBUTION

In this subsection the distribution of the nine grapsoids and two ocypodids on the various types of shore is
described from field observations. The vertical zonation and the apparent reaction to cover and salinity of these species is described and feeding habits are briefly mentioned.

4.21 MATERIALS AND METHODS

In the collection of distributional data localities ranging from fully exposed rocky coasts to sheltered bays and estuaries around the east and north coasts of Tasmania were studied (see text-figure 1). Several of these were examined throughout the four years 1962-65. At each locality, data on the type of shore and the dominant organisms were collected. Identifications of molluscs were checked against descriptions and illustrations given by May (1958) and Macpherson & Gabriel (1962) and barnacles were identified from Pope (1945). Densities of each species of crab were measured by collecting all the crabs in an area of one square metre. The location of samples on each shore was chosen in a random fashion over the whole of the intertidal area, along selected zones or along vertical transects from low tide level to high tide level. Shore zones were estimated mainly from study of major zoning organisms. The major levels were estimated by use of tidal information supplied by the Hobart Marine Board. Relative abundance was judged from collections and counts made in the field. The scheme outlined by Endean, Kenny
A Stephenson, (1956) is used here to describe relative abundances. Thus relative abundances are considered in five categories: dominant, co-dominant, subdominant, very common, common (less than 20 but more than 5 specimens found), present (no more than 5 specimens found). These abundances are relative to other grapsids and ocypodids only. The crabs were usually counted in the field and measured across the widest part of the carapace with vernier calipers. In the majority of samples the individuals of each species were measured only with an accuracy sufficient to place them in one of three groups termed "juveniles", "small adults" and "large adults". The size demarcating juveniles and adults was chosen after determination of the lower size limit for ovigerous females. The size demarcating small and large adults was placed arbitrarily at about the middle of their size range (see table 6).

**TABLE 6** Arbitrary size groupings of four species of grapsids used in ecological surveys.

<table>
<thead>
<tr>
<th>Species</th>
<th>Maximum carapace width of &quot;juveniles&quot;</th>
<th>Minimum carapace width of &quot;large adults&quot;</th>
</tr>
</thead>
<tbody>
<tr>
<td>B. spinosus</td>
<td>7.9 mm</td>
<td>12.0 mm</td>
</tr>
<tr>
<td>C. granulosus</td>
<td>12.0 mm</td>
<td>19.0 mm</td>
</tr>
<tr>
<td>R. quadridentatus</td>
<td>12.3 mm</td>
<td>19.0 mm</td>
</tr>
<tr>
<td>P. gaimardii</td>
<td>14.9 mm</td>
<td>30.0 mm</td>
</tr>
</tbody>
</table>
In the study of the food of the various species, the stomachs were dissected out of about 10 specimens of each species and the contents examined under a dissecting microscope.

Temperatures were measured in the field with a portable Wheatstone bridge and thermistor. Relative humidities were measured in the field with cobalt thiocyanate paper and a Lovibond humidity test kit.

Salinities were determined from collections of water made in test tubes measuring 6" by 1", sealed with a cork which was taped to the tube securely to minimize evaporation. The test tubes were first rinsed three times in the water from which the sample was collected. Calculation of the salinity values was made from two or three titrations of approximately 0.28 N silver nitrate (precise normality determined by titration against sodium chloride of known normality) against 5 millilitre samples of the water, using potassium chromate as an indicator (Strickland and Parsons, 1960).

The mechanical composition of soft substrates was determined from field samples collected in 4" x 1" test tubes sealed with screw-on lids, by the Bouyoucos method (Bouyoucos, 1928) as modified slightly for use by the undergraduate classes of the University of Sydney Faculty of Agriculture. Particles were grouped according to the international, rather than U.S. levels, only the hydrometer
readings at 5 and 120 minutes being considered.

The distributions of the species according to the type of shore are given in table 7 and text-figure 31.

4.22 FULLY EXPOSED AND SEMI EXPOSED CLIFFS, PLATFORMS AND ECOULDER BEACHES

The most conspicuous intertidal crab of fully exposed cliffs and platforms is undoubtedly L. variegatus. This species is frequently seen scuttling over the platforms when the tide is out. At Bicheno (text-figure 32A; plate 9A) and at Binalong Bay on the east coast, large numbers are found fairly high up on the shore sheltering in crevices in the upper midlittoral zone and supralittoral fringe, the area subjected to flying spray.

Careful searches of many areas at Bicheno where only vertical or horizontal crevices with high entrances were found revealed no crabs but in horizontal crevices with low entrances the species was invariably found. At Bicheno, on one occasion, at least 20 were observed sheltering at the back of a very deep horizontal crevice about 10 metres long situated near a blowhole and thus subject to constant dripping of water across the entrance. Densities of this species thus vary quite widely, only one or two sometimes being found in long vertical crevices whilst in horizontal crevices groups of 5-10 are not uncommon within an area of one square metre.
As the tide recedes the crabs emerge from the crevices and commence feeding, moving down as they do so to the lower parts of the shore among the coralline algae. They move fairly slowly, on the tips of their ambulatory appendages and when feeding sit semi-erect with the legs flexed at right angles, spending several minutes in each spot before moving on. Between short bouts of feeding an individual may move back into a nearby crevice, or at other times into an adjacent remnant pool of sea water where it lowers its body into the water, then elevates itself again and moves off. They appear to prefer to feed in areas of the platforms shaded by surrounding low cliffs or large blocks or stacks rather than the open parts of platforms. *L. variegatus* sometimes feeds under water, collecting algae from around the rim of the larger pools. These crabs are at all times very agile, running quickly into nearby crevices when disturbed and moving rapidly along crevices, from which they are removed only with the greatest difficulty. The long, sharp, spine-like hairs on the ambulatory dactyli are undoubtedly of tremendous assistance to them. On one occasion, for instance, at Nicheno in November 1965, one large adult male was seen running across a sloping part of the rock platform well within the reach of larger waves. As a large wave came in the animal 'froze in its tracks', was covered by the wave and remained in the same place for a
TABLE 7  Distribution of all species with respect to type of shore classified according to substrate and wave action. Each figure gives the number of localities at which each species was found. Localities at which less than five specimens were found (L. variegatus - sheltered platforms, B. spinosus - muddy estuaries) are not included here.

<table>
<thead>
<tr>
<th>Type of shore</th>
<th>Number of localities</th>
<th>Species</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fully exposed cliffs, platforms and boulder beaches</td>
<td>11</td>
<td>L. variegatus</td>
</tr>
<tr>
<td>Semi exposed cliffs, platforms and boulder beaches</td>
<td>11</td>
<td>L. octodentatus</td>
</tr>
<tr>
<td></td>
<td></td>
<td>B. spinosus</td>
</tr>
<tr>
<td></td>
<td></td>
<td>U. granuloculus</td>
</tr>
<tr>
<td></td>
<td></td>
<td>P. quadridentatus</td>
</tr>
<tr>
<td></td>
<td></td>
<td>P. gainardi</td>
</tr>
<tr>
<td></td>
<td></td>
<td>P. laevis</td>
</tr>
<tr>
<td></td>
<td></td>
<td>P. capensis</td>
</tr>
<tr>
<td></td>
<td></td>
<td>A. cordiformis</td>
</tr>
<tr>
<td></td>
<td></td>
<td>L. latifrons</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th></th>
<th>L. variegatus</th>
<th>L. octodentatus</th>
<th>B. spinosus</th>
<th>U. granuloculus</th>
<th>P. quadridentatus</th>
<th>P. gainardi</th>
<th>P. laevis</th>
<th>P. capensis</th>
<th>A. cordiformis</th>
<th>L. latifrons</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fully exposed</td>
<td>7</td>
<td>1</td>
<td>0</td>
<td>4</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>6</td>
<td>0</td>
</tr>
<tr>
<td>Semi exposed</td>
<td>0</td>
<td>6</td>
<td>1</td>
<td>10</td>
<td>0</td>
<td>8</td>
<td>0</td>
<td>0</td>
<td>2</td>
<td>0</td>
</tr>
<tr>
<td>Sheltered</td>
<td>0</td>
<td>1</td>
<td>9</td>
<td>8</td>
<td>3</td>
<td>5</td>
<td>6</td>
<td>1</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Sandy, muddy</td>
<td>0</td>
<td>0</td>
<td>2</td>
<td>2</td>
<td>4</td>
<td>0</td>
<td>6</td>
<td>2</td>
<td>0</td>
<td>3</td>
</tr>
<tr>
<td>Open estuaries</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>7</td>
<td>0</td>
<td>10</td>
<td>2</td>
<td>0</td>
<td>8</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
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<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
few moments after the wave had receded, then continued running in the original direction. On another occasion, at Dinalong Bay, several were seen manoeuvring themselves gingerly down a vertical crevice about twice as wide as their bodies. They generally proceeded sideways but sometimes spread themselves across the crevice holding on with some of the legs of both sides.

Examination of stomach contents confirms that this species feeds on the algae encrusting the rocks. In feeding this algae and associated material is scraped off by the fingers of the chelae which are quite deeply scooped at their tips.

*P. capensis* occurs commonly on fully exposed rocky coasts. It is also a crevice dweller but lives low down on the shore in the infralittoral, sometimes in deep pools, amongst giant fucoid algae. According to B.C. Mollison, who has observed the behaviour of this species on several islands in Bass Strait, *P. capensis* moves up with the incoming tide to feed. It appears to be a rather solitary species.

Examination of stomach contents shows that *P. capensis* feeds on red and green encrusting algae. This is undoubtedly scraped off by the horny, spooned tips of the fingers of the chelae.

Where there are no boulders or similar loose material no other grapsid is found on fully exposed coasts. On
semi-exposed coasts where there are no boulders,

*L. octodentatus* sometimes occurs in shallow horizontal crevices. At Rocky Cape, on the northwest coast, this species occurs high up in the supralittoral and uppermost part of the midlittoral amongst small littorinid snails. According to Miss Elizabeth Pope (personal communication) this species was found by her and Miss Isobel Bennett along the north coast of Tasmania in burrows on the top of high cliffs. *L. octodentatus* has short spine-like hairs on the ambulatory dactyli which presumably provide assistance in moving in crevices as they do in *L. variegatus*.

Where boulders occur in large banks or scattered in groups over the platform *C. granulosus* and *P. quadridentatus* are the dominant shore crabs.

*C. granulosus* is distributed throughout the upper midlittoral. It is particularly common where patches of water remain at low tide or under piles of boulders amongst algae where the relative humidity at low tide is at least 95%. In such situations densities in this species mostly range from 20-50 and sometimes up to 140 or more per square metre (table 8). Higher up on the shore towards the supralittoral fringe, where littorinid snails are common, densities are lower, down to 14 per square metre. Similarly, in the lower midlittoral, densities are also low but higher than towards the supralittoral fringe. Individuals of *C. granulosus* spend much of their time crawling around among
TEXT-FIG. 31. Distribution of the 11 species with respect to substrate and wave action. The width of each bar is proportional to the percentage occurrence in each of five kinds of habitat (see Table 7). Dotted lines indicate marginal occurrence.
the rocks and sometimes merge on to the tops of boulders. They readily move beneath boulders when disturbed but are not capable of quick movement down the sides of boulders and often fall off when navigating near vertical faces.

*P. quadridentatus* inhabits the lower midlittoral, reaching densities of 8 - 23 per square metre (table 8), rather lower than those achieved by *C. granulosus*. For the most part, this species resembles *C. granulosus* in its ecological distribution and the two nearly always occur together. Their vertical distributions frequently overlap around the lower part of the midlittoral zone (text-figure 32B). Both species lack prominent tufts of hairs between the bases of the legs.

A good example of the differences in vertical distribution of *C. granulosus* and *P. quadridentatus* on a semi-exposed boulder beach is apparent at Ninepin Pt., beyond Gordon on the south east coast (text-figure 33A) (studied sporadically throughout 1963 to 1965 and surveyed in detail on 12 January, 1964 and again on 1 February, 1965).

The pattern of distribution of these two species observed at Ninepin Pt. is found on semi-exposed rocky beaches throughout the northwest coast and is unmodified by the presence of *L. octodentatus* at some boulder beaches, such as Low Head at the mouth of the Tamar River. This species, previously mentioned as sometimes occurring in crevices on some semi-exposed cliffs is commonly found on boulder
beaches, especially semi-exposed ones. Here it is almost entirely confined to the supralittoral zone where masses of the isopod *Licia australiensis* are found and the relative humidity is as low as 75%. In the present survey this kind of habitat has been the one at which this species has most often been taken, both on the northwest and east coasts. Densities of this species are rather low, seldom more than 6 per square metre. Often, only one or two may be found in an area of this size and the distribution is frequently bunched, several groups occurring along a 100 or so metre strip separated by large areas where the species is absent. The maximum size of individuals at all these localities is around 35 mm. It is frequently found in association with fresh water seepages, particularly along the northwest coast.

The salinity of a small stream near boulders at Tesselated Pavement, Pirates Bay where this species occurs was 4.68‰. It does not appear to extend into the mid-littoral. It was not found at several fully exposed boulder beaches along the east coast, notably Binalong Bay and Bicheno. Examination of the stomach contents of individuals collected at Pirates Bay shows that this species feeds both on plant material including algae and on the isopod *Lidia australiensis*. The tips of the fingers of the chelae are cylindrical and not spooned.

At Pirates Bay, in southeastern Tasmania, most of the above species were found on the wide platform known as the
Text Fig. 32. Diagrammatic representation of vertical distribution and ecological significance of the eleven species of grapsids and acarpids at six localities: A, fully exposed platform and adjoining sandy beach at Blackman; B, semi-exposed platform with scattered boulders at Pluteys Bay; C, sheltered sandstone platform and adjoining stony, sandy estuary at Pittwater; D, muddy estuary and adjoining rocky beach at Umina; E, muddy estuary at Woy Woy; F, muddy estuary at mouth of Illawarra Creek, Blackman Bay. Levels on the graph extracted mainly from study of major zonation organisms: HWS, mean level of high spring tides; HSN, same, neap tides; MSL, mean sea level; LSN, mean level of low spring tides; LSS, same, spring tides.
Tesselated Pavements (text-figure 32B; plate 10A).

4.23 SHELTERED BOULDER AND STONY BEACHES

In quiet bays and inlets where boulder or stony beaches occur the two dominant species are again those found in similar habitats on exposed coasts, *C. granulosus* in the upper midlittoral and *P. quadridentatus* in the lower midlittoral. On stony beaches both species generally become rather sparse, seldom achieving densities of more than 10 per square metre (table 8) and there is frequently a marked reduction in maximum size. For instance, at Gordon where the beach is composed of small stones, *C. granulosus*, whilst occurring in densities up to 167 per square metre, reaches a maximum size of only 15 mm carapace width (according to samples taken on 24 May, 1963 - text-figure 34A) whereas at boulder beaches such as Tarcoona (text-figure 34C; plate 11A) and Sandy Bay, this species reaches a maximum size of 28 mm or more (numerous samples from 1963 through 1965). On stony beaches (such as at Oyster Bay - text-figure 34B) densities are generally around 5 per square metre.

Examination of stomach contents of individuals of both species collected at Sandy Bay indicates that the food comprises green algae. In both species the tips of the fingers of the chelipeds are only very weakly excavated as spoons.
TABLE 8 Densities (number of individuals per square metre) of five species of grapsids in seven kinds of habitat. The upper row of each set gives the mean density (and the number of samples) and the lower the standard deviation (s). The second to last row gives the maximum measured density and the last row gives details of the habitat carrying that density — intertidal zone (UML, upper midlittoral; LML, lower midlittoral), degree of exposure to wave action and type of substrate. In the case of the maximum densities given for *C. granulosus* and *B. spinosus* higher values have been recorded but differ from those given here comprising mainly juveniles (*C. granulosus*) or being an extrapolation from a ¼ square metre sample (*B. spinosus*).

<table>
<thead>
<tr>
<th>Species</th>
<th>C. granulosus</th>
<th>P. quadridentatus</th>
<th>B. spinosus</th>
<th>P. gaimardi</th>
<th>H. haswellianus</th>
</tr>
</thead>
<tbody>
<tr>
<td>Number of localities</td>
<td>8</td>
<td>6</td>
<td>3</td>
<td>3</td>
<td>5</td>
</tr>
<tr>
<td>Habitat</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Semi-exposed platform and scattered boulders</td>
<td>13.4 (7)</td>
<td>6.5 (2)</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td></td>
<td>(17.09)</td>
<td>(4.95)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Semi-exposed boulder beach</td>
<td>39.8 (31)</td>
<td>16.5 (6)</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td></td>
<td>(35.37)</td>
<td>(7.29)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sheltered boulder beach</td>
<td>15.3 (25)</td>
<td>10.0 (17)</td>
<td>2.5 (8)</td>
<td>8.4 (7)</td>
<td>–</td>
</tr>
<tr>
<td></td>
<td>(14.92)</td>
<td>(8.19)</td>
<td>(1.92)</td>
<td>(4.31)</td>
<td></td>
</tr>
<tr>
<td>Sheltered platform and stony beach</td>
<td>33.5 (13)</td>
<td>4.8 (10)</td>
<td>19.6 (42)</td>
<td>5.9 (11)</td>
<td>27.8 (13)</td>
</tr>
<tr>
<td></td>
<td>(365.79)</td>
<td>(6.36)</td>
<td>(19.38)</td>
<td>(5.24)</td>
<td>(23.54)</td>
</tr>
<tr>
<td>Stony estuary</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>13.0 (10)</td>
<td>–</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>(7.67)</td>
<td></td>
</tr>
<tr>
<td>Open mud bank</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>21.8 (8)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>(21.31)</td>
</tr>
<tr>
<td>Maximum density</td>
<td>149</td>
<td>29</td>
<td>81</td>
<td>25</td>
<td>68</td>
</tr>
<tr>
<td>Locality and habitat of maximum density</td>
<td>Taroma UML semi-exposed boulder beach</td>
<td>Sandy B. LML sheltered boulder beach</td>
<td>Pittwater UML sheltered platform</td>
<td>Pittwater UML sheltered stony estuary</td>
<td>Elwick B. UML sheltered stony estuary</td>
</tr>
</tbody>
</table>
On sheltered boulder or stony beaches two additional species, *B. spinosus* and *P. gaimardii* occur.

Where the beach consists mainly of boulders or larger stones or where the accumulation of silt begins to give the beach a characteristic muddy appearance, *P. gaimardii* is the more often found. This species lives in the lower midlittoral and sometimes extends into the upper midlittoral, always occurring under stones and often in remnant pools (text-figure 32C). In such a habitat it reaches densities of around 13 per square metre (table 8). Large adult individuals, more than 30 mm carapace width, are sometimes found in such habitats (text-figure 34 I).

This species appears to feed mainly on green algae. Whilst being kept in the laboratory, individuals of this species were seen to scrape encrusting green algae off the surfaces of rocks (Lynette B. Donne, personal communication). The tips of the fingers of the chelae are only weakly excavated as spoons.

Where the stones are small, *B. spinosus* is the more common. This species occurs also where stones are scattered on a sandstone platform. Like the other species just discussed *B. spinosus* always occurs under stones, where the relative humidity is generally above 95% but sometimes reaches 75-80%. It is most common in the upper midlittoral but may extend over much of the intertidal zone and so overlap the distributions of species such as *P. gaimardii* and
and *P. quadridentatus* (text-figure 32C); sometimes it occurs under stones in remnant pools. In dryer sandy habitats it frequently constructs very simple excavations under stones. It reaches densities of up to 81 per square metre at certain localities such as Pittwater but is often found in densities of less than 5 per square metre (table 8; text-figure 34 D,E). Beaches of small stones (e.g. Oyster Cove) generally carry smaller populations of *B. spinosus* (text-figure 34B).

*B. spinosus* appears to feed mainly on algae. The tips of the fingers of the chelae are weakly spooned with several scattered stout hairs towards the tips. There are tufts of hairs between the bases of the ambulatory legs, especially between the first and second and second and third legs.

Three localities, Dunalley Bay, Sandy Bay and Howden, provide particularly good examples of the above patterns of distribution. At Dunalley Bay (text-figure 33B, plate 12A) where a beach of large boulders forms the upper part of an extensive sandy estuary, all four species typical of sheltered shores of this type occur. (This locality was studied on several occasions and the main survey was carried out on 31 January, 1965). The boulders in the lower part of the shore are covered towards their bases by masses of tubes of the polychaete *Caleolaria caespitosa*. *P. gaimardii* extends throughout the whole of the beach and, except in the uppermost parts, is represented in larger numbers than any
TEXT. FIG. 33. Vertical distribution of four species of grapsids at two localities in south eastern Tasmania. Each value for density is the mean of two samples 1 square metre in area.
other species. Where it is most abundant there are many more large individuals than small. Elsewhere, particularly at the upper and lower parts of the shore large individuals are comparatively rare. The other three species appear to be represented in approximately equal abundances, *P. quadridenticatus* being most abundant low down on the wetter parts of the shore, *C. granulosus* and *B. spinosus* higher up. Largest individuals of the former were found about the middle of the species' range whilst all samples containing *B. spinosus* were dominated by small adults.

Along parts of the shoreline of Sandy Bay, near Hobart, studied on numerous occasions, the intertidal part of the beach becomes rather muddy (plate 11B). Three species occur here, their ranges overlapping around the centre of the midlittoral. *P. gaimardi* and *P. quadridenticatus* dominate the lower, and *C. granulosus* the upper midlittoral. On the cleaner stony and boulder beaches of Sandy Bay only *P. quadridenticatus* and *C. granulosus* are found.

At Howden, North West Bay (Plate 10B), on the south east coast (also studied throughout 1963-65 and surveyed mainly on 9 November, 1965) the shore consists of a moderately wide, gently sloping sandstone platform with scattered stones and remnant pools not much below high tide level. *Brachynotus spinosus* is common in these pools and reaches local concentrations of 82 per square metre (as estimated from 2 square
metro samples). Stony beaches carrying small populations of *P. crassipes*, *P. gaimardii* and *P. quadridens* flank this platform. The sandstone platform and adjoining stony beach and sandy estuary carries the same species distributed in a manner similar to that at Howden (text-figure 33C).

Only at a few localities is this pattern described for sheltered stony shores modified. Towards the mouth of the Proser River, above Orford, on the east coast, and at Double Creek and MacLaine’s Creek, slightly further north, *P. laevis* is found in the upper sublittoral, often occurring together with its congener, *P. gaimardii*. (The comparative distribution of these two species at Orford and at Double Creek was studied in October 1965). In the upper parts of the Proser River (text-figure 32B), where the shore consists of a narrow stony beach, *P. laevis* is quite common in the upper sublittoral, just below *H. haswellianus* where the substrate comprises as much as 35% silt and clay. The salinity of the water at low tide here reaches as low as 2.5‰. *P. gaimardii* is rare at these localities and those individuals present are usually only small adults and juveniles. Near the mouth of the river at Orford (plate 98) both *P. laevis* and *P. gaimardii* occur in burrows in the extensive *Kostera* marsh (see below). At Double Creek (plate 14B) both species show a similar distribution up to about 50 metres above the mouth. Both species are commonest
under stones and in burrows in the mud (silt and clay together 12%). About 30 metres above the mouth both species are less common but *P. laevis* occurs slightly higher up on the shore. A further 20 metres upstream both species are slightly less common but large individuals of both species still occur. At these localities *P. laevis* is generally most abundant higher up on the shore, in the upper sublittoral zone, whilst *P. caimardii* is usually found in the lower sublittoral. These areas are subject to some freshwater influence and an appreciable amount of silt is present also. At numerous other east coast localities, mostly where silt is absent and the substrate is almost entirely sand, *P. caimardii* is present and *P. laevis* absent.

In those localities where large amounts of silt accumulate or on soft sandstone platforms, for instance, at Alwick Bay (Plate 12B) a further species, *H. haswellianus*, occurs high up on the shore in the upper sublittoral and supralittoral under small stones, often in small burrows. Where large flat stones as well as small stones are present largest numbers are found under the former.

Stomachs of individuals of this species collected at Hoggy Creek and Alwick Bay contained fragments of stems of plants. The tips of the fingers of the chelae are not spooned but bear scattered short hairs.

*L. oculamentatus* has been found at only two sheltered beaches, at Kingston, where one large adult male was found
TABLE 9  Percentage composition and moisture content at time of low tide of substrate occupied by nine species, together with relative humidity of habitat and salinity of water.

<table>
<thead>
<tr>
<th>Species</th>
<th>% Sand$^1$</th>
<th>% Silt$^1$</th>
<th>% Clay$^1$</th>
<th>% Moisture$^2$</th>
<th>Relative humidity (%)$^3$</th>
<th>Salinity (%)$^2,4$</th>
</tr>
</thead>
<tbody>
<tr>
<td>L. octodentatus</td>
<td>-</td>
<td>-</td>
<td></td>
<td>-</td>
<td>75</td>
<td>4.7 (1)</td>
</tr>
<tr>
<td>B. spinosus</td>
<td>-</td>
<td>-</td>
<td></td>
<td>-</td>
<td>85</td>
<td>25.1 – 36.7 (9)</td>
</tr>
<tr>
<td>C. granulosus</td>
<td>-</td>
<td>-</td>
<td></td>
<td>-</td>
<td>95</td>
<td>31.9 (1)</td>
</tr>
<tr>
<td>H. haswellianus</td>
<td>77.9 (5)</td>
<td>7.2 (5)</td>
<td>14.9 (5)</td>
<td>6.5 – 52.2</td>
<td>-</td>
<td>0 – 24.5 (7)</td>
</tr>
<tr>
<td>P. quadridentatus</td>
<td>-</td>
<td>-</td>
<td></td>
<td>-</td>
<td>-</td>
<td>33.7 – 34.9 (2)</td>
</tr>
<tr>
<td>P. gaimardii</td>
<td>93.3 (4)</td>
<td>2.3 (4)</td>
<td>4.3 (4)</td>
<td>-</td>
<td>-</td>
<td>6.5 – 35.9 (13)</td>
</tr>
<tr>
<td>P. laevis</td>
<td>91.4 – 95.0</td>
<td>02 – 4.1</td>
<td>4.2 – 4.5</td>
<td>22.3 – 30.2</td>
<td>-</td>
<td>5.8 – 35.9 (8)</td>
</tr>
<tr>
<td>P. latifrons</td>
<td>69.8 (5)</td>
<td>6.8 (5)</td>
<td>23.4 (5)</td>
<td>-</td>
<td>75</td>
<td>7.2 – 29.8 (6)</td>
</tr>
<tr>
<td>H. cordiformis</td>
<td>81.0 (7)</td>
<td>4.0 (7)</td>
<td>15.0 (7)</td>
<td>19.7 – 37.8</td>
<td>-</td>
<td>6.5 – 29.8 (4)</td>
</tr>
<tr>
<td>H. latifrons</td>
<td>86.1 (4)</td>
<td>2.9 (4)</td>
<td>10.9 (4)</td>
<td>-</td>
<td>75</td>
<td>6.5 – 29.8 (4)</td>
</tr>
</tbody>
</table>

$^1$Each set gives the mean (and number of samples) and below this, the range.  $^2$Only the range is given (and the number of samples).  $^3$Only the lower limit is given.  $^4$Salinity is that from samples of water taken at low tide.
in a remnant pool high up in the supralittoral and at Pirates Bay, near Fossil Island, at the mouth of a stream, where one small adult male was found under stones, again in the supralittoral. Prominent tufts of hairs arise from between the bases of the ambulatory legs, especially between the first and second and second and third legs.

At only two sheltered beaches, the southern part of Pirates Bay and at Coles Bay, Freycinet Peninsula, *L. variegatus* was found in the upper midlittoral in shallow, vertical crevices on moderately wide platforms. Only one individual was found at each locality.

4.24 ESTUARIES

Estuaries are the typical habitat of three species of grapsids, *H. haswellianus*, *P. gaimardi* and *P. laevig* and the two ocypodids, *H. cordiformis* and *H. latifrons*.

*P. gaimardi* is usually found in the shallow pools under large scattered stones which are embedded in the sand or mud and its distribution frequently extends into the upper midlittoral. Pittwater (text-figure 32C; plate 13A) and Eaglehawk Bay provide examples of such localities but this species also constructs well made burrows in *Zostera* marshes, especially in the lower midlittoral and extends well into the sublittoral from where it is taken in reasonably large quantities by fish such as the flathead.
Platycorda bazzanali Cuvier & Valencianos) and possibly others (S.R. Guilex and Lynette S.邓, personal communication). The burrows are fairly large and straight and extend into the mud at a low angle. In constructing the burrows the crabs scrape up the mud with the legs of one side and drag it off a short distance. The excavated material is thus deposited in a pile not far from the burrow entrance. These crabs which construct burrows are of all sizes and large adults are common. Small crabs sometimes construct shallow burrows in sandy banks just above high tide. At Isthmus Bay, Flinders Island, on extensive sandy flats, large numbers of this species are found in the infralittoral fringe using clusters of the tunicate Fyrea bracteolata as temporary shelters. At two localities, Pipe Clay Lagoon and Norfolk Bay, investigation of the burrows on several occasions showed that large males were present but no females were found. The density of burrows in these situations is around 2 per square metre.

While P. gaimardii thus lives under stones and also in burrows, its preference for stones at many localities is evident. It would appear that adults only construct burrows in firm mud such as in marshes or lagoons colonized by Zostera. In nearly all localities absence of either stones or Zostera is correlated with absence of P. gaimardii.

P. laevig, as already mentioned, occurs at a few localities with P. gaimardii. At Blackman Bay at the mouth of
TEXT-FIG. 1A. Histograms showing size distribution of 6 species of gastrid at 8 loc'i. Vertical axis represents frequency (intervals of 2 underlined); horizontal axis, carapace width divided into 10 cm groups. Samples were collected as follows: A, C, L. 14 cm; B, D, 20 minutes random searching; E, total of 5 non-adjacent 1 square metre samples; F, G, 10 minutes random searching; H, 60 minutes random searching; I, U. 14 of 13 non-adjacent 16 cm square metre samples; J, 20 minutes random searching.
Brean Creek (text-figure 32B: plate 14A), large adults of both sexes of P. laevis are found in burrows around high tide level, in banks of mud which comprise 50% silt and clay. The burrows are well made, vertical and expand into slightly larger chambers after about six to twelve inches. At this locality small adult and juvenile P. gaimardii are found slightly lower down on the shore in the stream bed in small burrows. However, neither P. gaimardii nor P. laevis possess strong tufts of hairs between the bases of the ambulatory legs.

H. haswellianus has already been mentioned as occurring on sheltered stony beaches. At numerous estuaries where stones are absent this species is found in mud and earth banks in the upper midlittoral and supralittoral, sometimes up to two feet above high tide level, in extremely well made semi-vertical burrows which often form a complex network with their entrances close together. Sometimes, as at Margate (plate 13B), this species shows a distinct preference for burrowing near the scattered stones or under large clods of earth (text-figure 32B). It is an aggressive species and strongly defends small areas by raising its body on partly unflexed legs and stretching out its chelae which may be flexed in front of the face or unflexed and forwardly stretched. H. haswellianus extends considerable distances up rivers (text-figure 35B,C) and is common where salinities are as low as 6°/oo. Individuals of H. haswellianus possess
prominent tufts of hair between the bases of the ambulatory legs.

Open estuaries and the banks of streams, where the mud is at all firm, are the almost exclusive domain of the two scyphodids (text-figure 32D, E, F; plate 13B). Both live only in burrows which are sometimes near stones but never under them. Both species have prominent tufts of long hair between the bases of the ambulatory legs, especially between the first and second and second and third legs.

The burrows of M. cordiformis are made in firmer mud in the upper part of the shore right up to the limit of high spring tides and are vertical, round and fairly deep, extending to the water table where they enlarge into chambers, the bottoms of which are usually covered by water. This species actually tolerates a very wide amount of variation in the constitution of the substrate, from colloidal clay through organic muds comprising 30% silt and clay to very sandy mud comprising less than 5% silt and clay (table 9). Moisture content of the substrates in which they burrow ranges from fully saturated to 135% water by weight (data from samples collected at the time of extreme low tide). Relative humidities in the burrows are always above 95%. Both species extend considerable distances up streams and rivers and tolerate low salinities (table 9; text-figure 35B, C). M. latifrons burrows in the wetter part of the mud flats, in runnels or large areas which remain moist even at low tide. The substrate
TEXT-FIG. 35. Distribution of nine species of grapsids and ocypodids along River Derwent: A, map of lower reaches of river; B, distribution of the species along the river; C, number of species at the 13 localities shown in A; B and C are based on the scale of miles at the bottom of C.
usually comprises at least 80% sand and generally more, with moisture contents as low as 23% by weight. The burrows extend into the mud at a low angle for about six inches. Both species are active at low tide, feeding on small particles of organic matter which they sift from the mud. The tips of the fingers of the chelae are prominently excavated as spoons and the inner edge of the spoon on the fixed finger is fringed with hairs. The excavations are best developed in *H. cordiformis* but the hairs much shorter. (Feeding, burrowing and other behaviour of these two species is described in detail in section 5).

Both species of ocygodids are subject to some predation by white fronted herons (*Notophoyx novaehollandiae* (Latham)), silver gulls (*Larus novaehollandiae* Stephens) and possibly other estuarine waders.

**4.25 CONCLUSIONS**

From the field observations described above it is apparent that in their broad horizontal patterns of distribution the species fall into three groups:

1. those preferring fully exposed cliffs and platforms, sheltering in cervices - *L. variegatus* and *P. capensis*;

2. those preferring semi-exposed or sheltered boulder or stony beaches, sheltering under the boulders or stones - *C. eximiosus*, *P. quadridentatus*, *P. spinosus* and
I. octodentatus; and

3. those preferring sheltered shores such as estuaries, lagoons or the banks of streams, sometimes sheltering under stones and sometimes constructing burrows - P. naimardii, P. laevis and H. haswellianus, or never under stones but always in semi-permanent burrows - H. cordiformis and H. latifrons.

The species of the last group are almost the only ones exposed to low salinities.

There are, within these patterns, differences in the species' vertical distributions and the resultant pattern is further modified by the availability of certain types of cover (for summary see table 20).

Morphological features such as the presence of spines on the legs of species living on exposed cliffs (L. variegatus, L. octodentatus, P. capensis), dense tufts of hairs arising from the bases of the ambulatory legs of species living in areas subject to silt (H. haswellianus and the two ocypodids, also L. octodentatus and B. spinosus but not Paragrapbus species) appear to be correlated with the ecological distributions.

The available data indicate that all species feed on the organisms most abundant in their surroundings. Only for L. octodentatus is there evidence of a carnivorous diet. L. variegatus, P. capensis and, to a lesser extent
P. mimardii, have the tips of the fingers of the chelae excavated as spoons and almost certainly feed on algae which they scrape from the surfaces of stones. The acy-podids also have spooned fingers but these serve to collect mud pellets from which the food is extracted by the mouthparts.

4.3 BREEDING AND MoulTING CYCLES

In this subsection the variation from month to month in the proportions of moulting individuals, of females carrying eggs and of juveniles is considered. These cycles were studied to find to what extent the periods of breeding overlapped in each species and to determine the relations between breeding cycles as estimated by counts of ovigerous females, and moulting cycles.

4.31 MATERIALS AND METHODS

In the investigation of breeding and moulting cycles, two species, *Cyclograpsus granulosus* and *Brachynotus spinosus*, were selected for special study. Two to four samples were collected at approximately monthly intervals from May, 1963 to April, 1965. Three localities carrying populations of *C. granulosus* differing insignificantly in size range and breeding habits, and one locality at which *B. spinosus* occurred, were studied. At each, samples were collected
TEXT-FIG. 36. Breeding and moulting cycles in C. granulata (A, B) and B. spathula (C, D). Percentage of adult females carrying eggs (crosses), adult females moulting (filled circles) and adult males moulting (open circles) computed by pooling data for the two size classes of adults for corresponding months of successive years.
from habitats carrying relatively the largest number of adults. Initially, sampling involved measuring, to the nearest millimetre, the carapace width of all crabs collected from an area of one square metre. This procedure was modified later in favour of examination of a larger number of individuals by collecting for a standard time (generally 20 minutes for C. granulosus and 10 minutes for E. spinosus) over a larger area, each crab being measured to an accuracy sufficient to place it in one of the three size groups - "juveniles", "small adults" and "large adults" (see 4.21 - table 6). In addition to size, the following data were also collected for each individual: sex, whether or not it had recently moulted (a crab was considered to have recently moulted if the cardiac and intestinal regions of the carapace could be easily depressed - see Hiatt, 1948: 149) and, in the case of a female, whether or not it was carrying eggs.

4.32 CYCLES IN C. GRANULOSUS AND E. SPINOSUS

In the two intensively studied species (see tables 10 and 11 and text-figure 36), ovigerous females are found throughout seven or eight months of the year, from July or August through February (late winter to late summer) and are most common in November and December. The rate of increase in numbers of ovigerous females appears to be slow initially but after the peak is reached the rate of decr
<table>
<thead>
<tr>
<th>Year</th>
<th>1963</th>
<th>1964</th>
<th>1965</th>
</tr>
</thead>
<tbody>
<tr>
<td>Month</td>
<td>May</td>
<td>Aug</td>
<td>Oct</td>
</tr>
<tr>
<td>Day</td>
<td>30</td>
<td>13</td>
<td>5</td>
</tr>
<tr>
<td>Locality</td>
<td>Ta</td>
<td>Ta</td>
<td>Ta</td>
</tr>
<tr>
<td>Sample</td>
<td>337(4)</td>
<td>240(3)</td>
<td>129(2)</td>
</tr>
<tr>
<td>Juveniles</td>
<td>37.6</td>
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</tr>
<tr>
<td>%Moulting</td>
<td>-</td>
<td>-</td>
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<td>0-11</td>
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<td>-</td>
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<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>0-6</td>
<td>-</td>
<td>0-50</td>
<td>0-100</td>
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<tr>
<td>0-25</td>
<td>50-82</td>
<td>0-100</td>
<td>55-100</td>
</tr>
</tbody>
</table>

**TABLE 10.** Moulting and breeding cycles in *Cyclograpsus granulosus*. The figures for sample in row 5 give the total number of individuals in the sample (and the number of samples). The figures for juveniles (row 6), small adult males and females (rows 9 and 12), large adult males and females (rows 17 and 20), are percentages of the total number in the sample which each of these groups comprised. The figures for percentage moulting and ovigerous are percentages of these individual groups and the row below each gives the range of these between samples.

Localities: Ta, Taroona; Go, Ninepin Pt., near Gordon; SB, Sandy Bay.
sperm relatively fast. Large adults appear to breed to a much greater extent than do smaller ones, beginning earlier and finishing later; they may possibly breed twice each season with peaks separated by about three months (October and January in C. granulosus, slightly earlier in B. spinosus). These latter features were obvious only in C. granulosus in 1963-4. Total chi-square tests for all samples indicate a significant difference in breeding intensity between the two size classes in both species. Tests between samples of C. granulosus for each month indicate significant differences between size groups in October 1963 and January 1964. These differences between the size groups are indicated in text-figure 37 which shows the size constitution of ovigerous females of C. granulosus in relation to the proportion of all adult females in samples for five months of the 1963-4 breeding season.

Moulting in adults takes place twice a year in C. granulosus with peaks around the end of the breeding season in March and again near the beginning of the succeeding season. Males appear to moult slightly earlier than females in C. granulosus. The moult near the beginning of the breeding season seems to be participated in by small adults only, that at the end of the breeding season by all adults. In B. spinosus moulting seems to occur only at the end of the breeding season, with a peak around February in females and
**TABLE 11.** Moulting and breeding cycles in *Brachynotus spinosus.* The data is arranged as in the previous table for *C.granulosus*, locality: Pit., Pittwater.

<table>
<thead>
<tr>
<th>Year</th>
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<th>1964</th>
<th>1965</th>
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<tr>
<td>Sample</td>
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<td>66(3)</td>
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<td>Juveniles</td>
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<td>Females</td>
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<tr>
<td>%Moulting</td>
<td>0</td>
<td>0</td>
<td>15.4</td>
</tr>
<tr>
<td>%Ovigerous</td>
<td>0</td>
<td>9.1</td>
<td>32.1</td>
</tr>
<tr>
<td>Males</td>
<td>15.6</td>
<td>4.5</td>
<td>5.6</td>
</tr>
<tr>
<td>%Moulting</td>
<td>0</td>
<td>0</td>
<td>100</td>
</tr>
<tr>
<td>Large adults</td>
<td>33.5</td>
<td>36.3</td>
<td>10.2</td>
</tr>
<tr>
<td>%Moulting</td>
<td>0</td>
<td>0</td>
<td>50.0</td>
</tr>
<tr>
<td>%Ovigerous</td>
<td>0</td>
<td>20.8</td>
<td>54.5</td>
</tr>
<tr>
<td>Males</td>
<td>15.6</td>
<td>4.5</td>
<td>5.6</td>
</tr>
<tr>
<td>%Moulting</td>
<td>0</td>
<td>0</td>
<td>100</td>
</tr>
<tr>
<td>Large adults</td>
<td>33.5</td>
<td>36.3</td>
<td>10.2</td>
</tr>
<tr>
<td>%Moulting</td>
<td>0</td>
<td>0</td>
<td>50.0</td>
</tr>
<tr>
<td>%Ovigerous</td>
<td>0</td>
<td>20.8</td>
<td>54.5</td>
</tr>
</tbody>
</table>
April in males.

In populations of any species of animal it would be expected that younger, usually smaller individuals would be proportionally more numerous than older ones. This is no less likely in the species studied here. Since ovigerous females are most abundant at certain times of the year, providing development of early and late hatched larvae takes the same time, it would also be expected that the proportion of juveniles (post larval individuals) would fluctuate, being especially high at a certain time of the year. In the samples of the species studied here, however, whilst large adults are less frequently taken than smaller ones, juveniles seldom make up the bulk of the sample. This is undoubtedly due to the fact that they are at all times more difficult to capture because of their small size and so pass unnoticed or escape under rocks or into crevices.

The relative number of juveniles does appear to fluctuate, with peaks of abundance around March and possibly December in *C. granulosus* and around January in *B. quinquus*. Moulting in juveniles appears to take place throughout the year with peaks coinciding with those for adults. It should be emphasized here that most of the individuals classed as juveniles are larger than the first crab stage after megalopa.

### 4.33 OTHER TASMANIAN SPECIES

The periods over which ovigerous females occur in eight other Tasmanian species is shown in table 12 where data
TABLE 12  Months in which ovigerous females of ten species have been taken during the present studies. Crosses indicate months in which females are known to be ovigerous; a's, months in which they are known to be not ovigerous; dashes indicate that only small samples were collected and that ovigerous females and soft specimens were not present.

<table>
<thead>
<tr>
<th>Species</th>
<th>Months of the year</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Jun</td>
</tr>
<tr>
<td>L. octodentatus</td>
<td></td>
</tr>
<tr>
<td>B. spinosus</td>
<td>a</td>
</tr>
<tr>
<td>C. granulosus</td>
<td>a</td>
</tr>
<tr>
<td>H. haswellianus</td>
<td></td>
</tr>
<tr>
<td>P. quadridentatus</td>
<td>a</td>
</tr>
<tr>
<td>P. gaimardii</td>
<td></td>
</tr>
<tr>
<td>P. laevis</td>
<td></td>
</tr>
<tr>
<td>P. capensis</td>
<td></td>
</tr>
<tr>
<td>H. cordiformis</td>
<td>a</td>
</tr>
<tr>
<td>H. latifrons</td>
<td>a</td>
</tr>
</tbody>
</table>
are compared with the results for the two species discussed above. In H. haswellianus, H. quadridentatus and H. rainard-
dii there is evidence to suggest that breeding and moulting cycles are related temporally in the same fashion as in
C. granulosus and H. spinosus. Paracarcinus species (perhaps including P. lacou) apparently finish breeding earlier and
may commence earlier than either C. granulosus or H. spinosus.
H. intestinalis breeds at about the same time as these two and
in L. edentatus, H. haswellianus and H. cardiformis oviger-
ous females occur later.

4.34 CONCLUSIONS

The data obtained on breeding and moulting cycles shows
clearly that in adults, moulting reaches a peak about two
months after the time at which ovigerous females are most
abundant. Small adults also appear to moult prior to the
commencement of breeding. The small percentages of moulting individuals may be due to the fact that a moulting crab
generally hides away to prevent predation whilst it is soft
immediately after exuviation. The time taken for the carap-
pace to harden after exuviation is also undoubtedly much
shorter than that during which the developing eggs are
carried under the female. (Broekhuysen, 1941; Hiatt, 1943;
females in all species are common in summer and the breeding
cycles of all species overlap to a considerable extent.
TEXT-FIG. 37. Size distribution of ovigerous females (filled area) of C. granulosa, compared with size distribution of all females larger than 9 mm carapace width from August 1963 to January 1964. N is total number of animals in sample.
There do appear to be slight differences amongst the species in the timing of breeding. Those species living low down on the shore (P. primordii, E. quadridontatus, H. latifrons) reach maxima in occurrence of ovigerous females earlier than those living higher on the shore (E. octodentatus, E. granules, H. haswellianus and H. cyciformis). The latter species, those living high on the shore, are also mainly ones with geographical distributions extending into warm temperate regions. The reasons for such differences are probably due to species' differential responses to temperatures. It would be expected that species inhabiting warmer areas would require higher temperatures to initiate breeding.

4.4 GILL NUMBERS AND RELATIVE VOLUME OF THE GILLS

As was mentioned in the general introduction (section 1.5) adaptations to terrestrialness in brachyuran crabs include reduction in the volume of the gills in relation to the body. Since it has already been demonstrated (section 4.2) that the species differ in their vertical zonation, some living higher on the shore in less moist habitats than others, it was considered worthwhile to investigate the gill volumes of the species to determine to what extent differences do exist in this feature.
4.41 MATERIALS AND METHODS

In assessing the relative volume occupied by the gills, the crabs were placed in 15% chromic acid for 24 hours, the legs removed at their fracture plane, the gills dissected out at their bases and the body (cephalothorax, abdomen and viscera), legs and gills allowed to dry on filter paper for five minutes. The body was then placed in a graduated cylinder and the volume of water displaced was noted. The legs were then placed in the cylinder and the resultant displacement of water again noted. The gills (and epipodites) were separately placed in another smaller, graduated cylinder (Hiatt, 1948: 145). In the case of small species (Brachynotus spinosus and Helograpsus haswellianus) volumes were estimated from two or three crabs at a time.

4.42 GILL NUMBERS

The maximum number of gills (excluding epipodites) found in the species studied here was 18 (Table 13). Of the Grapsidae, the grapsine L. variegatus and the plagusine P. capensis have 18 gills (nine on each side). These are pleurobrancho on the fifth and sixth thoracic segments (corresponding to the first and second ambulatory legs), an anterior and posterior arthrobranch on the cheliped and third maxillipede, an anterior arthrobranch on the second maxillipede and p...
sesarmines and the varunine, B. spinosus, possess 16 gills, differing from L. variegatus in lacking an anterior arthrobranch on the second maxilliped. In the grapsine L. octodentatus an anterior arthrobranch is also absent from the second maxilliped and the pleurobranch on the sixth thoracic segment is vestigial.

Of the Ocypodidae, H. latifrons has 16 gills arranged as in the majority of the grapsids, but H. cordiformis has only 12 gills, the least number of any species dealt with here, the podobranch of the second maxilliped being lost and the pleurobranch of the sixth thoracic segment being vestigial.

4.13 RELATIVE GILL VOLUMES

The sesarmines, with the possible exception of H. haswellianus, have relatively large gill volumes ranging from 5.24 to 5.98% of the body and 3.17 - 3.67% of the total volume; in H. haswellianus the gills occupy as large a volume as in other sesarmines relative to the body only, but less relative to the total volume. In L. variegatus the gills occupy slightly smaller relative volumes. In P. capensis, B. spinosus and L. octodentatus the gills occupy a much smaller volume, 3.35 - 3.18% of the body and 1.72 - 2.3% of the total volume. In the ocypodids the gill volume relative to the total volume is small (1.4 - 2.3%) although in H. latifrons the gills occupy 5.11% of the body only, as
TABLE 15  Number of gills and their volume, in relation to body and legs and to body only, in the eleven species. In the third and fourth column the first figure is the mean and the range is given in parentheses. Those species occurring in the infralittoral are listed last.

<table>
<thead>
<tr>
<th>Species</th>
<th>Number of gills</th>
<th>Percentage of total volume occupied by gills</th>
<th>Percentage of body volume occupied by gills</th>
<th>Number of animals tested</th>
</tr>
</thead>
<tbody>
<tr>
<td>P. capensis</td>
<td>18</td>
<td>1.72 (1.6-1.9)</td>
<td>3.35 (3.2-3.6)</td>
<td>2</td>
</tr>
<tr>
<td>P. gaimardii</td>
<td>16</td>
<td>3.19 (2.3-4.5)</td>
<td>5.28 (3.6-6.3)</td>
<td>6</td>
</tr>
<tr>
<td>P. laevis</td>
<td>16</td>
<td>3.44 (3.4-3.5)</td>
<td>5.41 (5.1-5.7)</td>
<td>4</td>
</tr>
<tr>
<td>P. quadridentatus</td>
<td>16</td>
<td>3.17 (2.4-4.8)</td>
<td>5.98 (4.6-9.1)</td>
<td>6</td>
</tr>
<tr>
<td>H. latifrons</td>
<td>16</td>
<td>2.33 (1.7-2.9)</td>
<td>5.11 (5.1-6.1)</td>
<td>5</td>
</tr>
<tr>
<td>C. granuloculus</td>
<td>16</td>
<td>3.67 (3.0-4.3)</td>
<td>5.68 (5.0-7.5)</td>
<td>4</td>
</tr>
<tr>
<td>L. variegatus</td>
<td>18</td>
<td>2.93 (2.3-3.9)</td>
<td>5.66 (4.8-7.9)</td>
<td>4</td>
</tr>
<tr>
<td>E. spinosus</td>
<td>16</td>
<td>2.31 (2.2-2.4)</td>
<td>3.80 (3.7-3.9)</td>
<td>6</td>
</tr>
<tr>
<td>H. cordiformis</td>
<td>12</td>
<td>1.43 (1.2-1.7)</td>
<td>2.61 (2.3-3.9)</td>
<td>4</td>
</tr>
<tr>
<td>H. haswellianus</td>
<td>16</td>
<td>2.62 (2.6-2.7)</td>
<td>5.25 (4.8-5.7)</td>
<td>5</td>
</tr>
<tr>
<td>L. octodontatus</td>
<td>14</td>
<td>2.00 (1.8-2.2)</td>
<td>3.40 (2.5-4.3)</td>
<td>4</td>
</tr>
</tbody>
</table>
high as in the sesarmines. In H. cordiformis the gills occupy less volume than in any other species studied here.

Adjusting the volume of the gills to account for large total volume differences in the various species and calculating the adjusted mean volume per gill shows that on the average P. sanensis, C. crangon, B. spinosus, L. octodentatus and H. cordiformis have smaller gills than do the other species.

In all species, the epipodites constitute a very small fraction (less than 10%) of the gill volume.

4.42 CONCLUSIONS

The method used to determine gill volumes has given rather poor results in the case of some species. Of course, the larger the diameter of the cylinder used, the less accurately the displaced volume can be measured. Where were used which scarcely exceeded in diameter the width of the carapace of the particular species being measured, best results were still obtained where each measurement included more than one crab. Prior treatment of the crab with chronic acid appeared to make little difference to the result.

Those species living higher on the shore generally possess lower gill volumes relative to the total volume of the body and legs. The values in relation to volume of the body only do not correlate with increasing height on the shore quite as well. This is rather unexpected, since per-
centage of total volume should show variations with differences in relative size of the chelipods and legs according to species and sex. Further consideration reveals differences according to habitat and behaviour rather than merely with the zone on the shore typically inhabited by the species. Thus, species like C. granulosus and H. haswelli which live high on the shore have rather high relative gill volumes; however, these species are nearly always found under stones or in burrows where relative humidities are high. Again, L. variegatus shelters in crevices but comes out on to the open shore to feed in the shade of boulders and cliffs; its relative gill volume is higher than that of L. octodentatus which lives even higher on the shore. Both the ocypodids, which spend considerable time on the open mud flats, have very low gill volumes.

There seems little correlation between gill numbers and height on shore normally inhabited by the species.

4.5 MOUTHPARTS

The basic structure of the mouthparts in brachyurans was well described by Borradaile (1922). The fact that, in animals, the structures associated with the mouth differ according to the nature of the food and the way in which that food is collected, is so well known that this generalization need not be elaborated further. Within the
Brachyura, differences in the arrangement of the hairs on the maxillipeds and in the modifications of the hairs, have been particularly well demonstrated in some American species of fiddler crabs (Uca). These differences have been correlated with the type of substrate in which the particular species feeds (Crane, 1941a; Altevogt, 1957a; Miller, 1961).

4.51 MATERIALS AND METHODS

All six pairs of mouthparts were studied for the eleven Tasmanian species dealt with here. Each appendage was dissected away from its attachment with fine forceps. Special attention was paid to the structure and arrangement of hairs on the endopodites, palps and endites. Observations were made with a Zeiss Opton binocular stereomicroscope and detailed structure was studied through an Olympus EH microscope. Photomicrographs were taken with an Olympus PM6 camera. Terminology used here for the mouthparts follows that employed by Borradaile (1922) and Miller (1961).

The account of the mouthparts follows a comparative approach, each appendage being dealt with in turn.

4.61 THIRD MAXILLIPED

The third maxillipeds are of importance taxonomically and are illustrated for most species in section 3.

In all species the endopodite is expanded and strongly flattened and the exopodite slender and weakly flattened;
the flattening is especially well exhibited by the large ischium and slightly smaller merus of the endopodite, the remaining segments, carpus, propodus and dactyl, which form the 'palp', being subcylindrical and slender.

The ischium has its medial edge toothed only in *L. octodentatus*, *H. spinosus* and *P. gaimardii* in all of which the teeth are small and rounded; in others the medial edge is entire.

The ischium in *C. cranosus*, *H. hassellianus*, all *Panaque* species and *P. capensis* bears dense longitudinal rows of hairs on both the outer and inner surfaces. These rows are situated close to the medial edge and the hairs are longest and especially dense on the outer surface midway along. In *C. cranosus* the hairs are plumose and in *P. gaimardii* they are piliferous. The same species have the palp moderately or densely hairy also, especially on the inner surface and at the tip of the dactyl. The hairs of the carpus are piliferous in all except *P. quadridentatus* and *P. capensis*.

In the other grapsids the endopodite is only sparsely hairy except on the inner surface of the propodus. In *L. variegatus* especially, the hairs are sparse. In this second group the hairs are simple.

In the ocypodids the endopodite bears many dense rows of distally plumose hairs on the outer surface of the ischium and a few isolated hairs on the inner surface. The
TEXT FIG. 18. Left appendicularia, outer aspect, of Tasmanian graspea (a-g) and oxyphida (h-i). a. t. exserta; b. t. octodentata; c. t. spinosa; d. t. kanei; e. t. quadridens; f. t. pansula; g. t. exposia; h. m. conforma; i. m. latifrons.
pulp is densely fringed by hairs which are plumose on the
campus of H. latifrons but otherwise simple.

4.62 SECOND MAXILLIPED

The second maxillipeds are more pediform than either of the other two pairs of maxillipeds, the endopodite being only moderately expanded proximally and the inner surface usually flattened or weakly concave, the outer surface more or less strongly convex. The longest segment is the merus (text-figure 38).

In C. granulosus, H. haswellianus and Paragrapsus species the ischium and merus are densely fringed with hairs medially, especially on the outer surface where they are arranged in two to four rows. Those on the medial edge of the merus are plumose in all of this group. In H. haswellianus (text-figure 38d), P. gaimardii (text-figures 38f, 39b) and P. laevis the proximal hairs of the merus are very long, almost as long as the palp; in C. granulosus and P. quadri-dentatus (text-figures 38e, 39a) they are much shorter. In E. spinosus (text-figure 38c) and P. capensis (text-figure 38g) the hairs on the ischium and merus are only moderately dense; they are plumose in E. spinosus and simple in P. capensis.

In the remaining grapsids (L. variegatus and L. octo-dentatus) the merus is only sparsely haired. The hairs are long and distally plumose in L. octodentatus (text-figure 38b)
but short and simple in \textit{L. variegatus} (text-figure 38a).

In both ocypodids the hairs of the ischium and merus are very long and those arising on the inner surface are distally plumose (text-figure 39c,d); in \textit{H. latifrons} they are less dense than in \textit{H. cordiformis}. Those arising from the medial edge and outer surface are fine and simple in \textit{H. latifrons} but in \textit{H. cordiformis} they are stout and "woolly", bearing circlets of short, apically directed processes which basally are long, slender and sharp and towards the tip are short, stout and blunt (text-figure 40c). In all species, the inner surface of the merus bears few hairs.

The carpus in all species is naked or very sparsely haired.

In the arrangement of hairs on the two distal segments of the palp, two main groups again emerge amongst the grapsids but the content of the groups is different (plate 8). In all species the edge of the dactyl bears 10-15 stout spine-like hairs. These are very long and sharply pointed in \textit{P. capensis}; in the other species they are short, stout and blunt. They extend almost right around the edge in \textit{H. haswellianus} and \textit{P. capensis} but are virtually confined to the tip in the remaining grapsids.

In the species of the first group (\textit{L. octodentatus}, \textit{H. haswellianus}, \textit{P. gainardii} and \textit{P. laevis}) there is a dense fringe of long hairs overlying and almost concealing these
TEXT-FIG. 39. Merus of left second maxillipeds, inner aspect, of Tasmanian grapsids (a, b) and ocypodids (c, d):
3. P. quadridentatus, b, P. zainardi; c, H. cordiformis; d, H. latifrons.
spine-like hairs and also extending along the whole length of the lateral edge of the propodus and along the distal part of the medial edge; in *E. spinosus* the dactyl is slightly less hairy.

In the species of the second group (*L. varienatus*, *C. granulosus*, *P. quadridentatus* and *P. capensis*) the hairs are likewise distributed along the lateral edge of the propodus and on the medial edge are confined to the distal portion but are very sparse; on the edge of the dactyl they are also sparse, the spine-like hairs being clearly visible. The inner surface of the propodus and dactyl bears short stout hairs in all grapsids.

In the two ocypodids, some of the hairs of the dactyl are quite different from those found in the grapsids. These hairs are of the type usually called "spoon-shaped" or "spooned" (Crane, 1941a). They are distally expanded, with blunt tips, the surface of the distal part inwardly concave. In *H. cordiformis* the hairs at the tip of the dactyl are quite short with broad-spooned tips, the edges of the spoon incised into broad lobes (text-figure 40a); similar but much shorter hairs are present on the inner surface of the dactyl. On the outer surface are longer hairs with more slender spoons and weakly incised edges (text-figure 40b), whilst the lateral and medial edges bear very long hairs with only weakly expanded tips, their edges fairly strongly incised distally and bearing slender "spines" basal to the tip (text-figure 40c).
Long hairs, which may or may not be laterally incised, densely fringe the propodus laterally and medially; the carpus also bears a few simple hairs and moderately long, simple hairs arise from the inner surface of the propodus (plate 8B).

In H. latifrons the spooned hairs are of only one type: long and slender with weakly expanded tips, deeply incised edges distally and spinate edges midway along (text-figure 40d). These are present in two or three rows on the distal edge of the dactyl. The palp is otherwise fringed laterally and medially by a dense array of long simple hairs (plate 8F).

4.63 FIRST MAXILLIPED

The first maxilliped is the most modified of all the maxillipeds. The endopodite is a large flattened structure with a medially projecting lobe towards the tip and two endites at the base, the distal elongate oval in shape and arising from the basis and the proximal, projecting transversely from the coxa and subpentagonal in shape.

Among the grapsids, the distal endite is more than half the length of the endopodite in L. octodentatus, B. spinosus and P. capensis (text-figure 41b); in the remaining species (e.g., P. quadridentatus, text-figure 41a) it is about onethird the length of the endopodite. In the ocypodids (text-figure 41c, d) the distal endite is slightly more than
TEXT-FIG. 40. Modified hairs from the dactyl of the second maxilliped of *Heloecius cordiformis* (a-c) and *Hemiplus latifrons* (d) (front view to the left, side view to the right): a, spooned hair from tip of dactyl; b, spooned hair from outer surface of dactyl; c, laterally serrate hair from lateral edge of dactyl; d, weakly spooned hair from tip of dactyl; e, "woolly" hair from medial edge of merus of second maxilliped of *H. cordiformis*.
a third the length of the endopodite in H. cordiformis and about one half the length in H. latifrons.

In all species the medial edge of the endopodite, the anterior edge of its medial projection, the medial edge of the distal endite and the distal edge of the proximal endite are the more densely hairy. In general, the same kind of hairs as are found on the dactyl of the second maxilliped are found also on the medial edge of the distal endite of the first maxilliped and the kind found on the bases of the second maxilliped are distributed towards the tip of the proximal endite. Thus, the medial edge of the distal endite bears, at least along the distal half, stout, spine-like hairs in the grapsids and spooned hairs in the ocypodids.

In the grapsids the spine-like hairs are overlain by long hairs which in most species are arranged in up to four more or less dense rows. These hairs are plumose in L. octodentatus, H. haswellianus, P. gaimardii and P. inaevis and simple in the other grapsids. In most species the outer surface of the distal endite bears scattered short hairs.

In H. cordiformis broad, spooned hairs are present about midway along the medial edge and weakly expanded, spinate hairs proximally and around the distal part of the lateral edge. In H. latifrons weakly spooned, spinate hairs are present along almost the entire edge and are overlain by simple hairs. The outer surface of the distal endite bears scattered hairs in both ocypodids.
The proximal endite bears a dense fringe of hairs around all free edges and sparser hairs on the outer surface in \textit{L. octodentatus}, \textit{H. haswellianus}, \textit{P. caimardii} and \textit{P. laevis} but in the remaining grapsids the edges are sparsely hairy except distally and the outer surface is naked or sparsely hairy. The distal hairs are particularly long in \textit{P. capensis}.

In \textit{H. cordiformis} the proximal endite bears long "woolly" hairs around the distal edge and plumose hairs around the remainder of the edge, the outer surface being naked. In \textit{H. latifrons} the whole surface and the free edges are densely hairy, the distal hairs being plumose.

The medial edge of the endopodite bears a single dense row of plumose hairs in \textit{C. granulosus}, \textit{H. haswellianus} and \textit{Paragrapsus} species and a single, sparse row of hairs in the other grapsids; in \textit{P. capensis} the hairs are plumose, in the others simple.

In both ocypodids the medial edge of the endopodite bears a single dense fringe of long plumose hairs.

4.64 MAXILLAE

The two pairs of maxillae both consist of a number of transversely elongated, flattened lobes; those of the second maxilla are termed "endites", those of the first maxilla (maxillule), "laciniae".
TEXT.FIG. 41. Left first maxillipeds, outer aspect, of Tasmanian grapsids (a, b) and ocypodids (c, d): a, *P. quadridens*; b, *P. capensis*; c, *H. cordiformis*; d, *H. laetusrns*.
The arrangement of hairs on the dactyl of the second mandilliped, which are repeated on the distal endite of the first mandilliped are again repeated on the medial edge of the distal endite of the second maxilla. Similarly, the medial edge of the proximal endite of the second maxilla bear hairs of a similar type and arrangement to those found on the mesus of the second mandilliped and the proximal endite of the first mandilliped. Thus, in the grapsids there are stout spine-like hairs on the distal endite of the second maxilla and in the ocypodids the distal endite bears spooned hairs.

Both the lacinae of the first maxilla bear spines in the grapsids and spooned hairs in the ocypodids although the outer one possesses stronger spines or better developed spooned hairs than does the inner.

The fringes of simple or plumose hairs overlying or underlying the spine-like or spooned hairs are much less dense on the maxillae than on the mandillipeds.

4.65 MANDIBLE

In all species of the two families the medial edge of the mandible is sharp, with a single more or less blunt tooth somewhat distally. The palp, which is attached to the inner surface of the distal edge distally bears hairs of the type found on the dactyl of the second maxilliped - spine-like in the grapsids, spooned in the ocypodids.
CONCLUSIONS

Summarizing, two main groups of species are apparent:
1, those in which there are more or less dense coverings of hairs on the palp of the second maxilliped, the distal endite of the first maxilliped and the distal endite of the second maxilla (*L. octodentatus*, *B. spinosus*, *P. gaimardii*, *P. laevis* and the two ocypodids); and
2, those in which the hairs are sparse on these regions (the remaining grapsids).

The hairs on the merus of the second maxilliped, the proximal endites of the first maxilliped and second maxilla are sparse in *L. octodentatus* among the first group of grapsids and *H. latifrons* and are also sparse in *L. variegatus* and *P. capensis* which belong to the second group.

The first group of species are those inhabiting areas where silt is abundant. Amongst these, only *L. octodentatus* lives in habitats where wet sand is not abundant. As in the second group of species, the densest fringes of hairs on the second maxilliped merus are found in the species inhabiting wet sandy areas. Species like *L. variegatus* and *P. capensis* which live in areas where both sand and silt are absent have the sparsest arrangement of hairs.

Spine-like hairs appear to be characteristic of the grapsids and spooned hairs of the ocypodids. The grapsids
undoubtedly feed on more macroscopic material than do the ocypodids. However, the absence of strong teeth on the medial edge of the ischium of the third maxilliped also seems to indicate that large animals are relatively unimportant in the diet of these crabs.

4.6 EXPERIMENTAL STUDY OF HABITAT SELECTION

So far it has been demonstrated that each species has a characteristic ecological distribution and the volume occupied by the gills and the arrangement of different types of hairs on the mouthparts appear to be adjusted to suit the characteristic habitats of each species. Many of the species also possess morphological adaptations to their habitat, such as spines on the ambulatory legs, spooned chelae, etc. Field observations of the distributions of species certainly provides some information on optimal conditions and the extent to which various factors limit distributions. However, reactions of species to various environmental factors may be modified by other factors which are not readily apparent, such as interspecific competition for space, food, etc. and the activities of predators. Isolated in the laboratory, the full range of species' tolerances and preferences may be investigated. The experiments described here were designed to determine these behavioural preferences and to find what correlation there was between these
and the distribution observed in the field.

4. MATERIALS AND METHODS

The habitat preferences of eight species were studied by means of three types of experiments.

1. Comparison of animals in (a) a system which presented a choice between sea water or fresh water and (b) one in which no choice was available (control).

2. Determination of short term (2 hours) temporal variation in species' behaviour in the situation outlined in 1(a) above.

3. Comparison of the long term (24 hours) behaviour of animals in a system which presented a choice between two different kinds of substrate, each of which was half covered by sea water.

The first two types of experiment are for convenience here designated freshwater tolerance experiments and the third, substrate preference experiments.

The eight species studied were Leptograpsus octodentatus, Brachynotus spinosus (only briefly studied in relation to substrate preference), Cyclograpsus granulosus, Helograpsus haswellianus, Paragrapsus quadridentatus and P. gaimardii, Heloccius cordiformis and Hemiplus latifrons.
All crabs used in the experiments were intermoult specimens (mainly adults) with the carapace hard. In the study of freshwater tolerances in *P. gaimardii*, the behaviour of small adults (carapace width less than 25 mm) was compared with that of large adults (carapace width more than 30 mm). Except in a few cases (in relation to substrate preferences - see below) each species was studied independently.

The experiments on freshwater tolerances were carried out in rectangular plastic trays placed in a plywood box covered by a plywood lid. The plastic trays were of two sizes: 'small' (8 x 3 3/4 inches with steeply sloping sides and ends 2 1/2 inches high, one side of which was cut down to 1 inch) and 'large' (9 3/4 x 7 1/2 inches with vertical sides and ends 2 1/2 inches high, one side of which was cut down to 1 1/2 inches). The large trays were used in studying large crabs. Four trays were placed in pairs, side by side in each box, the members of each pair having their 'cut down' sides adjacent. The two pairs of trays were separated by a plywood partition of the same height as the wooden box (approximately 6 inches). Thus, the animals could not escape from the box and only a negligible amount of light entered. In all, 16 'chambers' (i.e., 32 trays) were used, two to six crabs of a single species being placed gently in one tray of each and left undisturbed for varying amounts of time. The number of crabs in each chamber was kept low so as to minimize, as far as possible,
movement out of the tray in which they were placed due to effects of crowding.

In experiments of the type outlined in 1(a) and 2 above, one of the trays contained fresh water (tap water) and the other sea water. In 1(a) the crabs were alternately placed in sea water and fresh water. In 1(b) both trays contained sea water.

In experiments of type 1 the animals were left for at least 12 hours and the number in the two trays counted at the end of that time. The experiments were repeated several times for each species.

In the second type of experiment the animals were left for 5, 10, 15, 20, 30, 60 or 100 minutes, after which time their distribution was noted. A new experiment was begun after an interval, between experiments, during which the crabs were maintained in sea water for 5-120 minutes (average time 30 minutes), the shorter intervals being used for longer experiments (60-100 minutes). The average duration of these experiments was 20 minutes. Two to six such experiments were conducted each day, three to ten for each time, the fresh water being changed at the beginning of each set of experiments for each time and all water at the beginning of each day's experiments. The trays in which the crabs were maintained between experiments contained only sea water which was changed once daily.
The experiments were completed within, at the most, eight days from the time of collection of the animals; during this time they were not fed. It was found that all species could survive in these trays of seawater for at least a month, provided the water was changed regularly. The experiments were carried out at room temperature (15-25°C).

During the conduct of these experiments it became apparent that some species were showing a significant tendency to move out of water and on to the sides of the trays or boxes. The uncut edges of the small trays projected outwards for about 5/8". In some cases the crabs settled on these. The large trays were not shelved and the crabs merely clung to the sides. It was therefore possible to study concurrently species’ tolerance to fresh water and to immersion in water.

The experiments on substrate preferences were carried out in large plastic trays 2'6" x 1'3" and 3" deep surrounded by a shelf 1" wide. Plywood enclosures of slightly greater dimensions but one foot high were placed on top of the shelf surrounding each tray. The trays were partly filled with sand, mud and earth. In nearly all cases, two kinds of substrate were placed in each tray, one kind in each half; pebbles or stones were placed in layers or in groups and arranged so as to cover all of one kind of substrate or the whole tray. Sea water was placed in the tray so as to cover about half of each of the two substrates. That part of the
substrate covered by water was about half an inch deep, that uncovered, about 2\(\frac{1}{2}\) inches deep; the covered and uncovered portions were separated by a bank about two inches high. Sea water was changed, and the portion not covered by water moistened, at the beginning of each experiment.

From two to twelve crabs, but generally four to six, were placed in the centre of each tray and their position was noted after about 24 hours. The crabs placed in each tray were generally of one species but several experiments were carried out in which individuals of two or three species were placed in a tray together. Each crab in each experiment thus had a choice of at least four kinds of habitat, \textit{viz.}, sand below water, sand above water, mud below water, mud above water, etc.; where a group of stones was placed in each quarter of the tray there were eight choices available, \textit{e.g.} under stones on sand below water, on open sand below water, under stones on sand above water, etc.

Experiments were repeated several times for each species under each particular set of conditions. All experiments were generally completed within two weeks of the time of capture of the crabs. During this time they were not fed and between experiments were maintained as described above.

\textbf{Note:} Mechanical analysis of the three kinds of substrate used in experiments showed that the "sand" contained less
TABLE 1.4 Variation in proportion of crabs remaining in water of different salinities. The first column (control) gives the proportion remaining in the tray in which the crabs were placed; results from the first column are obtained from experiments where both trays contained sea water. The second column (sea water) gives the proportion remaining in the tray containing sea water and the third column (fresh water) gives that remaining in the tray containing fresh water; the results are obtained from experiments in which one tray contained fresh water and the other sea water. The fourth column gives the probability that results in any row are not significantly different. (Note: the number in brackets after each proportion in columns 1-3 is the total number of animals used in each part of the experiment.)

<table>
<thead>
<tr>
<th>Species</th>
<th>Control</th>
<th>Sea water</th>
<th>Fresh water</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>P. quadridentatus</td>
<td>0.40 (20)</td>
<td>1.00 (8)</td>
<td>0.00 (12)</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>B. spinosus</td>
<td>0.52 (23)</td>
<td>1.00 (8)</td>
<td>0.00 (25)</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>C. granulosus</td>
<td>0.59 (34)</td>
<td>1.00 (15)</td>
<td>0.00 (19)</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>H. latifrons</td>
<td>0.46 (28)</td>
<td>1.00 (8)</td>
<td>0.00 (20)</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>P. gaimardii</td>
<td>0.63 (30)</td>
<td>1.00 (5)</td>
<td>0.19 (16)</td>
<td>&lt;0.005</td>
</tr>
<tr>
<td>H. haswellianus</td>
<td>0.52 (19)</td>
<td>1.00 (7)</td>
<td>0.00 (18)</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>H. cordiformis</td>
<td>0.60 (30)</td>
<td>0.78 (9)</td>
<td>0.38 (24)</td>
<td>&lt;0.100</td>
</tr>
<tr>
<td>L. octodentatus</td>
<td>0.50 (50)</td>
<td>0.94 (18)</td>
<td>0.06 (30)</td>
<td>&lt;0.001</td>
</tr>
</tbody>
</table>
remaining in fresh water against time) are exponential in form, decreasing quickly initially and slowly after longer times. In order to more easily calculate the rates of movement the raw data were transformed; percentages being expressed in angles (Snedecor, 1961: 316) and time logarithmically. The transformed data yields linear regressions. Table 15 gives the raw data for all species and times; text-figure 42 shows the transformed data compared for all the species over all times. The results are also compared in table 16 where the time taken for 50% of the crabs to move out of fresh water is compared for each species (see appendix 1).

The two groups are made up of *P. quadridentatus*, *E. spinosus*, *C. granulosus* and *H. latifrons* on the one hand and *H. haswellianus*, *L. octodentatus* and *H. cordiformis* on the other; *P. qaimardii* appears to be intermediate between these two. In the first group, only 10%, at the most, remained in fresh water after 100 minutes and the time for 50% emigration was around 5 minutes. In the second group, generally much more than 20% remained in fresh water after 100 minutes and the time for 50% emigration was around 25 minutes (more than 90 minutes in *H. cordiformis*). In the case of *P. qaimardii*, 20% remained in fresh water after 100 minutes and 50% had emigrated within 16 minutes. There were no significant differences between large and small
TABLE 15. Behavioural tolerance to fresh water in eight species — variation in percentage remaining at different times. Each set of data includes (line 1) range of means of all replicates for each time; (line 2) mean (and its standard error) calculated from pooled replicates for each time; (line 3) total number of crabs used for each time (and the number of replicates for each time).

<table>
<thead>
<tr>
<th>Species Time</th>
<th>P quadridentatus</th>
<th>B spinosus</th>
<th>C granulosus</th>
<th>H latifrons</th>
<th>P gaimardii</th>
<th>H haswellianus</th>
<th>L octodentatus</th>
<th>H cordifrons</th>
</tr>
</thead>
<tbody>
<tr>
<td>5 minutes</td>
<td>14–80</td>
<td>18–73</td>
<td>32–57</td>
<td>40–50</td>
<td>60–86</td>
<td>80–100</td>
<td>44–100</td>
<td>82–100</td>
</tr>
<tr>
<td></td>
<td><strong>44.3(9.93)</strong></td>
<td><strong>48.6(9.99)</strong></td>
<td><strong>47.9(12.49)</strong></td>
<td><strong>45.9(12.46)</strong></td>
<td><strong>73.9(7.32)</strong></td>
<td><strong>93.1(6.34)</strong></td>
<td><strong>67.1(4.70)</strong></td>
<td><strong>94.9(7.33)</strong></td>
</tr>
<tr>
<td></td>
<td>88 (5)</td>
<td>70 (5)</td>
<td>73 (4)</td>
<td>74 (4)</td>
<td>115 (6)</td>
<td>101 (4)</td>
<td>85 (10)</td>
<td>39 (3)</td>
</tr>
<tr>
<td>10 minutes</td>
<td>35–53</td>
<td>8–43</td>
<td>17–33</td>
<td>27–53</td>
<td>19–79</td>
<td>66–84</td>
<td>33–100</td>
<td>62–100</td>
</tr>
<tr>
<td></td>
<td><strong>23.3(8.45)</strong></td>
<td><strong>27.5(11.16)</strong></td>
<td><strong>25.7(7.28)</strong></td>
<td><strong>44.4(8.28)</strong></td>
<td><strong>51.8(8.26)</strong></td>
<td><strong>73.3(10.48)</strong></td>
<td><strong>59.2(4.92)</strong></td>
<td><strong>79.6(8.06)</strong></td>
</tr>
<tr>
<td></td>
<td>90 (5)</td>
<td>51 (4)</td>
<td>105 (6)</td>
<td>99 (6)</td>
<td>110 (6)</td>
<td>97 (4)</td>
<td>71 (10)</td>
<td>54 (5)</td>
</tr>
<tr>
<td></td>
<td><strong>5.7(5.80)</strong></td>
<td><strong>18.0(9.61)</strong></td>
<td><strong>44.9(2.33)</strong></td>
<td><strong>29.6(11.41)</strong></td>
<td><strong>48.0(7.14)</strong></td>
<td><strong>53.8(8.31)</strong></td>
<td><strong>52.5(4.99)</strong></td>
<td><strong>90.2(7.44)</strong></td>
</tr>
<tr>
<td></td>
<td>70 (4)</td>
<td>50 (4)</td>
<td>167 (8)</td>
<td>81 (4)</td>
<td>123 (7)</td>
<td>132 (6)</td>
<td>61 (10)</td>
<td>41 (4)</td>
</tr>
<tr>
<td>20 minutes</td>
<td>6–47</td>
<td>0–30</td>
<td>0–27</td>
<td>13–35</td>
<td>23–65</td>
<td>18–76</td>
<td>14–83</td>
<td>67–90</td>
</tr>
<tr>
<td></td>
<td><strong>19.3(7.89)</strong></td>
<td><strong>7.6(4.42)</strong></td>
<td><strong>15.7(9.99)</strong></td>
<td><strong>23.4(10.58)</strong></td>
<td><strong>50.4(8.33)</strong></td>
<td><strong>49.1(10.00)</strong></td>
<td><strong>56.9(4.95)</strong></td>
<td><strong>78.0(10.36)</strong></td>
</tr>
<tr>
<td></td>
<td>88 (5)</td>
<td>66 (6)</td>
<td>70 (4)</td>
<td>98 (4)</td>
<td>113 (6)</td>
<td>110 (5)</td>
<td>72 (10)</td>
<td>41 (4)</td>
</tr>
<tr>
<td>30 minutes</td>
<td>0–13</td>
<td>0–20</td>
<td>0–17</td>
<td>4–26</td>
<td>12–43</td>
<td>14–54</td>
<td>0–100</td>
<td>54–83</td>
</tr>
<tr>
<td></td>
<td><strong>4.3(12.83)</strong></td>
<td><strong>11.7(6.43)</strong></td>
<td><strong>9.8(5.95)</strong></td>
<td><strong>15.7(7.28)</strong></td>
<td><strong>22.3(5.94)</strong></td>
<td><strong>29.8(9.15)</strong></td>
<td><strong>58.3(4.93)</strong></td>
<td><strong>66.7(11.78)</strong></td>
</tr>
<tr>
<td></td>
<td>92 (5)</td>
<td>60 (5)</td>
<td>82 (5)</td>
<td>102 (5)</td>
<td>121 (7)</td>
<td>104 (5)</td>
<td>60 (10)</td>
<td>51 (4)</td>
</tr>
<tr>
<td>60 minutes</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>0–14</td>
<td>7–53</td>
<td>16–62</td>
<td>12–75</td>
</tr>
<tr>
<td></td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td><strong>5.8(4.72)</strong></td>
<td><strong>22.1(5.93)</strong></td>
<td><strong>29.7(11.42)</strong></td>
<td><strong>40.8(4.91)</strong></td>
</tr>
<tr>
<td></td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>86 (5)</td>
<td>140 (7)</td>
<td>74 (4)</td>
<td>76 (10)</td>
</tr>
<tr>
<td></td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td><strong>38 (5)</strong></td>
<td><strong>57.9(9.87)</strong></td>
<td><strong>40.8(4.91)</strong></td>
<td><strong>57.9(9.87)</strong></td>
</tr>
<tr>
<td>100 minutes</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>0–39</td>
<td>17–23</td>
<td>14–66</td>
<td>42–75</td>
</tr>
<tr>
<td></td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td><strong>10.6(5.13)</strong></td>
<td><strong>19.2(13.13)</strong></td>
<td><strong>32.7(4.65)</strong></td>
<td><strong>47.8(16.65)</strong></td>
</tr>
<tr>
<td></td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>104 (6)</td>
<td>52 (3)</td>
<td>49 (10)</td>
<td>23 (3)</td>
</tr>
</tbody>
</table>

adults of **P. gaimardii** in their behavioural tolerance to fresh water.
TABLE 16 Mean times (and 95% confidence limits) for 50% amigration from fresh water in eight species.

<table>
<thead>
<tr>
<th>Species</th>
<th>Mean time (minutes)</th>
<th>95% confidence limits (minutes)</th>
</tr>
</thead>
<tbody>
<tr>
<td>P. quadridentatus</td>
<td>3.57</td>
<td>1.75 - 7.28</td>
</tr>
<tr>
<td>B. spinosus</td>
<td>4.25</td>
<td>1.35 - 9.73</td>
</tr>
<tr>
<td>C. granulosus</td>
<td>4.34</td>
<td>1.02 - 23.07</td>
</tr>
<tr>
<td>H. latifrons</td>
<td>5.43</td>
<td>3.12 - 9.46</td>
</tr>
<tr>
<td>P. gainardii</td>
<td>13.49</td>
<td>8.59 - 26.66</td>
</tr>
<tr>
<td>H. haswellianus</td>
<td>23.28</td>
<td>11.91 - 48.42</td>
</tr>
<tr>
<td>L. octodentatus</td>
<td>28.13</td>
<td>10.20 - 78.20</td>
</tr>
<tr>
<td>h. cordiformis</td>
<td>90.99</td>
<td>41.30 - 200.4</td>
</tr>
</tbody>
</table>

4.63 BEHAVIOUR IN RELATION TO IMMERSION IN WATER

In their behaviour in relation to immersion in water (table 17 and text-figure 43) the species again appear to fall into two groups although the trends are not nearly as clear as in their behaviour towards fresh water. In one group (L. octodentatus, H. haswellianus, H. cordiformis and B. spinosus), there was a strong tendency to move out of water, the percentage increasing with time, whilst in the others (P. quadridentatus, H. latifrons and P. gainardii) there was almost the opposite, an appreciable percentage
moving out of water at first but soon returning to water. *C. granulosus* appears to belong to the first group but in this species there is little tendency for the percentage out of water to increase with time. In table 17 the behaviour of the eight species studied is compared in three
TABLE 17  Behavioural tolerance to immersion in water in eight species. The data were obtained from the experiments on tolerance to fresh water, the details of which are given in table 15.

<table>
<thead>
<tr>
<th>Species</th>
<th>Mean % of total out of water (over 30 mins)</th>
<th>Mean % of total at end of 30 mins</th>
<th>Maximum % out of water</th>
<th>Regression significant</th>
</tr>
</thead>
<tbody>
<tr>
<td>P. quadridentatus</td>
<td>11.0</td>
<td>8.9</td>
<td>16.7</td>
<td>No</td>
</tr>
<tr>
<td>H. latifrons</td>
<td>5.7</td>
<td>6.4</td>
<td>7.5</td>
<td>No</td>
</tr>
<tr>
<td>P. gaimardii</td>
<td>8.1</td>
<td>10.4</td>
<td>10.4</td>
<td>No</td>
</tr>
<tr>
<td>E. spinosus</td>
<td>13.7</td>
<td>16.6</td>
<td>20.0</td>
<td>Almost</td>
</tr>
<tr>
<td>C. granulosus</td>
<td>32.4</td>
<td>32.8</td>
<td>32.8</td>
<td>No</td>
</tr>
<tr>
<td>H. cordiformis</td>
<td>18.7</td>
<td>22.7</td>
<td>42.5</td>
<td>Yes</td>
</tr>
<tr>
<td>H. haswellianus</td>
<td>15.9</td>
<td>25.7</td>
<td>35.7</td>
<td>Yes</td>
</tr>
<tr>
<td>L. octodentatus</td>
<td>30.2</td>
<td>40.0</td>
<td>51.0</td>
<td>No</td>
</tr>
</tbody>
</table>
Different ways and text-figure 43 shows the data for these experiments plotted as in text-figure 42. Again, there were no significant differences between small and large adults of P. gaimardii.

TEXT-FIG. 43. Temporal behaviour of 8 species of grapsids and ocypodids in relation to immersion in water. Data plotted as in text-figure 42.
3.63 BEHAVIOR IN RELATION TO SUBSTRATE AND COVER

The preferences shown by the seven species towards substrate and cover can be most conveniently considered in three categories:

1. in relation to substrate above and below water;
2. in relation to cover; and
3. in relation to the nature of the substrate.

The results for the first and second aspects of their behaviour is shown for each species in tables 18 and text-figure 4-A.

The behaviour of the two ocypodids in relation to cover was not studied.

In most species a fairly large percentage settled amongst stones under water. Thus, in P. gaimardii, P. quadridentatus and H. latifrons, 80-100% of all individuals settled below water whilst in L. octodentatus, C. granulosus and H. haswellianus the percentage was between 50 and 70. H. cordiformis, on the other hand, showed a distinct tendency to settle above water.

Similarly, more than 50% of the individuals settled amongst or under stones in all species studied, C. granulosus showing the strongest preference for cover and P. gaimardii the least.

In C. granulosus and H. haswellianus preference for cover appears to be stronger than that for water since in three experiments in which stones were placed only over the
TABLE 18 Behavioural preference for substrate below water and for cover in seven species. The numbers in the square brackets of each set are the total number of crabs used in all experiments for each species (and the number of replicates).

<table>
<thead>
<tr>
<th>Species</th>
<th>Percentage settling below water</th>
<th>Percentage settling amongst stones</th>
</tr>
</thead>
<tbody>
<tr>
<td>L. octodentatus</td>
<td>52.3 [38 (20)]</td>
<td>79.2 [23 (6)]</td>
</tr>
<tr>
<td>C. granulosus</td>
<td>65.7 [132 (15)]</td>
<td>96.2 [32 (6)]</td>
</tr>
<tr>
<td>H. haswellianus</td>
<td>66.5 [181 (22)]</td>
<td>63.5 [55 (7)]</td>
</tr>
<tr>
<td>P. quadridentatus</td>
<td>55.3 [68 (14)]</td>
<td>63.9 [21 (6)]</td>
</tr>
<tr>
<td>P. gaimardii</td>
<td>100.0 [70 (17)]</td>
<td>50.0 [52 (14)]</td>
</tr>
<tr>
<td>H. cordiformis</td>
<td>13.6 [96 (11)]</td>
<td>-</td>
</tr>
<tr>
<td>H. latifrons</td>
<td>76.9 [43 (7)]</td>
<td>-</td>
</tr>
</tbody>
</table>
upper moist areas of the tray more than 90% of the indi-
viduals settled above water.

There appears to be a marked avoidance of small pebbles
by *P. gaimardii*. In four experiments with a total of
16 animals, an avoidance of small groups of stones was also
shown. The results for these experiments contrast rather
strongly with others in which a bank of large stones was
provided. The vast majority of individuals settled under
these stones.

*L. octodentatus*, *C. granulosus* and *P. quadzidentatus*
were all active and individuals of the first two species
spent some considerable time wandering among the upper layers
of stones. In all species except *H. haswellianus* the pres-
ence of stones did not affect the number settling below
water. In that species, however, slightly less than twice
as many settled above water where the whole tray was covered
by stones as did when there were no stones present (45% and
25% respectively).

In their preference for different substrates, the
species appear to fall into two groups, the grapsids prefer-
ing earth and the ocypodids mud. The results are given in
table 19; text-figure 44C compares the results for the five
species which showed a tendency to burrow. The height of
each column in this figure is proportional to a value com-
puted by summing the percentages per species preferring each
substrate in each of its two combinations and dividing by
three to give an estimate of the percentage preferring each substrate in the hypothetical situation where a choice of all three substrates was offered. It is apparent that only four species, *C. cramulosus*, *H. haswellianus*, *P. quadridentatus* and *P. gaimardii*, showed any degree of tolerance towards sand.

In tables 18 and 19 percentages are computed from individuals which constructed burrows as well as those which did not; unoccupied burrows are not included. This should be particularly emphasized in the case of *L. octodentatus*, *H. haswellianus*, *P. gaimardii* and the two ocypodids since these are the species which consistently constructed burrows. In *L. octodentatus*, *H. haswellianus* and *P. gaimardii* about half the number of individuals constructed burrows. Whereas in *L. octodentatus* and *P. gaimardii* preferences deduced from the positions of burrows only are in fairly good agreement with those taken from positions of the crabs at the end of 24 hours (ignoring burrows), in *H. haswellianus* there is a rather strong measure of disagreement between positions of burrows (occupied and unoccupied) and positions of animals.

There is a fairly strong tendency in this species to construct burrows above water and fewer burrows are constructed in the presence of stones. Thus, of the 73 burrows constructed by this species in all experiments, 56% were under water and 20% under stones. The results with regard to substrate
TABLE 19 Substrate preferences of seven species. The number in the first row of each set is the percentage preferring the first named substrate of each pair. The numbers in square brackets are the number of animals used in that particular combination (and the number of replicates).

<table>
<thead>
<tr>
<th>Species</th>
<th>Sand/Mud</th>
<th>Mud/Earth</th>
<th>Earth/Sand</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>L. octodentatus</em></td>
<td>32.0</td>
<td>36.3</td>
<td>57.1</td>
</tr>
<tr>
<td><em>C. granulosus</em></td>
<td>23.0</td>
<td></td>
<td>50.0</td>
</tr>
<tr>
<td><em>H. haswellianus</em></td>
<td>44.8</td>
<td>42.0</td>
<td>64.4</td>
</tr>
<tr>
<td><em>P. quadridens</em></td>
<td>25.0</td>
<td>46.1</td>
<td>30.0</td>
</tr>
<tr>
<td><em>P. gaimardii</em></td>
<td>52.5</td>
<td>25.0</td>
<td>66.4</td>
</tr>
<tr>
<td><em>H. cordiformis</em></td>
<td>10.4</td>
<td>80.5</td>
<td>56.0</td>
</tr>
<tr>
<td><em>H. latifrons</em></td>
<td>37.0</td>
<td>86.4</td>
<td>62.0</td>
</tr>
</tbody>
</table>
show a similar disparity, 37.5% of the burrows being constructed in earth or mud whilst 73% of the individuals were collected on one or other of these two substrates. *P. gaimardii*, on the other hand, often constructed burrows under stones. *L. octodentatus* showed a tendency to burrow into the bank separating the moist upper portion from the lower portion covered by water. Excavations were sometimes constructed in sand under stones. Both *C. granulosus* and *P. quadridentatus* made shallow depressions in sand beneath stones on some occasions.

In the two ocypodids the vast majority constructed burrows; indeed, in *H. cordiformis*, about twice as many burrows were constructed as there were individuals. This species showed a tendency to construct burrows in a very short time but left them shortly afterwards if they were in unsuitable material.

Text-figure 45 shows, for all replicates for the three combinations of substrates, the positions of burrows dug and occupied by individuals of *H. haswellianus*, *H. cordiformis* and *H. latifrons*. The strong preference of *H. haswellianus* for earth, of *H. cordiformis* for mud above water and of *H. latifrons* for mud below water, are shown fairly clearly. The slightly greater tolerance of sand by *H. haswellianus* is also shown.

From the few experiments with *H. spinosus* it would appear that there is a similarity in the behaviour of this species
to that *haswellianus* except for a stronger tendency
to settle under *sees*.

Finally, there does not seem to be any significant
departure in these results obtained from experiments with
single species, from the experiments in which two or three
species were placed together in the same tray.

4.65 CONCLUSIONS

Overall, the behaviour of the various species in these
laboratory experiments agrees fairly well with the prefer-
ences and tolerances which could be deduced from the field
observations described in section 4.2. Thus, the species
which exhibited little tolerance to fresh water (*P. quadrin-
dentatus, B. spinosus, C. granulosus* and *H. latifrons*) are
those living in habitats subject to little or no fresh water
influence. The only exception is *H. latifrons*. The
other species which showed a significant tolerance of fresh
water under experimental conditions, are those which inhabit
areas where low salinities are common; this is most marked
in *H. cordiformis, L. octodentatus* and *H. haswellianus*. There
is a clear disparity between species' behaviour under control
conditions and that where there was a choice available between
sea water and fresh water. Those species which spent consid-
erable times out of water (*H. cordiformis, L. octodentatus,
etc.*) are those living in the higher zones of the shore.
The absence of significant differences between large and small adults of \textit{F. gaimardii} in their behaviour in relation to fresh water and to immersion in water strongly suggests that the wider distribution of juveniles is not due to age differences in tolerances of physical environmental factors.

Almost all species showed a tendency to settle under cover. In the field most species are found under stones. \textit{F. gaimardii}, the only species which appears to deviate from this pattern, exhibited an avoidance of small stones and the inclusion of results from experiments where only small stones were present accounts, to some extent, for this deviation. Some, like \textit{H. cordiformis}, \textit{H. latifrons}, \textit{H. haswellianus} and \textit{F. gaimardii} constructed burrows under laboratory conditions. Field studies have shown these to be the species which are generally found in burrows. Generally, those species which construct burrows high on the shore (e.g. \textit{H. cordiformis}) burrowed above water under laboratory conditions. \textit{H. haswellianus}, which is often found in fairly wet areas of the higher parts of the shore tended to settle or burrow under water to a greater extent than did \textit{H. cordiformis}. Those species which burrowed mostly showed an avoidance of sand, as they do under natural conditions. Sand, whether wet or dry, provides poor material for semi-permanent burrows and the species, in the laboratory, merely reflect their avoidance of this under natural conditions.
Throughout, no significant differences are apparent between the results for those experiments conducted shortly after capture of the crabs and the results for the final experiments.

4.7 DISCUSSION

In the preceding subsections the distributions within Tasmania, of the eleven grapsid and ocypodid crabs have been considered in relation to various environmental factors, certain morphological features of the species have been outlined and the behaviour, in the laboratory, of most of the species towards certain kinds of habitat has been dealt with. Throughout, various interspecific differences have been mentioned. It is the purpose of this discussion to bring together these various ecological, anatomical and behavioural attributes of the species and to point out more clearly the ways in which the species differ from each other in relation to their occurrence in different habitats.

4.71 PATTERNS OF ECOLOGICAL DISTRIBUTION IN TASMANIA

In their patterns of distribution, the species can be ordered according to the five factors which seem most important; each of these can be in turn, further subdivided (see table 20). Considered in this way it is apparent that each species has a characteristic habitat, where it
occurs in greatest densities. In addition, each species is also found in a few similar habitats where it occurs in lower densities. The major factors appear to be substrate, wave action, salinity range, length of time for which each shore zone is uncovered by water and type of cover.

In these species inhabiting platforms, boulder and stony beaches the presence or absence of certain kinds of cover is of importance in determining species’ distributions and abundance. This is particularly exemplified by 

Loxocarcinus variomuratus which is absent from most coastal platforms where horizontal crevices with low entrances are not available and by 

Cyclograpsus granulosus which is present in large numbers where boulders occur but in small numbers where the beach consists only of stones.

In those species inhabiting sheltered estuaries and lagoons the composition of the substrate rather than the type of cover is partly or wholly important in determining the presence of species. Thus 

H. haswellianus, 

Paragrapsus lanvis and 

H. cordiformis certainly appear to tolerate, and probably prefer, less sandy areas than do Paragrapsus gaimardii and 

Hemiplus latifrons (table 9).

In that each species is most abundant in a certain zone on a particular type of shore (text-figure 32) there is a parallel with the distributions of other shore organisms although the limits of vertical zones are less clear in most cases because, unlike barnacles and molluscs - the major
TABLE 20  Summary of the ecological distribution of the eleven Tasmanian species of grapsid and ocypodid crabs in relation to type of shore, height on shore, salinity and cover.

<table>
<thead>
<tr>
<th>Habitat</th>
<th>L. variatus</th>
<th>L. octodentatus</th>
<th>P. spinosus</th>
<th>C. granulosus</th>
<th>H. haswelli</th>
<th>L. rubra</th>
<th>P. quadridens</th>
<th>P. galatheanum</th>
<th>P. laevis</th>
<th>P. capensis</th>
<th>P. cordiformis</th>
<th>Habitation</th>
</tr>
</thead>
<tbody>
<tr>
<td>platform</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>-</td>
<td>x</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>x</td>
<td>-</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td>boulder or stony beach</td>
<td>-</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td>sandy shore</td>
<td>-</td>
<td>-</td>
<td>x</td>
<td>x</td>
<td>-</td>
<td>x</td>
<td>x</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td>muddy shore</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td>fully-exposed</td>
<td>x</td>
<td>x</td>
<td>-</td>
<td>x</td>
<td>-</td>
<td>x</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>x</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td>semi-exposed</td>
<td>-</td>
<td>x</td>
<td>x</td>
<td>-</td>
<td>x</td>
<td>-</td>
<td>x</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td>sheltered</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td>supralittoral fringe</td>
<td>x</td>
<td>x</td>
<td>-</td>
<td>x</td>
<td>x</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>x</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td>upper mid-littoral</td>
<td>x</td>
<td>-</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>-</td>
<td>x</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td>lower mid-littoral</td>
<td>-</td>
<td>-</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>-</td>
<td>-</td>
<td>x</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td>infralittoral fringe</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td>high (^1)</td>
<td>x</td>
<td>-</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td>medium (^2)</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td>low (^3)</td>
<td>-</td>
<td>x</td>
<td>-</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>-</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td>crevices</td>
<td>x</td>
<td>x</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td>boulders or stones</td>
<td>-</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>-</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td>burrows</td>
<td>-</td>
<td>-</td>
<td>x</td>
<td>-</td>
<td>x</td>
<td>-</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>-</td>
<td>-</td>
<td></td>
</tr>
</tbody>
</table>

\(^1\) more than 30°/oo  \(^2\) 15-29°/oo  \(^3\) less than 15°/oo
zoning organisms - they shelter under stones or boulders where they are less subject to fluctuations arising from the rise and fall of the tide. These boulders or stones are confined to rather narrow bands on the shore the distribution of the species is rather more restricted (see text-figures 32C, 33B). Only Paramapsus gaimardii and P. laevis appear to have a vertical distribution extending through most of the intertidal region from upper midlittoral to infralittoral but their presence within the upper zones appears to depend on certain local factors.

Such vertical patterns of distribution are undoubtedly due to species' differences in tolerance to exposure to air. The work of M.J. Doty (see Moore, 1958: 340-4) on the distribution of intertidal algae on the Pacific coast of North America has emphasized the existence of critical levels on the shore at which maximum duration of exposure to air changes suddenly. Where tidal ranges are large such differences are accentuated and distributional limits extremely clear. Where tidal ranges are of small magnitude, as in Tasmania, the limits are likely to be rather poorly-defined. The most abrupt changes in the distributions of Tasmanian shore crabs appear to exist on open mud flats where the drier areas above the high water level of lowest neap tides are clearly separated from the wetter area below. In summer and at times of neap tides the upper area may be uncovered for several days at a time. H. cordiformis is abundant on
the upper part and *H. latifrons* on the lower, with little overlap of distributions (text-figure 32 D, E).

In estuaries, the upper levels of the shore and the surface organisms thereon, whilst subject to no less a range of salinity than lower levels, do experience rather lower minimum salinities (Moore, 1958: 192). Thus, although it is not clear from the data (table 9), species such as *Halococcus cordiformis* and *Halograptes baswellianus*, which live high on the shore, undoubtedly experience lower salinities than other, such as *P. gaimardii* and *Hemipala* *latifrons*, which live lower down. The distribution of *P. gaimardii* and *P. laevis* along the Frosser River appear to be due to this. Close to the mouth of the river (plate 9B) both species are found in the marsh in burrows. Just above the marsh and slightly further up the river, *P. laevis* occurs under stones in the upper midlittoral, in some areas at only a slightly lower level than *H. cordiformis*. The evidence suggests that *P. laevis* is able to tolerate lower salinities than can *P. gaimardii*.

There appear to be few differences between the various species in regard to the densities in which they occur in their typical habitats. Only *L. octodentatus* regularly occurs in low densities (less than 2 per square metre). Such low densities may be correlated with the carnivorous habits of this species, a feature noted for carnivorous tropical American crabs by Crane (1947: 93).
The occurrence of small numbers of crabs is correlated also with a general paucity of adults. This is particularly evident in *Cycloquadratus granulosus* (compare tables 7 and 8 with text-figure 34 A-C). The stony beach at Gordon, where small individuals of this species are present in high densities, presents an interesting situation requiring further investigation. Differences in distribution between large and small individuals have been previously noted amongst Californian xanthids (Knudsen, 1966b).

**4.72 PATTERNS OF ECOLOGICAL DISTRIBUTION OF TASMANIAN SPECIES OUTSIDE TASMANIA**

To obtain a realistic picture of the ecological distribution of a species, however, it must be considered throughout its full geographic range.

In general, the patterns shown by each species in Tasmania are not very different from those shown elsewhere. Especially is this true of those species with limited geographic distributions, such as *B. spinosus*, *C. granulosus*, *P. quadridentatus* *P. gaimardii*. Thus, Bennett & Pope (1952: 133) recorded *L. octodentatus* and *C. granulosus* (as *C. audouinii*) in Victoria from under boulders in the supralittoral fringe and upper midlittoral of exposed coasts. They also stated that *P. quadridentatus* (*P. gaimardii*, p.115) occurred slightly lower down on the shore but still in the supralittoral fringe. They considered that it
seemed to replace *Leptograpsus variegatus* in the habitat in which the latter species occurred in New South Wales. Their observations regarding *Paragrapsus* species do not agree with those of the present study and will be discussed further below. Hale (1927a) and Womersley and Edmonds (1958) recorded *L. variegatus* from South Australian coasts in the supralittoral fringe of rugged cliffs and *H. haswellianus* (as *Nelice haswellianus*) from the infralittoral ("upper sublittoral") of "sheltered coasts of moderate wave action" and from the "midlittoral" of muddy flats. Hale (1927a) however, stated that *H. haswellianus* was common in burrows in damp mud on marine flats in and around mangroves lining rivers - Womersley and Edmonds's observations suggest an ecological distribution for *H. haswellianus* slightly different from that observed in Tasmania. *P. capensis* occurs on most exposed coasts in South Australia (Hale, 1927a). George (1962) recorded *L. octodentatus* throughout Western and South Australia from supralittoral areas in estuaries, on granite coasts, near freshwater soaks and the edges of highly saline lakes. There they occur in both burrows and crevices. In New South Wales *L. variegatus* occurs on exposed and semi-exposed rocky coasts in crevices and sometimes under stones (Dakin, Bennett & Pope, 1952: 188). At some semi-exposed localities at least, small specimens are very abundant (personal observations, November, 1964). As
in Tasmania it occurs high on the shore. *Plagusia capensis* is found on similarly exposed shores but lower down. *H. cordiformis* and *H. haswellianus* occur on muddy estuarine flats as in Tasmania. *P. laevis* also inhabits muddy estuaries high on the shore under stones or logs, sometimes just below the level occupied by *H. cordiformis* (Dakin, Bennett & Pope, 1952: 196; B.M. Campbell, personal communication; personal observations November, 1964). In southern Queensland, *H. haswellianus*, *P. laevis* and *H. cordiformis* are again found in habitats similar to those occupied by the species in Tasmania (Snelling, 1959). *H. cordiformis* penetrates further along the Brisbane River than *H. haswellianus* and occurs in a lower zone.

Outside Australia, *L. variagatus* occurs on fully and semi-exposed rocky coasts in the upper midlittoral in crevices and under boulders both in New Zealand (personal observations, prior to 1962) and in Chile (Garth, 1957: 95).

Thus, only *P. quadridentatus* or *P. gaimardii* appears to differ significantly in its ecological range outside Tasmania. These differences can be almost immediately dismissed. Firstly, in regard to Dakin, Bennett & Pope’s (1952: 158) statement that *P. gaimardii* replaces *L. variagatus* in Tasmania, the present study shows quite clearly that this is not so. That *P. quadridentatus* in Victoria occupies a habitat similar to that occupied by *L. variagatus* in New South Wales, as suggested by Bennett & Pope (1953: 133),
also seems unlikely. In Tasmania these two species are clearly separated ecologically. The laboratory evidence would also appear to contradict such a possibility. *L. variegatus* apparently has a slightly wider ecological distribution outside Tasmania, at least in more northern parts of Australia.

There are reasonable correlations between habitat and three kinds of morphological adaptations. As already noted, spinate ambulatory dactyli are present in species roaming over exposed cliffs, the fingers of the chelae are excavated as spoons in those species which scrape encrusting algae from rock or sift particulate food from mud and tufts of hairs are present between the ambulatory legs of species inhabiting muddy estuaries. Spooned chelae have previously been noted in American xanthids, gracipsids and ocypodids which are predominantly eaters of encrusting algae or organic detritus (Crane 1947: 93). The tufts of hairs between the legs sift out fine silt and clay during intake of respiratory water through the major incumbent openings between the legs (see Arudpragasam & Naylor, 1964: fig. 7).

As already noted (section 4.25) there is little difference between the species in their feeding habits. MacIntyre (1959: 343, table 1) stated that at Lake Macquarie, New South Wales, *Paragrapus laevis* (= *Chasmagnathus laevis*) is a scavenger and carnivore. Should this be so in Tasmania (and there is no reason why it should not) this species
would contrast in this feature with its congener, \textit{P. gaimardii}, an algal feeder.

Horizontal and vertical patterns of distribution are universal amongst intertidal animals (see previous sections). Amongst the Brachyura they have been briefly described for western central American species (Crane, 1947), central eastern Australian species (Snelling, 1959), Californian Xanthidae (Knudsen, 1960b), Chilean species (Garth, 1957), East African species (MacNae & Kalk, 1962a, 1962b) and Jamaican Grapsidae (Hartnoll, 1965a). A major difference between the situation described here and those dealt with by most other workers, is the larger number of species present in tropical regions.

4.73 BREEDING AND MOLTING IN ECOLOGICALLY SIMILAR SPECIES

The non-Tasmanian species of Brachyura which have been well studied in regard to molting and breeding cycles show similar patterns to those exhibited by Tasmanian grapsids. In the central and northern Pacific species, \textit{Pachygrapsus crassipes} Randall, maximum percentages of ovigerous females are found from May to August with a peak in June and maximum percentages of molting adults are found from June to October with a peak around August or September (Hiatt, 1948). In the South African species \textit{Cyclograpsus punctatus}, largest numbers of ovigerous females are found from June to September (peak in July) and largest numbers of molting
adults from August to December (peak in September) (Brockhuysen, 1941). In this last species a second period of breeding occurs in January and February, followed by moulting in February through April. Wayler (1962) found that ovigerous females of the widespread *Carcinus maenas* (Linnaeus) were, in Plymouth, most common from February to June (late winter and early summer) and that moulting adults were most abundant in summer.

Peaks of occurrence of ovigerous females in these species are thus followed by peaks of moulting about two or three months later just as in *C. granulosus* and *B. spinosus* studied here. Differences between the two intensively studied Tasmanian species in the periodicity of moulting may be due to the fact that females copulate immediately after moulting in *C. granulosus*. In *B. spinosus*, which moults only once a year, it is almost certain that females copulate whilst hard. Such differences are apparently fairly widespread in Brachyura (Hartnoll, 1965b: 9).

Since there is a large overlap between most of the species in the time during which females are ovigerous it seems likely that, unless there are marked differences in the length of larval life, megalopae and young crabs of all species arrive on the shore within a few months of each other.
RELATIONS BETWEEN RELATIVE GILL VOLUMES AND SPECIES' ECOLOGICAL DISTRIBUTIONS

As in other species of Brachyura (see 1.4), those graspsids and ocypodids inhabiting higher areas on the shore generally possess lower gill volumes relative to the volume of the body (see table 13).

There appears to be better correlation between members of each subfamily in the number of gills than between number of gills and height on the shore occupied by the species. Thus, the Tasmanian sesarmines all have 16 gills (so do some Sesarma species which are almost terrestrial - Edney, 1960: 376, table 1). The varunine B. spinosus (and Hemicrapsus species - Hiatt, 1948: 145, table 1) also possesses 16 gills along with the macrophthalmine, H. latifrons. The graspsine L. variegatus (like the closely related Pachygrapsus crassipes, an upper midlittoral species, and the terrestrial Gecarcinidae) has 18 gills as does the infralittoral P. capensis; the graspsine L. octodentatus, has only 14 gills. Lastly, the ocypodine, H. cordiformis (like species of Uca) possesses only 12 gills.

The values of gill volume in relation to total volume obtained here are slightly higher for the lower midlittoral species than Hiatt obtained for ecologically similar species (more than 3% compared with less than 2.8%).
The arrangement and modification of hairs on the maxillipeds and inner mouthparts appears to show a reasonable correlation with habitat in *Uca* species (Crane, 1941a). For instance, species inhabiting muddy sandy shores, as opposed to shores of semi-liquid mud, possess numerous spooned hairs on the merus and palp of the second maxilliped and in some species, particularly those living in wet mud, "woolly" hairs are present on the merus of the second maxilliped. Miller (1961) has described in detail, for three species of *Uca*, the processes involved in separation of particulate food matter from the sand and other mineral material which is taken up with the food by these crabs. After the mud and sand is passed between the third maxillipeds it is mixed with water driven into the buccal chamber in front of the mouth by the beat of the scaphognathite, and the fine food material is gradually separated out from the heavy sand and mineral matter which is swept away from the central part of the external buccal chamber, adheres to the surrounding hairs and is then washed off and falls to the bottom of the mouth where it is extruded. The fine silt material is ingested with the food and excreted in the faeces (Miller, 1961). The food material adhering to the hairs is passed to the mouthparts close to the mouth by the palps of the second maxillipeds. This process has been termed the flotation.
process and was first analysed in species of *Uca* by Altenvoigt (1957a).

It would seem likely that any species which collects food material, whether macroscopic or microscopic, from the substrate, is faced with eliminating the heavy coarse mineral matter, presumably by a similar flotation process utilizing water from the branchial chamber. The repetition, in *Uca* species and those studied here, of similar hairs underlying one another on preceding mouthparts in corresponding positions supports the concept of repeated filtration.

Amongst the Tasmanian species, only the two cypodids possess hairs modified apically as spoons. The spooned hairs are confined to the palp of the second maxillipeds and the more distal parts of the medial edges of the anatomically preceding appendages, in contrast to many species of *Uca* where they are present also on the merus of the second maxilliped and proximal parts of the inner appendages. In *H. cordiformis*, the modifications of the hairs are greater than in *H. latifrons*. The well developed spoons of the hairs of the second maxilliped palps in the former species is further evidence of its ability to feed in dry sandy muds whilst the presence of "woolly" hairs on the medial edge of the second maxilliped merus, first maxilliped basal endite and lower parts of preceding segments is evidence of its ability to feed also in wet muds of low sand content. The
"woolly" hairs may also permit feeding in muds of high clay content since clay, when mixed with water of even moderately high salinity, becomes colloidal and would then behave like sand.

Similarly, the presence of spinate and lobate, weakly spooned hairs on the second maxilliped palp and distal parts of preceding segments in H. intifrons is evidence of this species' ability to feed only in wet sandy mud.

4.7b RELATIONS BETWEEN SPECIES' DISTRIBUTIONS IN THE FIELD AND THEIR BEHAVIOUR UNDER EXPERIMENTAL CONDITIONS

The habitat preferences shown by the species under experimental conditions in most cases show good correlations with those deduced from field observations. Similar agreement between observed distributions in the field and behaviour in the laboratory was obtained by Teal (1958) in a study of three species of Uca. The absence of significant differences between the results of experiments conducted shortly after the species were collected from the field and those for much later experiments were in contrast to the long term differences in behaviour after starvation, such as increased locomotor activity, which were recently described in the Pacific American varunine shore crab, Hemigrapsus oregonensis (Dana) (Symons, 1964).

Of the species which constructed burrows under laboratory conditions, one, L. octodentatus, was not consistently found
in burrows in the field in the present investigation although it does occur in this habitat in Tasmania (see section 4.22). The fact that individuals of this species under laboratory conditions showed a strong tendency to construct burrows, whereas they were taken from a stony beach where burrows were not constructed, provided interesting evidence of the maintenance of behavioural traits within each generation in situations where these traits were not normally exhibited. As mentioned above, *L. octodentatus*, occurs on the Australian mainland in burrows, sometimes on the banks of streams. The results obtained here are thus in agreement with the ecological distribution of this species. The only other species, the laboratory behaviour of which did not quite agree with field observations, is *H. haswellianus*. A greater percentage of individuals settled under water than was expected. This percentage was much greater than for *H. cordiformis* (table 18, text-figure 44) but about the same as in other species living in the upper midlittoral under stones (*e.g.* *C. granulosus*). The preference for moist natural conditions, and the higher relative gill volume may account for such behaviour in the laboratory.

Such agreement between distributions in nature and behaviour in the laboratory surely indicates that in nature the species' distributions are not effectively limited by competition with other crabs or other animals for space or
The results of the experiments carried out here on behavioural tolerance to fresh water are supported by previous physiological studies. Thus Edmonds (1935), in an investigation of the changes in ionic concentration of the blood in relation to different concentrations of sea water in several brachyurans, found that both *L. variegatus* and *H. cordiformis* exhibited marked hypotonicity to sea water over a wide range of external concentrations. *H. cordiformis* is able to survive for 41 hours in 2% sea water or even slightly lower concentrations but only for a very short time in fresh water.

Denne (1963, unpublished) found, from studies of the rates of scaphognathite beats at varying temperatures and salinities, that *P. gaimardii* was much more tolerant of lowered salinities and high temperatures than was *P. quadridentatus*. At a temperature of 25°C, 20 minutes immersion in 25% sea water resulted, in *P. gaimardii*, in an increase of about 5% in the rate of beating over that for 10 minutes immersion in 100% sea water at the same temperature. In *P. quadridentatus*, on the other hand, similar conditions resulted in a 100% increase in the rate of scaphognathite beat. Denne also found that *P. gaimardii* could survive in moist air for about 25 hours.
4.77 THE FACTORS LIMITING THE ECOLOGICAL DISTRIBUTIONS 
OF THE TASMANIAN GRAPSID AND OCYPODID CRABS

The distributions of the species studied here thus appear to be regulated by many factors. Most of these factors operate in several different ways and each species appears to react differently to each. Thus the ability of _Leptograpsus variicolor_ to withstand a limited amount of desiccation allows this species to extend high on the shore on beaches exposed to heavy wave action. The strongly depressed body is an adaptation to the crevice dwelling habit and the spines on the distal segments of the ambulatory legs allow it to roam over platforms subjected to pounding waves and to move along cliffs. This species is thus restricted to oceanic areas washed by highly saline water by factors other than its possible intolerance of low salinities. The apparent inability of most other grapsids to withstand desiccation restricts them to areas where stones or boulders occur. Those species which habitually construct burrows are limited by the availability of suitable substrate and the ocypodids at least, are also affected by the composition of the substrate through their ability to feed only in certain types of mud. The wider distributions of juveniles compared with adults surely result from the gradual extinction, in the marginal habitats, of individuals before they reach full maturity as a result of conditions intolerable to the species as a whole. That juveniles are present at all in habitats
where adults are mostly absent may be due to wider tolerance by the larvae and megalopae, of fluctuations in factors such as temperature and salinity (see Costlow, Brookhout & Monroc, 1962). Also in those species which consistently settle under stones, the juveniles would require smaller stones than would the larger adults. From the results of laboratory studies there would not appear to be any change in species' tolerances during postlarval life.

The accumulated evidence shows clearly that each species lives in a characteristic habitat and in some cases feeds in a characteristic fashion. To the extent that these habitats are species-specific the species are ecologically isolated from one another. That areas of overlap in these distributions occur does not nullify this. Each species shows at least some adaptations, of a morphological, physiological or behavioral nature, to its typical habitat. The very close agreement between the field observations and the results of the laboratory studies confirms the validity of the deductions from the former. In every case where closely related species have overlapping ecological distributions there are ecological factors which clearly distinguish them and help to maintain their specific distinctness. This is indeed the general situation among animals.
5. SOCIAL AND MAINTENANCE BEHAVIOUR IN THE TASMANIAN OCYPODIDAE

5.1 INTRODUCTION

The crabs of the family Ocypodidae are among the most typical crabs of the intertidal areas on open beaches and estuaries. All live in burrows which are usually at least semi-permanent. When the crabs are active the usually long eyestalks are held vertically giving the animals a characteristic appearance.

The ocypodids have been the subject of behavioural studies for more than a century. Thus Darwin (1871: 621) stated, "...it seems probable that the male in this species (Eliusinus sp.) has become gaily ornamented in order to attract or excite the female".

The crabs to which Darwin referred were the fiddler crabs (now known as Uca) and are characterized by the unequal development of the chelipeds in the adult male, one remaining very small and one becoming very large, sometimes exceeding the body in size and weight. The smaller (or minor) cheliped is used mainly in feeding, the larger (major) is waved in the air in a characteristic fashion. Much of the later work on species of Uca has been concerned
with elucidating the function of this waving or beckoning. Recent studies (Altevogt, 1955, 1957a; Crane, 1957, 1958) support the idea that waving "definitely plays a large part in courtship" (Crane, 1941a: 152). The contrasting views of various students of fiddler crab behaviour have been summarized both by Crane (1941a) and by Altevogt (1955). Thus Pearson (1913, 1914), studying Philippine species, Verwey (1930), Indonesian species and other workers all believed that waving was of importance in defence of the burrow and feeding area, but not in any way connected with sexual behaviour. On the other hand, evidence gathered by numerous workers supports the views expressed by Crane (see above).

Other ocypodids, in all of which the chelipeds are equally developed in males as well as in females (but unequally developed in both sexes in Ocypode species) also indulge in waving. In Dotilla species (Tweedie, 1950, 1963; Altevogt, 1957b) such waving is associated with fighting.

In the ocypodids so far accorded reasonably detailed study it has been found that distinct, more or less species-specific behaviour is associated with many activities. Particularly is this true of social behaviour, the reactions of one individual towards another. There is thus a parallel in these crabs to the behaviour of many other animals of which birds are undoubtedly the best known.
The study of the similarities and differences, in these stereotyped and largely innate behaviour patterns, has become the province of ethology (see recent reviews by Tinbergen, 1952; Bibl-Eibesfeldt & Kramer, 1958; Hinde & Tinbergen, 1958; Beer, 1963, 1964). As the pioneer workers in this field, Whitman and Heinroth, found in their respective studies of the behaviour of pigeons and waterfowl, "behaviour, as well as body form and structure, displays homologous traits" (Lorenz, 1958: 69). Thus, the behaviour of related species in comparable situations tends to include the same elements and hybrids sometimes exhibit elements which are known to exist in the behaviour of species related to the parent species themselves. Phylogenetical arrangements of species can be made out from ethological evidence alone; such arrangements may parallel those based on morphological evidence but are particularly useful where morphological evidence is inconclusive (Mayr, 1958).

It is this phylogenetical approach which has been taken by Crane (1941a et seq.) in her studies of fiddler crabs throughout the world. Thus, of twelve western central American Leu species, Crane (1941a: 152) found that, "each species proved to have a definite, individual display, differing so markedly from that of every other species observed, that closely related species could be recognized at a distance merely by the form of the display. Furthermore, related species had fundamental similarities of display
The study reported here was undertaken as part of the general investigation of the factors determining the distribution and abundance of the various species of shore crabs and also to determine the extent of the similarities and differences in the behaviour of the two Tasmanian ocypodids, *Holoccius cordiformis* and *Hemiplax latifrons*, to that of other ocypodids in particular and other Brachyura in general.

Before the commencement of this study some observations on the general behaviour of *H. cordiformis* had been published by Ward (1923). He briefly described the mode of feeding, burrow construction and the "calling gesture" or "semaphoring" - abrupt jerking of the chelipeds (i.e., waving). Ward stated (p. 243) that the latter behaviour was evidently directed towards nearby females". Waving is generally termed sexual display in the following account. A relative of the other species here studied, the New Zealand *Hemiplax hirtipes*, was studied by Beer (1959). Ritualized threat and fighting behaviour were noted in that species by Beer but apparently there is no sexual display as occurs in the other ocypodids mentioned above.

Some results of the present study have been previously reported in a preliminary fashion (Griffin, 1965).
5.2 MATERIALS AND METHODS

Field studies of the behaviour of the two species, *Heloeclis cordiformis* and *Hemiplus latifrons*, were carried out mainly at North-west Bay, Margate and Snug Bay near Hobart from August, 1963 through March, 1965 and particularly during the two summers, October, 1963 to February, 1964 and from October, 1964 to March, 1965. Observations were made with the aid of 8 x 30 binoculars from a distance not exceeding 50 feet and generally from about 15 feet.

Selected aspects of the behaviour of *H. cordiformis* were studied by placing about twenty crabs, marked on the back of the carapace with quick drying lacquer, in a large galvanized iron tank (the 'crabery') 8 feet x 4 feet and 4 feet deep. The tank was filled to a depth of from six to 24 inches with mud collected from a locality at which *H. cordiformis* was known to be common. Once a day, the crabery was slowly filled with tap water to a depth of a few inches above the highest part of the mud bank and the water was then allowed to drain slowly out over a period of three to four hours through an opening in one side seven inches from the bottom. The crabs lived fairly well under these conditions, feeding, burrowing and displaying normally. The majority lived for the two periods of two months during which the observations were carried out.
Analyses of the various ha a teristics of waving
in courtship display was made by studying 8 mm cine im-
taken at the rate of 16 frames per second, by counting
the number of waves in a standard time and a so by moving
a pen along a series of previously written numbers at the
rate of one number per second (as judged from a hand eld
wrist watch), crossing out the number at which the pen had
arrived each time a wave occurred.

Drawings are based on 35 mm photogaphs 8 mm cine
film, notes and drawings taken in the field and on collected
and preserved specimens.

5.3 ACTIVITY CYCLES

In both species individua s engage in several activ-
ities during the one day.

Counts of the number of individuals of H. cordiformis
engaged in various activities at different times during a
period of four hours in December, 1964 (see table 21) and
general observations on numerous occasions indicate the
following sequence of daily events. As the crabs emerge
after the tide has receded they immediately begin feeding.
After an hour or more, some begin displaying, others take
up aggressive wandering. This may continue as the domin-
an activity for almost the whole of the rest of the time
the tide is out. As the incoming tide nears their burrows
TABLE 21  Percentage of individuals of Heloscius cordiformis engaged in each of six kinds of activity during two, two-hour periods on 28, December and 20, December, 1964 at Snag Bay. The percentages are calculated from 5 minute observations of the individuals in an area of approximately 1 square metre (time of low tide approximately 11.15 a.m. and 1.00 p.m. respectively on the two days).

<table>
<thead>
<tr>
<th>Activity</th>
<th>28 December</th>
<th></th>
<th></th>
<th>20 December</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>11.40 am</td>
<td>12.00 noon</td>
<td>12.30 pm</td>
<td>12.40 pm</td>
</tr>
<tr>
<td>Resting</td>
<td>6.1</td>
<td>5.9</td>
<td>5.9</td>
<td>5.7</td>
</tr>
<tr>
<td>Wandering</td>
<td>15.2</td>
<td>35.3</td>
<td>17.9</td>
<td>12.9</td>
</tr>
<tr>
<td>Feeding</td>
<td>32.3</td>
<td>32.3</td>
<td>29.6</td>
<td>13.2</td>
</tr>
<tr>
<td>Burrow maintenance</td>
<td>0</td>
<td>2.9</td>
<td>0</td>
<td>7.5</td>
</tr>
<tr>
<td>Fighting and burrow defence</td>
<td>18.2</td>
<td>17.7</td>
<td>35.3</td>
<td>37.7</td>
</tr>
<tr>
<td>Sexual display</td>
<td>27.2</td>
<td>2.9</td>
<td>9.8</td>
<td>17.0</td>
</tr>
<tr>
<td>Number of individuals</td>
<td>33</td>
<td>34</td>
<td>51</td>
<td>53</td>
</tr>
</tbody>
</table>
many crabs begin collecting wet mud and wandering back to their burrow with it. Many plug their burrows. Others display almost until their burrow is covered by the tide. There also appears to be a short term fluctuation in activities. On some days most crabs will be repairing their burrows and on others displaying. There is certainly a long term seasonal fluctuation in activities. Sexual display is only found in summer and fighting is most common then. During winter, activity is at a low level, crabs sometimes not emerging for several days and then only to feed. At this time the mud flats at low tide present quite a different appearance from that of summer. On several occasions when the localities where these two species occur were visited there was little sign of their presence at all.

5.4 FEEDING BEHAVIOUR

In both species, feeding involves the scooping up of small pellets of mud by the open fingers of the chelae. These pellets are held on the inner side of the chelae between the tips of the two fingers during their transit to the third maxillipeds which gape to receive them. The pellets are placed near the top of the mouthfield and, after manipulation by the inner mouthparts, the material to be rejected forms as a large wet pellet at the bottom (see sections 4.5 and 4.7). This is removed roughly by
the fingers of one of the chelae or drops to the ground.

While feeding (text-figure 46a) the body rests close to, or on the ground and is often tilted back slightly, the last ambulatory leg usually directed at right angles to the ground and the front three directed increasingly forward. The merus of each leg is directed obliquely upwards, the more distal segments almost at right angles to them and obliquely meeting the ground, the dactyls sometimes bent inwards from the propodi. On other occasions the body is further forwards with the front three pairs of ambulatories almost at right angles to the ground and the last pair directed backwards. *H. latifrons* tends to sit further forward when feeding.

In both species feeding usually begins immediately upon emergence from the burrow. The crab moves sideways as it feeds, sometimes pausing in the one place for several seconds. *H. cordiformis* usually pauses often, *H. latifrons* tends to be always on the move.

Each chela generally supplies the mouth alternately; even after an interruption to move a piece of sand or some obstacle, this regularity may be maintained, the left chela supplying the mouth, as soon as the obstacle has been moved, if the right one has previously done so. However, the one chela may supply the mouth up to three times consecutively. While one chela is passing mud to the mouth the other is collecting more mud.
TEXT-FIG. 46. Social behaviour in Helicea carolina: a, feeding; b, emerging from burrow; c, 'burrow defence'; d, threat.
5.5 BURROW MAINTENANCE

The activities of both species are for the most part centred around the burrow. Much of an individual's time is spent modifying the burrow, the crab returns to it more or less briefly between bouts of feeding or sexual display and fights appear to be concerned mainly with possession of the burrow. During high tide, when the burrows are covered by the sea, the crabs retreat into their burrows.

The form of the burrow is different in the two species. In H. cordiformis it is a deep, round hole going straight down from the surface and ending in a larger chamber. In H. latifrons the burrow proceeds obliquely inwards at a shallow angle from the surface.

Both species burrow by scraping mud into a ball with the tips of the legs of one side. Both species enter and leave the burrow sideways. The mud is then passed across the 'face' with the aid of the chelipeds and deposited on the other side of the animal or pushed away by the chelae.

In H. cordiformis, as the burrow becomes deeper, the burrowing crab pauses momentarily at the entrance before emerging on to the open ground to deposit the excavated material (text-figure 46b). The perimeter of the burrow entrance becomes littered with the balls of excavated mud. The crab then returns immediately to its burrow, often entering in a slightly different direction from that in which
it last came out. *H. latifrons* on the other hand comes out of its burrow without pausing, deposits the excavated mud and returns immediately to its burrow without turning around. The excavated mud is thus heaped several inches from the burrow mouth.

Maintenance of the burrow comprises two kinds of activities: further enlargement of the burrow and (in *H. cordiformis*) collection of wet mud which is dragged into the burrow. When engaged in this last activity small pellets of mud are collected by the chelae as in feeding but are placed in front of the 'face' (the maxillipeds and the carapace surrounding the mouthfield) and held there by one of the chelae. A large number of pellets are collected on each expedition, the crab often moving sideways as it collects the mud. The ball of collected mud sometimes becomes almost as large as the body of the crab itself. The mud is dragged to the burrow and passed by the chelae to the undersides of the legs of the following side. The crab then enters the burrow leading side first, dragging the mud behind. Sometimes the mud ball is deposited at the entrance and dragged into the burrow by the legs of one side after the crab has entered the burrow. Sometimes as much as spent pushing pellets of excavated mud away from the burrow mouth. Usually the crab feeds as it does this.

Finally, in *H. cordiformis*, before the burrow is covered by the incoming tide, the entrance is closed by a mud plug.
This is either pushed up from the burrow itself or the crab collects the mud outside the burrow as previously described and drags the plug into the entrance after it with the legs of one side.

_H. latifrons_ was not observed collecting mud or plugging its burrow.

5.6 BURROW DEFENCE

On several occasions throughout the summer, individuals of both species, usually males, were observed standing motionless for fairly long periods of time near the burrow entrance, the body drying in the sun. This posture appears to be a burrow defence posture.

In _H. cordiformis_ (text-figure 46c) the body is elevated high off the ground, the ambulatories unflexed as far as possible, those of the two sides not very wide apart. Sometimes the first and last legs may be held clear of the ground. The chelipeds are partly or completely unflexed, parallel and hanging down or outstretched weakly. The chela remain motionless or move slightly.

In _H. latifrons_ the body is not quite as high off the ground and the chelipeds are flexed in front of the face.

In both species a mass of bubbles sometimes develop in front of the face whilst the crab is in this posture.
One male H. cordiformis, the body of which was completely dry when first noticed, remained motionless in this attitude for a further 41 minutes.

5.7 FIGHTING

In both species combats between males are strongly ritualized events with extensive use of the chelipeds, the body raised high off the ground on the tips of the ambulatory dactyli. In none of the numerous fig. s observed in both species was there any physical damage to the antagonists. Fights are almost always between males, seldom between a male and a female or between females. There are some important dissimilarities between the two species in their fighting behaviour.

5.71 FIGHTING IN H. CORDIFORMIS

In the threat posture (text-figure 45d) the body is held quite high off the ground, the ambulatoires being bent at right angles, the proximal segments directed straight out from the body. The chelipeds are held forward, a f lexed, in front of the body, the chelae wide apart, the tips of the fingers touching the ground or the he ped may be almost fully unflexed, chelae clear of the ground. The fins are usually wide open.

These poses are adopted at certain times when a male, wandering over the mud flats, approaches another crab near
its burrow. A fight generally follows, the defending male also raising itself on its legs and stretching out its chelipeds, fingers open. The two combatants approach one another with their chelipeds completely unflexed and held straight out in front. When about one cheliped's length away from each other, the chelipeds of one combatant reach over or under those of the other, and feeble attempts are made to grasp the opponent's legs or body (text-figure 47d). The two crabs then push backwards and forwards until one sinks to the ground and scuttles off. The victorious crab, whether it be the owner or the intruder, very often enters the burrow but may emerge shortly afterwards to feed, or modify the burrow. Fights generally last about 1-3 minutes.

Fights are sometimes not preceded by mutual threat but follow immediately upon an intruder's entry into an unoccupied burrow. On some occasions the two combatants may merely threaten each other momentarily or one may jerk its chelipeds in a quick vertical movement and the other immediately retreat.

Both ownership of the burrow and size of the crab are important determining factors in a fight. This is apparent both from observations in the field and from study of captive crabs. Of 12 closely studied fights between marked crabs in the crabbery the victor was the smaller in only one. The size disadvantage of the winner in this fight was 0.4 mm
carapace width and in three cases the size advantage of
the winner was as little as 1 mm. Of nine fights near
burrows the large intruder won all but two. In the field,
during one period of observation the intruder won only one
fight out of 10 seen.

The loser of a fight, especially if it be the owner of
the burrow, does not always retire quietly but may stay by
the burrow and sometimes attack the intruder as it emerges.
If beaten again the former owner usually retreats.

Whilst fights generally involve the same procedure time
after time, they sometimes become violent, drawn out, or a
third crab may involve itself. Thus, on two occasions, a
fight ended with the defeated male being tossed on its back;
the winner immediately commenced feeding normally. On anot-
other occasion a fight terminated in the combatants tumbling
over each other three times. On one of the occasions on
which a male was seen to attack a female, the male so viol-
ently grasped the female's legs that it nearly threw the
female out of the burrow.

Numerous instances of a third male being involved in a
fight were seen in the crabbery and several times in the
field. In one such instance two males were grappling and
pushing, neither giving way. The owner of the burrow was
soon attacked from behind by a male from a nearby burrow
but the two original combatants kept fighting each other.
The owner eventually went down its burrow and the third male
then attacked the first intruder. These two continued fighting, gradually moving away from the burrow until the third male eventually scuttled off. On another occasion a burrow owner was attempting to fend off an intruder. It eventually succeeded, the intruder wandering off and the owner retreating to its own burrow. There, however, it found a defeated male from a nearby fight. This second intruder was soon ejected but the owner was then again besieged by the original intruder. The owner at last sent this male off also.

One fight seen ended normally with the retirement of the smaller owner down its own burrow and of the defeated male towards its own burrow several inches away. But the intruder then moved back to the burrow of the small crab and abruptly pushed a heap of excavated mud in on top of the owner. The owner emerged momentarily, removed the mud and then retired again into its burrow. The larger crab quickly moved away, fed for a while and then entered its own burrow.

When physically ousted from their burrows and on other occasions too, crabs wander over the mud flats attacking burrow owners. Often, a crab will wander from one burrow to another attempting to evict owners, beginning by threatening the owner if it is outside its burrow, otherwise entering the burrow with hardly a pause. Large numbers of crabs may independently engage in such "aggressive wandering"
at the one time. Such behaviour seems particularly prevalent among the larger males. The intruder, if it defeats the owner, immediately sets about modifying the burrow as already mentioned, but may soon leave and attack another crab.

5.72 FIGHTING IN H. LATIFRONS

Fights in this species initially resemble those in H. cordiformis. The body is raised high off the ground, the legs only slightly bent and spread fairly wide from the body. The chelipeds are completely unflexed and extended forward and slightly upwards parallel to each other, fingers wide open. As the combatants approach each other closely the chelipeds of one cross over or under those of the other (text-figure 48c). The engaging of the chelae takes place in several abrupt movements, with pauses in between, during which the crabs stand motionless. There is a little pushing and feeble grasping of the opponent's legs during this stage of the combat. Then suddenly the chelipeds are moved outwards so that the tips of those of each opponent are touching (text-figure 48d). After a motionless pause in this position the body still raised high off the ground, quick mutual tapping of the tips of the chelae takes place. A few such tappings, separated by pauses, occur and then one crab suddenly sinks to the ground and retreats. This lateral extension of the chelipeds and mutual tapping
TIXT '10.47. Sodal behaviour in H. cordeformis, continued: a and b, sexual display: a, initial position; b, position at maximum elevation of body and chelipeds; c, copulation (female in foreground); d, fighting.
are quite unlike anything seen in H. cordiformis.

Fights may last for more than five minutes but sometimes they consist only of forward stretching of the chelipeds or standing motionless with outstretched chelipeds touching.

5.8 SEXUAL DISPLAY

Sexual display is indulged in only by males. In both species the body is elevated high off the ground and tilted back during display and the unflexed and forwardly stretched chelipeds raised and lowered. The form of the display is otherwise quite different in the two species.

5.8.1 SEXUAL DISPLAY IN H. CORDIFORMIS

At the beginning of display the body is close to the ground, the legs bent quite acutely and the chelipeds little more than half unflexed, the chelae at an angle of less than 45° to the ground, the fingers slightly open and touching the ground at their tips (text-figure 47a). Each wave involves the following sequence of events. The chelipeds are moved out sideways and unflexed a little and the body elevated slightly, the legs unbending to bring the angle between the proximal and distal segments to around 90°. When the fingers are almost as far apart as the width of the carapace they are lifted up and the body elevated further and tilted
back a little on the more unflexed ambulatories, the first pair sometimes lifting off the ground (text-figure 47b). When the chelae are almost horizontal and about level with the erect eyestalks they are suddenly jerked down until the fingers almost touch the ground and the crab returns to its original position, the body jerking down at the same time as the chelipeds which flex slightly. The two chelipeds generally move in unison but sometimes one does not reach as high as the other.

Each raising and lowering of the chelipeds ('wave') takes approximately 5/6 to 7/8 of a second, the raising of the chelipeds taking about 12 times as long as the terminal downward jerk. The interval between each wave of a series varies from two to six times the length of each wave, waves of short duration being separated by shorter intervals of time. Waving may sometimes be at the rate of more than one a second, six waves in five seconds are fairly common. Sometimes five seconds or more may elapse between waves. The number of consecutive waves in a series varies from two to twenty and is generally around 10. The animal may move sideways a few inches during a series of waves.

5.82 SEXUAL DISPLAY IN H. LATIFRONS

At the commencement of waving the body is close to the ground with the ambulatories folded in front of the 'face', the chelae at a low angle to
the ground, the fingers closed (text-figure 48a). As the
wave begins the body is elevated slightly, the chelipeds
unflex fully but are raised little. The chelipeds, with
the chelae now almost parallel and separated at their tips
by a distance barely exceeding the width of the carapace,
are raised and the body is further elevated, the ambulat-
ories unflexing; the fingers gradually open wide. The
body tips back until it is almost vertical, the chelipeds
reach vertically into the air and the front and sometimes
the back legs are lifted off the ground, the crab balanc-
ing on the widespread second and third legs (text-figure
48b). After a pause in this position the animal falls
forward rather quickly on to the front legs and the body
and chelipeds are lowered without a pause, the latter main-
taining their outstretched position. When the tips of the
fingers reach the ground the chelipeds are flexed and folded
in front of the face or without flexing they are raised high
almost immediately in another wave. Alternatively the cheli-
peds may flex in front of the face without reaching the
ground.

Each wave lasts from 3 to 12 seconds with intervals of
4 to 15 seconds between the end of one wave and the begin-
ing of the next, the shorter intervals usually occurring
between the shorter waves. There may be up to thirteen
waves per minute and more than fourteen waves in a series
but often there are as few as four or five. Of the three
components of the wave - upward stretching, rest and downward fall the second lasts the longest time and the first the shortest. The chelipeds are thus elevated quickly, rest for quite a while and fall fairly slowly.

The chelipeds often tremble slightly at their maximum elevation and sometimes move slightly laterally. When actively displaying the crab may move sideways a few steps on the tips of its legs.

In both species, males display near the entrance to the burrow and series of wavings are frequently interspersed with short bouts of feeding or, especially in H. latifrons, temporary retreat into the burrow.

Waving often appears to be initiated by, and the tempo of waving invariably increased at, the approach of a female. Moreover, a displaying male may also move sideways, or in H. latifrons, laterally jerk the chelae slightly at the appearance of a female. Whilst at most times the display of males does not appear to be directed at any particular female, a displaying male may turn around to face any female which approaches or emerges from a nearby burrow. Females, on the other hand, seldom take any apparent notice of the male's display. All these features were observed both in the field and in captive specimens of H. cordiformis.
Actual copulation in *H. rmis* was observed in the field on six occasions and attempted copulation in *H. latifrons* on three occasions. In both species copulation apparently takes place above ground near or at the entrance to the female's burrow and does not appear to be immediately preceded by display of the male. However, on one occasion a male which appeared to have attracted the attention of a female after some rapid displays moved into its burrow: the male appeared to be following the female but then moved off. And on another, a male which had just been displaying attempted to follow a female down its (the female's) burrow.

In *H. mi* copulation is generally immediately preceded by the male tapping quickly with the tips of its ambulatory dactyls on the back of the female's body or sometimes its legs. On many occasions males were seen at the entrances of burrows known to be occupied by females moving all the legs on one side quickly up and down. Tapping was sometimes interspersed with normal ecdysis. In most cases this resulted in the emergence of the female. If the female was not facing the male upon emergence did not turn around herself she was turned around by the male. The male's chelipeds were then placed around the side or over the top of the body of the female and flexed
so that the female was more or less enclosed. The male was sometimes tilted back and close to the ground or the two individuals were slightly elevated (text-figure 47c). The two crabs remain quietly in this position for several minutes. (The position of the abdomen was difficult to observe in all cases.) While in this position the male sometimes picked at the back of the female with his chelae. Either the male or female then disengaged itself and moves off, into its burrow or begins feeding.

On two different days several separate copulations were observed between the same pair within two hours. Males sometimes leave the female abruptly to chase away a wandering crab which appears to be entering the burrow of the copulating male.

Only one instance was observed which might indicate that copulation sometimes occurs below ground. A male approached a female and then went down its (the female's) burrow. The female wandered about close by for a short time and then followed the male only to partially emerge from the burrow almost immediately, collect a blob of mud and drag it back down the burrow closing the entrance.

On the three occasions on which attempted copulation was observed in H. latifrons the female was approached from behind. The male grabbed the female and made an effort to turn her around to face him. The female in all cases struggled violently and on one occasion the male held on to the female's legs with the fingers of his chelae.
TEXT-FIG. 46. Social behaviour in Hemiopus latifrons: a and b, sexual display: a, initial position; b, position at maximum elevation of body and chelipeds; c and d, fighting: c, first stage; d, final stage.
5.10 DISCUSSION

The behaviour of the crabs studied here is obviously stereotyped to a considerable extent. Thus feeding, burrow construction, aggressive behaviour and sexual display each occur with an almost monotonous similarity. Especially is this so of both aggressive and sexual behaviour, in the patterns of which there is most difference between the two species.

In their manner of feeding, *H. latifrons* and *H. cordiformis* resemble species of *Uca* (Pearse, 1912: 122; Crane, 1941a: 150; Altevogt, 1955: 707). This is particularly true of the placing of the food pellets in the top (anterior part) of the mouthfield and the rejection of pellets which form at the bottom (posterior part) of the mouthfield. In species of *Ocypode* the chelae, which are distally slightly concave but truncate and not spooned as in *Uca*, are used as "broad-toothed rakes" and the sand is scooped into the anterior end of the buccal cavity, rejected pellets forming at the posterior end (Crane, 1941b: 303; Tweedie, 1940: 322). These crabs, at least when they are young, are scavengers as well as detritus feeders. Species of *Dotilla* place the food pellets at the bottom of the mouthfield and the pellets of rejected sand form at the top (Tweedie, 1940: 317). In species of *Uca* and *Dotilla* the pellets of rejected material are nearly always wiped away by the chelipeds. The habit
of moving in a straight line from the burrow while feeding
leads, in Ocypode and Dotilla especially, to the develop-
ment of characteristic patterns on the sand or mud of lines
or rejected pellets radiating out from the burrow entrance.
Such patterns are poorly developed or absent in H. cordi-
formis and are not found in H. latifrons. All these ocyp-
odids, apart from Uca species, use both chelae in feeding.

The use of the legs of one side in burrow construction
is typical of all ocypodids so far studied. Beer (1959)
doubts that Hemiplax hirtipog constructs burrows at all
and in the scopinerines (and in the Nictyridae also) peculiar
temporary "igloos" are constructed (Tweedie, 1950, 1963).
In burrowing behaviour and in the nature of the burrow,
H. cordiformis, but not H. latifrons, thus most closely
resembles species of Uca and Ocypode in which a vertical or
near vertical burrow is constructed, with excavated material
either neglected near the entrance or carried away some
distance. In Ocypode caudichaudii Milne Edwards & Lucas
and O. ceratophthalmus Pallas excavated sand is taken some
distance from the entrance and then thrown away (Grane, 1943b:
306; Tweedie, 1950: 323). In a species found in the Eastern
Aden Protectorate, O. saratan (Forsskal) on the other hand,
evacuated sand is built into a volcano-shaped pile alongside
the burrow entrance, each successive load of sand being dumphed at the top of this pile (George & Knott, 1955: 20).

Similar burrowing behaviour is shown by O. ceratophthalmus
in Moçambique (Darras, 1963).

Fiddler crabs, like H. cordiformis, plug their burrows with mud or sand before the incoming tide (Pearsa, 1912: 117; Crane, 1941a: 150). They also carry mud into the burrow. In H. cordiformis the carrying of wet mud into the burrow and the plugging of the entrance probably maintains high relative humidity within the burrow but keeps actual water out (J.A. Beattie, personal communication). The habit of plugging the burrow has led, according to Crane (1941a: 157), to the development in species of Uca of the habit of building shelters which are used by males during display. The tendency of H. cordiformis to build high walls around the burrow entrance in damp mud and to remove excavated material from around the entrance of burrows built in dry mud would not, according to this viewpoint, appear to be of evolutionary importance. However, the origin of shelter building is by no means a settled question. The building of mounds by some Ocypode species and possibly the nature of burrow construction by Dotilla species surely provides some evidence for an origin from burrow construction. Crane's main argument against this is that in Uca species material for the shelter is usually collected separately, excavated material lying unused.

Of the behaviour patterns exhibited by H. cordiformis, the most difficult to satisfactorily interpret is that here called "burrow defence". This consists of an exact notionless
stance. Similar behaviour also occurs in H. latifrons although the body is rather close to the ground. This posture has been termed burrow defence because of its context and the reaction of other crabs to individuals in such an attitude. Thus the posture is only adopted near the burrow entrance and no crab standing in this attitude was seen attacked by another crab. Pearse (1912: 123, fig. 5), Crane (1943: 219) and Altvogt (1957a: 66-7, fig. 42) have observed extremely similar behaviour in species of Uca although there the chelipeds were elevated and widespread. Tweedie (1963) gives a photograph of a male Botilla nuctiroidae H. Milne Edwards posing in exactly the same position as that adopted by H. cordiformis. In H. cordiformis as in species of Uca, this posture, termed "posing" by Crane, resembles that associated with threatening behaviour towards other males. Both Pearse and Crane bring forward some evidence to suggest that such behaviour is associated with courtship display. Certainly this may be true of species like U. sexplicatus, Crane in which the pose lasts only a short time (in the order of seconds). It does not appear to be related to display in the two species here studied. Species of Uca also defend their burrow merely by pushing the major chela out of the entrance (Pearse, 1912; Crane, 1953).

As already mentioned, fairly strong differences in fighting behaviour are shown by the two species studied here
although there is a common element in the initial forward stretching of the chelipeds. This forward stretching is found also in species of *Potilla* (Tweedie, 1950: 319; Altwegg, 1957b). In *H. biptipes*, combats between males involve lateral stretching of the chelipeds but the body is held close to the ground and not elevated as in *H. latifrons*. In both species of *Hemiplax* fighting involves mutual tapping of the fingers of the chelae (Leec, 1959: 196, fig. 19). In species of *Uca*, fighting involves preliminary waving and tapping of the ground and terminates with interlocking of the major chelae and pushing (Pearse, 1912: 123; Crane, 1941a: 151; 1953). In *U. maracoani* (Latreille) threat and burrow defence both involve outward stretching of the minor as well as the major chela (Crane, 1958: 123-4).

In *Potilla mystiroidea* and *D. blanfordi* Alcock the winner of a fight executes a series of cheliped waves and body elevations (the triumph dance - Tweedie, 1950; Altwegg, 1957b: 335, fig. 8) which is similar to the waving of both Tasmanian species but especially to *H. cordiformis* in the relative timing of its components. Thus, the upward stretching is slow compared with the quick downward jerk. The absence of actual physical damage to the antagonists, noted in *H. latifrons* and *H. cordiformis*, is characteristic of combats between members of the same species in most animals.

Analysis of courtship display in fiddler crabs throughout the world (Crane, 1957) has shown the almost universal
applicability of the division of this behaviour into two
types - "vertical waving", in which the cheliped is usually
only partly unflexed, elevated and lowered in the same semi-
vertical plane and "lateral waving" in which the cheliped
is usually fully unflexed and stretched out laterally, then
elevated and returned with a circular motion to its original
flexed position in front of the 'face'. In addition, the
body may be elevated during waving and the crab may move
sideways on upright ambulatories. The vertical waving is
characteristic of, though not confined to, species in which
the eyestalks are set close together - the so-called
"narrow fronts", the lateral wave of the "wide fronts" in
which the eyestalks are widely separated proximally. Crane
considers the laterally waving wide-fronts the most phylo-
genetically advanced. In its courtship display H. cordi-
formis undoubtedly relates itself most closely with the
vertical wavers, being especially similar to species such
as U. marionis (Desmarest) (Altvogt, 1955: 709, fig. 12)
in which the body is also moderately elevated and the down-
ward jerk of very short duration.

The most distinctive features of the display of
H. latifrons are the parallel alignment of the chelae during
elevation, the chelipeds being unflexed before they are at
all raised, and the rather long pause at maximum elevation
of the body and chelipeds. In addition, the tempo of the
wave is rather slow. No close parallel seems to exist among
fiddler crabs, with the possible exception among the western central American species of *U. stylifera* (H. Milne Edwards), a narrow fronted species with a poorly developed lateral wave (Crane, 1941a: 171-2). That *H. hirtipes*, whilst so closely resembling *H. latifrons* in its fighting behaviour, should lack any courtship display whatever, is of considerable interest.

Both *H. latifrons* and *H. cordiformis* then, have displays of a fairly advanced type with almost maximum elevation of both body and chelipeds but without modification by the addition of "bowing" or "curtsies" or other special steps as are found in fiddler crabs (Crane, 1941a, 1957). It is possible that there is some significant geographical variation in the display of *H. cordiformis*. Thus, in Tasmanian populations, the chelae are elevated little further than the level of the top of the upright eyestalks, whereas Ward (1938: 243) states that (in New South Wales specimens) the chelipeds are thrown to their full extent above the carapace.

The female's habit in both Tasmanian species of ignoring displaying males and the male's habit of increasing the tempo of waving at the female's approach is well known in *Uca* species.

Not a great deal can be concluded regarding possible similarities in copulatory behaviour since so few observations have so far been made. In *H. hirtipes*, Beer (1959: 201) observed that the male seized the female without preliminaries
and adjusted her to the appropriate position for copulation. In species of Uca copulation may take place above ground or, in the more advanced species, in the burrow of the male (Crane, 1941a, 1958). It is generally preceded by very intense display and during copulation, or immediately before it, the male may 'stroke' the female with his ambulatory legs. In this feature there is a strong resemblance to H. cordiformis in which copulation is preceded by "tapping". During actual copulation in H. latifrons and H. cordiformis the female's abdomen must undoubtedly be lowered and the male's placed within it, the male's pleopods inserted into the gonopores of the female. This has been described for Uca maracoani by Crane (1958).

In fiddler crabs, there is a large amount of individuality and 'play', Crane (1941a) giving accounts of several most amusing incidents, including destruction of shelters and burrows, amongst western central American species. Such activities are developed to a moderate extent in H. cordiformis.

Individual, diurnal and seasonal rhythms of activity are well known in fiddler crabs (Pearse, 1912; Crane, 1943, 1958) and have also been noted in species of Ocypode (Crane, 1941b). There are again resemblances here to the behaviour of H. cordiformis.

Displacement behaviour, the sudden production of acts which closely resemble ones normally occurring under different
circumstances (Tinbergen, 1952), has not been definitely observed in H. cordiformis or H. latifrons although displacement feeding has been confirmed as occurring during fighting in fiddler crabs (Crane, 1957) and possibly occurs also in H. hirtipes (Beer, 1959: 201). Displacement cleaning of the major cheliped has been observed in H. maracoani by Crane (1958).

It is evident that both species have a reasonably large battery of social behaviour patterns. Within these patterns each species is again fairly advanced compared with related animals. However, there is not the amount of individuality of behaviour in these two species that the very advanced species of Uca show.

The present studies present additional supporting evidence for the at least partly sexual nature of courtship display or waving and the derivation of this behaviour from the aggressive posture adopted by most Brachyura (Crane, 1941a: 158-9; Hiatt, 1948; Beer, 1959; Bovbjerg, 1965; Schöne, 1961). Waving serves to advertise the presence of a male, the fact that it is in reproductive condition and that it is in possession of a burrow. Both the form of the wave and the intensity with which it is carried out convey, particularly to females, additional qualifying information concerning each male, including that identifying the species to which the individual belongs.
Finally, it has already been pointed out that there are similarities between the antagonistic behaviour of *H. cordiformis* and that of the scopimerines (*Petilla* species), usually regarded as a more primitive group of ocypodids. Resemblances between the 'triumph dance' of scopimerines, the sexual display of *H. cordiformis* and the vertical waving of 'narrow-fronted' *Oca* species have also been noted. These features, together with the employment of abbreviated waves (or juxts) by *H. cordiformis* in contacts between adult males, suggest that courtship display is a "derived activity" in the very broad sense of that term as used by Tinbergen (1952) and others. This suggestion, that waving in the advanced ocypodids has evolved from threat display, has already been more than hinted at by Crand (1941a).

Analysis of the various similarities and differences between the behaviour patterns of these ocypodids fully supports the close relationships, deduced on morphological evidence, between the Scopimerinae, *H. cordiformis* and other Ocypodinae. However, the quite different burrowing behaviour of scopimerines from that of other ocypodids, the rather different nature of aggressive and reproductive behaviour of *H. laridion* from that exhibited by *H. cordiformis* and other ocypodines and its similarity, especially in aggressive behaviour, gives further support to the isolation of these species and their relatives as three distinct
subfamilies. Further, the similarity in behaviour patterns of *H. latifrons* and *H. hirtipes*, again provides supporting evidence for the close relationship of these species within the Hacrophthalminae. Such support of morphological arguments by ethological evidence has been found within the genus *Uca* itself (Crane, 1957) and in many other groups of animals (Lorenz, 1958).
The studies reported here began with the aim of determining the kinds of habitats in which the various species of Tasmanian shore crabs were abundant and why, in some areas, several species were found together whereas in others only one was present. The basic unit dealt with has been the species - the species were looked at from the point of view of the factors governing their distribution rather than the habitats being studied to determine the totality of species which they could support. But units cannot be compared in any way without defining them and knowing their limitations in space. Therefore, the extent to which each species in Tasmania could be distinguished from other species was examined in detail. The results of these basic studies have been reported in the section (3) on taxonomy. The extent to which species can be distinguished is largely a reflection of their degree of spatial separation. More precisely, the magnitude of the genetical, and hence morphological or behavioural differences is usually proportional to the strength of the reproductive factors which isolate them in nature. It is the ways in which the species are separated, rather than the results of such separation, that are dealt with in the
sections on ecology and behaviour.

The eleven species of shore crabs belonging to the families Grapsidae and Ocypodidae in Tasmania are easily distinguished from each other. Generally, so are the species in any single area. Where each species is represented by a single population or by a few contiguous populations, as in the local situation, those species are distinguished, one from another, by marked discontinuities. But larger variation is evident in the wider situation where the area is greater and all, or nearly all, populations of a species are studied. Each species may then be very difficult to distinguish. This is especially so if small samples of the populations are extracted from their geographical or ecological context. This fact does not render less useful the concept of the species in either the local or the wider situation. The species is both a useful and a necessary concept. Mayr (1963) has summarized the very large amount of evidence which shows that species are also natural entities and not arbitrary categories, convenient pigeonholes. Some of the morphological differences between species have been discussed then in section 3.4 of the present report. The progress of the present studies from the species viewpoint is thus a valid one. To proceed with the study of their ecology without determining the validity of the units would not have allowed later comparison
with related species in other regions. The value of that part of the present study is seen in a consideration of the species of *Cyclograpsus*. Brockhuysen (1941), in South Africa, found that *C. punctatus* lived on sandy beaches and that ovigerous females were most common in winter. This species was formerly thought to be represented in Australia. However, Tasmanian populations of *Cyclograpsus* live on boulder beaches and ovigerous females are most common in summer. The realization that the South African and Tasmanian populations are not conspecific allows a rationalization of the otherwise difficult situation posed by their dissimilar biology.

Once the groundwork of the delimitation of species has been done one can proceed rather more safely to a number of other considerations of species' biology. Often the first result of a taxonomic study is that geographical regions inhabited by characteristic species become more obvious. Arguments about the limits of biogeographical regions and the usefulness of smaller subdivisions such as provinces have been numerous. Nearly always those who have criticised the concept of regions have considered the fact that the end points of geographical ranges seldom coincide for a number of taxa. The conclusion often reached is that where the limits cannot be fixed the category is of only limited usefulness or is non-existent. But implicit in such arguments is the often
unspoken concept that the boundary between regions must be some precise kind of line on one side of which are found one group of species and on the other, a quite different group. Clearly the effective realization of this depends on the level of discrimination. Study of the world-wide distribution of all terrestrial vertebrate animals which are reasonably well known permits the division of their distribution patterns into the six well known major zoogeographical regions (Darlington, 1957). But study of the boundaries shows that these are transition zones where the fauna of one region gradually changes over to the other. Similar transition zones surely separate subdivisions of the regions. In the case of western South America and New Zealand, Knox (1966) found, for intertidal invertebrates, the same kind of broad transition areas separating areas where there was a much greater tendency for the same species to occur together (see also Pawson, 1965). The present studies provide a little evidence for the possibility that amongst the subregions into which the Australian intertidal fauna might be divided is a south-western one which adjoins other distinct provinces towards the west in the eastern part of the Australian Bight, and to the east in the southern part of the mainland. Other studies on Brachyura (Stephenson, 1962; Griffin, 1966) suggest the existence of similar transition zones in the same areas. Different species, genera, families and classes of animals and plants react in differing degrees to the same environmental factors
(Pawson, 1961). The expectation that a boundary between regions of even a mildly homogeneous assemblage of animals, or plants, can be placed with an accuracy of a few miles is an unwarranted one. If the distribution of even a few species appears to stop geographically in or around the same area then this should focus attention on the environmental factors and the behaviour, in the broad sense, of the animals or plants in that area.

That distinct species have different tolerances to the same factors results in differences in their distributions within an otherwise uniform environment. Put this way, this rather self-evident statement suggests examination of species' physiology. But perhaps one might expect that both very closely related and virtually unrelated but similar species may have similar ecological requirements or tolerances. If they have, nevertheless, different distributions then attention might be focussed on their behaviour towards one another. This kind of approach begins from the assumption that no two closely related species can live in the same ecological niche or probably more precisely, as G.E. Hutchinson and E.S. Deevey put it, "...two species with the same niche requirements cannot form mixed steady-state populations in the same region" (Andrewartha & Birch, 1953). This has been called the "Volterra-Cause Principle" (Hutchinson, 1958). This theory is one which has occupied the attention of many ecologists and involves two much abused concepts, the niche and
competition. Hutchinson (1958) has considered the niche (or fundamental niche) of a particular species to be the multidimensional hypervolume delimited by all the environmental states which allow that species to exist indefinitely. The niche of a species thus includes all ecological attributes of that species and the way it behaves towards the environment. If the niche were extended to include all the characters which distinguish the species taxonomically the value of the Volterra-Gause principle is, of course nil. In that case, for one species to completely occupy the niche of another would require it to be sometimes another species which obviously is nonsense. Hutchinson's view then is that the fundamental niches of two distinct species may overlap or intersect, but not coincide. This definition of niche differs from some others previously proposed. Sometimes the term is used to mean something excluding at least partially, the habitat in which the species lives. Odum and Odum (1959: 27), for instance, consider "the habitat to be the organism's 'address' and the niche to be its 'profession', biologically speaking." Something similar appears to be intended by Ross (1957) when he states that several of six cognate species of leafhoppers in Illinois occupy the same niche at the same time, for he mentions behavioural differences between the species towards various environmental factors. Hutchinson's definition is used in the following discussion.
MacArthur (1959) considered that, in the strict sense, the word competition should be limited to the situation where "a number of animals (of the same or of different species) utilise common resources, the supply of which is short; or if the resources are not in short supply, when the animals seeking that resource nevertheless harm one another in the process". Thus, competition may occur where a large population of birds which nest in holes in trees seek nest sites in a forest in which the trees possess few holes. Or it may occur where beetles of one species come to have a much reduced fecundity when crowded with adults of another species compared with that where adults of the one species are crowded (see also Andeavortha & Browning, 1961; Browning, 1962; and Park, 1962).

Defined in this way the two concepts, niche and competition, are valuable ones. Both Birch and Hutchinson give many examples to show the results of competition and how the niches of sympatric species do not entirely overlap. Two, now well known, examples can be given here.

MacArthur (1959) studied the ecology of five species of warblers (Dendroica) living in coniferous forests in the north-eastern United States. The species are sometimes found together during the breeding season in relatively homogeneous nature forests. He found that each species behaved in such ways as to be exposed to different kinds of food, had different nesting habits and also differed from the others in its
territorial requirements. MacArthur concluded that these differences reduced competition and permitted the coexistence of the species. In other words each of the five species of barnacles occupied a rather different niche.

Connell (1961) studied the reasons for the fact that, on rocky coasts at Millport, Scotland, the small barnacle Chthamalus stellatus occurs higher on the shore than does the larger Balanus balanoides. The postlarval individuals of both species settle out from the plankton on rock throughout most of the intertidal zone, the smaller species settling slightly earlier than the larger. The larger species settled in larger numbers and grew faster than did the smaller. Connell observed that during its growth, Balanus smothered, undercut or crushed the small Chthamalus; Chthamalus was found to be able to survive on the shore at all the levels occupied normally by individuals of Balanus. The interspecific competition for the space on the shore contributed to the crowding of Chthamalus which tended to be smaller than in Balanus-free areas and hence to produce fewer offspring. Connell concluded that the lower limit for the higher living Chthamalus was set by the action of competition. In this case the two species tended to occupy rather similar niches, competition reducing distributional overlap.

Mayr (1963: 66-62) has given a number of examples of studies which suggested varying degrees of niche overlap.
some sympatric related species show considerable niche overlap and their distribution may be importantly limited by competition (Hailstone, 1951; Pitelka, 1951; Ripley, 1959), whilst others show little niche overlap and competition is minimized (Lack, 1945; Moreau, 1948; MacArthur, 1958; Teal, 1958; Crouell, 1962). Niche overlap is sometimes small whilst in other cases the differences may be very subtle.

There are also cases where investigation has been unable to show niche differences in a group of species. Sometimes the suggestion is made that the physical environmental factors cannot yet be measured nearly precisely enough. D.P. Wilson's experiments on the northern Atlantic chaetognaths, Sagitta elegans and S. setosa, showed, for instance, that two types of water which differed only in the kinds of organisms they usually supported, had quite different effects on the growth of these two animals (Lac, 1960). Analysis of the physical and chemical characteristics of the two waters did not reveal any differences between them, however.

The eleven species studied here readily appear to fit into the scheme of non-overlap or incomplete overlap of niches. Although several species are found often on the same shore and sometimes under the same stone or in nearby burrows they tend strongly to behave differently towards the intertidal environment. On the rock platform exposed
to full wave action, where the only kind of shelter available is crevices, two species, *Lepiocrangus variscatus* and *Placussia capensis*, are found. Both feed on encrusting algae and have the fingers of the chelae spooned to aid in the scraping of the algae from the rocks. They show other morphological adaptations to this general habitat in their strongly depressed body and distally spinate ambulatures. Both possess only sparsely hairy mouthparts. They also have relatively low gill volumes. But *L. variscatus* lives at a higher level on the shore and is active at the time of low tide when it moves down the platform with the retreating tide. *P. capensis*, on the other hand, is active when the tide is high. The total vertical ranges of the two species probably overlap very little. Because of this they undoubtedly feed on different species of algae.

On muddy estuaries two species, sometimes three or four, are found. The two acyopods, *Helocclus cordiformis* and *Neomelas latifrons*, both live in burrows and feed on organic detritus which they sift from the mud. The fingers of the chelae are spooned to aid in the scraping up of the mud pellets (although the arrangement of the hairs around the tips of the fixed fingers are slightly different in the two species). Both sort out the detritus and silt from the coarse sand with the aid of specially modified hairs on the mouthparts (but the nature and arrangement of hairs is qu'
different in the two). The two species are active at the same time, when the tide is low, feeding and burrowing. But taken into the laboratory H. cordiformis and H. latifrons behave quite differently with respect to fresh water and moreover, H. cordiformis seems almost to show an aversion to immersion in water, in contrast to H. latifrons. This behaviour reflects their distribution in nature. H. cordiformis lives higher on the shore than does H. latifrons and has a much lower relative gill volume. H. cordiformis also extends slightly further up streams and is found in areas subjected to lower salinities than those inhabited by H. latifrons. H. cordiformis also breeds later - males begin displaying later and vigorous females are most abundant later than in H. latifrons. These two species indeed show very little niche overlap. Holozranceus hastellianus is also sometimes found on muddy estuaries, generally higher up on the shore and under stones or clods of earth. Its higher gill volume is a reflection of its inability to tolerate long periods away from cover and in the laboratory it shows a strong tendency to settle under stones. In its behaviour towards fresh water and immersion in water it resembles H. cordiformis. Parozranceus chimpudii is occasionally found on mud flats. It nearly always occurs under stones or else in burrows, in those parts of the mud colonized by Zostera nana. Its behaviour in the laboratory and its relative gill volume reflect its vertical and horizontal distribution.
nature - it usually lives low down on the marsh in areas subjected periodically to low salinities.

In these examples from the present studies the species have all been only distantly related. But, in Tasmania there are three congeneric species, Paragrapsus quadridentatus, P. gaimardi and P. laevis. P. quadridentatus and P. gaimardi are sometimes found together under the same stones on sheltered boulder and stony beaches. P. gaimardi and P. laevis are sometimes found together in burrows low down on marshes inhabited by eel grass. P. quadridentatus and P. laevis have not been found on the same area of shore in the present studies. Field observations and study of mouthparts and laboratory behaviour reveal several marked differences between P. quadridentatus and P. gaimardi. For instance P. gaimardi often lives in burrows, the other never does, P. gaimardi tolerates fresh water to a greater extent than does P. quadridentatus and frequently occurs in estuaries at the mouths of rivers and in lagoons, its congener never is. P. gaimardi has a much denser array of hairs on the mouthparts than does P. quadridentatus. Whilst both prefer to settle under water, P. gaimardi is more tolerant of fresh water than is P. quadridentatus. Field studies reveal niche differences also between P. gaimardi and P. laevis, particularly in regard to substrate and perhaps salinity tolerances and ability to withstand dessication - P. laevis is sometimes found in larger
numbers higher on the shore than is \textit{P. gaimardi} (although the relative gill volumes are almost the same in both species). The two species probably utilize different food sources. There certainly appears to be room for more study of these three species, particularly \textit{P. gaimardi} and \textit{P. laevis}.

The demonstration of at least partial absence of niche overlap in these species through field observations and study of morphological attributes is of course not new. The ecological literature is full of such studies. But the demonstration, through laboratory studies of behaviour in relation to various environmental factors, that the different ecological distributions are largely those which each species would show at the present time, were other species absent, is perhaps of some value.

In the interpretation of the laboratory studies and in the extrapolation either way between field observations and results of laboratory studies, it has been assumed that each individual of the species has the ability, genetically determined through the course of evolution, to measure the environment and to select, for the most part successfully, those values of the environmental variables which will not lead to its death. This is surely as reasonable an assumption, and probably a more reasonable one (see for instance Thorpe, 1945) than the mechanistic approach presented by some schools of behavioural thought (Fraenkel & Cunn, 1940). Wilson (1960)
has summarized his earlier studies showing that larvae of
certain barnacles and other organisms were able to delay
metamorphosis until a suitable substrate was available for
settling. These larvae were able to continuously test the
environment and choose a particular one. Wilson's interpre-
tation is similar to that used here. Should brachyuran
larvae possess the same ability as those studied by Wilson
this would account in an important way for the absence of
young individuals from entirely unsuitable habitats and their
presence in suitable habitats and recruitment into the popu-
lation.

The conclusion already reached, that the niches of
these eleven species or these parts of them which are apparent
in the rather local situation are not importantly limited by
competition, seems a valid one.

That there is partial overlap in distributions in rela-
tion to some environmental factors is to be expected if the
reasoning already presented about overlap of geographical
distributions is valid. In the microenvironmental situation,
individual variation itself may account for some of this
marginal blurring of distributions.

Mayr (1963) has given examples of geographical variation
in species' niche size through less variation in adjustment
to one or more environmental variables. The best examples
come from studies on birds (see for instance D. Lack's
studies on Galapagos finches and D. Amadon's work on
Hawaiian birds quoted by Mayr, 1963: 83; also Kapfer & MacArthur, 1960; Kapfer, 1962). In these cases the shape of the bill may change, reflecting a change in feeding habits. These ecological situations parallel the cases of character divergence in morphological attributes (i.e. perhaps non-adaptive nature) discussed earlier in Tasmania, *L. variegatus* appears to be most closely limited to deep horizontal crevices on fully exposed cliffs and platforms while in New South Wales it is often found in more sheltered areas in shallow crevices. But the more limited distribution in Tasmania would appear to be due to competition, despite the fact that *Leptograpsodes octodentatus* is present in crevices on sheltered coasts in parts of northern Tasmania. The two species are very different in other ways.

These studies have hardly dealt with those intraspecific factors which might influence numerical sizes of populations except to a moderate extent in the behaviour of the two ocypodids. In these species the aggressive behaviour of individuals in the regions of the closely-spaced burrows certainly plays a part in regulating the number of adult individuals on a certain area of mud flat. The avian approach to the problem of the regulation of animal numbers has recently been taken up by Wynne Edwards (1962) although such spacing of animals, through each individual's possession of a defended area - the territory - in which no other member
of the same sex and species is tolerated, is now well known (Carpenter, 1958), again especially in birds. That amongst those species which show territorial behaviour, there are some in which the territory is large and some in which it is small and that those species which hold smaller territories occur in the higher densities, is of course obvious.

In the other species studied here there is apparently some considerable variation in the maximum densities in which each occurs. Partly this may be due to differences in maximum body size and the total biomass which particular habitats are able to support. These kinds of issues have not been investigated here. But in no case do any of the species appear to be suffering from overcrowding. Measurements of densities were carried out in part of the habitat of each species, under stones for instance, where the animal shelters. The individuals of each species, however, cannot spend all their time in such a situation for at certain times they must move out to areas where they feed, away from shelter, or even from the lower, wetter layers of stones to the drier upper ones.

Many aspects of the population biology of the eleven species have remained relatively untouched in the present study. Activity rhythms, breeding biology, larval ecology and, in Brachynotus spinosus, colour polymorphism, should provide ample opportunity for further study. So too should the study of temporal fluctuations in density. Finally,
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the generic groupings and relationships have not been considered. Other areas where further information is required have been already mentioned.

At the beginning of this discussion it was stated that the study aimed to determine what species were found in what habitats. In part, ecological studies aim at predicting the distribution and abundance of species under various sets of environmental conditions. The investigations reported in the previous pages have to some extent allowed such predictions for eleven, rather different, species of Tasmanian shore crabs.
7. SUMMARY

1. The report deals with nine Tasmanian species of Brachyura belonging to the family Grapsidae and two to the Ocypodidae.

2. The eleven species are the dominant brachyurans in the intertidal zone in Tasmania and are found on all shores except open, surf beaten, sandy ones.

3. The study is divided into three main sections which deal with the taxonomic status of the species in Tasmania, their ecological distribution and associated morphology and behaviour, and, in the case of the ocypodids, their social and maintenance behaviour.

4. Three of the species of Grapsidae are fully described and figured. These are Leptograpsus variegatus (Fabricius), Cyclograpsus granulosus H. Milne Edwards and Plagusia capensis de Haan. Three other Cyclograpsus species, the warm temperate Australian C. audouinii, the New Zealand C. lavaudi and the South African and Chilean C. punctatus, all originally described by H. Milne Edwards and the pan-tropical Indo-Pacific Plagusia dentipes de Haan, are also treated in detail.
5. The specific name capensis is retained here for the southern cool temperate species of Plagusia, pending designation of a neotype for Cancer chabrus Linnaeus which is conspecific with P. capensis; a lectotype is selected for P. capensis.

6. L. variegatus and P. capensis are confirmed as comprising geographically widespread sets of populations throughout most of the southern Indo-Pacific. These populations are not considered to warrant subspecific status. The group of Cycloecapsus species considered valid arise from partial splitting up of C. punctatus, formerly considered to be represented throughout temperate Australia as, at most, a subspecies, C. punctatus nudouiniai.

7. It has not been found possible to identify Cycloecapsus tasmanicus Jacquinot, originally described from Tasmania, with any Tasmanian grapsid or any species of Cycloecapsus.

8. One species, Paragrapus laevis (Dana), is added to the faunal lists of Tasmania. This species, previously known from the east coast of the Australian mainland, is here recorded from four localities in eastern Tasmania.
9. In *L. variegatus* and *P. capensis* there are marked morphological changes with growth apart from the usual ones associated with sexual dimorphism. Several characters, particularly in *L. variegatus*, show clinal variations.

10. *C. granulosus* and *C. andouinii* also show marked clinal variation leading to character divergence around their region of sympatry.

11. *P. capensis* can be easily distinguished from *P. dentipes* on the basis of at least seven characters. In some there is a marked resemblance, in adult *P. dentipes*, to juvenile *P. capensis*.

12. None of the species are confined to Tasmania but five species appear to be for the most part shared only with Victoria. Three others are represented throughout most of eastern Australia and one is present in western, but not eastern, Australia.

13. Four genera and two species are shared with temperate regions outside Australia. There, however, varunines are well represented in the intertidal zones, in contrast to the situation in Tasmania.

14. The distributions of the eleven species, within Tasmania, are described in relation to substrate, cover, wave
action, salinity and major tidal levels on the shore. The breeding and moulting cycles, the number and relative volume of the gills, the arrangement of particular types of hairs on the mouthparts and the behaviour, in the laboratory, in relation to fresh water, immersion in water, substrate and cover, are described.

15. The type of substrate, the availability of certain types of cover and the salinity of the water appear to be amongst the most important factors limiting the distribution of the species.

16. Breeding cycles last around three months, peaks of occurrence of ovigerous females being followed by peaks of occurrence of moulting about two months later. There is wide interspecific overlap in the timing of breeding.

17. Those species living highest on the shore and spending longest times away from cover have the lowest gill volumes relative to total volume.

18. In the Grapsidae the distal parts of the second maxillipeds and inner mouthparts bear stout spines. In the Ocypodidae these regions of the mouthparts bear "spooned" hairs. Those species living on open shores away from silt possess fewer supplementary hairs on
19. The species living on wave beaten rock platforms have spinate ambulatory dactyli. Those living in muddy areas have tufts of hair between the bases of the ambulatory legs.

20. Most of the grapsids feed on algae, those feeding on encrusting forms having the fingers of the chelipeds distally spooned. The octopods feed on detritus which is sifted out from the mud. The fingers of the chelipeds in these species are spooned and hairy.

21. Although the ecological distribution of each species overlaps that of others, each is most abundant in a particular type of habitat where other species do not occur in maximum abundances. Juveniles have a wider distribution than adults.

22. Leptograpsus variegatus and Plagusia capensis are found in crevices on fully exposed rock platforms, Cyclograpsus granulosus and Paraegrapsus quadridentatus on semi-exposed boulder beaches and Brachydrapus spinosus is usually found under stones on sheltered rock platforms. Paraegrapsus cainardii, P. lasius and Holograpsus hageniellus are always found on sheltered shores, sometimes under stones and sometimes in burrows. Leptograpsodes octodentatus is found in a wide range
of habitats from semi-exposed rocky cliffs where it shelters in crevices or in burrows in the bank to boulder beaches near fresh water seepages. The two ocypodids, *Heloccius cordiformis* and *Hemiplus latifrons*, are always found in burrows in muddy estuaries.

23. *Paragrapthus daimzdii*, *P. laevis*, *Helograpthus naswelllianus* and the two ocypod species extending some distances up rivers.

24. *L. octodentatus* and *H. naswelllianus* typically inhabit the upper part of the shore around the supralittoral fringe, *L. variocatus*, *C. granulosus*, *B. spinosus* and *H. cordiformis* are generally most abundant in the upper midlittoral, *Paragrapthus* species and *H. latifrons* are usually found in the lower midlittoral and infralittoral and *P. capensis* is nearly always found only in the infralittoral fringe.

25. In the laboratory, the behaviour of the species closely parallels their distributions in nature. Those species living in areas subject to very low salinities tolerate fresh water for longest times, those inhabiting the higher zones on the shore show some intolerance of immersion in water and those species which usually shelter under stones, settled under stones in laboratory experiments. The two ocypodids both constructed burrows in
the mud and *H. hamulians* burrowed in earth. *L. costodentatus* and *P. gaimardii* both sometimes constructed burrows in earth and sand.

26. The fundamental niches of the species actually show little overlap and interspecific competition for space seems not to be important in determining the limits of species' ecological distributions.

27. From field and laboratory observations it is apparent that the two scyphocids possess rather stereotyped behaviour patterns, particularly in relation to fighting and sexual behaviour.

28. The two species differ most widely in the form of their sexual display. That of *H. cordiformis* shows similarities to the display of vertically waving, narrow-fronted species of *Usa*.

29. The behaviour of *H. latifrons* is similar to that of the New Zealand *H. hirtipes*, which, however, lacks sexual display. The similarity between the two is seen most obviously in their fighting behaviour.

30. Defence of burrows by the males of each species probably limits the size of breeding populations of these two scyphocids.
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